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Effects of temperature and nitrogen supply on post-floral growth of wheat; measurements and simulations

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Abstract

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Warmth accelerates the rate of grain growth in wheat, but the temperature coefficient expressed as Q_{10} decreases gradually between 10 and 25°C. The rate of protein deposition responds more to temperature than the total grain dry matter accumulation rate. Warmth shortens the post-floral phase in cereals. The relation can be approximated by a direct log-linear relationship between temperature and duration, or by a heat sum above a minimum temperature. The proportion of the final amount of nitrogen in the shoot taken up by the roots after anthesis declines upon increase in the concentration of nitrogen in shoot dry matter at anthesis. The component shoot organs contribute to the total amount of nitrogen relocated from the shoot to the grains in amounts proportional to the amounts of nitrogen present in these organs at anthesis. Instantaneous effects of change in temperature on the apparent photosynthesis rate per plant were small. Differences in apparent photosynthesis per plant, which developed in time between temperature treatments or nitrogen treatments, were primarily attributable to the impact of these factors on the rate of leaf senescence. Measured respiration rates were compared with theoretically expected rates. There was agreement between calculated and observed growth respiration of grains. Measured respiration rates of non-grain organs (respiration related with maintenance and transport mainly) were considerably greater than theoretically expected rates, especially in roots. A dynamic simulation model is presented that describes and interrelates post-floral gross photosynthesis, respiration, grain growth, uptake and redistribution of nitrogen, and leaf senescence. According to model predictions final grain yield in the field (for Dutch climate and crop management) decreases by 30-40 $g \cdot m^{-2}$ per degree centigrade rise in temperature throughout grain filling (other input data fixed). This adverse effect of temperature can be offset by a concomitant increase in daily radiation of 130-180 $J \cdot cm^{-2} \cdot d^{-1}$ (PhAR). Yield differences between crops that differ in amount of shoot nitrogen at anthesis only are predicted to be 15-20%.

Free descriptors: wheat, grain growth, grain filling, grain yield, carbohydrate, nitrogen, temperature, radiation, photosynthesis, respiration, simulation, model.

Contents

1 Introduction

The original aim of the present study was to analyse the phenomenon of 'senescence' and the process of 'ageing' in wheat. Studies by Spiertz (1974, 1977) on temperature effects on grain filling showed the need to be better informed about the genetic and environmental variation of senescence of vegetative parts. In a first experiment it was therefore attempted to establish interrelations between photosynthetic capacity and several chemical constituents of the flag leaf of wheat as affected by air and root temperature. From the results of this experiment and from literature studies it was concluded that a more general picture should be drawn up of the impacts of temperature and nitrogen dressings on the carbohydrate and nitrogen economy of wheat in the grain-filling stage. Thus, in subsequent experiments a comprehensive plant physiological approach was adopted, with temperature and nitrogen supply as the main environmental factors under investigation.

In order to be able to throw more light on the dynamics of production and utilization of substrates during the grain-filling stage, four main types of measurements were carried out in different experimental systems of spring wheat. These were:

1. the 'classical', periodical analyses of growth: change with time in green leaf area and in dry weight per organ,
2. recordings of the carbon-exchange rates in the light and in the dark,
3. analyses of the quantities of non-structural, water-soluble carbohydrates (WSC),
4. analyses of uptake and redistribution of nitrogen.

As the experiments proceeded and data became available for interpretation and for comparison with literature, the need was felt to set up a framework of relations. The construction of a dynamic simulation model seemed to be the answer. In general, modelling is of value for two main reasons:

1. It provides a convenient way to integrate and interrelate data of diverse nature. Even more important is the fact that a model can be used to test the interpretation which is given to experimental results.
2. If successful, a model opens the opportunity to extrapolate beyond the range of conditions covered by the experiments. This is in particular valuable when temperature effects are studied, since the controlled environmental conditions which have to be used differ in many respects from field conditions.

Already during the course of the present study, the following coherent picture emerged from literature dealing with the effects of temperature (sometimes in combination with radiation) on grain growth in cereals:

Warmth (initially) enhances the kernel growth rate, but the accelerating effect seems to level off at temperatures above about 20°C to 25°C. Warmth also reduces the length of the grain-filling period. Radiation, or photosynthate supply, seems to be a modifying factor, affecting the degree and the duration of the temperature acceleration of the kernel growth rate. Thus, with respect to final yield, there seems to be an interaction between temperature and radiation. Furthermore, it appears that the nitrogen concentration in the kernels tends to be higher the higher the temperature. Relevant studies supporting this proposition are those by Wardlaw (1970), Sofield et al. (1974), Sofield et al. (1977a), Spiertz (1974, 1977). Ford & Thorne (1975), Ford et al. (1976) and Warrington et al. (1977), all with wheat; Andersen et al. (1978) for barley; and Chowdhury & Wardlaw, 1978 for wheat, rice and sorghum.

In order to reach further than already existing knowledge, and for modelling purposes, it became clear that the data should be evaluated to obtain:

1. a quantitative relationship between temperature and the duration of grain filling,
2. a quantitative relationship between temperature and the intrinsic or potential accumulation rate of non-protein components in the grains at non-limiting carbohydrate supply,
3. a quantitative relationship between temperature and the intrinsic or potential rate of protein accumulation in the grains.

A substantial part of this publication is devoted to the establishment of these relationships. This report will also treat (with special reference to treatment effects):

4. the distribution of dry matter and nitrogen at anthesis,
5. photosynthesis and respiration,
6. the contribution of various sources to grain nitrogen yield.

The effects of pests, diseases and water stress are not considered in this report.

2 Materials and methods

2.1 ARRANGEMENT OF EXPERIMENTS

The aim of the first experiment was to study temperature effects on several parameters for ageing of the flag leaf. Plants were grown on a nutrient solution (hydroponic) in a controlled environment (phytotron). The cultivar used was 'Yecora'. Until one week after anthesis, air and nutrient temperatures were kept at 15°C. Afterwards several combinations of air and nutrient temperatures were imposed, viz. 25/15, 20/15, 20/20, 20/15 and 20/10 (air/nutrient temperature in °C). From one week after anthesis onwards the following measurements were made at weekly intervals: rating of green area, recordings of net photosynthetic capacity at saturating irradiance (P_{max}), analyses of the contents of chlorophyll a + b, total nitrogen, nitrate and soluble protein. The objectives of Expt I were different from those of subsequent experiments and its description is included only because some results were useful within context of the main study.

In subsequent experiments, Expts II-VI, temperature and/or nitrogen effects were studied on crop performance during grain filling. The most relevant experimental conditions are summarized in Table 1. The following details are given in addition to this table: In all experiments graded seeds were used that were desinfected before planting. Anthesis was taken to be reached when at least 50% of the ears showed anthers on most of their spikelets.

In Expt II (cv. Bastion) plants were grown on a nutrient culture (hydroponics; see for technical details Subsection 2.3.1.). Fresh solutions, based on Hoagland plus micro-elements, were supplied about once a month, to make sure that nutrients were always in abundant supply. Twice weekly, pH was adjusted to 5.5. Also twice a week approximately 1.5 mg $FeSO_4$ was added per liter of culture solution, because cereals do not readily absorb Fe^{+++} from a nutrient solution (pers. comm. ing. A.A. Steiner, Centre for Agrobiological Reserach, Wageningen and the late Dr F. van Egmond, Dept. of Plant Nutrition, Agric. Univ. of Wageningen). All side tillers but one were removed at growth stage Feekes 10; thus in Expt II one plant consisted of the main axis and one side tiller plus their common root system. Subsequent regrowth of side tillers was only limited. Day length was gradually extended from 8 hours at planting to 16 hours at growth stage F7 to F8. The temperature of the nutrient solution was maintained at 15°C throughout the growth period for each treatment. Air temperature was kept at 15°C until 8 days after anthesis, when it was raised to 20°C for two out of three groups of

Table 1. Summary of experimental conditions in Experiments II-VI.

Experiment and treatment	Specification of treatments	Site	Root medium	No. of ears·m^{-2}	Radiation J·cm^{-2}·min^{-1} (PhAR)	Cultivar	No. of culms per plant
II 15 II 20 II 25	air temperatures 15, 20 and 25°C; transfer from 15 to 20 and 25°C at 8 and 9 d.a.a.; roots always kept at 15°C	phyto-tron	full nutrient culture	312	0.6	Bastion	2
III N1-16 III N2-16 III N3-16 III N1-22 III N2-22 III N3-22	3 levels of N supply imposed from F6-7 to heading; in total 66, 133 and 200 mg N given per culm in N1, N2, and N3, resp.; half of the plants transferred from 16 to 22°C at 6 d.a.a.	green-house	mixture of sand and peaty substrate in 5 l pots, 14 culms per pot	-	> 0.3	Adonis	1
IV A16 IV B22 IV C22 IV D22	varying air temperatures: IV A16 16°C throughout, transfer from 16 to 22°C at 6, 17 and 24 d.a.a. for B22, C22 and D22, resp., Roots always kept at 16°C	phyto-tron	nutrient solution regulated N supply	312	0.6	Adonis	2
VA N1 VA N2 VA N3	3 levels of N supply from F6-7 to heading; in total 40, 62 and 85 mg N given per culm in N1, N2, N3, resp.	out-doors 1977	see Expt III, 18 culms per pot	455	?	Adonis	1
VB -	no treatments, field crop	1977	clay soil	553	?	Bastion	?
VI N1 VI N2	2 levels of N supply from F6-7 to heading; in total ca 30 and 60 mg N per culm in N1 and N2 resp.; 16°C throughout growth	phyto-tron	sand in 5 l pots, 23 culms per pot	466	0.6	Adonis	1
VI subsidiary treatments	all combinations of 16 and 22°C and 3 light levels imposed at both N levels for 6 days; starting at 18 and 25 d.a.a.						

d.a.a. = days after anthesis

plants; the next day air temperature of one of the 20°C groups was raised further to 25°C. Thus three temperature treatments were created: 15/15, 20/15 and 25/15 (air/nutrient temperature in °C).
These treatments will be referred to by: Expt II 15, II 20 and II 25, respectively.

The plants in experiment III (cv. Adonis) were sown in 5 litre plastic pots on 19 August 1976. The pots contained a sterilized mixture of sand and peaty substrate. The pots were placed in a naturally-lit greenhouse; when natural light became limiting (early October), additional light was supplied by 400 Watt HPL lamps (one lamp per four pots). From planting onwards, day length was gradually extended from 8 to 16 hours, as described for Expt II.

Until growth stage Feekes 6-7, all pots were given equal amounts of nutrients (Hoagland plus micro-elements; dosings about once per 2 to 3 weeks). Next, three levels of nitrogen fertilization were imposed by varying the quantities of nitrogen supplied in subsequent dosings. Dosings were discontinued at ear emergence. Then, in total, 66, 133 and 200 mg nitrogen was given per plant in the N1, N2 and N3 treatments, respectively.

Until 6 days after anthesis temperature was kept at 16°C. Then half of plants were transferred from 16°C to 22°C. Thus six treatments were created; these will be abbreviated by Expt III N1-16 (lowest nitrogen dressing, 16°C) through Expt III N3-22 (highest nitrogen dressing, 22°C).

At growth stage Feekes 10.5, all side tillers were removed. Thus a plant consisted of the main axis only in Expt III. A vigorous regrowth of tillers occurred in the respective N2 and N3 treatments at both temperatures, no regrowth appeared at the lowest level of nitrogen nutrition. During kernel filling all regrown tillers were excised regularly for the determination of their dry weight and nitrogen contents. The arrangement of pots did not allow analyses to be made with unit ground area as a reference basis.

In Expt IV (cv. Adonis) the same experimental set up was used as in Expt II, though it was modified at some points. Excision of all side tillers but one was carried out earlier than in Expt II, viz. at growth stage Feekes 3. Regrowth of side tillers was negligible and ended completely after stem extension. Thus, as in Expt II, one plant consisted of a main axis and one side tiller plus their common root. Another major difference with Expt II was, that the basic nutrient solution lacked nitrogen (see Schrobb 1951, p. 154, for composition). Nitrogen was added in small quantities twice a week, in the form of calcium or potassium nitrate (less than 1 mg N added per culm per day). Nitrogen supply was regulated in order to prevent excessive tillering. Until anthesis the tanks were cleaned out about once per 4 to 6 weeks. Adjustment of pH and addition of $FeSO_4$ were similar as described for Expt II. Day length was gradually extended from an initial 8 hours to 16 hours at growth stage Feekes 7.

The nutrient temperature was maintained at 16°C throughout the growth pe-

riod for all treatments. Air temperature was 16°C, but on three occasions after anthesis a group of plants was transferred to 22°C, thus creating four treatments. These will be referred to by: Expt IV A16, the standard population, kept at 16°C throughout the experiment; Expt IV B22, transferred to 22°C air temperature at 6 days after anthesis; Expt IV C22, transfer at 17 days after anthesis; and Expt IV D22, transfer to 22°C air temperature at 24 days after anthesis. The first samplings in Expts IV B22 through D22 took place on the third day after transfer from 16° to 22°C air temperature.

Plants in Expt VA (cv. Adonis) were sown in pots outdoors on 4 March 1977; pots and growth medium were similar to the ones described in Expt III. After full emergence, plant numbers were reduced to 18 per pot and the pots were arranged to form a closed canopy. The outer pots were not used in the experiment but served as guard rows; at first one row, later two. At growth stage F3 all side tillers were removed. Regrowth of tillers stopped completely at early stem extension. Thus one plant consisted of the main axis only in Expt VA. Nutrients (Hoagland plus micro-elements) were given at equal rates in all pots until growth stage F7 (24 May 1977). At that stage 30 mg N had already been given per plant (culm). Then three treatments were created that differed in nitrogen supply; total amounts of nitrogen given (at heading) were 40, 62 and 85 mg N per culm. In this report these treatments are referred to as Expt VA N1 to N3, respectively.

The climatic conditions during the 1977 season in Wageningen have been described by Spiertz & van de Haar (1978). It can be described as relatively cool, dark and wet, at least during the kernel-filling phase, when the mean daily temperature was about 16°C. This is rather fortunate because in most experiments under controlled conditions one or more treatments were grown at 16°C. The date of anthesis in Expt VA. was 23 June in all treatments.

To gain some information from field grown crops it was decided to arrange a plot in a nearby field of 'Bastion' spring wheat, grown under normal agricultural management in 1977; this experiment is designated Expt VB. Sowing was done on 8 March. Nitrogen was applied at a rate of 90 $kg \cdot ha^{-1}$. The date of anthesis coincided approximately with that in Expt VA. Figures expressed per culm represent the average value for many types of tillers.

Plants in Expt VI (cv. Adonis) were sown in 5-litre plastic pots in steamed sand. The experiment was conducted in the phytotron. After full emergence plant number was reduced to 23 per pot. Pots were arranged to form a closed canopy. All side tillers were removed at growth stage Feekes 3. Thus in Expt VI one plant consisted of the main axis only. Regrowth of new tillers stopped completely at early stem extension. Day length was regulated as described for Expts II-IV. Air temperature was maintained at 16°C throughout the growth period. Until growth stage Feekes 7 all pots received equal amounts of nutrients (Hoagland plus micro-elements). At that stage of development 10 mg nitrogen had been given per culm. Beyond stage F7 pots were allotted to two levels of nitrogen supply. Dosings were discontinued at ear

emergence. Plants at the lowest level of N nutrition were given 30 mg N per culm in total (Expt VI N1), whilst plants at the higher N dosing (Expt VI N2) received 60 mg N per culm in total.

Throughout the growth period plants were moved at regular intervals from spot to spot and from one growth room to another. Unfortunately, the experiment could not be continued till complete ripeness of Expt VI N2.

At 18 and 25 days after anthesis subsidiary treatments were started in both Expt VI N1 and VI N2, consisting of all combinations of two temperatures (16 and 22°C, designated by T1 and T2, respectively) and three radiation levels (0.2, 0.4 and 0.6 $J \cdot cm^{-2} \cdot min^{-1}$ PhAR at ear level, designated L1, L2 and L3, respectively). Day length was extended from 16 to 22 hours in all subsidiary treatments. So the daily quantity of incident PhAR in the L3 treatment was greater than in the main treatments of Expt VI, with also 0.6 $J \cdot cm^{-2} \cdot min^{-1}$ at ear level, and that of the L2 treatments was about equal to the daily quantity in the main treatments. In this report the subsidiary treatments are abbreviated by (for instance) Expt VL N1 L1 T1 (lowest N dressing, lowest light level and 16°C) or Expt VI N2 L3 T2 (highest N dressing, highest light level, 22C°). Both series of subsidiary treatments lasted six days.

In all experiments under controlled environmental conditions the relative humidity was maintained at 70 to 80%. Fungal diseases and infestation with aphids were prevented or controlled by spraying with pesticides. In experiments under controlled conditions, foot rot, caused by Fusarium spp., could not be prevented completely; severely attacked plants had to be disdiscarded.

Some observations were made of the effect of tiller removal on the development of the remaining main axis. At anthesis the dry weight per detillered culm was higher than the dry weight of the main axis of untreated plants. This is presumably attributable to the difference in culm density; crop dry weight in $g \cdot m^{-2}$ was higher in untreated plants. It appeared, however, that plant morphology (in terms of height, shape and size of organs, shoot/root ratio) was not fundamentally altered when tillers were excised early. The main advantage of detillering is a more uniform stand. Furthermore, an effect of nitrogen supply on ear density could be avoided in this way.

2.2 OBSERVATIONS IN EXPTS II-VI

Growth analyses In each experiment growth analyses were performed during the grain-filling period with sampling intervals of 7 to 14 days. Plants were dissected to separate the following parts:

- ear; when possible separated in grains and chaff plus rachis,
- flag leaf blade,

- second leaf blade,
- lower leaf blades,
- first plus second internodes plus leaf sheaths,
- lower internodes plus leaf sheaths,
- roots (not recovered from the field crop).

Growth analyses were less detailed in Expt IV, as well as in Expts VA and VB during the first half of the grain-filling period.

Fresh weights were measured immediately after dissection of the respective plant parts. The green area of the leaf blades was determined with an electronic planimeter (Paton Industries, Australia). When fresh and dry weights of leaf blades were measured, no distinction was made between green and non-green tissue. Roots from pot-grown plants were recovered by washing away the substrate. In order to facilitate washing, pure sand was used in Expt VI. After fresh weight and green area determinations, plant parts were chopped. The samples were oven-dried at 70°C for 24 hours and weighed immediately after they were taken out of the oven. When the grains were big enough to be recoverd, about one week after anthesis, ears were threshed and grain numbers counted. Grain and chaff and rachis samples were redried and weighed.

Next, samples were bulked (generally in duplicate samples) ground and a (sub)sample of the powered material was sealed in plastic, awaiting chemical analysis.

No real replicates were taken in Expt II; at each sampling 30 plants were taken. In Expt III each figure is the mean of 7 replicates: 6 pots of 12 plants each supplemented by the sample taken for respiration measurement, which consisted of 12 plants (2 plants taken form each of the 6 pots). At each sampling date 3 samples of 14 plants were taken in Expt IV. In Expt VA 6 pots with 18 plants were harvested at each sampling occasion. Each figure for growth analysis in Expt VB (field crop) represents the weighted mean of 2-4 replicates of 0.25-0.125 m^2 each. In Expt VI 6 pots with 17 plants each furnished 6 replicates, whilst 2 replicates of 18 plants were obtained from respiration samples (6 plants taken from each of the 6 pots).

Photosynthesis In Expts II and IV apparent photosynthesis of a microcanopy was measured at regular intervals in all treatments. Each figure obtained is the mean of several observations on one lot of plants (30 in Expt II and 42 in Expt IV). Root respiration contributed to net CO_2 exchange. Technical details of measurements of photosynthesis and respiration are dealt with later.

In Expt III only a few measurements from each of the six treatments (2 temperatures, 3 N levels) could be obtained early after anthesis, because part of the equipment was destroyed in a fire. These few data are not presented. In Expt VA 7 pots were placed in the enclosure. Again, each figure is the mean of several observations on the same sample. Within each experi-

ment all successive photosynthesis measurements were made at a fixed light level. In Expt II photosynthesis was recorded throughout the day (16 hours). Since no diurnal pattern appeared, save for a slight decline towards the end of the light period, measurements were extended over a period of 2-3 hours only in subsequent experiments. No apparent photosynthesis rates were determined in Expts VB (field crop) and VI.

Respiration In Expt II only night-time respiration was measured in complete shoots, and in excised roots, ears, and stems and sheaths. In total 12 plants were involved, no replicates were taken. In Expt III night-time respiration was recorded in one replicate (n=12) of the following excised organs: ears, leaf laminae, and stems and sheaths (no root respiration measured). In Expt IV, VA and VB three replicate recordings were made with excised ears, leaf laminae, stems and sheaths, and roots. No roots were recovered from Expt VB. The side tiller shoots from Expt IV were measured intact. Samples were taken a few hours from dawn, just after midday and around dusk. Sample size was 18 plants in Expts IV and VA; 40-60 culms were taken in Expt VB because there was more variation between culms. Two replicates of 18 plants were taken in Expt VI, one at the start and one at the midst of the light period. Worthwhile noting is, that no diurnal pattern in respiration was observed in Expt IV (phytotron), but in Expt VA (pots outside) the midday respiration rates tended to be higher than in the other replicates, at least on sunny days. Technical details of respiration measurement are dealt with later in this chapter.

Chemical analyses Standard chemical analyses included N-Kjeldahl and water-soluble carbohydrates (WSC). No WSC determinations were done in Expt IV. Furthermore, starch was determined in most grain samples (except for Expt VI). In several selected samples analyses were made of cell wall constituents (CWC), carbon percentages, the fractional composition of WSC and the degree of polymerization of frustosans. Soluble protein was measured in leaf laminae, stems and sheaths and roots in a treatment subsidiary to Expt IV A16. Analyses of chlorophyll a + b were performed on leaf laminae in Expt VA and VB.

Abnormalities Frequent sampling and the numerous types of analyses enabled deviating samples to be traced. It appeared, that the data from samplings at 18 and 19 days after anthesis were somewhat out of range in Expt II 15 and II 20, respectively. The first sampling from Expt II D22 at 27 days after anthesis gave also somewhat unexpected results. Possibly some sampling error was involved. Likewise, a few strange figures were obtained from Expt VA N3 at 29 days from anthesis, possibly because of transient inadequate water supply. In the subsidiary treatments of Expt VI, some unexpected results were obtained in the treatments for the middle light level at 16°C.

Presumably climatic control was not as appropriate than assumed.

In experiments performed in the phytotron poor seed setting was noticed in many spikelets in the upper half of some ears, also at relatively cool temperatures, e.g. 15°C or 16°C. The frequency of this phenomenon was not recorded, but it may have appeared in about 10 to 20% of the ears. Furthermore, in all experiments and treatments, except in the field crop (Expt VB), plants showed for some time during the vegetative phase quite often symptoms resembling potassium deficiency. Generally extra potassium was supplied. Growth was never hampered, and the only lasting after-effects of the transient symptoms were yellow leaf tips (1-2 cm). Possibly potassium was not involved at all, but some agent inherent to artificial conditions.

2.3 TECHNICAL DETAILS OF METHODS AND PROCEDURES

2.3.1 Design and operation of the nutrient-culture system

In Expt I, II and IV plants were grown on a nutrient culture system (hydroponic). The tanks were 94 cm wide, 170 cm long and 50 cm deep. In total 220 plants could be placed on one tank. The outer rows were excluded from the experiments and served as guard rows. Seeds were germinated in fine silver sand. After one week the sand was washed away and the grain of the seedling was wrapped in a piece of plastic foam, which was placed in a one-centimeter-diameter hole in a 8 cm × 8 cm plastic square. The plastic squares were placed on a stainless steel framework above the nutrient solution. Roots of neighbouring rows were separated by plastic plates, which hung into the solution. Entangling of roots within a row was prevented by separating the roots manually a few times during early growth. The solution in the tanks was circulated continuously. The temperature of the solution could be controlled adequately. The solution was aerated by small air bubbles, escaping from finely perforated rubber tubes, connected to an air compressor.

In Expt II plants could not be moved easily within and between growth rooms. In Expt IV this problem was solved, resulting in more uniform plants.

2.3.2 Description of equipment for carbon-dioxide-exchange measurements

A mobile installation for measurement of CO_2-exchange was available. Carbon dioxide concentrations were measured by infra-red gas analysers (IRGA's) (URAS, made by Hartmann & Braun, Frankfurt/Main).
The system consisted of two sub-units:
1. Enclosure for measurement of CO_2-exchange in crops. The main circuit consisted of the enclosure (a Perspex cage); a fan, operated at a capacity of 1000 m^3 per hour; a temperature conditioning unit; and 24-cm diameter, air-tight, insulated tubes, by which the various parts of the cir-

cuit were connected to each other. Via a by-pass, air was led through an IRGA continuously. The signal from this IRGA was transmitted to a set of instruments which regulated the injection of pure CO_2 gas into the circulating air, for maintaining a preset equilibrium CO_2 concentration in the enclosure. The circuit was not completely closed. Outside air was forced into the enclosure at a rate such that it created an overpressure equivalent to a 2-3 cm water column. Under field conditions this overpressure is necessary to prevent CO_2 from the soil from entering the enclosure.

2. A separate system consisting of 5 or 7 channels, in which leaf photosynthesis or respiration chambers could be fitted. The actual number of available channels was 5 when system 1 was simultaneously in operation. In principle the design of this unit was as follows. Outside air was scrubbed free of CO_2 by passing through a sodalime tower. If necessary, part of the air was dried by passing through a silica-gel tower. Pure CO_2 was then injected at a constant rate into the CO_2-free (and dried) air. The thus obtained air, with a stable CO_2 concentration (in total 2 $m^3 \cdot hour^{-1}$), was divided over the channels. The air velocity was adjusted manually per individual channel (needle valves and flow rate meters). Leaf photosynthesis or respiration chambers were fitted in all channels but one. A sample of outlet air of each chamber was sucked back to the second IRGA (1 $litre \cdot min^{-1}$ per chamber). Measurement of the CO_2 concentration in outlet air of the blank channel gave a value of the CO_2 concentration of the inlet air of the other channels. The air tubes leading to or coming from the chambers were wrapped in an electric heating coil (to prevent condensation of water in the tubes) and covered by insulating material.

In both system 1 and 2 temperature was measured with thermocouples and radiation by a Kipp solarimeter. Temperatures, CO_2 concentrations and dew points were printed on two paper-roll recorders and input on magnetic tape once per run (one run lasted about 7 minutes). Incident radiation and the rate of CO_2 injection into system 1 were recorded more frequently per run. The paper-roll recorder output enabled constant control of operation and served as a safety output in case computer processing of the magnetic tape failed. The IRGA's were calibrated once or twice daily with calibration gasses produced by Wüsthoff gas mixing pumps.

Leaf chambers Chambers for measurement of flag-leaf photosynthesis were made of Perspex. The inner dimensions were: length 500 mm, width 25 mm and height 8 mm. Two Perspex strips (diameter 2.8 mm) at the bottom wall and one running at the centre of the top wall kept the leaves flat and stretched. The air inlets and outlets were placed in the bottom wall; the outlet was positioned near the base of the leaf. The chambers were sealed with some plastic putty. A thermocouple was attached to the lower surface of the leaf. Air velocities ranged from about 150 to 300 $litre \cdot h^{-1}$, aiming at a

maximum difference in CO_2 concentration between inlet and outlet air of about 30 ppm.

In relatively young flag leaves (shortly after anthesis) it took about three quarters of an hour or more before a stable net carbon-exchange rate was established (Expt I); in older leaves the period in which equilibrium was achieved was shorter. Keys et al. (1977) found a rather stable rate within minutes of fitting a flag leaf in a chamber; they observed a decline in photosynthesis rates after 10-15 minutes. Osman & Milthorpe (1971a) measured a maximum and stable rate of photosynthesis in the fourth leaf of wheat four hours after the start of the recordings.

Crop enclosure for photosynthesis measurements The enclosure system for crop photosynthesis measurements, described above, was actually designed to be operated on one square metre plots in the field. In the present experiments it was not possible to use a cage larger than 0.4 m^2 ground area. This meant an aggravation of relative errors, especially for small carbon-exchange rates of the crops. For this reason, and because of other technical difficulties, the scatter in photosynthesis measurements was often bigger than in other measured attributes, for instance respiration.

Respiration chambers Equipment was developed to measure respiration rates of excised organs. Basically the set-up consisted of a big, temperature controlled water bath and a number of double-walled plastic cylinders. The space within the inner cylinder served as a measuring cuvette, connected to the IRGA system-2. Samples were placed in containers with some water, which in turn were placed in the inner cylinders. Temperature control was achieved by forcing water of the desired temperature through the space between inner and outer cylinder and back into the water bath. The cylinders were wrapped in insulating material. The temperature of the samples was recorded by thermocouples. The tubes varied in length from 50 cm to 110 cm; the diameter of the inner space was 7 cm.

Measurement of root respiration was slightly different, in that roots were placed in a bottle with water of pH 4.5 to 5.0. The air inlet reached nearly to the bottom of the flask. Temperature was controlled by putting the bottle in a water bath where the desired temperature was maintained.

2.3.3 Evaluation of the technique of respiration measurement

There was concern at to whether the rates of respiration measured on excised organs would deviate from measurements on intact plants. Several tests were made to compare the rate of respiration of intact shoots with the sum of the rates determined in separate, excised organs. The difference between intact shoot and sum of component parts rarely exceeded 5%. Other test showed no discrepancy between respiration rates in intact and excised

mature roots.

The time lapse before a stable carbon efflux was reached, was about an hour or less for aerial organs and one hour and a half or more for roots. Yamaguchi (1978) also reported a longer equilibration period for roots than for shoots with equipment of basically similar design. During the last experiment it was discovered that the equilibration period for roots could be shortened by leading compressed air through the bottle before commencing of the recordings, or by minimizing the amount of water.

In mature, excised organs the rate of respiration was rather constant for several hours, and even during a whole night. The respiratory carbon efflux from young shoots and young roots (4-6 weeks old) tended to decline somewhat during the night (data not presented).

2.3.4 Methods of chemical analyses

Water-soluble carbohydrates (WSC) were measured on an automatic analysing device, using anthrone (Expt II), and ferricyanide (Expts III-V). WSC were weighed as glucose; thus some amount of inaccuracy is involved as part of the WSC consisted of fructosans.

Starch contents were estimated by subtraction of the amount of WSC (determined separately) from the amount of starch plus WSC (measured together after hydrolization with amyloglucosidase). Starch was weighed as $(C_6H_{10}O_5)_n$.

Total nitrogen, including nitrate, was determined by the Kjeldahl method as modified by Deijs (1961) or by an automatic analysing device (Expt VI), using alkaline salicylate. Separate analyses of nitrate (by a specific electrode) in Expt I showed that nitrate-N constituted only a few percentages of total-N after anthesis. Schouls (pers.comm. 1977) never found substantial accumulation of nitrate in wheat during kernel filling and therefore further nitrate analyses were omitted.

Soluble protein was measured according to Lowry et al. (1951), and chlorophyll determinations were based on the method of Arnon's (1949).

Carbon was determined with a micro-analysis. The dry matter was burnt at high temperature in pure oxygen. The carbon dioxide was collected by a specific absorber and measured by the weight increase of the absorber. Analyses were performed by Mr H. Jongejan of the Department of Organic Chemistry of the Agricultural University of Wageningen. Cell wall constitents (CWC) were estimated by the method of Van Soest (1977). Measurements of the fractional composition of WSC and of the degree of polymerization of fructosans were performed by Dr W. Kühbauch of the Lehrstuhl für Grünlandlehre der Technische Universität München. The procedures have been described by Kühbauch (1973) and Kühbauch & Voigtländer (1974). Nitrate reductase activities were assessed by an in-vivo method by Mr D.R. Verkerke (Centre for Agrobiological Research, Wageningen).

3 Results

3.1 CROP CHARACTERISTICS

3.1.1 Features of crop performance

Analyses of the experimental plant communities will have some relevance for field conditions when crop characteristics, reflecting crop performance in global terms, show values commonly observed under field conditions. Such characteristics are the mean crop growth rate, the relative uptake of nitrogen after anthesis and the harvest indices for dry matter and nitrogen.

The increments in total DM after anthesis (in $g \cdot m^{-2}$) and the crop growth rate (CGR; $g \cdot m^{-2} \cdot day^{-1}$) of most of the plant communities (15°C, 16°C and outdoors) are displayed by Table 2.

The CGR figures are only approximations because the accumulation of DM did not exactly end at the last sampling date. A mean CGR of about 150 $kg \cdot ha^{-1} \cdot day^{-1}$ may seem somewhat small, but then it must be remembered that the stage of declining growth prior to maturity was included in the interval over which the rates were calculated. It appears from Table 2 that differences in total DM accumulation between experimental systems were rather attributable to differences in duration of growth than to differences in CGR. Most crop growth rates under (semi)controlled conditions were not substantially different from that of the field crop Expt VB. Furthermore,

Table 2. Increment in total dry matter (DM) and approximate crop growth rates (during grain filling) in plant communities grown at 15°C, 16°C or outdoors.

Experiment and treatment	Interval considered (days after anthesis)	Increment in total DM ($g \cdot m^{-2}$)	Approximate crop growth rates ($g \cdot m^{-2} \cdot day^{-1}$)
II 15	4-68	870	14
IV A16	5-58	870	16
VA N1-N3	1-53	620	14
VA N1-N3[a]	1-53	715	16
VB[a]	7-48	620	15
VI N1	4-48	520	12
VI N2	4-48	750	16

a Roots excluded

the total amounts of DM produced during the post-floral stage are in the order of magnitude normally obtained under Dutch field conditions.

Between 60% and 85% of the total amount of N present in the shoot (roots not considered) at maturity was already taken up before anthesis, the figure of the field crop (Exp VB) was 69% (Table 3). These values are rather common for field conditions (Austin et al., 1977; Spiertz & Ellen, 1978; Spiertz & van de Haar, 1978; all on winter wheat).

The harvest indices in Table 3 bear on shoot dry matter only. The harvest indices for dry matter (HIDM) ranged between 0.42 en 0.50 for plant communities grown at 15°C and 16°C or outdoors; that for the field crop was 0.42. The HIDM was generally smaller the higher the temperature during grain filling (Expt II and III N1) or the earlier during grain filling the transfer was made from 16°C to 22°C (Expt IV). The overall range of values is the same as commonly observed under field conditions (e.g. Spiertz & Ellen, 1978;

Table 3. The relative uptake of nitrogen after anthesis and harvest indices for dry matter (DM) and nitrogen (N).

Experiment and treatment	Percentage of final amount of N in the shoot already present at first sampling date after anthesis	Harvest indices	
		DM	N
II 15 ma[a]	80	0.43	0.68
II 15 st[b]	85	0.45	0.70
II 20 ma	80	0.36	0.57
II 20 st	85	0.38	0.60
II 25 ma	80	0.33	0.53
II 25 st	85	0.34	0.53
III N1-16	83	0.45	0.76
III N1-22	83	0.42	0.74
IV A16 ma	58	0.47	0.82
IV A16 st	60	0.49	0.84
IV B22 ma	58	0.43	0.77
IV B22 st	60	0.44	0.79
IV C22 ma	58	0.45	0.80
IV C22 st	60	0.46	0.80
IV D22 ma	58	0.46	0.82
IV D22 st	60	0.48	0.82
VA N1	81	0.50	0.79
VA N2	76	0.49	0.72
VA N3	74	0.48	0.68
VB (field crop)	69	0.42	0.68
VI N1	81	0.42	0.68
VI N2	85	0.41	0.61

a ma = main axis
b st = side tiller

Spiertz & van de Haar, 1978; Gallagher & Biscoe, 1978; Ellen & Spiertz, 1980).

The harvest indices for nitrogen (HIN) ranged between 0.68 and 0.82 for the low temperature treatments, including experiments outdoors; for the field crop it was 0.68. In Expt VA (pots outdoors), the HIN was smaller the higher the nitrogen dressing. The same tendency holds for HIDM in this experiment. The harvest indices for nitrogen were also smaller the higher the temperature, or the earlier during grain filling the transfer was made from 16°C to 22°C. The overall range of values is similar to the one commonly observed under field conditions (Austin et al., 1977; Spiertz & Ellen. 1978; Spiertz & van de Haar, 1978; Ellen & Spiertz, 1980).

The harvest indices for DM and N of the side tillers in Expt II and IV were generally above those of the main culms. There was no significant correlation between HIDM and HIN.

Data from the N2 and N3 treatments at both temperatures of Expt III were excluded from Table 3. This was done because it is difficult to interpret and to account for the amount of DM and N invested in continuously regrowing side tillers. Table 4 shows the amount of DM and N involved in tiller regrowth in those treatments. The figures represent cumulative amounts per culm, invested after several complete excisions of tillers between anthesis and 44 or 45 days later in the respective 16°C and 22°C treatments. The amounts of DM and N involved were bigger at the lowest temperature and at the highest N dressing.

The cumulative amounts of DM and N in side tillers was also expressed in percent of the grain DM and N yield (Table 4). These figures indicate that the side tillers in those treatments acted as important sinks for DM and N. This has to be kept in mind when further analyses of those treatments are presented.

The characteristics of the experimental plant communities presented hith-

Table 4. Data about cumulative amounts of dry matter (DM) and nitrogen (N), invested in regrowing side tillers at both temperatures in the respective N2 and N3 treatments in Expt III. (See for intermediate figures Appendix A).

Treatment :	N2-16	N2-22	N3-16	N3-22	
interval anthesis to:	44	45	44	45	days later
Cumulative amount of DM invested in side tillers:					
in mg per culm	420	333	746	405	
in % of grain DM	20	19	39	24	
Cumulative amount of N invested in side tillers:					
in mg per culm	13	11	27	15	
in % of amount of N in grains	25	21	57	30	

erto do not advise against extrapolation of trends to field conditions because important features of crop performance were basically similar to those of field crops.

3.1.2 Detailed description of the crops shortly after anthesis

For a more detailed description of the respective crops Table 5 contains data about dry weights per organ, green leaf areas and specific leaf areas. All data relate to the first sampling after anthesis. Results of statistical analyses of effects of nitrogen dressings are included. The data about specific leaf areas were not subjected to statistical processing.

Table 5 shows that the dry weights per culm of ears, leaf blades and of stems and sheaths were high in the main shoots of Expt II and small in the field crop (Expt VB); the difference in dry weight per organ as well as in total shoot dry weight amounted to a factor 3 between these two extremes.

In Expts III and VA nitrogen treatments had no or negligibly small effects on both dry weights and green areas of the respective organs at anthesis. In Expt VI the dry weights of all organs, except those of the lower internodes and roots, were significantly higher at the highest nitrogen dressing; green leaf areas were affected likewise.

The relative distribution of shoot dry matter over ears, leaf blades and stems and sheaths can be derived from the data in Table 5. It appeared that at anthesis on average a fraction of 0.17 (with a coefficient of variation, c.v., of 12%) of the dry matter was present in ears, 0.23 (c.v. 10%) in leaf blades and 0.60 (c.v. 4%) in stems and sheaths. Thus it can be noted that the total shoot dry matter present at anthesis was distributed in fairly fixed proportions over aerial organs.

Inclusion of root dry weight in this approach led to some difficulties because the shoot to root ratio (abbreviated by S/R) varied considerably between experiments. As shown by Table 5 S/R ratios ranged from 3 to 6.9.

Around anthesis the specific leaf area of flag leaves was on average 1.87 $dm^2 \cdot g^{-1}$ (n = 7, c.v. = 7%), that for second leaves amounted to 2.15 $dm^2 \cdot g^{-1}$. Specific leaf areas for the lower leaves are somewhat less reliable since a varying amount of dead leaves did contribute to the dry weight but not to the green area. The same holds of course for specific leaf areas calculated for bulked leaves per culm. A tendency can be noted towards a higher specific leaf area in plants grown outdoors or in the green house (Expts III, VA, VB) compared to phytotron grown plants (Expts II, IV, VI).

The total number of leaves formed until heading was not recorded. At anthesis the number of predominantly green leaves was about 5 per culm.

Table 5. Dry weight (DW, mg), leaf areas (cm^2), specific leaf areas (SLA, $dm^2 \cdot g^{-1}$) and shoot/root ratio's (S/R) at first samplings after anthesis from Experiments II-VI.

Attribute	Expt II, 4 d.a.a.		Expt III, 3 d.a.a.			Expt IV, 5 d.a.a.		Expt VA, 1 d.a.a.			Expt VB	Expt VI, 4 d.a.a.		
	ma	st	N1	N2	N3	ma	st	N1	N2	N3	7 d.a.a.	N1	N2	signi-ficance
ear dry weight	760	510	420a	381a	412a	530	450	311	314	326	253	376	451	****
flag leaf:														
area	38.0		20.7a	19.0a	21.2a							24.5	30.6	****
dry weight	230		106	100	118							126	167	****
SLA	1.65		1.95	1.90	1.80							1.94	1.83	
second leaf:														
area	44.4		20.7ab	17.4a	21.1b							17.8	23.6	****
dry weight	260		90ab	82a	99b							86	108	
SLA	1.71		2.30	2.12	2.13							2.07	2.18	
lower leaves:														
area	61.0		61.4a	79.4b	73.0b							19.3	46.4	****
dry weight	350		383a	406a	419a							340	369	*
SLA	1.74		1.60	1.96	1.74							0.57	1.26	
total of leaves:														
area	143.1	-	104.8a	115.8a	115.2a	99.3	85.6	121.9	127.1	123.4	55.7	61.6	100.4	
dry weight	840	630	579a	588a	636a	670	530	444	462	471	272	552	644	
SLA	1.71		1.81	1.97	1.81	1.48	1.62	2.74	2.75	2.61	2.05	1.11	1.56	
DW 1st+2nd internodes	1200		807a	665b	718ab							829	943	****
DW lower internodes	890		695a	613a	593a							642	652	ns
DW total stem	2090	1830	1502a	1278b	1311b	1670	1430	1498	1466	1469	783	1471	1595	ns
DW shoot	3700	2970	2670	2410	2540	2870	2140	2250	2240	2270	1310	2400	2710	
DW root	970		828	659	774	1760		462	435	557	-	704	728	ns
S/R	6.9		3.0	3.4	3.0	3.0		4.9	5.2	4.1		3.4	3.7	

d.a.a. = days after anthesis; ma = main axis; st = side tiller. Figures followed by different letters indicate a statistically significant difference between means in Expt III (Tukey's Honest Significant Difference Test, $P < 0.05$). No statistically significant differences were found among nitrogen treatments of Expt VA. For Expt VI statistically significant differences are indicated by the number of stars, where **** = $P < 0.001$, *** = $P < 0.01$, ** = $P < 0.1$; ns = no statistically significant differences.

3.1.3 Numbers of ears, spikelets and kernels

Important characteristics of a wheat crop are the number of ears per square metre, the number of spikelets per ear, and the number of kernels per ear (or per square metre). These attributes are given in Table 6. With respect to ear densities it suffices to remark that these were attained by manipulating the crop and not as a result of free tillering, except in the field crop Expt VB. Furthermore it is recalled that the arrangement of pots did not permit unit ground area to be used as a reference basis for data of Expt III.

Spikelet numbers were generally counted on a few occasions only; the total number (including empty ones) ranged between 18 and 26. In Expt VI the number of empty spikelets in the basal parts of the ear was counted more systematically. This was done because from a visual judgement a nitrogen effect was expected. It appeared that the total number of spikelets increased by two with more nitrogen, whilst the number of empty spikelets had decreased by two.

The number of kernels per ear was determined at several sampling occasions, starting at about mid-kernel filling. Counts of several harvests were averaged and data of all treatments within an experiment were bulked when significant nitrogen and/or temperature effects were not found. Only in Expt VI more kernels per ear were found with more nitrogen. Variation in temperature from one week after anthesis onwards had no effect on seed setting.

The number of kernels per square metre varied considerably between experiments, viz. from about 13 000 in Expt IV to almost 21 000 in Expt VI N2.

3.2 FEATURES OF GRAIN GROWTH

3.2.1 Ear-growth curves

As a simplification, the period of grain filling can be subdivided in three consecutive stages. During the first one or two weeks after anthesis the rate of dry matter gain is relatively small. In literature this is called the 'initial lag period'. During the second stage, the growth rate is almost constant, it extends over most of the grain-filling period and is often called 'the linear phase'. It is in this stage that the bulk of the grain dry matter is produced. During the third, or maturation stage, the rate of dry matter accumulation can be small. Sometimes a decline in dry weight shows up after a maximum is reached.

Ear-growth curves, obtained in experiments grown outdoors or at 15°C or 16°C under controlled conditions, are given in Fig. 1. From Expts III and VA the curves of the respective N2 treatments were included only. These curves show the features mentioned above. However the curves are given

Table 6. Ear, spikelet and kernel numbers.

Experiment	Number of ears per m^2 ground area	Approx. total no. of spikelet per ear	Number of grains per ear	Number of grains per m^2
II ma	312	26	63.1	19 080
II st		nm	59.2	
III	-	21.5	46.4	-
IV ma	312	21.2	44.2	13 070
IV st		nm	39.6	
VA	455	18.0	39.9	18 150
VB	553	18.2	28.8	15 930
VI N1	466	20.4(3.7)[a]	36.9	16 970
VI N2	466	22.3(2.3)[a]	45.2	20 790

ma = main axis; st = side tiller; nm = not measured
a Values in brackets indicate total number of empty spikelets per ear.

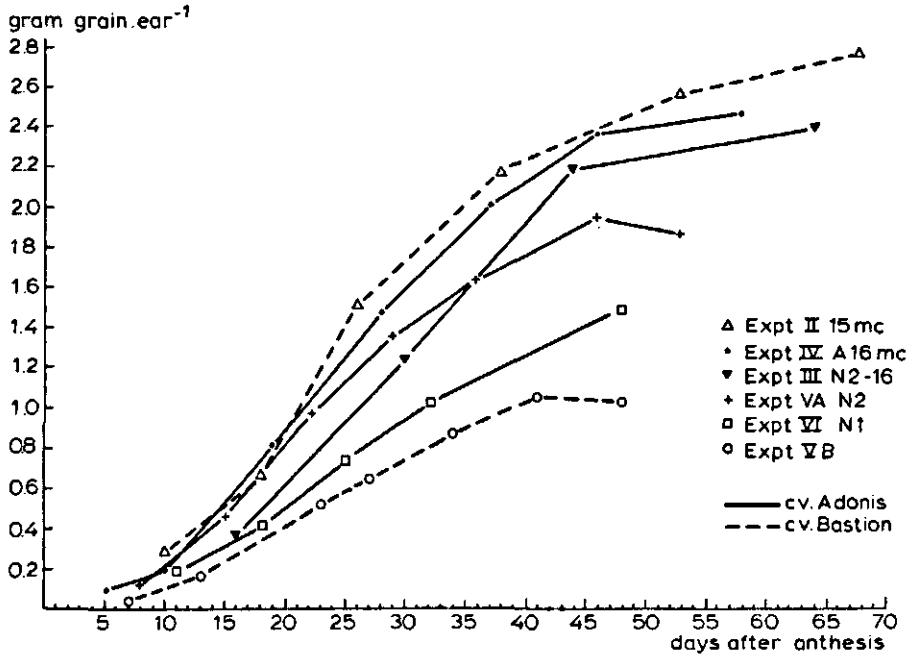

Fig. 1. Changes with time in grain dry weight per ear; data from different experiments with moderate temperature regimes (15°C, 16°C, outdoors).

primarily to stress the variation between experiments with respect to grain growth rate, the duration of the grain-filling period and grain yield on a one culm basis. These differences were mainly attributable to differences in experimental conditions, since only two varieties were use (viz. cv. Bastion, represented by broken lines and cv. Adonis, represented by solid lines).

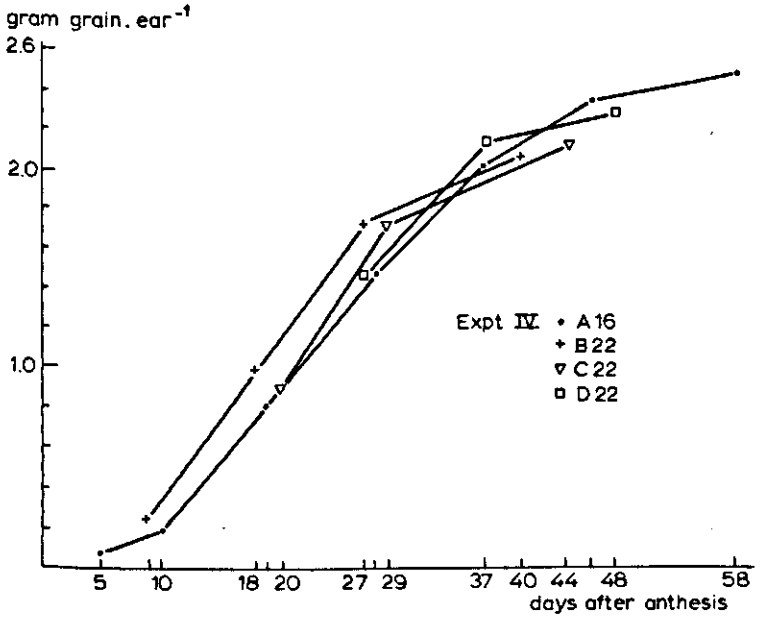

Fig. 2. Effect of temperature on change with time in grain dry weight per ear. Data from Expt IV; treatment A16 kept at 16°C air temperature continuously; treatments B22, C22 and D22 transferred from 16°C to 22°C air temperature at 6, 17 and 24 days after anthesis, respectively. Root temperature 16°C in all treatments.

3.2.2 General picture of temperature effects on grain growth

Temperature effects on grain growth were in principle similar in all experiments. Warmth shortened the 'initial lag', in most cases increased the rate of DM accumulation during the 'linear stage', and shortened the total period of grain filling.

These effects are shown by an example of the ear-growth curves of the main culms in Expt IV, which are depicted in Fig. 2. With respect to the shortening effect of warmth on the initial lag it has to be remembered that the first figure of Expt IV B22 (at 9 days after anthesis) relates to the third day after transfer from 16°C to 22°C. Apparently, the linear stage had already commenced in Expt IV B22, whilst it started a few days later in Expt IV A16. Fig. 2 shows also that ear-growth rates increased in response to higher temperatures, irrespective of the stage of grain filling. Likewise, the total period of grain filling was shorter, the earlier the plants had been subjected to higher temperature. Again, the number of points drawn in Fig. 2 are not completely convincing, because the cessation of DM accumulation is not displayed. However, in all treatments the last samplings were taken when ears and top internodes had lost all green coloration and thus bear on a similar stage of development.

It appears from these results that the temperature prevailing at any point in time during grain filling exerts a distinct effect on both (potential) grain growth rate and rate of development.

3.2.3 Dry matter and nitrogen accumulation rates per kernel

The DM (dry matter) and N (nitrogen) accumulation rates during the second or almost linear stage are convenient parameters to characterize grain growth further. These rates were calculated by simple linear regressions, relating total grain dry weight or amount of nitrogen to time. Only those figures were included that fell on an approximately straight line, as judged by eye. The intervals chosen in this way and the growth rates, given by the slopes of the regressions, are presented in Table 7.

First of all it is of interest to note that the periods of constant ni-

Table 7. Accumulation rates of dry matter (DM) and nitrogen (N) per grain during the linear stage of grain growth as well as Q_{10}-values.

Experiment and treatment	Interval d.a.a.	mg DM·grain^{-1}·day^{-1}	Q_{10} base = 15°C or 16°C	Q_{10} base = 20°C	Interval d.a.a.	µg N·grain^{-1}·day^{-1}	Q_{10} base = 15°C or 16°C	Q_{10} base = 20°C
II 15 ma	10-38	1.08		1.52	18-53	17.27		2.38
II 20 ma	11-17	1.33	1.52		11-37	26.62	2.38	
II 25 ma	12-16	1.74	1.61	1.71	12-24	37.72	2.18	2.00
II 15 st	26-38	0.94		1.60	26-38	19.24		2.11
II 20 st	11-25	1.19	1.60		11-37	27.94	2.11	
II 25 st	12-19	1.50	1.60	1.59	12-24	34.26	1.78	1.50
III N1-16	16-30	1.51	ca 1.0		16-30	27.64		
III N1-22	10-17	1.54	ca 1.0		10-31	31.15	1.22	
III N2-16	16-30	1.34	ca 1.0		16-44	30.73		
III N2-22	10-17	1.32	ca 1.0		17-38	38.75	1.47	
III N3-16	16-30	1.20	ca 1.0		16-44	29.68		
III N3-22	10-31	1.26	ca 1.0		10-31	36.59	1.42	
IV A16 ma	10-37	1.57			10-46	26.33		
IV B22 ma	9-27	1.89	1.36		9-27	38.34	1.87	
IV A16 st	10-37	1.48			10-46	25.17		
IV B22 st	9-27	1.81	1.50		9-40	34.31	1.68	
VA N1	8-29	1.52			8-36	22.72		
N2	8-29	1.51			8-36	26.12		
N3	8-29	1.47			8-36	25.41		
VB	13-34	1.18			7-48	18.23		
VI N1	11-32	1.07			11-48	18.43		
VI N2	11-32	1.06			11-48	21.12		

ma = main axis; st = side tiller; d.a.a. = days after anthesis

trogen deposition rates were longer than those of constant total dry matter accumulation rates.

By inspection of treatments grown outdoors or at 15°C and 16°C under controlled conditions it can be seen that the rates of total dry matter accumulation varied between about 1.1 and 1.5-1.6 mg DM·kernel^{-1}·d^{-1}. In fact, the grain growth rates in the two experiments with cv. Bastion (Expts II 15 and VB) were in the same order of magnitude, viz. about 1.1 mg DM·kernel^{-1}·d^{-1}. In the other experiments with cv. Adonis the mean grain growth rate was about 1.5 mg DM·grain^{-1}·d^{-1}. However there were exceptions within cv. Adonis: rates were lower in the N2 and N3 treatments of Expt III and in Expt VI.

In Expts VA and VI kernel growth rates during the linear stage did not differ between nitrogen treatments. In Expt III the kernels grew faster at the lowest level of nitrogen application, at least until about 4 weeks after anthesis. The rates for the N3 treatments were slightly smaller than those of the N2 treatments. In this particular experiment the smaller grain growth rates with more nitrogen had possibly some link with the greater drain of assimilates to regrowing side tillers.

Temperature drastically enhanced the growth rates during the linear stage in Expts II and IV; the Q_{10} for the rate of total DM accumulation in the grains was about 1.5. According to the figures in Table 7 the linear growth rates were not enhanced by temperature within each nitrogen treatment of Expt III. However, at 16 days after anthesis grain dry weights per ear were far smaller in the 16°C treatments than at 17 days after anthesis at 22°C, for instance 340 mg grain DM·ear^{-1} was found in N1-16, against 540 mg grain DM·ear^{-1} in N1-22. Expt III thus seems to represent an example where warmth reduced the initial lag, whilst the potentially higher kernel growth rate could not be realized due to lack of substrates. Of course, the latter statement needs to be confirmed by analyses of the carbohydrate economy later in this report.

Nitrogen deposition in treatments grown outdoors or at 15°C or 16°C under controlled conditions ranged between 17-18 and 25-30 µg N·kernel^{-1}·d^{-1}. The former figures seem representative for cv. Bastion, and the latter for cv. Adonis.

The rate of nitrogen deposition was smallest in the respective N1 treatments of Expts III, VA and VI. Temperature generally enhanced the rates of N accumulation in the grains; the Q_{10} for this process was generally higher than that for total DM accumulation rate.

Additional data about DM and N accumulation rates in grains and Q_{10} values are given by Table 8. These figures are from temperature treatments, which were imposed at later stages of grain filling. It appears from Tables 7 and 8 that representative values for the Q_{10} for DM and N accumulation rates were about 1.5 and around 2.0, respectively, over the range of temperatures tested. There were deviating figures, some of which undoubtedly due

Table 8. Effect of temperature on the rates of dry matter (DM) and nitrogen (N) accumulation per grain in treatments imposed later during grain filling.

Experiment and treatment	Interval d.a.a.	mg DM grain^{-1}. day^{-1}	Q_{10} base = 16°C	Interval d.a.a.	µg N grain^{-1}. day^{-1}	Q_{10} base = 16°C
IV A16 ma	19-28	1.66		19-28	23.98	
IV C22 ma	20-29	2.09	1.47	20-29	37.43	2.10
IV A16 st	19-28	1.77		19-28	24.30	
IV C22 st	20-29	2.27	1.51	20-29	42.56?	2.54?
IV A16 ma	28-37	1.46		28-37	ca 25.0	
IV D22 ma	27-37	1.45?	1.00?	27-37	36.88	ca 1.91
IV A16 st	28-37	1.06		28-37	24.80	
IV D22 st	27-37	1.74?	2.28?	27-37	43.0?	2.51?
VI N1 16[a]	18-31	-		18-31	16.10	
VI N1 22	18-31	-	ca 1.0	18-31	23.49	1.88
VI N2 16	18-31	-		18-31	20.80	
VI N2 22	18-31	-	ca 1.0	18-31	33.29	2.19

a Data from subsidiary treatments of Expt VI averaged over three radiation levels and both series.
? = questionable figure; ma = main axis; st = side tiller; d.a.a. = day after anthesis

to experimental errors (Section 2.2) some presumably due to lack of substrates, as will be elaborated later.

3.2.4 Effects of temperature and radiation on grain growth in the subsidiary treatments of Expt VI

The ear dry weights obtained in the subsidiary treatments of Expt VI are shown in Fig. 3. These treatments consisted of all combinations of three light levels and two temperatures, imposed for 6 days in both nitrogen treatments, starting on 18 and 25 days after flowering. The data of the highest and of the lowest light level are given in Fig. 3 only. For reference part of the grain growth curves of the main treatments VI N1 and VI N2 are shown (solid lines; daily quantity of radiation about equal to that in the omitted L2 light level of the subsidiary treatments).

The general pattern is that temperature dit not affect grain growth; whilst grain growth was faster the higher the radiation flux density. The absence of a temperature enhancement of grain growth, and its response to radiation flux density both point at a limiting substrate supply in Expt VI. A limiting substrate supply, in turn, might explain why the grain growth rates were lower in Expt VI than in other experiments with cv. Adonis. It

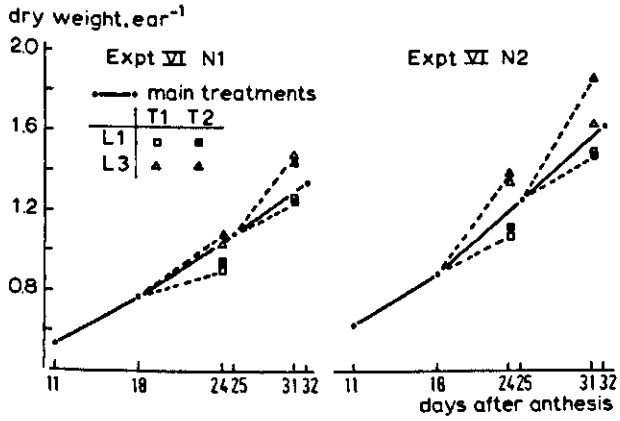

Fig. 3. Effects of temperature and radiation on ear dry weights in the subsidiary treatments of Expt. VI. The change with time in the main treatments, VI N1 and VI N2, is given by solid lines. T1 = 16°C, as in the main experiments; T2 = 22°C. L1 = 0.17 J·cm^{-2}·min^{-1}, L3 = 0.54 J·cm^{-2}·min^{-1} (PhAR: photosynthetically active radiation).

is because they led to this hypothesis that the results of the subsidiary treatments were included.

3.2.5 *Grain DM and N yields; durations of post-floral periods*

Information about grain dry matter and nitrogen yields, as well as data about the duration of the grain-filling periods are given by Table 9.

In the moderate temperature treatments (outdoors, 15°C and 16°C) grain DM yields ranged from 1.02 (field crop Expt VB) to 2.76 gram per ear (Expt II 15 main axis). Individual grain weights at maturity ranged between 35.4 mg in Expt VB to more than 55 mg in Expt IV A16. When converted to grams per square metre the smallest yields appeared in the field crop, viz. 564 g·m^{-2}. The highest yields were achieved by the plant communities of Expt VA (pots outdoors). These plants produced about 880 g·m^{-2} under climatic conditions largely similar to those for the field crop.

Between those experiments or treatments within a cultivar, which had about equal kernel growth rates during the linear stage, the differences in grain dry matter yield per unit ground area were attributable to either differences in duration of the grain-filling period or in number of kernels per square metre or both. For instance, in spite of the longer duration of grain filling in Expt IV A16, the relatively small number of grains per unit area (about 13 000) did not allow this plant community to outyield those of Expt VA with about 18 000 grains per m^2 and a shorter post floral period.

It is of interest to note that in Expts II and IV the differences in grain yield per ear between main axis and the one side tiller left were

Table 9. Grain dry matter (DM) yields, expressed per ear, per grain and per unit land area; grain nitrogen (N) yields per ear; and duration of DM accumulation.

Experiment and treatment	Grain DM yield			mg N·ear^{-1} in grains	Duration anth.-mat.[a] (days)
	g·ear^{-1}	mg·grain^{-1}	g·m^{-2}		
II 15 ma	2.76	43.7	830	65.1	68
II 15 st	2.56	43.2		57.6	
II 20 ma	2.01	31.9	602	56.1	47
II 20 st	1.85	31.3		53.3	
II 25 ma	1.58	25.0	465	48.7	33
II 25 st	1.40	23.6		43.3	
III N1-16	2.12	45.7	-	43.9	ca 64
III N2-16	2.39	51.5	-	51.2	ca 64
III N3-16	2.23	48.1	-	49.3	ca 64
III N1-22	1.69	36.4	-	45.9	ca 43
III N2-22	1.84	39.7	-	54.3	ca 43
III N3-22	1.77	38.1	-	51.7	ca 43
IV A 16 ma	2.47	55.6	738	53.2	58
IV A 16 st	2.26	57.1		48.6	
IV B 22 ma	2.05	46.4	610	52.0	37
IV B 22 st	1.86	47.0		46.9	
IV C 22 ma	2.12	48.0	630	50.5	40
IV C 22 st	1.92	48.5		44.2	
IV D 22 ma	2.29	51.8	685	52.6	48
IV D 22 st	2.10	53.0		46.2	
VA N1	1.88	47.1	855	37.4	ca 49
VA N2	1.95	48.9	887	ca 40.0	ca 49
VA N3	1.94	48.6	883	41.4	ca 49
VB	1.02	35.4	564	21.7	ca 45
VI N1[b]	1.48	40.1	690	29.3	48
VI N2[b]	1.77	39.2	825	39.1	> 48

ma = main axis; st = side tiller.
a anth.-mat. = anthesis till maturity.
b Treatment VI N2 discontinued before complete maturity.

solely attributable to differences in grain numbers between the two types of tillers.

Within Expt III the respective N1 treatments (16°C and 22°C) dropped behind with respect to final yield per ear because the grain growth rate slowed down earlier than in the N2 and N3 treatments. Leaf senescence proceeded also at a faster rate in the N1 treatments.

In Expt VI the differences in yield per unit area were mainly attributable to differences in grain number per m^2 since the growth rates per kernel were similar in both nitrogen treatments.

Temperature did not affect grain numbers within Expts II, III and IV. Thus the only component of yield affected by temperature was the final kernel dry weight. In all experiments warmth exerted a negative impact on

final kernel dry weight. The accelerating effects of warmth on the transition from the initial lag to the linear stage and on the kernel growth rate were not big enough to compensate for the shorter duration (under the present experimental conditions). The drastic effects of temperature on duration will be discussed in more detail in Section 4.8.

Temperature did not affect final grain nitrogen yield per ear in Expts III and IV (Table 9). The stimulating effect of warmth on the deposition of proteins in the grains was apparently large enough to compensate for the shorter duration of protein accumulation. However, in Expt II, with cv. Bastion, grain nitrogen yield was smaller the higher the temperature during grain filling.

In Expts III, VA and VI grain nitrogen yields per ear were smaller at the respective N1 levels of nitrogen nutrition.

Between the nitrogen treatments of Expts. III and VA there were no differences in the length of the period of dry matter accumulation in grains. At the time when Expt VI had to be discontinued the N2 plants were not fully ripe yet. However, a possible continuation of grain filling in this treatment would presumably have been a matter of a few days, since the ears of both nitrogen treatments started to loose water at the same time. Based on these findings it is justified to state that nitrogen had only a minor influence on the duration of grain filling in the present experiments.

The duration of grain filling was generally longer under controlled conditions with a moderate temperature economy than outdoors: about 60 versus 45 days.

3.2.6 *Changes with time in the nitrogen concentration in grain dry matter*

The results presented so far indicate that accumulation of carbohydrates and proteins are regulated by different mechanisms. This can be demonstrated in further detail by analyses of the changes with time in the nitrogen concentration in grain dry matter. Two examples will be elaborated in more detail. Fig. 4a is taken from Expt IV and was chosen to illustrate temperature effects; Fig. 4b gives the time courses of the N concentration in grains as affected by nitrogen treatment in Expt VA. For reference purposes, data from the field crop Expt VB are included in this graph.

In virtually all experiments and treatments a two-stage pattern was observed: nitrogen concentrations declined until about the mid-kernel filling stage and increased towards maturity. At the beginning of grain filling the nitrogen concentration amounted to 26-27.5 $mg \cdot g^{-1}$ in Expts II, III, IV and VB, and to 23.5 $mg \cdot g^{-1}$ in Expts VA and VI. At mid-kernel filling the nitrogen concentrations ranged between 16.5 and 21 $mg \cdot g^{-1}$. At warmer temperatures nitrogen concentrations increased earlier whilst the final concentrations were higher than under cooler conditions. With respect to the effects of nitrogen dressings it can be noted that the differences in grain

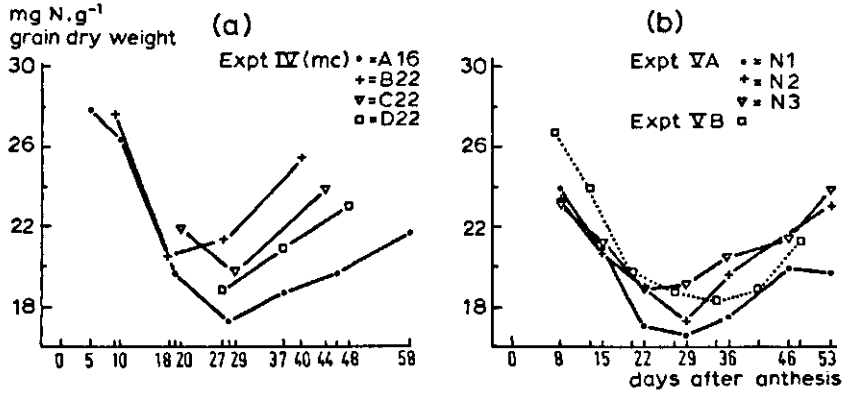

Fig. 4. Changes with time in nitrogen concentrations in grain dry matter. (a). Effects of temperature, data from Expt IV. (b). Effects of nitrogen treatment in Expt VA (pots outdoors); data from the field crop, Expt VB, are included for reference (dotted line).

nitrogen concentrations were generally small during the first weeks after anthesis. As time progressed the plants supplied with more nitrogen took advantage over less well fertilized plants with respect to both concentration and absolute amounts of nitrogen in the grains.

Figs 4a en 4b show that the time course of nitrogen concentration in the grains was basically similar in the field crop VB, in plants grown in pots outdoors (Expt VA), and a moderate temperatures in the phytotron (Expt IV A16).

3.2.7 Change with time in chemical composition of grains

Figures 5a-d depict the cumulative fractional chemical composition throughout kernel filling of Expts II 15, II 25, VA N1 and VB, respectively. Three groups of components were determined: water-soluble carbonhydrates (further abbreviated by WSC), protein (N content times 5.95) and starch.

Between 5 and 10 days after anthesis, when grain could be recovered separately for the first time, the WSC mass fraction was 30-50% of total grain DM. At moderate temperatures (15°C, 16°C, outdoor treatments) the WSC fraction declined rapidly until about 25 days after anthesis. However, measured in absolute units, the amounts of WSC generally increased during this period. Beyond 20-25 days after anthesis the fraction of WSC was small, i.e. between 3% and 6%, and remained fairly stable. The rate of decrease of the WSC fraction in the first half of kernel filling was faster at higher temperatures, demonstrated by Fig. 5a and 5b. Later during kernel filling the WSC fraction of grain dry matter generally did not show differences between temperature treatments.

As early as 8-10 days after anthesis starch percentages over 10% were

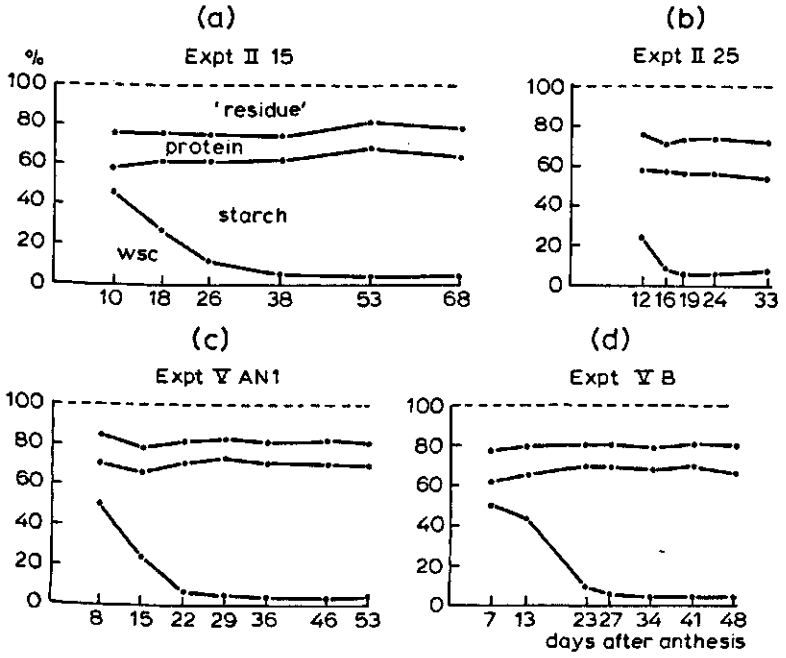

Fig. 5. Examples of the change with time in the cumulative proportional chemical composition of grain dry matter for the following constituents: water-soluble carbohydrates (WSC; basal part), starch, protein and 'residue' (uppermost fraction, consisting of the fraction of the dry matter not identified as WSC, protein or starch). Data from Expt II 15 and II 25, respectively, illustrate the effects of temperature.

measured at moderate temperatures. In Expt II 25 the starch percentage was already 33% at 12 days after anthesis (4 days after transfer from 15°C to 25°C). Starch became the most predominant compound beyond 3 weeks after anthesis in all cases.

Protein, actually nitrogen concentration, has been treated in detail in subsection 3.2.6. It suffices to remark here that the fraction of protein, as read from the width of the protein band in Fig. 5a-d, was smallest at mid-kernel filling, and that it was greater under warmer conditions.

Between 70% and 85% of the total grain dry matter was generally caught in these three types of compounds. At the beginning of grain filling the proportion of unidentified compounds was generally greater than near maturity, whilst it was smaller at moderate than at warm temperatures. With more nitrogen (Expt III, VA) the proportion of unidentified compounds tended to increase. Furthermore the starch fraction in the dry matter of mature grains was somewhat smaller at higher nitrogen dressings, for instance 65.3% and 62.5% in VA N1 and N3, respectively.

The change with time in fractional chemical composition of grains did not differ between the field crop and the other cases analyzed.

3.3 THE NITROGEN ECONOMY

3.3.1 Initial and residual mass fractions of nitrogen

The initial and residual mass fraction of nitrogen in dry matter (mg $N \cdot g^{-1}$DM) are shown by Table 10. Initial nitrogen fractions stand for the nitrogen concentrations at the beginning of the grain-filling period; the term residual nitrogen fraction refers to the nitrogen concentration measured at ear maturity. Mass fractions of nitrogen in roots and in stems and sheaths were expressed per gram dry matter (DM) minus water-soluble carbohydrates (WSC), as non-structural carbohydrate contents fluctuated considerably within and between treatments, especially at maturity.

The weighted mean initial mass fraction of nitrogen (concentration) in shoot dry matter varied considerably between experiments and treatments; the smallest value observed was 13 mg $N \cdot g^{-1}$ DM and the highest value was twice that large. Intitial nitrogen fractions of root tissue ranged between 11 and 38 mg $N \cdot g^{-1}$ (DM-WSC); the average figure for all treatments and experiments amounted to 19 $mg \cdot g^{-1}$. Initial nitrogen concentrations in stems and sheaths ranged between 10 and 23 $mg \cdot g^{-1}$ (DM-WSC), the average value was 16 $mg \cdot g^{-1}$. The smallest, greatest and average figures for initial nitrogen fractions of leaf blade tissue were 20.8, 40 and 33 mg $N \cdot g^{-1}$ DM, respectively. Corresponding figures for chaff and rachis were 14, 24 and 19 mg $N \cdot g^{-1}$ DM.

A comparison of the mean initial nitrogen concentrations in the respective organs (bottom of Table 19) shows that on average the highest nitrogen concentrations were found in leaf-blade tissue and the smallest in stems and leaf sheaths. The coefficients of variation indicate that initial nitrogen concentrations varied least in chaff and rachis and leaf blades, and most in roots.

An other feature shown by Table 10 is the relatively small initial nitrogen concentration in the field crop, Expt VB, compared to experiments under (semi-) controlled conditions. Furthermore, it is shown that the objective was attained indeed to grow plants substantially differing in nitrogen concentrations in Expts III, VA and VI. Nitrogen was abundantly available in the nutrient culture experiment II and was frequently supplied in small quanties in nutrient culture experiment IV. This different manner of nitrogen supply resulted in much smaller nitrogen concentrations in Expt IV.

At the end of the grain-filling period the residual nitrogen fractions in root tissue ranged between 8 and 28.5 mg $N \cdot g^{-1}$ (DM-WSC); in stems and sheaths values ranged between about 3.5 and 11 mg $N \cdot g^{-1}$ (DM-WSC).

Residual nitrogen fractions of leaf blade tissue ranged between 7 and 23 mg $N \cdot g^{-1}$ DM. High residual concentrations were observed especially in treatments II 20 and II 25. In these treatments not all of the leaves were senesced when ears were ripe. Residual mass fractions of nitrogen in the dry matter of chaff and rachis ranged between 4 and 12 mg $N \cdot g^{-1}$DM.

Table 10. Weighted mean initial nitrogen (N) fractions of shoot dry matter (DM), initial and residual nitrogen fractions per organ and final N fractions of grain dry matter, all in mg N per gram dry weight.

Experiment and treatment	Weighted mean initial N fraction of shoot DM	Roots[a]		Stems & sheaths[a]		leaf		Chaff & rachis		Grains (final)
		initial	residual	initial	residual	initial	residual	initial	residual	
II 15	22	37.8	17.0	20.7	7.9	38.4	15.7	17.5	6.3	23.6
II 20			28.5		10.6		23.3		8.3	27.9
II 25			27.2		11.0		23.3		9.1	30.8
III N1-16	18	12.2	11.4	14.2	4.1	30.3	8.3	22.9	5.4	20.7
III N1-22			12.2		5.2		8.3		6.8	26.5
III N2-16	26	19.9	13.4	21.4	6.5	37.5	9.0	24.2	9.4	21.4
III N2-22			16.9		6.8		13.7		11.0	31.1
III N3-16	26	20.4	16.0	23.6	9.0	40.0	15.9	21.7	10.2	22.1
III N3-22			21.0		7.6		17.9		12.5	30.3
IV A16	14	22.6	15.0	10.8	3.6	26.5	6.7	15.1	4.1	21.5
IV D22			14.5		3.6		6.9		4.7	22.5
IV C22			14.4		4.1		7.7		4.7	23.4
IV B22			16.4		4.3		9.6		5.8	25.3
VA N1	17	13.2	8.0	13.0	4.4	35.1	10.9	17.8	6.3	19.7
VA N2	20	19.7	12.6	17.1	8.2	36.1	14.2	18.6	7.6	23.0
VA N3	21	18.2	16.7	17.7	10.3	37.8	17.4	18.7	8.7	23.8
VB	17			11.8	5.7	29.3	15.5	15.0	8.2	21.3
VI N1	13	10.1	7.8	9.5	3.6	20.8	8.6	14.1	4.5	19.8
VI N2	20	15.8	-	15.7	-	29.7		15.1		
mean		19.0		16.0		32.9		18.2		21.7[b]
coefficient of variation (%)		40		29		18		19		7

a N fractions corrected for water-soluble carbohydrates.
b Mean for treatments at 15°C or 16°C and outdoors.

Residual nitrogen fractions were generally higher under warmer conditions, except in Expt IV C22 and D22. Treatment effects on residual nitrogen contents will be dealt with in more detail later.

The final mass fractions of nitrogen in grain tissue were greater with higher doses of nitrogen fertiliser. In Expt III, however, the effect was relatively small, as can be seen from the figures 21.0, 21.4 and 22.1 mg $N \cdot g^{-1}$ grain dry matter for the N1, N2 and N3 treatments at 16°C, respectively. Final nitrogen fractions of grain tissue were strongly affected by temperature. The highest value observed was in the 25°C treatments of Expt II, viz. 31 mg $N \cdot g^{-1}$ DM. Averaged for treatments with a moderate temperature economy (15°C, 16°C, outdoors) the final nitrogen concentration in grains amounted to 21.7 $mg \cdot g^{-1}$. Compared to the wide range in mass fractions of nitrogen in dry matter of vegetative parts, the final nitrogen concentrations grain dry matter was rather stable when considered for approximately equal temperatures.

3.3.2 The relative nitrogen distribution at anthesis

The absolute amounts of nitrogen per organ at anthesis varied considerably due to variation in culm sizes (between experiments) and in nitrogen concentrations (between and within experiments). Therefore is was decided to present the initial nitrogen distribution in relative terms. This seemed appropriate since it was found in Subsection 3.1.2 that the initial dry matter was distributed over shoot organs in relatively fixed proportions.

Table 11 contains the relative distributions of nitrogen at the beginning of grain filling. To facilitate comparisons with cases where roots were not analyzed (field crops) the relative distributions were also calculated for above-ground organs only (Table 11). In Expt IV the root was relatively large and contained therefore relatively much more nitrogen than roots in other experiments. For that reason the mean relative distribution, averaged over experiments and treatments, was calculated with and without the data from this experiment (Table 11).

Apart from Expt IV, the relative amount of nitrogen in the roots at the beginning of grain filling ranged between 14% and 22% and amounted to 19% on average. Between 35% and 43% of the initial amount of nitrogen was located in stems and sheaths; the average was 38%. Leaf blades contained between 30% and 35% of the initial amount of nitrogen, with an average of 32%. In the ear structures (chaff and rachis) there was between 10% and 16% of the initial amount of nitrogen with an average of 12%.

Looking at aerial organs only, with inclusion of data from Expt IV, the relative distribution of nitrogen at the beginning of grain filling over stems and sheaths, leaf blades, and chaff and rachis was on average 46%, 39% and 15%, respectively. Since the respective coefficients of variation were relatively small, it seems justified to conclude that the initial

Table 11. Relative distributions of initial amounts of nitrogen, whole plants and shoots only.

Experiment and treatment	Whole plant				Shoot only		
	percentage of initial N in				percentage of initial N in		
	roots	stems and sheaths	leaf blades	chaff and rachis	stems and sheaths	leaf blades	chaff and rachis
II	19.1	40.3	29.5	11.1	49.8	36.5	13.8
III N1	20.4	30.6	33.1	16.0	38.4	41.5	20.1
III N2	20.9	34.6	33.2	11.3	43.8	42.0	14.3
III N3	22.2	36.1	31.6	10.1	46.5	40.6	12.9
VA N1	13.7	38.9	35.0	12.5	45.1	40.5	14.4
VA N2	15.7	42.5	31.1	10.7	50.4	36.9	12.7
VA N3	16.8	42.7	30.3	10.1	51.3	36.5	12.2
VB	-	-	-	-	42.7	41.4	15.9
VI N1	19.2	37.8	30.2	12.9	46.7	37.3	16.0
VI N2	18.4	40.4	30.6	10.6	49.6	37.5	13.0
IV	33.5	26.9	27.3	12.3	40.5	41.0	18.5
mean (IV excl.)	18.5	38.2	31.6	11.7	46.4	39.1	14.5
coefficient of variation (%)	14.5	10.3	5.7	16.1	8.7	5.9	16.1
mean (IV incl.)	20.0	37.1	31.2	11.8	45.9	39.2	14.9
coefficient of variation (%)	26.9	13.9	7.0	15.2	9.2	5.8	17.0

amount of shoot nitrogen was distributed in fairly fixed proportions over component parts. This conclusion is reinforced by considering the large variation in culm sizes between experiments and in nitrogen mass fractions between, but also within, experiments. However, with respect to effects of variation in nitrogen supply, the refinement can be made that the proportion of initial shoot nitrogen in stems and sheaths tends to increase with more nitrogen, at the expense of the proportion in leaf blades. These results indicate a larger nitrogen buffer capacity for stems and sheaths than for leaf blades.

3.3.3 The relative contribution of various sources to grain nitrogen yield

The contribution to grain nitrogen yield of aerial organs can be assessed by expressing the amount of nitrogen removed from each organ as a percentage of grain nitrogen yield. The remaining proportion of grain nitrogen yield, not derived from depletion of aerial organs, must originate from the roots. The 'gross' contribution by roots consists of two components: nitrogen removed from root tissue and a net uptake of 'new' nitrogen from the soil.

Table 12. Relative contribution (%) to final grain nitrogen (N) yield from different sources.

Experiment and treatment	Contribution by N removal from aerial organs:			'Gross' root contribution[a]
	stems and sheaths	leaf blades	chaff and rachis	
II 15	40.4	29.2	11.0	19.4
II 20	36.4	22.0	11.4	30.2
II 25	41.0	26.7	12.5	19.8
III N1-16	30.1	35.3	16.5	18.1
III N1-22	25.5	34.6	14.7	25.2
IV A16	20.7	24.8	10.5	44.0
IV D22	20.9	25.4	10.3	43.4
IV C22	20.4	25.7	10.9	43.0
IV B22	18.9	22.4	9.5	49.5
VA N1	31.1	35.1	9.7	24.1
VA N2	28.9	31.8	8.1	31.2
VA N3	27.1	30.9	7.5	34.5
VB	25.0	28.5	7.2	39.3
VI N1	32.1	25.8	11.3	30.8
VI N2	33.2	24.7	10.0	32.1

a 'Gross' root contribution consists of N removal from root tissue plus net N uptake from the root medium.

Figures of the relative contributions to grain nitrogen yield are presented in Table 12. Data from the N2 and N3 treatments of Expt III were disregarded because re-growing side tillers acted as a second sink for nitrogen in these treatments. Stems and sheaths contributed between 20% and 40% to grain nitrogen yield; the average over all treatments amounted to 29%. Nitrogen removal from leaf blades accounted for on average 28% of grain nitrogen yield, with figures ranging between 22% and 35% for individual cases. The corresponding figures for chaff and rachis were: average 11%, with a range between 7% and 17%. The most variable source consisted of the combined contributions of nitrogen removal from roots plus additional nitrogen uptake (together designated 'gross' root contribution), the figures ranged between 18% and 50%, and the average proportion was 32%.

Distinct treatment effects on 'gross' root contribution can be noted. Compared to the controls at 15°C (Expt II 15) or 16°C (Expts III N1-16 and IV A16), this proportion increased when plants were transferred to 20°C (II 20) or 22°C (III N1-22, IV B22) early after anthesis. Since equal grain nitrogen yields were noted in Expt IV A 16 and B22 (Section 3.2.5) the stimulation of nitrogen uptake by temperature readily explains the higher residual nitrogen concentrations in non-grain parts in Expt IV B22.

Early transfer to the hot temperature of 25°C (Expt II 25) or late transfer from 16°C to 22°C (Expts IV C22 and D22) did not result in higher root contributions to grain nitrogen yield. Furthermore, 'gross' root contribution to grain nitrogen yield increased with higher doses of nitrogen supply in Expts VA and VI. However, the data from the latter experiment are tentative, because the N2 treatment was not fully ripe when the experiment had to be discontinued.

A higher 'gross' root contribution to grain nitrogen yield with more nitrogen or at higher temperature implies a smaller contribution by nitrogen removed from shoot organs. Table 13 shows the proportions that component shoot parts contributed to the total amount of nitrogen removed from the shoot. The fact that the figures are largely similar for each temperature treatment or nitrogen treatment within experiments indicates that all shares of individual shoot organs were diminished to the same extent, when 'gross' root contribution to grain nitrogen yield increased due to treatment, or in other words, the proportions that component shoot parts contributed to the total amount of N removed from the shoot were not responsive to treatment induced changes in 'gross' root contribution to grain nitrogen yield.

An even more interesting conclusion can be drawn by comparison of the data in Table 13 (within experiments data from N treatments considered separately and for temperature treatments data combined) with those about the initial relative nitrogen distribution over shoot organs, presented in Table 11. The figures in both tables are practically, if not exactly, equal for each experiment and/or N treatment. This implies that the proportions

Table 13. The proportions (%) component parts contributed to the total amount of nitrogen removed from the shoot during kernel filling.

Experiment and treatment	Stems and sheaths	Leaf blades	Chaff and rachis
II 15	50.4	36.2	13.6
II 20	52.2	31.5	16.3
II 25	51.1	33.3	15.6
III N1-16	36.8	43.1	20.1
III N1-22	34.1	46.3	19.6
IV A16	37.0	44.3	18.7
IV D22	36.9	44.9	18.2
IV C22	35.8	45.1	19.1
IV B22	37.2	44.1	18.7
VA N1	41.0	46.2	12.8
VA N2	42.0	46.2	11.8
VA N3	41.4	47.2	11.4
VB	41.2	46.9	11.9
VI N1	46.4	37.3	16.3
VI N2	48.9	36.4	14.7

that individual shoot organs contributed to the total amount of N removed from the shoot were numerically equal to the initial proportion of shoot nitrogen present in these organs. The data of Expt VA, and to a smaller extent also those of Expt VB, deviated somewhat from this pattern in that stems and sheaths contributed less to N removal from the shoot than in proportion to the initial amounts, whilst leaf blades contributed more. These deviations can be explained by non-metabolic losses of leaf dry matter and thus of N losses which occurred in these experiments (Subsection 3.4.4). In the present type of analysis nitrogen losses through shedding of leaves would indeed cause the relative contribution of leaf blades to grain nitrogen yield to be overestimated.

3.3.4 Summary of treatment effects on the nitrogen economy

Some features of the nitrogen economy and the treatment effects will be summarized and demonstrated by cumulative nitrogen distribution graphs. Fig. 6a shows the distribution of nitrogen throughout the grain-filling period in Expt IV A16. From each sampling date the amounts of nitrogen present in roots (lowest lines), in stems and sheaths, in leaf blades, in chaff and rachis and in the grains were superimposed; thus the uppermost line represents the total amount of N in the plant. Fig. 6a depicts the pattern of nitrogen relocation from component parts of the plant in detail. Furthermore it can be seen that nitrogen uptake continued throughout the kernel-filling period, although at a decreasing rate.

Fig. 6b serves to show the effect of temperature on the nitrogen economy of Expt IV. The upper lines represent the total amount of nitrogen per plant in treatments IV A16, B22 and C22; the amounts of nitrogen in non-grain parts are given by the lower lines. The time courses for amounts of nitrogen in the grains is depicted in Fig. 6c for all treatments of Expt IV. The duration of nitrogen deposition in grains was shorter the earlier plants were transferred from 16°C to 22°C. The shorter duration was fully compensated for by an increased rate of nitrogen accumulation in the grains, because there was next to no difference in final grain nitrogen yields between temperature treatments. In Expt IV B22 (early transfer to 22°C) the higher rate of N deposition in grains was achieved by a faster rate of N depletion from vegetative parts and by a larger additional uptake of nitrogen by the roots compared to IV A16 (Fig. 6b). This led eventually to higher residual nitrogen concentrations (Table 10) and a smaller harvest index for nitrogen (Table 3). Though less clearly, the same features apply to Expt III N1-22 and to Expt II 20, except that in the latter case the shorter duration of N deposition in grains was not fully compensated for by an increased rate. Thus grain nitrogen yields were smaller in Expt II 20 than in II 15 (Table 9). In treatment IV C22, and also in IV D22, the faster rate of N deposition in grains was achieved by a faster removal of N from vegetative organs only

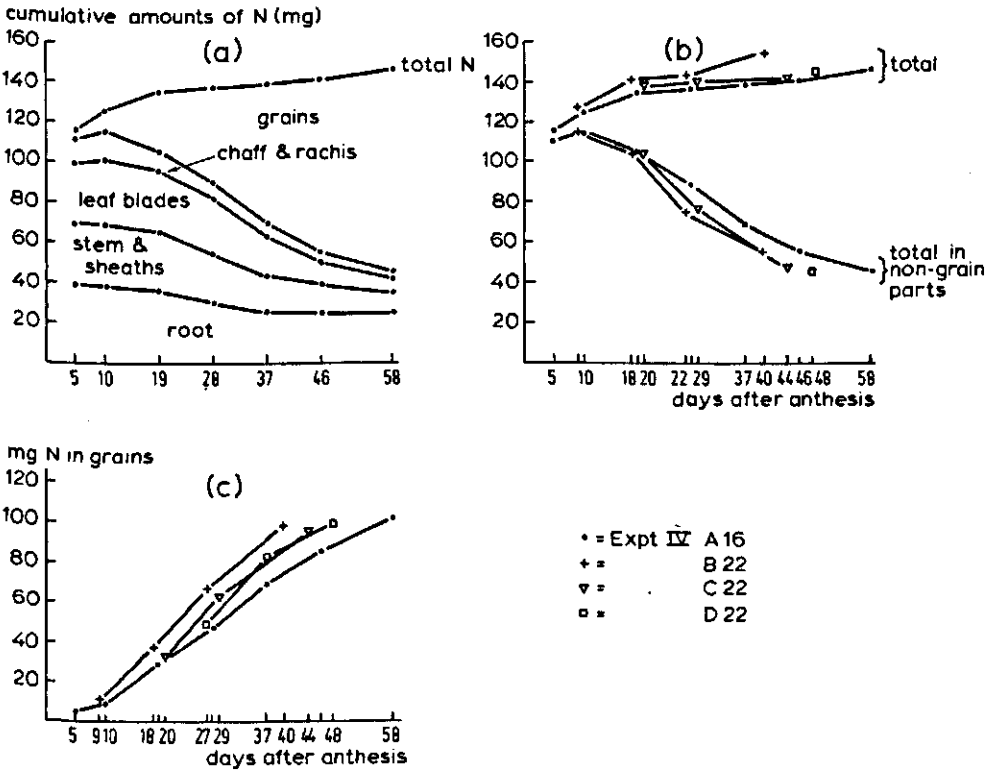

Fig. 6. Graphical representation of the nitrogen economy, as affected by temperature in Expt IV. All data bear on the whole plant (main axis plus one-ear-bearing side tiller plus their common root). (a). Change with time in the cumulative distribution of nitrogen over constituent plant parts. (b). Temperature effects on the change with time in the total amount of nitrogen per plant (uppermost lines) and in the amount of N in non-grain organs (lower lines). (c). Temperature effects on the change with time in the amount of nitrogen in the grains.

(Fig. 6b) and not by an enhancement of N uptake by the roots. Thus the residual amounts of nitrogen and the harvest indices for nitrogen were similar in Expts IV A16, C22 and D22.

Figs 7a en 7b show the cumulative nitrogen distributions as affected by nitrogen treatment in Expts VA N1 and N3. These graphs indicate a continued uptake of nitrogen after anthesis, which was somewhat greater in the N3 treatment. Initial and residual amounts of nitrogen were clearly superior in the N3 treatment. The smaller harvest index for nitrogen (Table 3) with more nitrogen was brought about by a greater increase in residual nitrogen in vegetative parts than in grain nitrogen yield. The cumulative nitrogen distribution graphs emphasize that the relocation of nitrogen from vegetative organs to the grains is one of the most significant processes in the grain-filling stage of cereals.

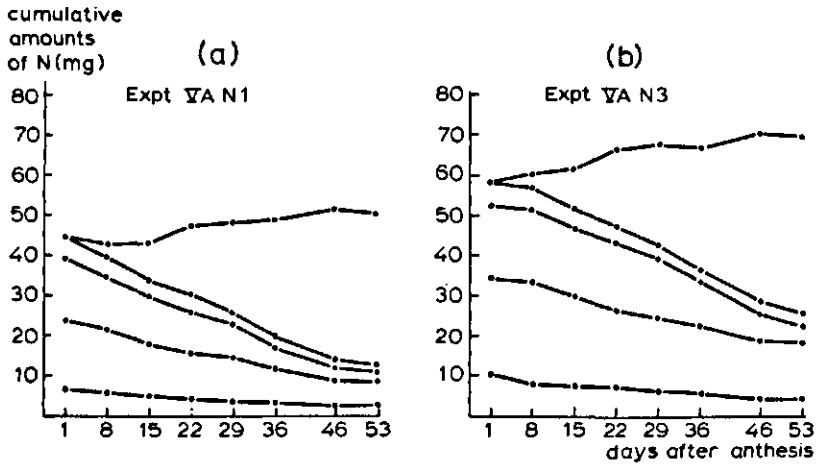

Fig. 7. Graphical representation of the effects of nitrogen treatments on the change with time in the cumulative distribution of nitrogen, illustrated with data from Expt VA N1 (a) and Expt VA N3 (b). From bottom to top the amounts of nitrogen in roots, stems and leaf sheaths, leaf blades, chaff and rachis, grains; the uppermost line represents the total amount of N per plant (cf. Fig 6a).

3.3.5 Nitrate reductase activities

Some analyses of nitrate reductase activities were performed in plants of Expt IV. The results are given in Table 14. At four weeks before anthesis the specific reductase activity in vivo (designated NRA-FW in Table 14) was clearly higher in shoots than in roots (although the fresh weight of roots is not a really dependable measure). The results obtained with this method suggest that about a third to a quarter of the nitrate was reduced in the roots at that stage of development. In the second batch of plants, harvested two weeks after anthesis, the NRA-FW was highest in leaf blades and lowest in stems and sheaths. Intermediate figures were found for roots. Per plant organ the nitrate reductase activity was also higher in leaf laminae than in the stem plus leaf sheaths, but the absolute activity of the root approximated that of the total shoot. So it seems that in older plants a bigger proportion of the nitrate was reduced in the roots, about 42% to 53%.

The estimates of the proportion of nitrate reduction in roots are only dependable if the reductase activities in vivo really reflect what happens during growth in the intact plant. Analyses of nitrogen uptake rates were available for the second batch of plants and it appeared that the real rate if nitrate assimilation was much smaller than the rate derived from the nitrate reductase activity measurements. Thus, it seems that the present data at best will only provide qualitative information, even when not taking into account that the number of observations is only small.

Table 14. Nitrate reductase activity (NRA) in vivo per organ and nitrate reductase shoot/root ratio; data from Experiment IV.

Growth stage	Plant number	Organ	Fresh weight (g)	NRA-FW[a]	NRA per organ	NRA total plant	NRA shoot/root ratio
4 weeks before anthesis	1	shoot	22.2	1.27	28.2	38	2.8
		root	24.2	0.41	9.9		
	2	shoot	19.9	1.14	22.7	34	2.0
		root	22.1	0.51	11.3		
2 weeks after anthesis	1	leaf blades	5.3	3.34	17.6		
		stem and sheaths	21.9	0.41	9.0	55	0.9
		root	24.7	1.15	28.3		
	2	leaf blades	5.0	3.76	18.8		
		stem and sheaths	24.1	0.51	12.3	53	1.4
		root	23.9	0.93	22.3		
	3	leaf blades	4.8	3.36	16.0		
		stem and sheaths	24.2	0.52	12.7	68	0.7
		root	25.7	1.52	38.9		

[a] NRA-FW = nitrate reductase activity in mole·g^{-1} fresh weight·h^{-1}

3.4 CHEMICAL ANALYSES OF CARBOHYDRATES, CARBON AND CELL WALL CONSTITUENTS

3.4.1 *Water-soluble carbohydrate contents per organ*

Chaff and rachis After anthesis the mass fractions of WSC in dry matter of chaff and rachis generally increased to 100-150 mg·g^{-1} DM at 2 to 3 weeks after anthesis, then WSC concentration declined; at maturity low concentrations in the order of 10 to 30 mg·g^{-1} were found. The absolute amount of WSC, which was stored after anthesis and subsequently metabolized, ranged between 20 and 65 mg per ear in treatments grown outdoors or at 15°C or 16°C under controlled conditions.

Leaf blades The range in the WSC fractions of the dry matter of leaf blades was between 40 and 80 mg·g^{-1} throughout kernel filling. Only when increment in ear dry weight was small relative to assimilate production, e.g. shortly after anthesis, or in some experiments near ear maturity, the fraction of WSC sometimes reached levels of 100 to 120 mg·g^{-1}.

Stems and leaf sheaths Fig. 8a-d show the courses of the amounts of WSC in the stems and sheaths in mg per culm in Expts II-VB. Data of Expts II and IV refer to the main axis only.

In the first place, only treatments will be considered grown at moderate temperatures (15°C, 16°C, outdoors). It can be noted that the amounts of stored WSC increased initially after anthesis. There were differences between experiments in the period during which accumulation continued as well

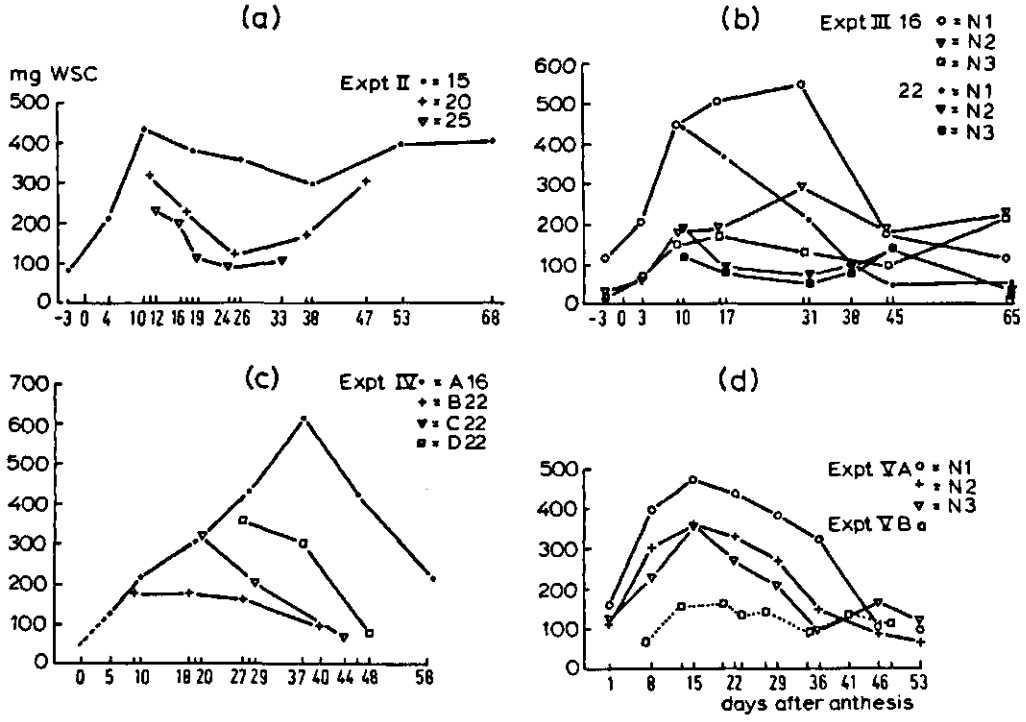

Fig. 8. Effects of temperature and nitrogen treatments on changes with time in the amounts of water-soluble carbohydrates (WSC) per (main) culm; data from Expts II-VB.

as in the maximum WSC concentration reached. These attributes are displayed in Table 15. As a rule the amounts of WSC decreased during the second half of the grain-filling period, however in some cases a rise in WSC contents was observed towards maturity. This phenomenon occurred in experiments where ear maturity preceded complete senescence of the vegetative parts, for example in Expts II, III N2 and III N3.

Temperature effects are obvious in Expts II and IV. The general picture is that after transfer to a warmer temperature (either early or later during grain filling) no further storage of WSC occurred (Expt IV B 22), or that carbohydrates already present were metabolized rapidly (Expts II 20, II 25, IV C22, IV D22). The asynchronous senescence of ears and vegetative parts is particularly clear in Expt II 20, where the amount of WSC in stems and sheaths increased notably during the later stages of grain filling.

The effects of temperature, described for Expts II and IV, also apply to the N1 treatment of Expt III. The amounts of WSC in stems and sheaths in the N2 and N3 treatments were generally small throughout kernel filling. At 16°C the quantities were somewhat higher than at 22°C. The sink strength of growing grains and side tillers was apparently so great that concurrently produced photosynthates were consumed immediately.

Table 15. Observed maxima in the water-soluble carbohydrate (WSC) fractions of stems and sheaths (mg per g dry matter).

Experiment and treatment	Observed maxima in WSC fractions of stems and sheaths ($mg \cdot g^{-1}$)	Day after anthesis of observations
II 15 ma	177	10
III N1-16	298	30
III N2-16	194	30
III N3-16	148	64
IV A16 ma	287	37
VA N1	264	15
VA N2	205	15
VA N3	202	15
VB	159	20

ma = main axis only

At anthesis there were slightly more WSC at the lowest level of nitrogen nutrition in Expt VA. As time progressed larger differences between the nitrogen treatments appeared: more WSC were stored and subsequently metabolized the lower the level of nitrogen nutrition. At maturity the differences had disappeared.

The pattern of change of WSC in stems and sheaths in the field crop Expt VB was largely similar to that in the pot experiment done under similar climatic conditions (Expt VA). The maximum amount of WSC in stems and sheaths, measured at 20 days after anthesis in the former experiment was equivalent to 880 $kg \cdot ha^{-1}$.

At maturity the amounts of WSC in stems and sheaths were generally not or not much smaller than at anthesis. This implies that carbohydrates produced before anthesis contributed nothing or only slightly to grain yield.

Roots Figures 9a and 9b show the time courses of the amounts of WSC in roots of Expts II and IV, respectively (nutrient culture experiments). Broken lines in Fig. 9a indicate the continuation after ear maturity.

Until about 25 days after anthesis the amount of WSC in roots was low in all temperature treatments of Expt II (approximately 16 $mg \cdot g^{-1}$ DM). Beyond that time the amounts increased, first in the 25°C treatment and latest at 15°C. At 25°C the rise in WSC was only small, but at 15°C and 20°C it was considerable. At ear maturity the mass fraction of WSC in root dry matter was 190 $mg \cdot g^{-1}$ in Expt II 20 and 160 $mg \cdot g^{-1}$ in Expt II 15; in both cases about 16% of the plant's total amount of carbohydrates was located in the roots.

In Expt IV A16 and B22 the amounts of WSC in roots were small until about 20 days after anthesis. Then enormous amounts of carbohydrates were stored. The treatments created by transfer of plants from 16°C to 22°C later

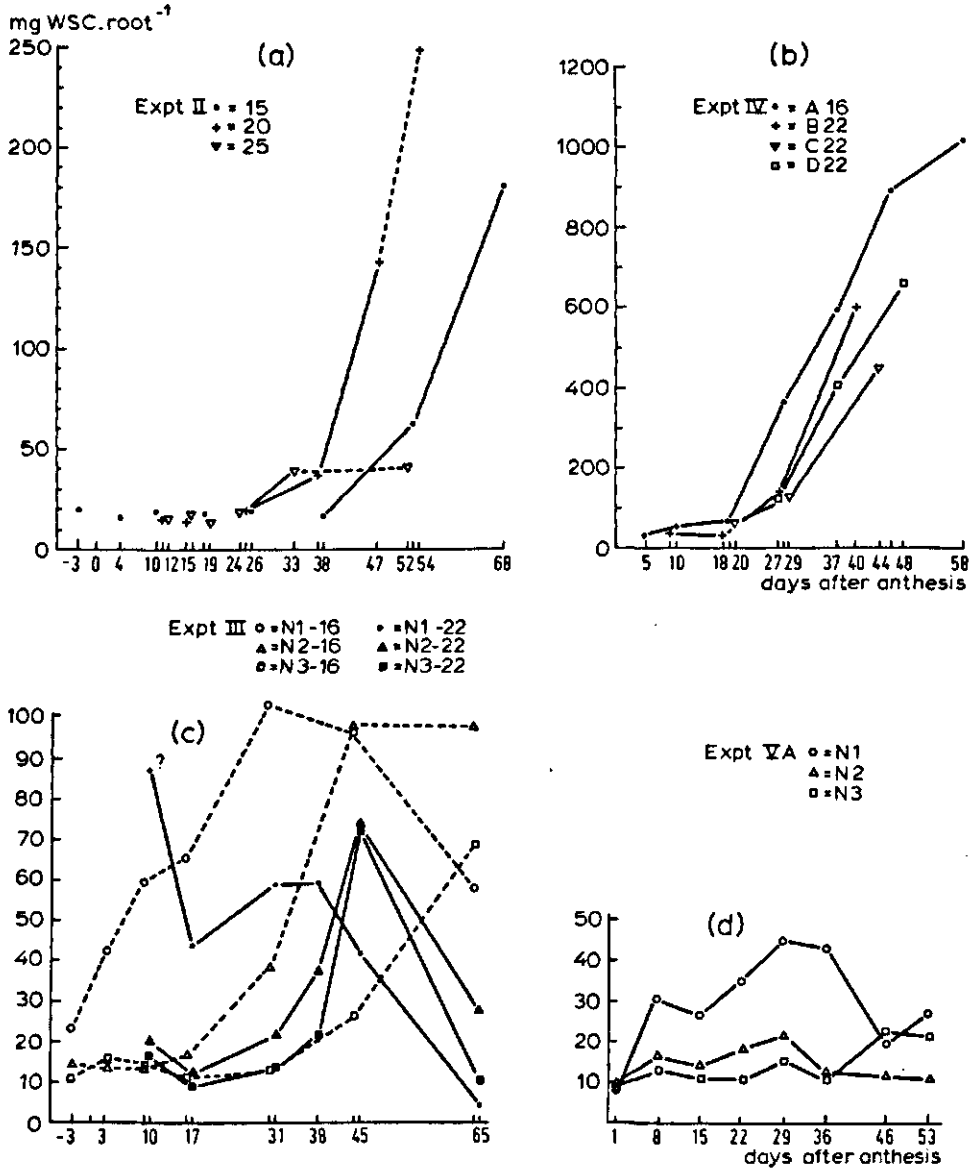

Fig. 9. Effects of temperature and nitrogen treatments on the amounts of water-soluble carbohydrates (WSC) in roots; data from Expts II, IV, III and VA. Root temperatures 15°C and 16°C in all treatments of Expts II and IV, respectively.

in grain filling (IV C22 and D22) showed first a lag in WSC accumulation in roots, but then it was resumed at a rate about equal to that at 16°C. The mass fraction of WSC in root dry matter was 380 $mg \cdot g^{-1}$ and 260 $mg \cdot g^{-1}$ at ear maturity in IV A16 and B22, respectively. At ear maturity about 70% of the plant's total quantity of WSC was located in the root in both treatments.

Figures 9c and 9d show the changes with time in the amount of WSC in roots of Expts III and VA, respectively. In these pot experiments the amount of WSC tended also to increase with time. It can be noted that in Expt III the onset of the rise in WSC occurred earlier the lower the nitrogen dressing and that it commenced earlier at 22°C. Between the last two sampling dates a decline in WSC quantities were noted in the treatments with the most advanced state of senescence (22°C treatments, N1 treatment at 16°C). Expressed as a fraction of root dry matter, the WSC fractions ranged between 10 and 160 $mg \cdot g^{-1}$ throughout grain filling in Expt III.

In Expt VA (Fig. 9d) the highest amounts of WSC in roots were found in the N1 treatment; the changes with time were not spectacular in the N2 and N3 treatments. Expressed as a fraction of root dry matter the WSC mass fractions varied between 10 and 110 $mg \cdot g^{-1}$ throughout grain filling in Expt VA.

No data are available about WSC contents in Expt VI. However, root dry weights increased between the last two samplings in both nitrogen treatments. This might reflect an increase in the amounts of WSC in roots towards maturity in this experiment.

3.4.2 *The composition of water-soluble carbohydrates*

To gain insight in the chemical form of water-soluble carbohydrates some samples were analyzed for the relative amounts of mono- and disaccharides on the one hand, and fructosans on the other hand. Moreover the distributions of molecular weights of fructosans were measured; these were characterized by their modal degree of polymerization (DP). The results are summarized by Table 16.

Most of the non-structural carbohydrates were present as mono- and disaccharides. In stem and sheath tissue there was a tendency towards a greater proportion of fructosans at increasing proportions of water-soluble carbohydrates ($r = 0.9$). The modal degree of polymerization of fructosans was rather similar for most samples and was about 6. Of course, longer and shorter fructosan chains were present as well. In fact, in most samples traces of fructosans with a DP up to 24 were detected. In Expt IV B22 virtually no carbohydrates accumulated in stems and sheaths. No long-chain fructosans were present in the sample analyzed from this treatment (number 3 in Table 16). The modal DP of 3 indicates that the relatively small amount of fructosans present in this sample consisted of trisaccharides mainly. The only sample of root tissue analyzed did not show a composition of carbohydrates different from that in stems and sheaths.

Table 16. Characterization of water soluble carbohydrates.

Experiment and treatment	Organ	Sample number	Day after anthesis of observations	WSC fraction ($mg \cdot g^{-1}$ dry weight)	Relative composition of WSC (%)		Modal degree of polymerization of fructosans
					mono- & di-saccharides	fructosans	
III N1-16	stems[a]	1	30	298	57.5	42.5	8
IV A16	stems	2	37	287	57.7	42.3	6
IV B2	stems	3	27	94	83.3	16.7	3
VA N1	stems	4	15	264	71.9	28.1	6
VA N3	stems	5	15	202	74.4	25.6	6
VB	stems	6	14	156	79.9	20.1	6
IV A16	roots	7	37	261	65.4	34.6	6

a stems = stems and leaf sheaths

Table 17. Mass fractions of carbon in dry matter per organ and weighted means per plant ($mg\ C \cdot g^{-1}DM$).

Organ	Expt IV A16 10 d.a.a.	Expt IV A16 37 d.a.a.	Expt IV C22 44 d.a.a.	Expt VB 13 d.a.a.	Expt VB 41 d.a.a.
kernels	450	439	449	436	447
chaff and rachis	462	453	446	445	420
leaf blades	425	413	414	431	431
stem and sheaths	442	430	449	436	449
root	406	422	422	-	-
weighted mean of aerial parts	443	434	444	436	435
weighted mean of total plant	428	430	437	-	-

d.a.a. = days after anthesis.

3.4.3 Mass fractions of carbon in the dry matter

The results of carbon analyses are presented in Table 17. Each figure is the mean of two replicate determinations. On purpose samples were selected from an experiment conducted in the phytotron and from a trial outdoors. The number of data is too limited to permit definite conclusions, neither about the mass fractions of carbon (concentration; $mg\ C \cdot g^{-1}DM$) in dry matter of individual organs, nor about changes with time per organ. However it seems justified to conclude that the weighted mean mass fraction of carbon in wheat dry matter amounts to about 430 $mg \cdot g^{-1}$ in the grain-filling stage.

The results of some determinations in samples of about 6-week-old plants

(grown on nutrient culture) indicated also carbon fractions in vegetative shoots of about 430 $mg \cdot g^{-1}$, whilst a somewhat smaller figure was obtained for root material, viz. about 400 $mg \cdot g^{-1}$.

Biscoe et al. (1975) reported similar carbon mass fractions in shoots and roots of barley throughout growth: 436 and 397 $mg \cdot g^{-1}$, respectively.

3.4.4 Analyses of cell wall constituents

Analyses of cell wall constituents (CWC) were done to gain knowledge about the mass fraction that these compounds make up of the total dry matter in vegetative organs. Furthermore, time trends were evaluated.

Leaf blades The mass fractions of CWC in dry matter of leaf blades ranged between 0.35 and 0.60 $g \cdot g^{-1}$. The variation in these figures was primarily caused by differences in the amounts of proteins and water-soluble carbohydrates. This follows from the fact that the ratio between the amount of CWC and the residual dry weight (=total dry weight minus the amounts of proteins and water-soluble carbohydrates) was always close 0.60.

If it is assumed that the plant does not break down cell wall constituents itself, the amount of these substances should remain constant in non-growing organs. In indoor experiments the amount of CWC in leaf blades did not change during the kernel-filling period indeed. This is shown in Table 18 by the data of Expts III and IV. Outdoors, dead leaf blades can be torn off (wind and rain) and microbial activity may also result in loss of structural tissue. In Expts VA en VB (pots outside and field crop, respectively) the

Table 18. Examples of the change with time in the amount of cell wall constituents (CWC) in leaf blades.

Experiment	Treatment	Days after anthesis of observations	CWC in all leaf blades per culm (mg)
III	all N1, N2, N3 at 22°C	8 and 9	244 (n=6; c.v.: 1.6%)
		44	230 (n=3; c.v.: 6.6%)
IV	A16	5	353
		37	360
		58	340
VA	N2	1	203
		15	190
		29	199
		46	167
		53	144

c.v. = coefficient of variation.

amount of CWC in leaf blades decreased, especially during the second half of kernel filling. This is shown in Table 18 by example of Expt VA N2. In this particular case about 30% of the structural tissue was lost during the kernel-filling period.

Stems and sheaths The mass fractions of CWC in dry matter of stem and sheaths tissue ranged between 0.55 and 0.75 $g \cdot g^{-1}$. The variation in these figures was due to differences in the amounts of proteins and water-soluble carbohydrates, as the ratio between the amount of CWC and the residual dry weight was always very close to 0.80.

Examples of the change with time in the amount of CWC in stems and sheaths are given in Table 19. It appeared that the deposition of CWC may continue until about 10 days after anthesis. After that time the amount of CWC remained always constant.

Roots The mass fractions of CWC in root dry matter ranged between 0.48 and 0.78 $g \cdot g^{-1}$. The variation in these figures was brought about by differences in the amounts of proteins and water-soluble carbohydrates, as the ratio between the amount of CWC and the residual dry weight was always close 0.80.

In experiments grown on nutrient culture (hydroponics) the amount of CWC in roots hardly changed with time (Expts II and IV, Table 20). In contrast, with pot-grown plants, the amount of CWC in roots declined especially during the second half of the grain-filling period (Expts III and VA, Table 20). Some of the old root branches may have broken off when washing away the substrate to recover the roots. Microbial activity may have played

Table 19. Examples of the change with time in the amount of cell wall constituents (CWC) in stems and leaf sheaths.

Experiment	Treatment	Day after anthesis of observations	CWC per stem and leaf sheaths (mg)
II	15	-3	1 190
		4	1 260
		10	1 440
		53	1 420
IV	A16	5	1 160
		10	1 230
		37	1 250
		58	1 230
	B22	40	1 200
	D22	27	1 230
		37	1 230
VB	-	7	540
		13	690
		27	650
		48	670

Table 20. Examples of the change with time in the amount of cell wall constituents (CWC) in roots.

Experiment	Treatment	Day after anthesis of observations	CWC per root (mg)
II	15	4	550
		38	550
		68	550
	20	47	580
	25	52	570
III	N1-16	3	489
		44	335
		64	304
III	N3-16	3	450
		44	320
		64	310
IV	A16	10	1 270
		28	1 230
		46	1 310
		58	1 240
	B22	40	1 190
	C22	44	1 140
VA	N1	8	320
		36	290
		46	225
VA	N3	8	290
		36	250
		46	240

a role too. In the present examples about 20% to 30% of the amount of CWC in roots was lost during the grain-filling period.

3.5 FEATURES OF LEAF SENESCENCE

3.5.1 Ageing parameters in flag leaves in Expt I

Expt I concerned the establishment of temperature effects on a number of parameters of senescence in the flag leaf. These were: green area, rate of photosynthesis at saturating light intensity (P_{max}), and the amounts of chlorophyll (a+b), soluble protein and nitrogen. An example of the relationships between the relative values of these variables is presented in Fig. 10. The relative figures 100 were assigned to the values at 11 days after anthesis. From three days before to eleven days after anthesis the amounts of the chemical constituents considered were rather constant, except for the amount of soluble protein which decreased.

Fig. 10 shows that the change in photosynthetic capacity of the flag

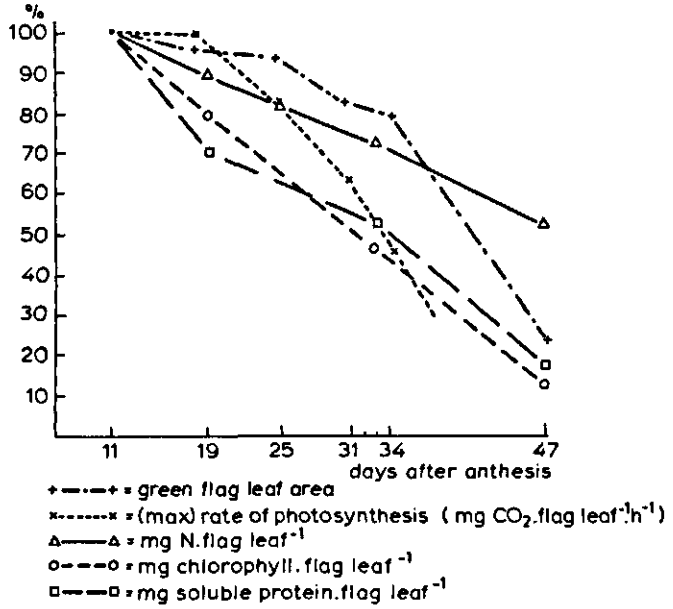

Fig. 10. Patterns of decline of flag leaf attributes. Data taken from Expt I (cv. Yecora); treatment: 20°C air temperature, 10°C of nutrient solution. Absolute values of attributes at 11 days after anthesis were assigned the value 100%.

leaves was not intimately associated with the change in one of the other variables. In treatments grown at other combinations of air and root temperatures similar patterns of change were observed, with greater rates of decline the higher the air temperature. Root temperature acted in a similar way as air temperature, but the effects were far less pronounced.

3.5.2 Treatment effects on leaf senescence in Expts II-VI

The initially small or non-significant differences between the nitrogen treatments of Expts III and VA with respect to green area and dry weight of leaves (Table 5) became larger as time progressed. The data of Table 21 serve to illustrate this. From Expt III the data are given of the sampling date when for the first time significant nitrogen treatment effects appeared on dry weight and green area of the top two leaves, viz. in the harvest at 31 days after anthesis at 22°C and at 44 days after anthesis at 16°C. From Expt VA, a set of data is given from the sampling at 29 days after anthesis; that is the first sampling with separate dissection of the upper leaf layers. Significant effects of nitrogen on leaf attributes might have thus occurred earlier. From both experiments, data obtained at or near ear maturity are included in Table 21 as well.

It can be derived from Table 21 that green leaf areas and leaf dry weights

Table 21. Some data from Expts III and VA on leaf senescence as effected by nitrogen dressings.

Experiment and treatment	Day after anthesis	Flag leaf blades		Second leaf blades		Lower leaves blades	
		DM (mg)	green area (cm^2)	DM (mg)	green area (cm^2)	DM (mg)	green area (cm^2)
III N1-16		76a	1.2a	63a	0.6a	406a	0.0a
III N2-16	44	106b	17.1b	91b	16.0b	429a	31.2b
III N3-16		121b	18.8b	99b	17.1b	410a	29.0b
III N1-16		84a	0.0a	68ab	0.0a	386a	0.0a
III N2-16	64	80a	0.2a	66a	0.1a	398a	0.0a
III N3-16		109b	8.9b	92b	8.5b	388a	15.8b
III N1-22		95a	14.8a	80a	11.5a	429a	5.5a
III N2-22	31	115a	19.4b	94ab	19.9b	452a	47.3b
III N3-22		113a	19.2b	99a	19.3b	468a	56.0b
III N1-22		81a	0.0a	68a	0.0a	420a	0.0a
III N2-22	45	114b	8.5b	96b	12.2b	374a	22.1b
III N3-22		115b	18.0c	114b	19.9c	397a	40.9c
VA N1		136a	31.5a	115a	30.1a	126a	8.4a
VA N2	29	177b	38.5b	136b	35.8b	155b	28.3b
VA N3		168b	36.8b	140b	36.7b	150b	30.5b
VA N1		79a	0.0a	55a	0.0a	83a	0.0a
VA N2	46	85a	0.3a	67b	0.3a	84a	0.0a
VA N3		95b	1.5b	75b	1.0b	98b	1.3b

Different letters behind treatment means in a column indicate statistically significant differences, calculated by Tukey's Honest Significant Difference Test ($P < 0.05$).

declined earlier in time in plants given less nitrogen (Expts III and VA) or subjected to a higher temperature (Expt III). At or near maturity the largest green laminar areas were obtained at the highest nitrogen dressings. So leaf senescence, as reflected in the declines in green area and dry weight of leaves, proceeded slower with more nitrogen and at the cooler temperature.

Treatment effects on leaf senescence, including those of temperature, were quantified further by calculation of the integrals of leaf area in cm^2 per culm and time in days (Table 22). For reasons of simplicity, these integrals were called LAD (leaf area duration), although this term is usually reserved for the integral of LAI and weeks. In experiments with different nitrogen treatments LAD values were computed from the first sampling date after anthesis till ear maturity in the respective treatments; in experiments with variation in temperature, LAD values were computed from the date of imposition of treatments.

LAD increased with nitrogen supply, although the differences were relatively small between the respective N2 and N3 treatments of Expts III and

Table 22. Treatment effects on LAD values (cm^2 green area·days) per (main) culm.

Integration interval	LAD values of treatment					
a. Effects of temperature on LAD in Expt II.	II 15	II 20	II 25			
from 11 d.a.a. till ear maturity of II 25 at 33 d.a.a.	2 223	2 207	1 903			
from 11 d.a.a. till ear maturity in II 20 at 47 d.a.a.	3 309	3 246				
b. Effects of treatments on LAD in Expt III.	N1-16	N1-22	N2-16	N2-22	N3-16	N3-16
1 d.a.a. till ear maturity (nitrogen effect)	2 862		4 908		5 444	
9 d.a.a. till ear maturity (temperature effect)	2 015	1 516	3 953	3 176	4 504	4 193
c. Effects of temperature on LAD in Expt IV.	A 16	B 22				
9 d.a.a. till ear maturity	3 150	2 485				
d. Effects of nitrogen on LAD in Expt VA.	N1	N2	N3			
1 d.a.a. till maturity	3 316	4 123	4 315			

d.a.a. = days after anthesis

VA. Expt VI N2 had to be discontinued before ripeness, but the difference in LAD between the two nitrogen treatments of Expt VI would presumably have grown to a factor 2 (data not presented).

The impact of temperature on LAD seemed to depend on the level of nitrogen nutrition. This follows readily from the data of Expt III (Table 22): in treatment N1-22 (lowest nitrogen dressing) the LAD value was about 25% smaller than in N1-16, whilst the difference between temperature treatments was only 7% at the N3 level of nitrogen nutrition. Furthermore, temperature hardly affected LAD in Expt II with nitrogen rich plants (Table 22), whilst LAD was far smaller at 22°C than at 16°C in Expt IV, an experiment with relatively low nitrogen contents.

3.5.3 Chlorophyll contents of leaf blades in Expts VA and VB

The leaf laminae of the treatments of Expt VA appeared to have a deeper green colour, the higher the nitrogen dressing. Analyses of chlorophyll were made because the suspected differences between nitrogen treatments might be a factor of importance with respect to assimilate production; analyses in Expt VB (field crop) were made for reference purposes. The time courses for

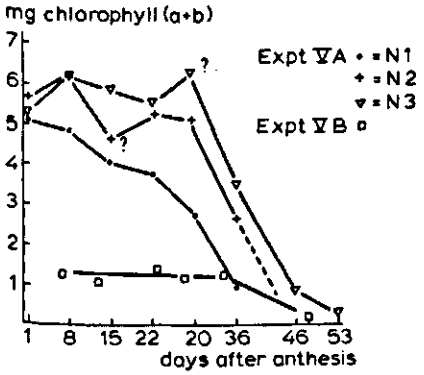

Fig. 11. Changes with time in the total amount of chlorophyll (a+b) in leaf blades per culm as affected by nitrogen treatments in Expt VA, data from Expt VB are given for reference.

the average amount of chlorophyll a+b (measured separately) in the total mass of leaf blades per culm are plotted in Fig. 11. Each point represents the mean of 2-4 replicates; the coefficients of variation for replicates ranged between 4% and 12%.

At anthesis the amount of chlorophyll in Expt VA N1 was slightly lower than that in the N2 and N3 treatments. However, as time progressed the differences between the nitrogen treatments became larger.

The differences in amounts of chlorophyll between the treatments were not reflected in differences in photosynthesis rates until late in the grain filling stage (see Section 3.6, Fig. 16).

In Expt VA the chlorophyll content (a+b) amounted to 0.4-0.5 $g \cdot m^{-2}$ green leaf area, except during the last few weeks prior to maturity when lower values were obtained. Chlorophyll content was considerably smaller in the field crop Expt VB. Here it ranged between 0.2 and 0.3 $g \cdot m^{-2}$ green leaf area during most of the grain filling period.

3.5.4 *Relationships between amount of nitrogen and green area of leaves*

In literature a link has been suggested between removal of nitrogen from vegetative parts and their senescence (e.g. Sinclair & de Wit, 1976). For that reason the relationships between the decrease with time in amount of N in leaf blades and the decrease of green area of leaf blades were examined. Of course such analyses will not yield results of fundamental significance, but they may enable leaf senescence to be related to the nitrogen economy in simulation models.

Some examples will be elaborated, viz. data from Expt IV, representing the temperature effects in other experiments as well, and data from Expts VA and VI, showing the impact of nitrogen dressings, thereby representing

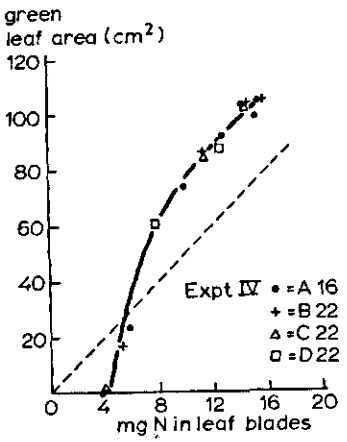

Fig. 12. The relationship between the decline of the green leaf area and the amount of nitrogen in the leaf blades. Data taken from successive harvest in all temperature treatments of Expt IV (main culms only).

also Expt III.

In Fig. 12 values are plotted of cm^2 green area per culm (ordinate) against the amount of nitrogen of the leaf blades in mg, as obtained in successive harvests in all treatments of Expt IV. A rather smooth pattern was obtained, with data of different temperature treatments forming one curve. Such curves do not pass through the origin since there is a residual amount of nitrogen left in the leaf blades when green area is zero.

Fig. 13 depicts similar relationships for Expts VA and VI; only data of the N1 and N3 treatment of Expt VA are included in this graph. The curves of Fig. 13 exhibit the same basic shape as the ones found for Expt IV. Green area at anthesis was similar in all nitrogen treatments of Expt VA but the nitrogen contents of leaves were higher for greater nitrogen supply. In Fig. 13 this is reflected in a displacement to the right of data points of VA N3 relative to VA N1. This displacement was maintained for all green leaf areas, and, although this was only small when green area approached zero, the data indicate that there is more residual nitrogen left in leaves (which lost all green coloration) for higher nitrogen dressings. In Expt VI green areas and the amounts of nitrogen in leaves at the beginning of grain filling were significantly different between the two nitrogen treatments. The plot of green area against amount of nitrogen in leaves gave an apparently smooth curve for combined data of both treatments. However, the N2 treatment was discontinued before ripeness and a displacement to the right relative to VI N1 might have appeared when more data could have been collected. This can be inferred from the fact that the lowest point (relating to the latest sampling) dropped already from the curve drawn in Fig. 13.

Between experiments green areas differed at a certain amount of nitrogen. This can be inferred from position of the curves in Figs 12 and 13 relative

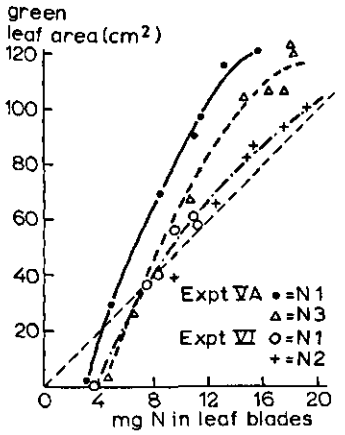

Fig. 13. The relationship between the decline of the green leaf area and the amount of nitrogen in all leaf blades per culm, as affected by nitrogen treatments in Expts VA and VI. (————) data from Expt VA N1; (– – – – –) data from Expt VA N3; (– · – · – · – · –) data from Expts VI N1 and N2. All curves were fitted by eye. The broken reference lines has a slope of 5 cm^2 green leaf per mg nitrogen.

to the reference lines. (These reference lines have a slope in both graphs of 5 cm^2 green area per mg nitrogen in leaves). This means that there is no intimate link between the amount of nitrogen in leaves and green leaf area.

3.6 APPARENT PHOTOSYNTHESIS RATES PER PLANT

In the phytotron Expts II and IV, the photosynthesis recordings could not be performed in the growth rooms. The plants had to be moved to a special measurement cell with an other light source than in the growth rooms. The results indicated that the amount of PhAR intercepted during measurement must have been far greater than during growth in Expt II. For that reason photosynthetic rates were transformed into relative rates by assigning the value 100 to the maximum rate, which was measured in Expt II 15 at 4 days after anthesis. Fig. 14 shows the time courses of apparent relative photosynthesis rates of all treatments of Expt II. In this experiment photosynthesis declined gradually with time. At higher temperatures the decline was faster, though the difference between Expts II 15 and II 20 was only small. In Expts II 20 and II 25 the accumulation of dry matter in the ears ceased when the relative photosynthesis rates were still 33% and 29%, respectively. These figures clearly demonstrate that ear maturation preceded senescence of vegetative parts in this experiment.

In Expt IV the light conditions during measurement and growth matched better: there was no discrepancy between growth derived from CO_2 exchange recordings and from growth analyses. Therefore Fig. 15 shows absolute appa-

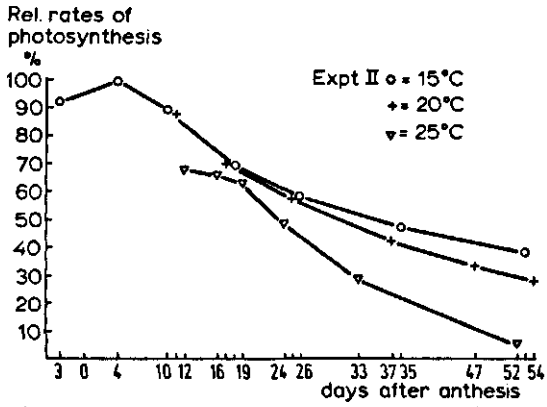

Fig. 14. The pattern of change with time of the relative rate of apparent photosynthesis, as affected by temperature in Expt II. Values of 100% were assigned to the rate measured in treatment II 15 at 4 days after anthesis. All recordings were made at a similar level of radiation.

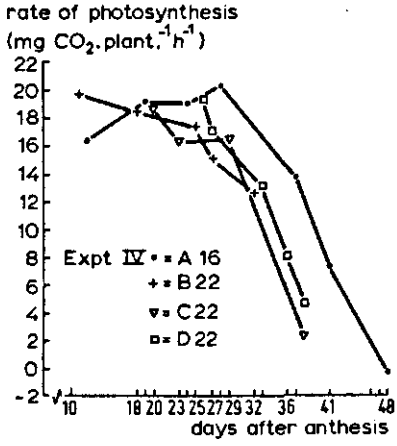

Fig. 15. The pattern of change after anthesis in apparent photosynthesis per plant, as affected by temperature in Expt IV. All recordings were made at a similar level of radiation (approximately 0.6 $J \cdot cm^{-2} \cdot min^{-1}$ PhAR at ear level).

rent photosynthetic rates of all treatments of Expt IV. Plant density was 156 plants$\cdot m^{-2}$ (312 ears), thus the maximum photosynthetic rates measured were equivalent to 30 kg $CO_2 \cdot ha^{-1} \cdot h^{-1}$. The overall pattern of change with time in treatment IV A16 differed substantially from that in II 15 in that the photosynthetic rate remained almost constant during the first 4 weeks after anthesis. After that it declined at a quite constant rate. Transfer of plants from 16°C to 22°C (the respective starts of treatments B22, C22 and D22) had no immediate effect on apparent photosynthesis. The most conspicuous temperature effect was an earlier onset of the stage of rapid de-

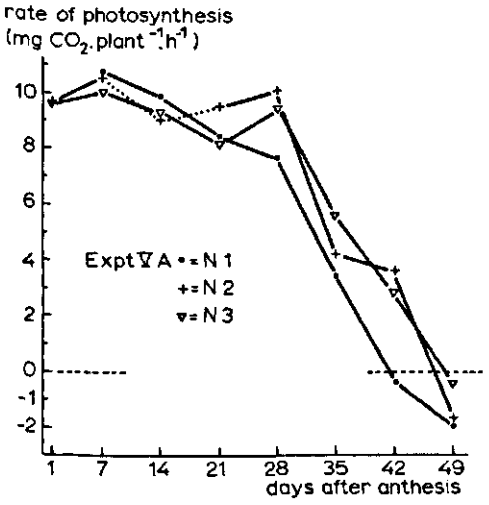

Fig. 16. The pattern of change in apparent photosynthesis per plant after anthesis, as affected by nitrogen treatment in Expt VA. All recordings were made at a similar level of radiation (approximately 0.6 $J \cdot cm^{-2} \cdot min^{-1}$ PhAR at ear level).

cline of photosynthesis. This phenomenon is nicely depicted for treatment IV D22 as compared to IV A16 (Fig. 15).

In Expt VA (plants in pots outdoors) measurements of photosynthesis were performed at constant irradiance throughout the grain-filling stage. Fig. 16 reveals that there were only marginal effects of nitrogen treatment on apparent photosynthesis in this experiment. Only an earlier decline in photosynthesis was apparent at the lowest level of nitrogen nutrition. It is of interest to note that the overall pattern of change with time in photosynthesis resembled that in Expt IV. There was an equally long period after anthesis during which photosynthesis remained rather stable, followed by a stage of continuous decline. Plant (culm) density was 455 plants$\cdot m^{-2}$ in Expt VA. Thus it can be derived from Fig. 16 that under the conditions of measurement the highest measured photosynthetic rates of the micro-canopies were equivalent to about 50 kg $CO_2 \cdot ha^{-1} \cdot h^{-1}$.

3.7 DATA ABOUT RESPIRATION

3.7.1 *Outline of data presentation*

During grain filling the time courses of respiration were generally similar for each organ in all low temperature treatments. Just to provide a general picture of respiration, the change with time will be shown per organ from a representative experiment.

Next, respiration rates of individual organs will be compared when ex-

pressed on several reference bases. Of course this approach will not yield much insight in the factors controlling respiration. It was adopted just to roughly relate respiration to various crop attributes. It does provide a rather suitable way to show the differences between experiments and treatments, too. Furthermore, some reference bases will be shown to provide a better guess about the level of respiration than others. In the first instance data will be tabulated from each experiment and treatment grown at 15°C or 16°C or outdoors (measured at 16°C). From all treatments one observation was made in the interval between 7 and 11 days after anthesis and thus these were selected. Anthesis would have been a more obvious check point, but there are no reliable data available from each treatment at that stage of development.

3.7.2 Changes with time in respiration per organ

A representative set of time courses was obtained in Expt V A N1. These are depicted in Fig. 17. Ear respiration increased in rate after anthesis and reached a maximum when one-quarter to one-third of the total grain-filling period had passed. Thereafter a gradual decline occurred. In some experiments leaf laminar respiration rate showed only a slight decline for several weeks, followed by more rapid decrease toward maturity. In other experiments a gradual decline was observed from shortly after anthesis onwards. It will be shown that the pattern of leaf laminar respiration mirrorred

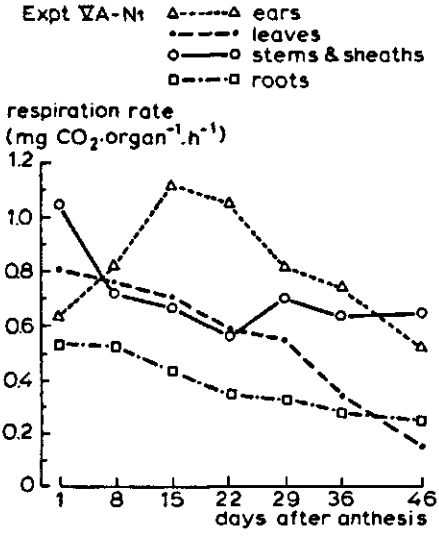

Fig. 17. A representative example of the patterns of change after anthesis in respiration rates of separate plant organs. Data taken from Expt VA. Temperature during measurement 16°C; 1 mg $CO_2 \cdot culm^{-1} \cdot h^{-1}$ is equivalent to 455 mg $CO_2 \cdot m^{-2} \cdot h^{-1}$.

Table 23. Ear respiration rates shortly after anthesis from treatments grown at 15°C or 16°C or outdoors; respiration rates expressed on various reference bases.

Experiment and treatment	Day after anthesis	Ear respiration rates ($mg\ CO_2 \cdot ear^{-1} \cdot h^{-1}$)	($mg\ CO_2 \cdot g^{-1}DM \cdot h^{-1}$)	($mg\ CO_2 \cdot g^{-1}N \cdot h^{-1}$)	($mg\ CO_2 \cdot m^{-2} \cdot h^{-1}$)	($\mu g\ CO_2 \cdot grain^{-1} \cdot h^{-1}$)
II 15	10	1.17	1.23	66	365	18.85
III N1-16	9	0.64	0.95	49	-	13.79
III N2-16	9	0.86?	1.54?	68?	-	17.91
III N3-16	9	0.65	1.14	49	-	14.01
IV A16	10	0.94	1.47	79	293	21.26
VA N1	8	0.83	1.73	99	378	20.34
VA N2	8	0.90	2.00	109	410	22.05
VA N3	8	0.83	1.77	98	378	20.34
VB	7	0.49	1.96	105	271	17.01
VI N1	11	0.67	1.26	73	312	18.15
VI N2	11	0.81	1.29	73	373	19.02
mean		0.80	1.48	79	348	18.43
coefficient of variation (%)		23	23	27	14	15

closely the time course of the green area. The respiration rate of stems and sheaths decreased markedly during the first one or two weeks after anthesis, followed by a long-lasting stable phase until maturity. The term 'plateau value' in this paper refers to the rate of stems and sheaths respiration during that stable phase. Generally, root respiration declined gradually throughout the kernel-filling period.

3.7.3 Ear respiration

Table 23 contains the ear respiration rates of all treatments grown at 15°C, 16°C or outdoors as obtained on a sampling date between 7 and 11 days after anthesis. Respiration rates ranged between 0.49 and 1.17 mg $CO_2 \cdot ear^{-1} \cdot h^{-1}$ with an average rate of 0.8. Corresponding figures per gram ear dry matter were between 0.95 and 2.00 mg $CO_2 \cdot h^{-1}$ with an average value of 1.48 mg $CO_2 \cdot g^{-1}DM \cdot h^{-1}$. The wide range in specific respiration values indicates that the dry matter mass as such was not a predominant determinant of the intensity of respiration. The same held for nitrogen content. For, when expressed per gram nitrogen, respiration ranged between 49 and 109 mg $CO_2 \cdot h^{-1}$, the average being 79 mg $CO_2 \cdot g^{-1}N \cdot h^{-1}$. Per unit ground area ear respiration amounted on average to 348 mg $CO_2 \cdot m^{-2} \cdot h^{-1}$; the highest and smallest figures encountered were 410 and 271 mg $CO_2 \cdot m^{-2} \cdot h^{-1}$, respectively. Expressed per kernel the figures varied from 13.79 to 22.05 µg $CO_2 \cdot kernel^{-1} \cdot h^{-1}$; the average value was 18.43 µg $CO_2 \cdot h^{-1}$.

The coefficients of variation at the bottom of Table 23 were large, viz. 14-23%. The variation in ear respiration shortly after anthesis was smallest when related to unit ground area or to the number of kernels per ear (counted on later sampling dates).

3.7.4 Respiration of leaf blades

Table 24 shows leaf laminar respiration rates from treatments grown at 16°C or outdoors and measured on a sampling date between 7 and 11 days after anthesis. The total mass of leaf blades of one culm respired on average 0.64 mg CO_2 per hour; the highest and lowest values were 0.76 and 0.31 mg $\cdot culm^{-1} \cdot h^{-1}$. Expressed per gram leaf DM respiration amounted to 1.27 mg $CO_2 \cdot h^{-1}$ on average; the extremes were 0.57 mg $CO_2 \cdot g^{-1}$ DM$\cdot h^{-1}$ and 2.04 mg $CO_2 \cdot g^{-1}$ DM$\cdot h^{-1}$. Corresponding figures per gram nitrogen were in a range from 26-63, with an average of 44 mg $CO_2 \cdot g^{-1}$ N$\cdot h^{-1}$. Calculated per unit ground area, leaf laminar respiration amounted to 272 mg $CO_2 \cdot m^{-2} \cdot h^{-1}$, with lowest and highest values of 144 mg $CO_2 \cdot m^{-2} \cdot h^{-1}$ and 346 mg $CO_2 \cdot m^{-2} \cdot h^{-1}$, respectively. When related to green leaf area it varied between 52.9 mg $CO_2 \cdot m^{-2}$ green area$\cdot h^{-1}$ and 98.7 mg $CO_2 \cdot m^{-2}$ green area$\cdot h^{-1}$, with 66.6 mg $CO_2 \cdot m^{-2}$ green area$\cdot h^{-1}$ as an average.

Within Expts III and VA the amount of carbon dioxide respired per hour

Table 24. Leaf blade respiration rates shortly after anthesis from treatments grown at 16°C or outdoors; respiration rates expressed on various reference bases.

Experiment and treatment	Day after anthesis	Leaf blade respiration rates				
		(mg $CO_2 \cdot culm^{-1} \cdot h^{-1}$)	(mg $CO_2 \cdot g^{-1} DM \cdot h^{-1}$)	(mg $CO_2 \cdot g^{-1} N \cdot h^{-1}$)	(mg $CO_2 \cdot m^{-2}$ land area $\cdot h^{-1}$)	(mg $CO_2 \cdot m^{-2}$ green area $\cdot h^{-1}$)
III N1-16	8	0.71	1.04	37	-	72.0
III N2-16	8	0.70	0.97	26	-	60.8
IV A16	10	0.69	1.11	45	215	65.7
VA N1	8	0.76	1.77	57	346	65.2
VA N2	8	0.73	1.55	43	333	60.4
VA N3	8	0.72	1.50	39	328	59.8
VB	7	0.55	2.04	63	304	98.7(?)
VI N1	11	0.31	0.57	48	144	52.9
VI N2	11	0.58	0.92	36	270	62.1
mean		0.64	1.27	44	277	66.4
coefficient of variation (%)		22	37	26	27	20

by the total mass of leaf blades of one culm varied little between nitrogen treatments. In these experiments respiration was smaller, the higher the nitrogen dressing when expressed per gram nitrogen. The latter held also for the two N dressings of Expt VI.

The coefficients of variation were large, irrespective of reference base (20-37%). The smallest variation was found when leaf respiration was related to its green area, although the coefficient of variation at the bottom of Table 24 is not too convincing (20%). This high value is due to the extreme value measured in Expt VB at 7 days after anthesis. On subsequent sampling dates far smaller values were found. In fact, leaf laminar respiration was fairly stable throughout the grain-filling period when related to green area (16°C, outdoors). Only during the last week or so did the green area drop relatively faster than the respiration rate. Data from this period were excluded from the calculations in Table 25, which shows that averaged over experiments and treatments, leaf laminar respiration at 16°C amounted to 68 (± 3) mg $CO_2 \cdot m^{-2}$ green area$\cdot h^{-1}$ during most of the grain-filling period. Averaged over all data points of treatments kept at 22°C, this value was 84 mg $CO_2 \cdot m^{-2}$ green area$\cdot h^{-1}$. The difference in leaf respiration per unit leaf area suggests that in the long term the temperature coefficient was 1.43 (though not really appropriate, the temperature coefficient was quoted as Q_{10}).

3.7.5 Respiration of stems and sheaths

It should be noted that for all measurements, stems and leaf sheaths were never separated, but always treated together.

The left hand part of Table 26 contains stem and sheaths respiration rates from treatments grown at 15°C, 16°C or outdoors, measured on a sampling date between 7 and 11 days after anthesis. Absolute values ranged between 0.33 mg $CO_2 \cdot h^{-1}$ and 0.99 mg $CO_2 \cdot h^{-1}$; on average one stem plus its leaf sheaths respired 0.62 mg $CO_2 \cdot h^{-1}$. Expressed per gram dry matter, stem and sheaths respiration amounted to 0.39 mg $CO_2 \cdot h^{-1}$ on average, the smallest and highest values were 0.21 mg $CO_2 \cdot g^{-1}$ DM$\cdot h^{-1}$ and 0.51 mg $CO_2 \cdot g^{-1}$ DM$\cdot h^{-1}$,

Table 25. Mean leaf blade respiration per unit area green throughout kernel filling at 16°C and 22°C.

Experiments	Temperature treatments (°C)	Number of observations	mg $CO_2 \cdot m^{-2}$ green leaf area$\cdot h^{-1}$		
			mean	95% confidence interval	coefficient of variation (%)
III, IV, VA, VB, VI	16, outdoors	49	68.2	65.0-71.5	16.5
III, IV	22	16	83.9	77.7-90.0	13.8

Table 26. Stem and sheaths respiration rates, on various reference bases. Data obtained shortly after anthesis and means of the stable phase (= plateau-values)[b].

Experiment and treatment	Day after anthesis	Respiration rates shortly after anthesis				Respiration rates during rest of grain-filling phase		
		(mg $CO_2 \cdot stem^{-1}$)	(mg $CO_2 \cdot g^{-1}$ DM$\cdot h^{-1}$)	(mg $CO_2 \cdot g^{-1}$ N$\cdot h^{-1}$)	(mg $CO_2 \cdot m^{-2} \cdot h^{-1}$)	plateau-value per stem[a] (mg $CO_2 \cdot h^{-1}$)	plateau-value (mg $CO_2 \cdot g^{-1}$(DM-WSC)$\cdot h^{-1}$)	plateau-value (mg $CO_2 \cdot m^{-2} \cdot h^{-1}$)
II I5	10	0.99	0.41	24	309	1.03	0.52	321
III N1-16	8	0.59	0.33	33	-	0.61	0.46	-
III N2-16	8	0.65	0.43	23	-	0.58	0.46	-
III N3-16	8	0.68	0.45	21	-	0.65	0.52	-
IV A-16	10	0.63	0.36	40	197	0.60	0.38	187
VA N1	8	0.72	0.40	45	328	0.66	0.50	300
VA N2	8	0.78	0.45	34	355	0.70	0.50	319
VA N3	8	0.72	0.43	28	328	0.73	0.53	332
VB	7	0.40	0.51	46	221	0.31	0.39	171
VI N1	11	0.33	0.21	27	152	0.36	-	168
VI N2	11	0.45	0.26	21	207	0.49	-	228
mean		0.62	0.39	31	262	0.61	0.47	253
coefficient of variation (%)		29	23	30	29	32	12	28

a stem = stem and sheaths
b plateau-values are a mean of several observations.

respectively. Corresponding figures per gram nitrogen were 31 mg $CO_2 \cdot h^{-1}$ with a range between 21 and 46 mg carbon dioxide per gram N per hour. In Expts III, VA and VI there was at least a tendency towards lower values, the higher the nitrogen dressing. On average stems and sheaths respired 262 mg CO_2 per unit ground area per hour, the smallest and highest values were 152 mg$\cdot m^{-2} \cdot h^{-1}$ and 355 mg$\cdot m^{-2} \cdot h^{-1}$, respectively. Judging from the coefficients of variation at the bottom of Table 26 stem and sheaths respiration shortly after anthesis varied considerably between experiments and treatments, irrespective of reference basis.

After 1-2 weeks after anthesis the rate of respiration of stems and sheaths was fairly stable within each treatment (cf. Fig. 17 and Appendix D). The figures in the three right hand colums of Table 26 represent stem and sheaths respiration rates averaged over the whole period of stable CO_2 efflux (plateau values). Each figure is a mean of several observations in time. When expressed per culm the mean stem and sheaths respiration rates bearing on most of the grain-filling period were practically equal to the values measured between 7 and 11 days after anthesis. This indicates that the stage of stable carbon dioxide efflux from stems and sheaths had commenced between 7 and 11 days after anthesis in most experiments. Only in Expt VB (field crop) was a stable rate of stem respiration reached at a somewhat later point in time (different figures in the two parts of Table 26: viz. 0.40 mg $CO_2 \cdot culm^{-1} \cdot h^{-1}$ and 0.31 mg $CO_2 \cdot culm^{-1} \cdot h^{-1}$).

The dry weight of stems and sheaths varied considerably during the grain-filling period, due to changes in water-soluble carbohydrate (WSC) contents. Therefore plateau values were related to DM minus WSC. The coefficient of variation of stem and sheaths respiration per gram DM-WSC seems rather small (12%). However, WSC data were not available from Expt VI, and when figures from this experiment are included in the calculation, assuming a WSC content of about 150 mg$\cdot g^{-1}$DM, the coefficient of variation would rise to a value of 22%. Under this assumption the plateau values of stem and sheaths respiration would be 0.25 mg $CO_2 \cdot g^{-1}$(DM-WSC)$\cdot h^{-1}$ and 0.30 mg $CO_2 \cdot g^{-1}$ (DM-WSC)$\cdot h^{-1}$ in Expt VI N1 and N2, respectively.

3.7.6 The effect of temperature on respiration rates of stems and sheaths in the long term

Because of its stability during most of the grain-filling period respiration of stems and sheaths seems a suitable variable to examine the effect of temperature in the 'long term'. Table 27 gives respiration rates of stems and sheaths, averaged over the stable period for different temperature treatments. It can be seen that the Q_{10} was smaller the earlier after anthesis plants were moved from 16°C to 22°C in Expt IV. The mean stable stage stem and sheath respiration rate at 22°C, calculated with data of Expts III and IV, amounted to 0.57 (± 0.09) mg $CO_2 \cdot g^{-1}$(DM-WSC)$\cdot h^{-1}$. Compared to a figure

Table 27. Long-term effect of temperature on plateau-values of respiration of stems and sheaths as Q_{10} values.

Experiment and treatment	Q_{10} values for temperature ranges		
	15-20°C	15-25°C	16-22°C
II 15 and II 20	1.38		
II 15 and II 25		1.48	
III N1-16 and III N1-22			1.15
III N2-16 and III N2-22			1.92
III N3-16 and III N3-22			1.48
IV A16 and IV B22			1.47
IV A16 and IV C22			1.69
IV A16 and IV D22			2.02
subsidiary treatments in VI N1			1.20
subsidiary treatments in VI N2			1.37

of 0.46 at 16°C this result indicates a Q_{10} of 1.43 in the long term; a similar value for the long-term temperature coefficient was found for respiration of stems and sheaths at different temperatures in Expt II (Table 27), as well as for leaf laminae (Subsection 3.6.6).

3.7.7 *Root respiration*

Table 28 contains root respiration rates from treatments kept at 15°C or 16°C or outdoors, measured at a sampling date between 7 and 11 days after anthesis.

In absolute amounts, root respiration varied between 0.46 and 5.11 mg $CO_2 \cdot root^{-1} \cdot h^{-1}$. This means a ten-fold difference between the extremes. However it should be considered that the values of Expts II and IV are presumably higher than in other experiments, because one root sustained two shoots in these trials and only one in the other experiments.

When related to root dry matter, respiration varied from 1.06 mg $CO_2 \cdot g^{-1}$ $DM \cdot h^{-1}$ to 2.58 mg $CO_2 \cdot g^{-1} DM \cdot h^{-1}$. Specific respiration rates of the nutrient culture experiments II and IV were substantially higher than in pot experiments VA and VI viz, on average 1.16 mg $CO_2 \cdot g^{-1} DM \cdot h^{-1}$ in the latter experiments against 2.10 mg $CO_2 \cdot g^{-1} DM \cdot h^{-1}$ and 2.58 $CO_2 \cdot g^{-1} DM \cdot h^{-1}$ in Expts II and IV, respectively.

Between experiments root respiration per gram nitrogen ranged between 52 mg $CO_2 \cdot h^{-1}$ and 115 mg $CO_2 \cdot h^{-1}$, with an average figure of 78 $mg \cdot h^{-1}$. Corresponding figures per square meter were in the range of 209 to 798 (averge 368) mg $CO_2 \cdot m^{-2} \cdot h^{-1}$.

The last column of Table 28 shows the proportion of root respiration in total plant respiration on the sampling dates considered. In Expt IV this

Table 28. Root respiration rates shortly after anthesis in treatments grown at 15°C, 16°C or outdoors expressed on various reference bases.

Experiment and treatment	Day after anthesis	Root respiration rates				Root respiration as fraction of total plant respiration
		(mg CO_2 · root^{-1}·h^{-1})	(mg CO_2 · g^{-1}DM·h^{-1})	(mg CO_2 · g^{-1}N·h^{-1})	(mg CO_2 · m^{-2}·h^{-1})	
II I5	10	1.89	2.10	56	295	0.20
IV A16	10	5.11	2.58	52	798	0.54
VA N1	8	0.52	1.06	91	237	0.18
VA N3	8	0.46	1.15	52	209	0.17
VI N1	11	0.66	1.14	115	304	0.34
VI N2	11	0.79	1.30	99	363	0.30
mean			1.16[a]	78	368	
coefficient of variation (%)			9	36	59	

a Refers to Expts VA and VI

fraction was extremely high, viz. 0.54. In the other experiments it ranged from 0.17 to 0.34. With respect to this attribute, the nutrient culture experiment II did not deviate from pot experiments.

3.7.8 The temperature coefficient of respiration in the short term

The instantaneous effect of temperature on respiration was determined in a number of separate tests. For that purpose the carbon efflux rates were recorded of individual samples at two temperatures differing bij 4-7°C. The overall range of temperatures tested was between 14°C and 27°C. A rather representative Q_{10} value was about 2.2 in vegetative organs, irrespective of treatment, age, kind of organ, temperature range etc.. It appeared that the Q_{10} for ear respiration was somewhat smaller in these tests, viz. 1.7-1.8. Presumably this was due to the fact that not all of the dense ear tissue reached the new temperature. Moreover, the ears were densely packed in the measuring cuvette.

The comparisons of respiration rates in low temperature treatments with those of high temperature treatments (measured a few days after imposition of the higher temperature) allowed also additional estimates for Q_{10} values to be calculated. As a rule these Q_{10} values were in the range of 1.8 to 2.4 and often close to 2.2. This was also the case for ears.

These data suggest that the application of a conventional Q_{10} value of 2.0, or even a somewhat higher value, is justified in the case of wheat during grain filling, at least in the short term. As shown for leaf blades and stems and sheaths, it might be safer to adopt a Q_{10} value of about 1.4

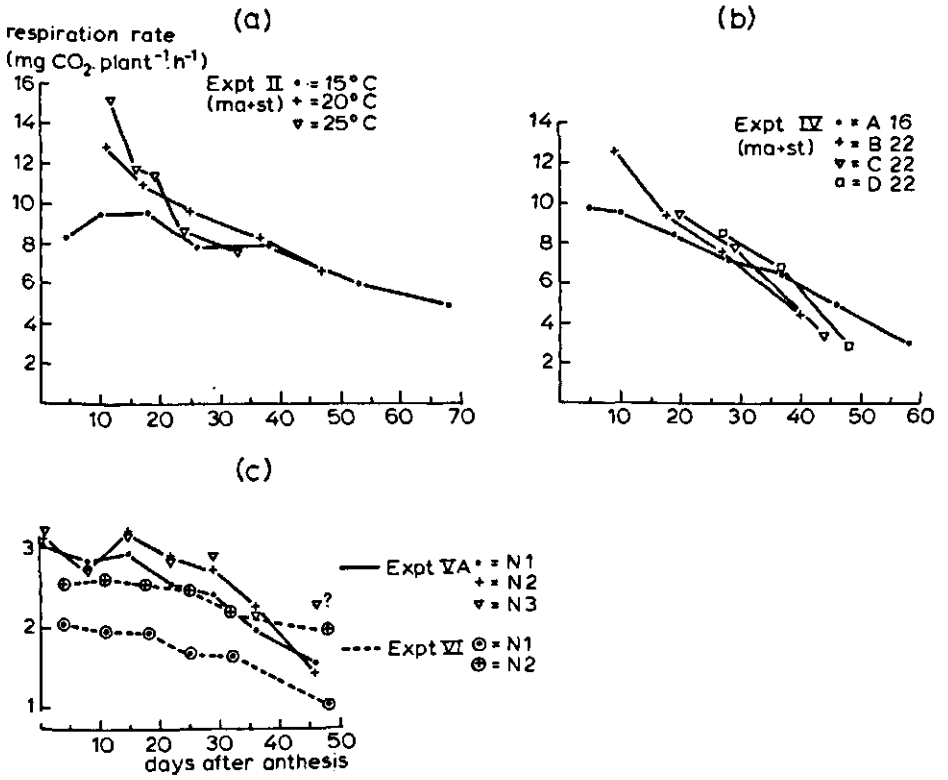

Fig. 18. Treatment effects on the change with time in whole plant respiration rates. Data from the nutrient culture Expts II and IV displayed in (a) en (b), respectively, show the effects of air temperature on respiration; 10 mg $CO_2 \cdot plant^{-1} \cdot h^{-1}$ is equivalent to 1.56 g $CO_2 \cdot m^{-2} \cdot h^{-1}$. (c) Effects of nitrogen treatments in Expts VA and VI; 3 mg $CO_2 \cdot plant^{-1} \cdot h^{-1}$ is equivalent to about 1.4 g $CO_2 \cdot m^{-2} \cdot h^{-1}$.

to 1.5 for the 'long term', at least when comparing fixed temperature treatments.

3.7.9 Treatment effects on changes with time in total plant respiration rates

Temperature effects on the time courses of total plant respiration rates in Expts II and IV are depicted in Fig. 18a and 18b, respectively. Respiration was enhanced following a transfer from a lower to a higher temperature. When the transfers were made early after anthesis (Expts II 20 and 25, Expt IV B22), respiration rose relatively more than after late transfer (Expts IV C and D22). The initial temperature enhancement of respiration was smaller in Expt IV than in Expt II. This is plausible, because root respiration constituted a larger part of total plant respiration in Expt IV

than in Expt II (roots always kept at the lowest temperature). As time progressed temperature effects on respiration diminished, or even reversed, as plants aged more rapidly at higher temperatures.

Fig. 18c depicts the changes with time in total plant respiration rates as affected by nitrogen treatments in Expts VA (solid lines) and Expt VI (broken lines). Initially there were no differences between the nitrogen treatments of Expt VA. However, between two and six weeks after anthesis total plant respiration rate was about 10% lower in the N1 treatment. The same trend could be observed for separate aerial organs, although not as marked as appeared in Fig. 18c for the sum of measurements on individual organs. Shortly after anthesis there were considerable differences in total plant respiration rates between the two nitrogen treatments of Expt VI; these difference became even bigger as time progressed. Until green areas started to differ, total shoot respiration rates did not differ systematically between nitrogen treatments of Expt III (data not shown).

In all cases displayed by Figs. 18a-c, total plant respiration rates declined gradually with time. At ear maturity respiration still proceeded at a rather high level, but was bound to decline soon after recordings were discontinued.

3.7.10 Effect of radiation on respiration rates of stems and sheaths

In the first series of the subsidiary treatments of Expt VI, recordings were made of the respiration rates of stems and sheaths; measurements were made on the third day after the imposition of three radiation levels and two temperatures. The results are given by Fig. 19. When expressed per culm, stem respiration was higher at the highest of both nitrogen dressings (equal ear densities). This was also found in the main treatments of Expt VI (specific respiration rates in the N1 treatment about 20% smaller than those in the N2 treatment). There was an effect of temperature; for most treatments the temperature coefficient, quoted as Q_{10} was about 1.25. There was also a tendency towards higher respiration rates with higher levels of radiation. However, the effect of radiation was rather small considering that radiation differed in ratios of 1:2:3 between treatments, and that recordings were made on the third day after imposition of treatments.

3.7.11 Miscellaneous respiration data

On a few occasions very high respiration rates were recorded in leaf blades that were nearing complete senescence. Such peaks usually showed up in one of the replicate samples measured on one day. This gives the impression that by chance measurements were performed at the time when some kind of climacteric, heralding the final stage of development, occurred.

In Expt II peculiar, but very systematic, fluctuations were observed in

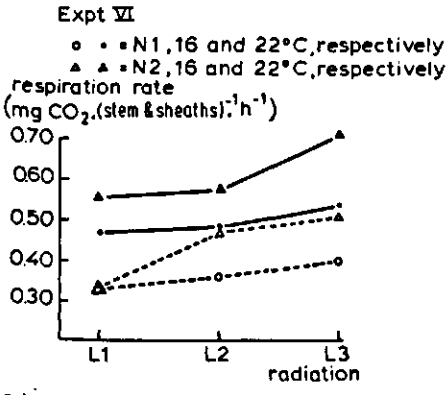

Fig. 19. Effects of temperature and radiation on respiration rates of stems and sheaths in the subsidiary treatments of Expt VI. Recordings made on the third day after imposition of treatments. L1, L2 and L3: 0.17, 0.32 and 0.54 $J \cdot cm^{-1} \cdot min^{-1}$ (PhAR) with 22 hours day length. Conditions of main experiment: 16°C, 0.6 $J \cdot cm^{-2} \cdot min^{-1}$ (PhAR) with 16 hours day length.

rates of respiration of roots and of stems and sheaths. Respiration in both organs oscillated with frequencies of several days. Relatively high stem and sheaths respiration was always accompanied by relatively low root respiration and vice versa (cf. the data in Appendix D). The oscillations were observed in all treatments. The fluctuations did not relate to addition of NO_3^- to the root medium, nor to pH adjustment.

In Expt IV the relationship was examined between the respiration rate and the amount of soluble protein in leaf blades, stems and sheaths, and roots. Observations were made on 5 occasions between 14 and 45 days after anthesis. For each organ, there was no close association between respiration and soluble protein. Between organs, respiration per gram soluble protein differed widely. At 14 days after anthesis, for instance, leaf blades, stems and sheaths, and roots respired 19, 38 and 269 mg CO_2 per gram soluble protein per hour at 16°C, respectively.

4 Discussion

4.1 TREATMENT EFFECTS ON PLANT PERFORMANCE

Courses of total dry matter (DM) accumulation suitably illustrate the integrated treatment effects, composed of effects on photosynthesis, respiration, grain growth, leaf senescence and accumulation and depletion of water-soluble carbohydrates (WSC), on plant performance.

Fig. 20 depicts the changes with time in total dry matter (of main axis + side tiller + root) and of total non-grain dry matter as affected by temperature in Expt IV. Between 10 and 28 days after anthesis the rate of DM accumulation was 148 mg·plant^{-1}·d^{-1} in IV A16, while it amounted to 129 mg·plant^{-1}·d^{-1} in treatment B22. During the first 9-days intervals after each of the two successive transfers from 16 to 22°C, the negative impact of temperature was in the same order of magnitude: e.g. between 20 and 29 days after anthesis, the growth rate was also 129 mg DM·d^{-1} in IV C22, whilst still 148 mg·plant^{-1}·d^{-1} at 16°C.

A decrease of about 13% in the rate of increment of total DM at 22°C relative to 16°C is plausible in view of results of carbon-exchange recordings. Initially after imposing 22°C, apparent photosynthesis rates were not really affected (Fig. 15), but warmth enhanced night respiratory carbon losses (Fig. 18b). As time progressed the differences in respiration rate per plant diminished between temperature treatments, but at the same time differences in apparent photosynthesis increased. Ultimately, dry matter accumulation

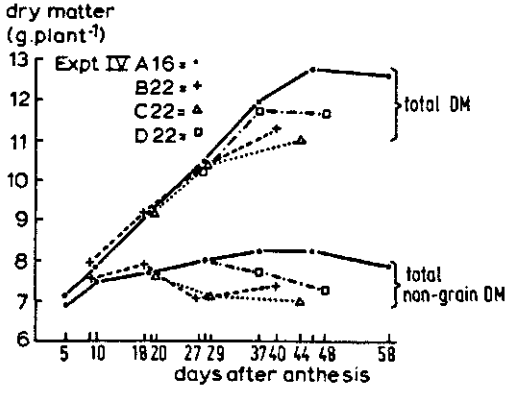

Fig. 20. Effects of temperature on the change with time of total dry matter per plant and non-grain dry matter per plant; data from Expt IV (whole plants).

stopped earlier, the earlier the transfer from 16°C to 22°C was made, as warmth enhanced senescence; the latter is reflected in a smaller LAD (Table 22).

Initial temperature effects on total dry matter gain were rather small, which indicates that the dynamics of storage and metabolization of WSC must have been different between temperature treatments. As structural growth of the vegetative parts ceased soon after anthesis (Subsection 3.4.4) the differences between treatments in non-grain total dry weight (Fig. 20) represent differences in amounts of WSC per plant. Thus it can be deducted that at 16°C, accumulation of WSC occurred throughout the grain-filling period, except during the last sampling interval prior to maturity. Some accumulation of WSC occurred early after initiation of treatment B22, but the general picture is that reserves were metabolized after imposition of the higher temperature. These features were shown more directly already by the time courses of the amounts of WSC in stems and sheaths (Fig. 8c); the differences in patterns of change between WSC contents of stems and sheaths and total non-grain dry matter (Fig. 20) are mainly brought about by the enormous accumulation of carbohydrates in the roots in this experiment (Fig. 9b).

In Expt II the rates of total dry-matter production per plant (main axis + side tiller + root) was about 100 mg DM·plant^{-1}·d^{-1} in both II 15 and II 20. This figure bears on the period between 10 and 47 days after anthesis; that is the period between transfer from 15°C to 20°C and ear maturity in II 20. As the integration of the green area per plant (in cm^2) and time (in days) gave a similar figure for both treatments over this period (Table 22), no or only small temperature effects on dry matter gain would appear reasonable at first sight. However, in view of temperature impact on carbon exchange, similar to the pattern described for Expt IV, one would expect a somewhat smaller increment in dry matter at 20°C in comparison to 15°C.

A slight effect of temperature on the rate of dry matter gain in Expt II implies differences between the 15°C and 20°C treatments in the dynamics of storage and depletion of WSC: grain growth was initially faster at 20°C, so WSC were metabolized (Fig. 8a); later grain growth rates were smaller at 20°C and then more reserves were stored than at 15°C (beyond about 25 days after anthesis Fig. 8a).

Fig. 21 depicts the time courses of total DM accumulation as affected by temperature and nitrogen treatments in Expt III. Root dry weights and the cumulative dry weights of regrown side tillers are included in the total dry weight. The curves were drawn excluding the points obtained at 9 and 10 days after anthesis, because the relatively high dry matter weights observed at those dates, were mainly caused by a transient and unexplained peak in root dry weights.

Initial effects of temperature on total dry matter gain were small, as was found in Expts IV and II. The rate of DM accumulation slowed down ear-

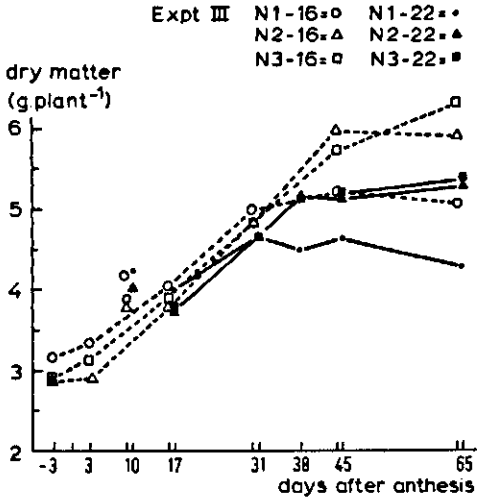

Fig. 21. Effects of temperature treatments and nitrogen treatments on the changes with time in total dry matter per plant in Expt III. The cumulative dry weight of regrowing but regularly excised little side tillers is included in the total dry weight of the N2 and N3 treatments.

lier at the lowest level of N nutrition (N1) and at the highest temperature. This is in accordance with figures on leaf senescence (Tables 21 and 22). At both temperatures reserve carbohydrates hardly accumulated in the N2 en N3 treatments (Fig. 8b). With a relatively small adverse effect of temperature on the rate of total DM production, and a lag in time in grain production at 16°C compared to 22°C (Subsection 3.2.2), there must have been a greater surplus of carbohydrates at 16°C than at 22°C in the N2 and N3 treatments. As illustrated by the data in Table 4 the plants at 16°C used their more favourable carbohydrate supply to produce more side tillers. In the N1 treatment (no regrowing side tillers) considerable amounts of WSC were stored during the first half of kernel filling (Fig. 8b). Transfer from 16°C to 22°C (treatment III N1-22) resulted in an immediate consumption of reserves; at 16°C the reserves were not metabolized before the later stages of growth. Between 30 and 44 days after anthesis the grain growth rate was 45 mg DM·ear^{-1}·d^{-1} in N1-16 and 55 mg·ear^{-1}·d^{-1} in both N2 and N3-16. Increment in total plant dry weight was much smaller in N1-16 than in the other two treatments, viz. 16 mg DM·plant^{-1}·d^{-1} against 73 mg DM·plant^{-1}·d^{-1}. So during this particular period (when leaves senesced rapidly in III N1-16) previously stored assimilates were a major substrate for grain growth in this treatment. In the N2 and N3 treatments grain growth during the later stages of grain filling was not supported by previously stored reserves at both temperatures, simply because there were none or because reserve levels even increased (Fig. 8b).

Fig. 22 shows how the accumulation of total dry matter (including roots)

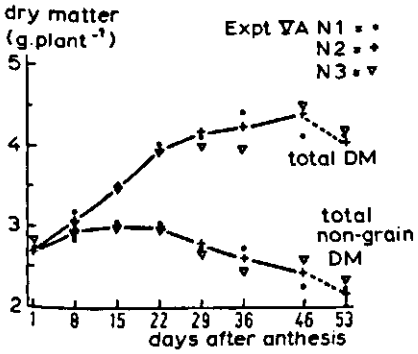

Fig. 22. Effects of nitrogen treatments on the change with time in total dry matter per plant and in non-grain dry matter per plant; data from Expt VA (lines drawn through point of the N2 treatment only).

and of total non-grain dry matter was affected by nitrogen treatments in Expt VA. Until 22 days after anthesis there were no differences between treatments in total DM nor in total non-grain DM. The differences beyond that date are not of systematic nature and might reflect an increasing inter-pot variation, due to the cumulative effects of "little accidents" happening to the plants. The amounts of WSC present in stems and sheaths were about equal at the beginning and end of the grain-filling period, both within and between treatments.

In Expt VI plants of the two nitrogen treatments differed in many attributes. Between 4 and 48 days after anthesis the rates of total dry matter accumulation amounted to 25 and 38 mg DM·plant^{-1}·d^{-1} in Expts VI N1 and N2, respectively.

4.2 THE ROLE OF TEMPORARILY STORED ASSIMILATES

4.2.1 Contribution to grain yield

The rate of DM accumulation in grains is generally not equal to the concurrent rate of substrate production; in other words: usually there is no steady state.

"Sink strength" of ears and of vegetative parts is small around anthesis; i.e. during the very ontogenetic part of grain filling, when the highest possible photosynthetic rates can be achieved (present experiments; de Vos, 1977; Spiertz & van de Haar, 1978). The excess of carbohydrates is stored in the vegetative parts, in particular in stems (and leaf sheaths?) (present experiments; and, for example, Spiertz & Ellen, 1978, Spiertz & van de Haar 1978, Apel & Nátr 1976, Gallagher et al., 1976 and many other reports). During later stages of grain filling, or at relatively high temperatures, grain growth rate can exceed net daily photosynthetic substrate

production. Under the latter conditions grain growth can be sustained by substrate sources other than concurrent production. These substrates were produced either before or after anthesis.

The last few decades, many researchers have been intrigued by the question of the role of temporarily stored assimilates with respect to yield formation. The apparently easiest assessment of the pre-anthesis assimilate contribution to grain yield is obtained by the calculation of the ratio between the weight decrease of stems during grain filling and grain yield (Gallagher et al., 1975). Although the bulk of the dry weight of vegetative organs and reserve carbohydrates are located in the stems it is in principle better to base the calculations on the weight decrease of all vegetative aerial organs, as was done by Gallagher et al. (1976). In their papers Gallagher et al. reported cases for barley where the pre-anthesis contribution exceeded 50%.

This growth analysis method has its shortcomings. In the first place the bulk of the proteins, found in grains at maturity, constitute already a part of the crop dry weight at anthesis. The weight of the relocated proteins represents a minimum contribution of pre-anthesis assimilate to grain yield, even when for more than one possible reason no net change in non-grain shoot dry weight is observed between flowering and maturity. The contribution of relocated protein can be calculated with the following general formula:

$$(a \times b) \times (1 - c/d),$$

where

a = the final nitrogen concentration in grain tissue (%),
b = the conversion factor between nitrogen and protein,
c = the fraction of total nitrogen taken up after anthesis, preferably corrected for nitrogen depletion of roots,
d = nitrogen harvest index.

Substitution of representative values for a-d of 2.1, 5.7, 0.25 and 0.7, respectively, yields 7.7% 'pre-anthesis contribution' to grain yield from relocated protein. The maximum possible value equals the grain protein concentration; this is under conditions where no additional nitrogen was taken up after anthesis. Most of these parameters can be measured rather simply, requiring only a limited number of samples to be taken.

In the present experiments the minimum contribution to grain yield due to protein relocation calculated with the general formula amounted to 12.3% in Expt II 15, 10.8% in Expt III N1-16, 9.1% in IV A16, 9.8% in IV B22, 10.1% in VA N2, 6.7% in VB (field crop), and 9.1% in Expt VI N1.

In principle a separate evaluation of protein relocation opens the possibility to look more closely at the role of non-structural carbohydrates if the latter components are not measured directly.

The growth analysis method leads to misinterpretation when structural tissue is either gained or lost after anthesis. (cf. Bidinger et al., 1977).

In order to test changes in structural dry weight one could measure the crop's total amount of cell wall constituents, for instance at anthesis, about two weeks later and at maturity.

Other workers have made inferences about the contribution of temporarily stored assimilates to grain yield from (combined) data about stem respiration, and/or the (re)distribution of assimilated ^{14}C and/or the dynamics of storage and metabolization of water-soluble carbohydrates. Relevant studies are those by Wardlaw and Porter (1967), Rawson & Hofstra (1969), Rawson & Evans (1971), Apel & Nátr (1976), Austin et al. (1977b), Bidinger et al. (1977), Makunga et al. (1978), Spiertz & Ellen (1978) and Austin et al. (1980).

However, in most attempts it was not possible to construct a complete picture of production, storage and utilization of assimilates. To arrive at some estimates for relocation assumptions had to be introduced for the rates of one or more component processes. Most figures ranged between 5% and 20% of the pre-anthesis assimilate contribution to grain yield.

A shortcoming of all the methods employed to tackle the problem seems to be that post-anthesis substrate production is implicitly underestimated, because no allowance is made for conversion losses of substrate in the ear. In the present experiments these respiratory losses constituted about 20-40% of the increment in grain dry matter over the period between 10 days after anthesis and ear maturity. This means that per gram increment in ear dry matter, on average about 0.3 g glucose has to be produced concomitantly to meet the energy requirement of the entire ear.

Whatever the approach to the problem of various authors there is concensus on one point in the literature, namely that the contribution to grain yield of non-concurrently produced assimilates is relatively larger under adverse conditions, like heat, drought and sub-optimal nitrogen supply. In the present experiments, also, there was a smaller spare production of carbohydrates at higher temperatures and with lower nitrogen dressings. It is worthwhile to note that a greater relative contribution of stored assimilates under adverse conditions does not necessarily imply the involvement of greater quantities of material.

One can take the view that it is irrelevant to calculate the contribution to grain yield of non-concurrently produced assimilates more accurately than has been done up to now. Key questions that deserve a higher priority are whether high carbohydrate levels invoke either an inhibition of concurrent photosynthate production or an apparently wasteful combustion of carbohydrates. If such negative impacts do not occur under field conditions, high reserve levels (up to about mid-kernel filling) can be considered as useful and benificial. Of course this does not apply to cases where high reserve levels are due to growth limiting conditions (e.g. nitrogen deficiency or too few kernels).

4.2.2 Sink-source relationships

Several workers have reported a dependency of the rate of photosynthesis (of the flag leaf) of wheat and barley on the rate of ear growth (King et al., 1967; Evans & Rawson, 1970; Rawson & Evans, 1971).

Other workers have concluded that photosynthesis was independent of the rate of assimilate utilization by the ear (Apel & Peisker, 1973; Apel et al., 1973b; Austin & Edrich, 1975). Rawson et al. (1976) found an association between the photosynthesis rates of the upper two leaves and the assimilate requirement of the ear (altered by DCMU or partial sterilization) only when the tiller culms were kept defoliated.

In the present experiments stem respiration rates were stable during most of the grain-filling period. Apparent photosynthesis rates were more or less constant for about 4 weeks after anthesis in Expts IV and VA (whilst the earlier decline in Expt II will be shown to be related to a different pattern of leaf senescence (Subsection 4.3.2)). However stem carbohydrate levels changed considerably during the period of stable rates of photosynthesis and stem respiration. These findings indicate that neither accumulation of WSC, resulting in WSC proportions of 250-400 $mg \cdot g^{-1}$, nor metabolization of WSC invoked feed-back on either production or utilization of assimilates in aerial organs. It is of interest to note here that a possibly too high osmotic pressure is apparently avoided by conjugation of momomers (Subsection 3.4.3).

A discussion on sink-source relationships should also touch upon the impact if any, of the WSC concentration in vegetative organs on grain growth rates. This relationship will be dealt with in more detail in Subsection 4.6.4, there it will be concluded that the grain growth rate is largely irresponsive to carbohydrate concentrations if the latter exceed some threshold value.

The results of the present experiments strongly suggest that water-soluble carbohydrates can be regarded, indeed, as a true reserves. The level (content) of reserves depends on the rate of production and on the rate of utilization, both of which are regulated by different mechanisms.

The fact that during the first weeks after anthesis the mass-fraction of WSC can rise to 250 or 350 $mg \cdot g^{-1}$ in stems and sheaths (Spiertz & Ellen, 1978; Spiertz & van de Haar, 1978; present experiments), suggests that production and utilization rates in wheat are rather unbalanced around anthesis. The following calculations serve to quantify this phenomenon. In Expt IV A16 126 mg grain dry matter was produced and 45 mg WSC was stored per plant per day, averaged over the period between 10 and 37 days after anthesis. The mean daily respiration rate amounted to 130 mg glucose. Storage thus amounted to $(45)/(126 + 130) \times 100 = 18\%$ of utilization. However, Expt IV might represent a case where an excessive carbohydrate production did invoke 'wasteful' respiration of roots (see Subsection 4.5.4). A similar calcula-

tion with data taken from Expt VA N1 bearing on the first two weeks after anthesis showed that here storage was 23% of utilization.

4.2.3 Carbohydrate economies of spring wheat and winter wheat

The winter wheat crops, described by Spiertz & van de Haar (1978) were grown at 50 m distance from the spring wheat crop, designated Expt VB in the present study. Around anthesis the WSC concentrations in stems and sheaths amounted to 300-400 $mg \cdot g^{-1}$ in the winter wheat crops and to only 90 $mg \cdot g^{-1}$ in the spring wheat crop. Per unit ground area the amount of WSC in stems and sheaths was about 35 $g \cdot m^{-2}$ in the spring wheat crop, whilst the minimum value in the winter wheats was 150 $g \cdot m^{-2}$. These data do suggest that the greater amount of WSC present at anthesis in winter wheat adds to its higher yield potential. Unfortunately, there are no supplementary data to test this hypothesis.

4.3 FACTORS AFFECTING PHOTOSYNTHESIS

4.3.1 Temperature

In the first experiment of the present series the rate of apparent photosynthesis of flag leaves (P_{max}) was slightly, though insignificantly, enhanced by temperature, when examined shortly after transfer from 15 to 20°C and 25°C (data not presented). In Expts II and IV no clear initial temperature effect was found on apparent photosynthesis of whole plants in the range 15°C to 22°C. Apparent photosynthesis dropped after transfer from 15 to 25°C in Expt II.

These findings will be placed against the background of earlier reports on the impact of temperature on photosynthesis, with special reference to cereals. Temperature effects on apparent, or net, and gross photosynthesis will be considered for individual leaves and for whole canopies. Gross photosynthesis will be defined by the sum of net photosynthesis plus respiration during the dark. Thus, in green cells an intrinsically similar rate of operation is assumed for the TCA cycle in light and in darkness (Chapman & Graham, 1974), whilst photorespiration will not be considered as a component of gross photosynthesis.

Planchon (1971) found no effect of temperatue in the range 17°C to 23°C on apparent photosynthesis of flag leaves of several wheat cultivars at anthesis. In similar plant material Bird et al. (1977) measured the highest gross and net rates of photosynthesis at 18°C. However, with plants grown at temperatures of 23°C and 28°C the photosynthesis-temperature response curve was fairly flat, whilst the peak at 18°C during measurement was more pronounced at growth temperatures of 13 and 18°C. Keys et al. (1977) found no clear temperature effect on net photosynthesis, for neither flag leaves nor second

leaves, of wheat grown at day/night temperatures of 18°C/14°C when measured between in the range of 13°C to 28°C. Wardlaw (1974) also observed only a moderate change in net photosynthesis of wheat flag leaves in the range of 15°C to 35°C; a maximum was observed at about 25°C. With barley seedlings, Ormrod et al. (1968) measured an optimum in apparent photosynthesis between about 16°C and 20°C in several cultivars (measured range 4°C to 34°C). However, in some cultivars the response curve was fairly flat, and in others it had a more pronounced peak.

A marginal response of net photosynthesis to temperature has been also reported for other species than Gramineae. Gaastra (1959), for instance, found practically no effect between 12°C and 27°C in leaves of tomato and turnip, at least when examined under normal CO_2 concentrations.

Bagga & Rawson (1977) came to the conclusion that in three wheat cultivars examined at anthesis, neither temperature history nor prevailing temperature affected the rate of net photosynthesis per unit area of either flag leaves or whole plants. De Vos (1977) found nothing but a marginal decline in net photosynthesis of field grown wheat as a result of an increase in temperature from 12°C to 20°C (measurements after anthesis with a crop enclosure method). At higher temperatures a decline in photosynthetic rate was observed, which became rather pronounced at 30°C. Apparently there was no interaction with irradiance.

Fukai & Silsbury (1977b) reported a clear interaction between the effects of immediate change in temperature and radiation in microplots of subterranean clover. At low levels of irradiance (0.3 $J \cdot cm^{-2} \cdot min^{-1}$ PhAR) net photosynthesis was inversely and linearly related to temperature, whilst at high levels (1.5 $J \cdot cm^{-2} \cdot min^{-1}$) net photosynthesis was directly and curvilinearly related to temperature. Lastly, Sale (1977) reported little effect on net photosynthesis of variations of temperature as large as 10°C on either side of the ambient temperature in field grown summer and winter vegetables.

In wheat, Stoy (1965) measured apparent photosynthesis and respiration rates at intervals of 5°C between 15 and 35°C. Three cultivars were examined in the three leaves stage; plants were grown indoors at 17°C/10°C day/night temperatures and photosynthesis recordings were carried out under near saturating radiation flux densities (1.8 $J \cdot cm^{-2} \cdot min^{-1}$ PhAR). Stoy found the highest net photosynthetic rates between 25°C and 30°C, whereas gross or true photsynthesis was highest between 30°C and 35°C. The lower optimum of net photosynthesis was due to the fact that the increment in 'dark respiration' (showing a more or less exponential relationship with temperature) exceeded the increment in gross photosynthesis at temperatures higher than 25°C. The following figures, derived from Stoy's work, are instructive: averaged over the three cultivars the relative rate of gross photosynthesis amounted to 87 at 15°C, to 94 at 20°C, 98 at 25°C, 100 at 30°C and 98 at 35°C. Dark respiration was on average 1.2% of gross photosynthesis at 15°C

and 6.4% at 35°C.

The difference between optimum temperatures of net and gross photosynthesis will be greater the lower the radiation flux density (and with increase in the ratio between heterotrophic and green tissue). This interaction with irradiance has been illustrated by the work of Fukai & Silsbury (1977b; cf. Nevins & Loomis, 1970).

It is of interest to note that some positive temperature response of gross photosynthesis seems likely in Expts II and IV, since there was no clear effect on net photosynthesis, whilst the initial acceleration of dark respiration would seem large enough to induce a measurable decline in rate of apparent photosynthesis on increase in temperature if the gross uptake were unaltered.

During the nineteen-seventies progress has been made in describing and quantifying the interacting effects on leaf photosynthesis of temperature, radiation and carbon dioxide and oxygen tensions (Jolliffe & Tregunna, 1973; Ehleringer & Björkman, 1977; Peisker & Apel, 1977; Ku & Edwards, 1977a, b, 1978; Tenhunen & Westrin, 1979; Tenhunen et al., 1979). As a rule net photosynthesis and quantum yield (that is the initial slope of the photosynthesis-absorbed quanta response curve) were found to decline at high temperatures in C3 plants, but there appears to be disagreement among various authors about the interpretation of results.

4.3.2 Long-term temperature effects on photosynthesis and on leaf senescence

It is interest to evaluate the extent to which 'long-term' treatment effects on photosynthesis are mediated by their impact on leaf senescence. For that purpose corresponding values of green leaf area and apparent photosynthesis (measured at a fixed radiation level), obtained from successive samplings in Expts II, IV and VA, were plotted in Figs 23 to 25. In all three cases analyzed there was a slightly curvilinear relationship between the size of green area and apparent photosynthesis. In Expt VA, however, the photosynthesis rate seemed initially not to drop in response to some decline in green area.

The data from different temperature treatments tended to form one curve. This implies that the differences in photosynthesis rate, which developed as time progressed (Figs 14 and 15), were primarily due to a faster decline in green area the higher the temperature.

The differences in the time course of photosynthesis between the nitrogen treatments in Expt VA (Fig. 16) were presumably also associated with differences in pattern of leaf senescence. However, the amount of data is too limited to permit any definite conclusions.

Additional evidence for the proposition that long-term temperature effects on photosynthesis are largely mediated by temperature effects on leaf senescence can be derived from Expt I. The stage of rapid decline in photosynthe-

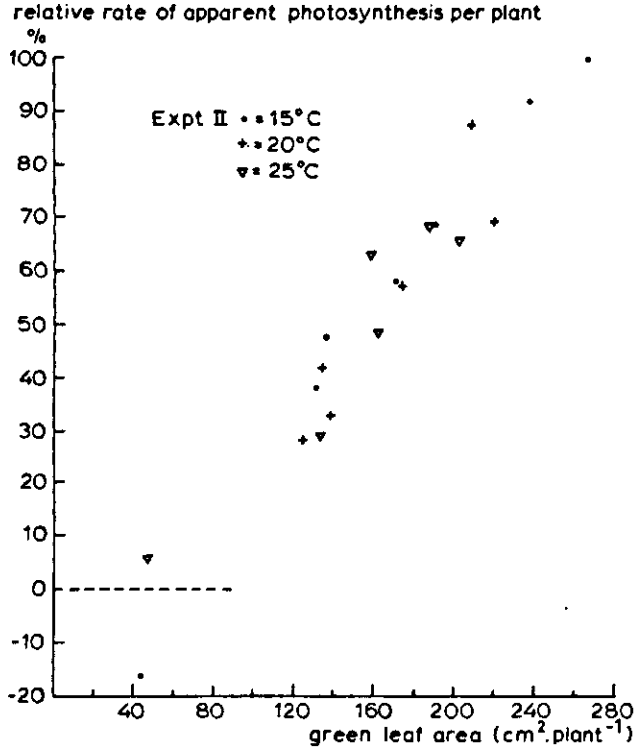

Fig. 23. The relationship between the decrease with time in the relative rate of apparent photosynthesis per plant and the green leaf area per plant; data from successive samplings in the three temperature treatments of Expt II. Data relate to the main axis plus side tiller.

sis of the flag leaf (measured under saturating light intensity) started at about 11 days after anthesis at 25°C/15°C (air/root temperature) and about one week later at 20°C/15°C. At 4 weeks after anthesis there was still no sign of an impending fall of photosynthesis at 15°C/15°C. Root temperature acted in a similar way as air temperature, but the effects were far less pronounced. These figures clearly demonstrate the long-term effect of temperature on the quantity of carbon dioxide fixed per flag leaf in Expt I. However, when photosynthesis rates per flag leaf, obtained from successive recordings, were plotted against green area remaining at the time of photosynthesis measurement, data points from all temperature treatments formed one curve (Fig. 26). This again indicates that the long-term temperature effects on photosynthesis are primarily mediated by temperature effects on leaf senescence.

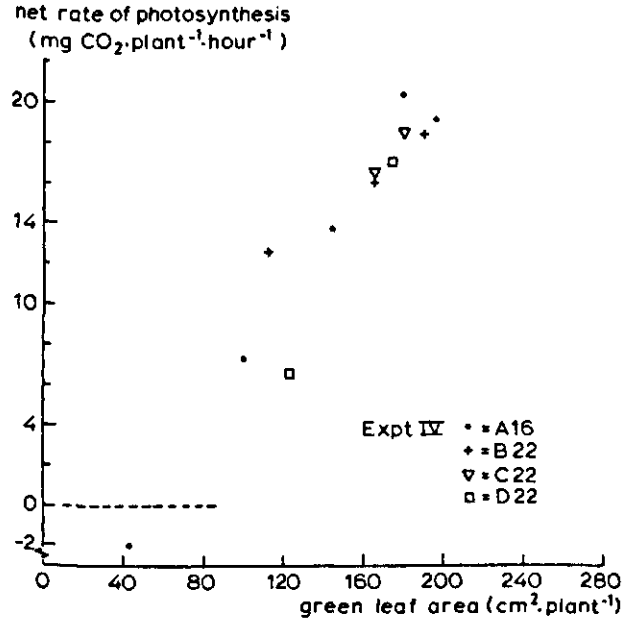

Fig. 24. The relationship between the decreases with time in the rate of apparent photosynthesis per plant and the green leaf area per plant; data from successive samplings in all four temperature treatments of Expt IV. Data relate to the main axis plus the side tiller.

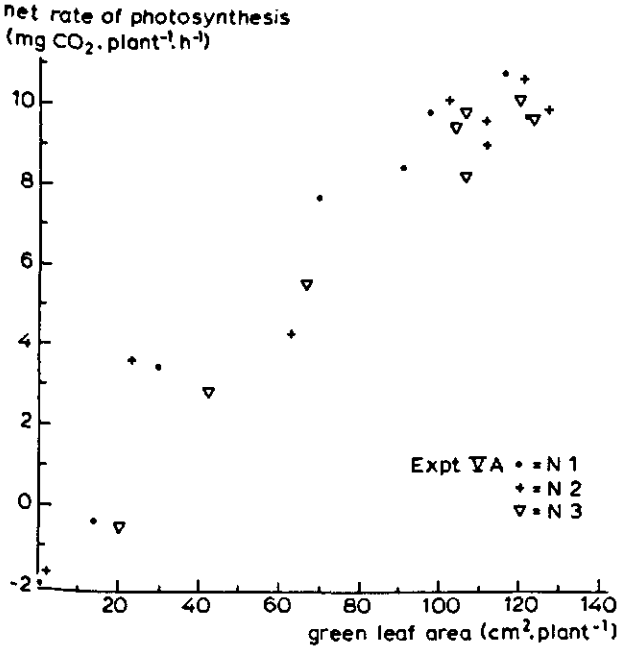

Fig. 25. The relationship between the decreases with time in the rate of apparent photosynthesis per plant and the green leaf area per plant; data from successive samplings in the three nitrogen treatments of Expt VA.

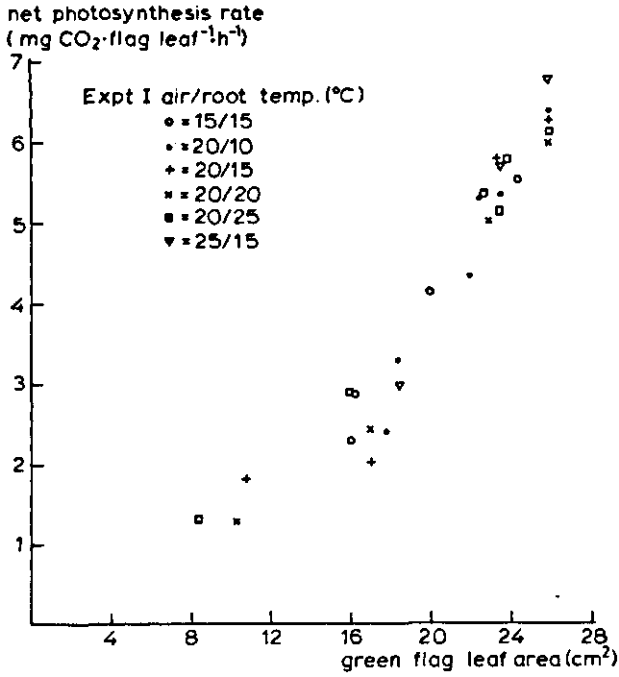

Fig. 26. The relationship between the decreases with time in the rate of flag leaf apparent photosynthesis at saturating radiation and the green flag leaf area; data from successive samplings in six temperature treatments of Expt I.

4.3.3 Leaf senescence and the photosynthetic capacity per unit green area

Radiation and green area are the two dominant factors that determine the rate of photosynthesis (Puckridge & Ratkowsky, 1971; Austin et al., 1976; Fukai & Silsbury, 1977b; Koh et al., 1978; Gallagher & Biscoe, 1979). A third factor involved is the photosynthetic capacity per unit green area at saturating radiation, P_{max}. Within the present context it is relevant to consider whether or not the P_{max} for remaining green tissue of a senescing foliage remains constant.

Osman & Milthorpe (1971b) described changes in photosynthesis of the fourth leaf of wheat in relation to age, nutrient supply and illuminance. Stoy (1965) observed no clear time trend in apparent photosynthesis of fully expanded flag leaves of wheat until the stage of rapid senescence commenced. Then rates drastically decreased. In similar material Dantuma (1973) and Angus & Wilson (1976) reported a gradual decline of P_{max} with time. In Expt I of the present series, P_{max} of flag leaves also declined continually with time: shortly after anthesis a value of 2.60 g $CO_2 \cdot m^{-2} \cdot h^{-1}$ was found; when green area had decreased by one third, P_{max} was only 1.47 g $CO_2 \cdot m^{-2} \cdot h^{-1}$.

It is of interest to mention in passing that in Expt I the initial P_{max} of

flag leaves represents a rather commonly observed value (cf. the respective compilations by Apel et al., 1973 and Angus & Wilson, 1976).

4.3.4 Effects of nitrogen on photosynthesis

In Expt VA no difference in photosynthesis was observed between nitrogen treatments initially after anthesis. At that time the plants had about equal green area, but differed substantially in nitrogen contents. Differences between nitrogen treatments became first apparent when green leaf areas started to diverge. Similary, Thomas & Thorne (1975), Pearman, Thomas & Thorne (1977) and Thomas, Thorne & Pearman (1978) showed that the rate of gross photosynthesis of flag leaves of wheat was not affected by nitrogen dressings (pot and field experiments). Beneficial effects of increasing amounts of nitrogen fertiliser on seasonal photosynthate production were due to a higher LAI and/or a longer duration of the green area. De Vos (1977) reported no differences in photosynthesis between two nitrogen treatments during the first 4 weeks after anthesis in winter wheat, at least when considered at 2.5 $J \cdot cm^{-2} \cdot min^{-1}$ incident radiation. At high radiation levels (5 $J \cdot cm^{-2} \cdot min^{-1}$) some benificial effect of more nitrogen could be detected earlier after anthesis. The latter finding is in agreement with observations of Spiertz & van de Haar (1978).

The results of all these studies point in the same direction, viz. that effects of nitrogen on photosynthate production are primarily brought about by effects on the size and the duration of the green area.

4.4 EVALUATION OF RESPIRATION FIGURES

4.4.1 Comparison with data in the literature

An answer to the question whether or not the rates of respiration, measured in the present experiments are reliable can be obtained by comparison with data in the literature. In the field crop of the present series (Expt VB; spring wheat) the rate of respiration shortly after anthesis amounted to 0.80 g $CO_2 \cdot m^{-2} \cdot h^{-1}$ at 16°C. This figures agrees well with those of de Vos (1977). He found a value of 0.76 g $CO_2 \cdot m^{-2} \cdot h^{-1}$ (2 successive seasons; crop enclosure method).

Ear respiration rates in wheat reported by Rawson & Evans (1971) were in the same range as observed in the present experiments, viz. 0.8-2.00 mg $CO_2 \cdot ear^{-1} \cdot h^{-1}$. In the present experiments, ear respiration rose to a maximum at 2-3 weeks after anthesis, after which it declined gradually (Fig. 17). Similar time courses were found by Evans & Rawson (1970), Rawson & Evans (1971), Damisch (1974), Sofield et al., (1977a), and Chowdhury & Wardlaw (1978).

Stoy (1965) also reported leaf respiration rates per unit area. In flag

leaves of wheat, grown in pots outdoors, he found figures ranging from 72 to 114 mg $CO_2 \cdot m^{-2} \cdot h^{-1}$ (measured in the post-floral stage at 20°C; his Table 31, 3 cultivars). Much in agreement with these figures are the present ones, viz. 68 mg $CO_2 \cdot m^{-2} \cdot h^{-1}$ at 16°C and a corresponding figure of 84 mg $CO_2 \cdot m^{-2} \cdot h^{-1}$ at 22°C. In another field experiment with wheat, Stoy (1965, his Table 23) found rates ranging between 110 and 190 mg $CO_2 \cdot m^{-2} \cdot h^{-1}$ at a relatively low level of nitrogen nutrition, against figures of between 13 and 200 mg $CO_2 \cdot m^{-2} \cdot h^{-1}$ at a higher N dressing.

In the present experiments stem and sheaths respiration (in absolute amounts per culm) declined during the first one or two weeks after anthesis. Thereafter it remained fairly stable until about one week before maturity (Fig. 17). This pattern of change with time of stem (and sheaths) respiration corroborates the results of Stoy (1965), Rawson & Evans (1971) and Austin et al., (1977a).

Althought dry weight is not a particular useful reference basis for stem and sheaths respiration (Subsection 3.7.5), it is the only one available to compare the present results with others. In six winters wheat cultivars, Austin et al., (1977a) noted stem respiration rates ranging from 0.28 to 0.35 mg $CO_2 \cdot g^{-1}DM \cdot h^{-1}$ (mid July 1975, 15°C). Stoy found values (perhaps at 20°C) around 0.40 mg $CO_2 \cdot g^{-1}DM \cdot h^{-1}$ averaged over three cultivars grown in pots outdoors. Rawson & Evans (1971) grew six wheat cultivars, all under similar conditions in a phytotron. Between cultivars stem respiration rates varied from 0.19 to 0.68 mg $CO_2 \cdot g^{-1}DM \cdot h^{-1}$ (measured at 20°C between 15 and 17 days after anthesis). These data suggest some genetic effect; however in the present experiments the variation was about just as large within a cultivar.

Accounting for differences in temperature during measurements, and reference bases, it appears that the range of observed stem and sheaths respiration rates is similar to those quoted from literature.

Data about root respiration in wheat are relatively scarce in literature. Osman (1971) recorded root respiration in wheat plants grown on nutrient culture under controlled conditions as well as from roots of field grown plants. At about one week before anthesis root respiratory rates amounted to 2.45 and 1.83 mg $CO_2 \cdot g^{-1}DM \cdot h^{-1}$ for nutrient culture and field grown plants, respectively. The former figure agrees reasonably with the specific root respiration rates measured early after anthesis in the present nutrient culture experiments II and IV (2.10 and 2.58 mg $CO_2 \cdot g^{-1}DM \cdot h^{-1}$, respectively). Osman's figure for field grown wheat corresponds to 1.16 mg $CO_2 \cdot g^{-1}DM \cdot h^{-1}$ as an average for the pot experiments VA en VI early after anthesis. With respect to these comparisons one has to be reminded that the plants differed in age and that the specific root respiration rate decreases gradually with age. For instance, Osman found that the specific root respiration rate in four-week-old plants easily exceeded 4.0 mg $CO_2 \cdot g^{-1}DM \cdot h^{-1}$. The author found similar values for plants of that age (data not presented).

From the comparisons of present respiration figures with literature data, one can conclude that the present measurements are not systematically wrong.

4.4.2 The temperature coefficient (Q_{10}) for respiration

One of the most conspicuous features of respiration concerns its temperature sensitivity. In short-term measurements the Q_{10} was on average about 2.2. This rather conventional value was found irrespective of growth temperature, kind of organ or age of organ; the overall range of temperatures tested was 14°C to 27°C.

Although a Q_{10} of about 2 is indeed rather common, this value cannot be regarded as a natural constant. When temperature coefficients for respiration are calculated over a broad range of temperatures, say between 5°C and 35°C, a decline in Q_{10} on increase in temperature is generally observed (Forward, 1960; Stoy, 1965; Fukai & Silsbury, 1977). Moreover Q_{10} may shift as the duration of the temperature change increases. Analyses of respiration rates of stems and sheaths and leaf blades from plants grown at different, but fixed temperatures, enabled some sort of long term Q_{10} to be established in the present experiments (see Subsection 3.7.6); this long term Q_{10} was about 1.4, i.e. much smaller than in short term measurements. An interesting connection can be made with the work of Fukai & Silsbury (1977b), who observed a greater impact of temperature on photosynthesis and respiration after an immediate change in temperature than between treatments grown at different, but fixed temperatures. Apparently, temperature effects on carbon exchange rates level off in the long run.

4.5 THE INTERPRETATION OF RESPIRATION FIGURES

4.5.1 Short review of relevant literature

McCree (1970; cf. McCree, 1974; McCree & Silsbury, 1978) and Thornley (1970, 1976) developed models in which respiration is assumed to consist of a growth component, directly proportional to the increment in new tissue, and a maintenance component, directly proportional to the dry mass already present. Several other authors fitted their data on respiration and growth (or photosynthesis) with such a two-component model. Relevant studies are those by Hesketh et al., 1971; Robson, 1973; Biscoe et al., 1975; Hansen & Jensen 1977, Walker & Thornley, 1977; Moldau & Karolin, 1977; Hansen, 1978; Kimura et al., 1978. Yokoi et al., 1978; and Hansen, 1979. Although there are differences in symbols and units, or approach between authors, most of the results can be expressed in Thornley's Y_g and M. The 'true growth efficiency', Y_g , is the fraction of substrate C retained in the 'new' tissue after biosynthesis, while M is the maintenance coefficient, expressed in gram C per gram C already present per day. Various values have been reported

for both Y_g and M, with Y_g generally ranging from about 0.65 to 0.90, depending on conditions, growth stage and whether the analyses were done on whole plants or individual organs. Values for M range generally between 0.010 and 0.060 g $C \cdot g^{-1}C \cdot d^{-1}$. In those studies quoted above where temperature effects were studied it appeared that Y_g was independent of temperature, whilst M responded strongly to temperature, usually with a Q_{10} between about 1.8 and 2.2.

Thornley (1977) proposed a more flexible model, in which maintenance cost is not a fixed 'tax on property', but depends on the rate at which labile compounds desintegrate. According to Barnes & Hole (1978) this newer formalism can be reconciled with the original two-component model, if in the latter maintenance costs are related to protein content rather than to dry weight. Hole & Barnes (1980) extended the two-component model in order to be able to account for gradual ontogenetic change in Y_g and M.

Penning de Vries and collaborators followed a different approach. Using knowledge about biochemical pathways they computed the 'production values', 'carbon dioxide production factors' and 'oxygen requirement factors', by which the conversions between substrate (glucose) and end products (proteins, carbohydrates, lipids, lignin, organic acids and minerals) can be characterized rather universally. The values of these characterizing variables are believed to be independent of temperature or species. Relevant references are Penning de Vries et al., 1974; Penning de Vries 1975a; de Wit et al., 1978. Furthermore, Penning de Vries (1975b; cf. de Wit et al., 1978) gave estimates for maintenance cost, based on estimates of energy requirements of component processes. At 25°C maintenance cost were estimated to amount to about 15-25 mg glucose per gram dry matter per day; numerically these figures are about equivalent to 0.015 to 0.025 g $C \cdot g^{-1}C \cdot d^{-1}$, i.e. smaller than most M values derived from regression analyses.

4.5.2 Ear respiration and ear growth

Preliminary analyses revealed a direct relationship between ear respiration rate (Y, expressed in mg $CO_2 \cdot ear^{-1} \cdot d^{-1}$) and ear growth rate (X, expressed in mg $DM \cdot ear^{-1} \cdot d^{-1}$). In all individual data sets it was found that data points obtained during the first weeks after anthesis were positioned higher in the graphs (higher respiration rates at any growth rate). Fig. 27 based on Expt IV, shows an example of the association between ear respiration rate and ear growth rate.

In fact the slopes and intercepts of the regressions on individual data sets appeared to be very similar and for that reason data from several experiments and treatments were bulked; the results of the regression calculations are summarized in Table 29. The first regression equation of Table 29 relates to the first weeks after anthesis (Expts III-VI all treatments); Equation 2-4 bear on the remaining and longest parts of the

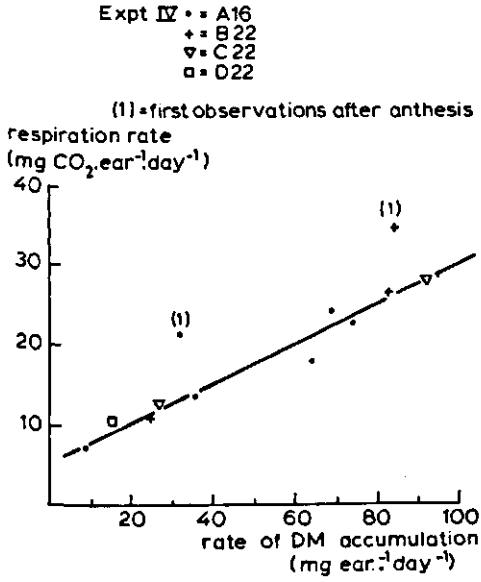

Fig. 27. A typical example of the relationship between the respiration rate of ears and the growth rate of ears; data taken from Expt IV.

Table 29. Simple linear regressions of ear respiration rate (Y) in mg $CO_2 \cdot ear^{-1} \cdot d^{-1}$ on ear growth rate (X) in mg $DM \cdot ear^{-1} \cdot d^{-1}$; data from Expts III-VI.

Stage of kernel filling[a]	Temperature (°C)	Y = a + b X					Equation number
		a	b	S.E.	n	r^2	
1		13.02	0.22	0.03	18	0.75	1
2	16	7.61	0.24	0.03	25	0.79	2
2	22	7.20	0.24	0.02	8	0.94	3
2	16, 22	7.59	0.24	0.02	33	0.84	4

[a] 1 = data from the first two weeks after anthesis; 2 = data from the remaining and longest part of the grain-filling period.

grain filling periods. Equation 2 was derived from low temperature treatments only (16°C, outdoor experiments), whilst only 22°C treatments were selected to obtain Equation 3. The last calculation in Table 29 bears on data of 16°C and 22°C treatments with exclusion of figures obtained early after anthesis. Table 29 shows that in both distinguished stages of grain filling about 0.24 g CO_2 is produced per gram increment in grain dry matter. Temperature effects did not appear, neither on slope (b term) nor intercept (a term; Equations 2, 3 and 4, Table 29). A comparison of Equations 1 and 4 reveals that the rate of ear respiration at zero growth rate (the intercept a) was twice as high early after anthesis than at later stages of

grain filling.

An interesting question is whether the slope of the regression equations in Table 29 (i.e. the growth component of ear respiration) will correspond to the one expected when the concepts of Penning de Vries (Penning de Vries et al., 1974; Penning de Vries, 1975a) are applied. For reasons of simplicity, grain dry matter was supposed to consist of protein and non-protein, or 'carbohydrates', thus ignoring the small quantities of lipids and ash present. In order to solve this question, multiple regressions were worked out relating protein growth rate and 'carbohydrate' growth rate to ear-respiration rate. Preliminary results (Vos, 1979) pointed to an encouraging agreement between calculated and theoretically expected coefficients. More detailed analyses did not yield consistent results, and the conclusion had to be drawn that a multiple-regression technique is not a suitable tool for this problem. Therefore an other approach was followed. Growth respiration of ears was calculated by multiplying the 'carbohydrate' and protein growth rates of grains with the CO_2-evolution coefficients, derived from Penning de Vries (1975a), viz. 0.17 and 0.74, respectively. Next calculated growth respiration was subtracted from total measured ear respiration. The remaining part of respiration was always in the order of magnitude given by the intercepts of Equations 2-4 in Table 29. This result indicates that growth respiration of ears can be derived from the coefficients of Penning de Vries (1975a; cf. Penning de Vries et al., 1980).

A more superficial calculation leads to the same conclusion: if each additional unit of grain dry matter consists for about 12% of proteins and about 88% of 'carbohydrates', the theoretically expected slope of the regression equations of Table 29 would be $(0.12 \times 0.74) + (0.88 \times 0.17) = 0.24$! Furthermore it is of interest to note that the slope of the regressions between ear respiration rates and ear growth rates declined when relatively more 'carbohydrates' were synthesized in the short-term treatments, subsidiary to the main treatments of Expt VI (data not presented).

The growth component of ear respiration (slopes in Table 29) can be expressed in Thornley's Y_g (Thornley, 1976). This gives a value of 0.87 g $C \cdot g^{-1}C$. Damisch arrived at an Y_g of 0.86 in wheat (Damisch, 1974) and at values between 0.87 and 0.91 in barley (Damisch, 1977).

A point of a principle nature, that has to be made is that unbiassed growth coefficients of respiration can never be derived from regression analyses that relate respiration rates to growth rates when part of the maintenance cost is directly proportional to the growth rate.

According to the regression equations of Table 29, a considerable part of ear respiration is not associated with increment in dry matter. Within the present-day concepts of respiration it is justified to assume that the extrapolated 'zero-growth' respiration rate represents the cost of maintaining ear structures and grains. In these concepts it is assumed that the maintenance costs are proportional to the total dry weight or to the amount of protein.

This is obviously not so in ears. Intuitively, the reason can be understood easily: beyond about two weeks after anthesis the accretion of grain dry matter consists largely of starch and storage proteins, which no longer partake in cell metabolism and which remain presumably unchanged once they are formed. Therefore it seems more realistic to use the ear dry weight or the amount of protein in the ear at the beginning of grain filling as a reference basis for maintenance cost. At that stage of development the ears in the present experiments weighed about 0.4-0.5 g. Shortly after anthesis (Equation 1, Table 29) the maintenance cost amounted thus to 26-33 mg CO_2 or 18-22 mg glucose per gram ear dry weight per day. Corresponding figures applying to most of the grain-filling period (Equation 4, Table 29) are 15-19 mg CO_2 or 10-13 mg glucose per gram ear dry weight per day. These are rather conventional values as indicated in Subsection 4.5.1.

Higher maintenance cost early after anthesis are not unlikely, since protein contents of ear structures are higher than later during grain filling. However, in a regression model as used at present, all respiration, which is not linked with measurable increment in dry matter, will be dumped into the maintenance component. The maintenance component of respiration of young ears may be overestimated in the present calculation, as a constructive sequence of events, such as cell formation, undoubtedly requires energy, while the dry matter gain is comparatively small.

In literature there is agreement on the temperature sensitivity of maintenance respiration (see, in addition to studies quoted above, Ryle et al., 1976). Therefore in regressions of ear respiration on ear growth rates, one would expect higher intercepts the higher the temperature. Fig. 27 and Table 29 show that this temperature dependency was not found in those data sets. A calculation of the maintenance part of ear respiration by subtracting growth respiration (Penning de Vries' coefficients) from total measured ear respiration showed no differences between 16°C and 22°C treatments in Expt IV. Throughout growth at these fixed temperatures, the maintenance respiration of ears amounted to about 6.2 mg $CO_2 \cdot ear^{-1} \cdot d^{-1}$. This is equivalent to 13 mg CO_2 per gram initial ear dry weight per day. Though the results of the shortterm treatments subsidiary to the main Expt VI were rather variable, they did indicate a Q_{10} for 'zero-growth' ear respiration in the order of 1.6-3.0.

4.5.3 *Interpretation of respiration in vegetative parts*

In a preliminary summary of this study (Vos, 1979) it was stated that the carbon efflux during kernel filling from non-growing vegetative organs could be regarded as maintenance respiration. This statement needs reconsideration because there are energy requiring processes other than maintenance that take place in these organs. For instance, additional uptake and assimilation of nitrate, relocation of nitrogenous compounds, transports of

enormous loads of carbohydrates to the grains and to other heterotrophis sites of utilization.

An account of the energy requiring processes will be given below, together with CO_2-evolution coefficients derived from the work of Penning de Vries and co-workers (Penning de Vries 1975a, 1975b; cf. de Wit et al., 1978). Subsequently, it will be examined wether computed rates of respiration agree with actually measured rates.

Energy requirements of nitrogen metabolism In wheat crops 0-50% of the amount of nitrogen present at maturity is taken up after anthesis (Austin et al., 1977b; Spiertz & Ellen, 1978). Nitrate is the predominant form in which nitrogen is taken up (Hewitt, 1979).

It can be derived from Penning de Vries (1975a) that 0.046 g CO_2 is produced per gram KNO_3 taken up in the root xylem. The cost of uptake of nitrate into the cell where it is reduced, the reduction itself, the formation of the primary nitrogenous compounds and their excretion into the phloem are estimated to give rise to the evolution of 0.6 g CO_2 per g protein ultimately produced (Penning de Vries 1975a, Fig. 20.1).

Whether these costs in terms of CO_2 evolution are paid depends on the site of reduction. In heterotropic organs like roots there are no other energy sources than ATP and reductant generated through glycolysis and the tricarboxylic acid cycle. However, when nitrate reduction is located in the leaves, no energy costs in terms of CO_2 evolution have to be considered if reduction takes place under conditions of illumination only, and/or when energy is drawn from the light reactions of photosynthesis (Beevers, 1976; Leech & Murphy, 1976; Raven, 1976a, 1976b; Miflin, 1980). This matter does not seem to be settled completely yet. Several points need further clarification and verification, for instance; the spatial distribution within a cell of the enzyme complexes involved, the type of co-factors accepted in a specific reaction and the competition for reductant and ATP between CO_2 reduction and other energy requiring reactions (cf. Aslam et al., 1979). Under field conditions, nitrate reduction in leaves might be apparently 'costless' more often than in phytotrons, as light saturation of the leaves which are most actively involved in nitrate reduction, occurs more often in the field than in relatively dark phytotrons.

A relevant question concerns the proportion to which roots and shoots participate in nitrate reduction. Several lines of inquiry indicate a substantial nitrate reduction in roots. Brunetti & Hageman (1976) observed equal root and shoot nitrate reductase activities (measured in vivo) in young wheat plants. This finding corroborates the few present data presented in Subsection 3.3.5. Kirkman & Miflin (1979) determined the ratio between reduced nitrogen and nitrate N in xylem exudates of wheat plants grown in a greenhouse. This ratio was believed to furnish information on the relative shares of roots and shoots in nitrate reduction. It appeared that the

ratio between reduced and non-reduced nitrogen increased with age: 0.6-1.6 at early stem extension, 1.6-3.7 during grain filling, whilst intermediate values were found at earing. The smallest figures bear on the highest nitrogen dressings (and N uptake rates); thus relatively more nitrogen was reduced in the shoot at higher N dressings. Wallace & Pate (1967) also showed an increase in the shoot/root reduction ratio on increase in nitrogen supply in peas.

According to Dijkshoorn (1971, 1973; personal communication, 1980) the bulk of the nitrate (that is 90% or more) is reduced in shoots. This postulate was derived from studies on production and transport of carboxylates under various nutritional treatments. Furthermore, he argued that the presence of organic nitrogen in xylem is not a suitable indicator of nitrate reduction in roots.

An other aspect of nitrate metabolism concerns the fate of the carboxylates that are concomitantly produced. Data of Kostić et al. (1967) indicate that in wheat at least two-thirds of the organic acids produced are decarboxylated in the roots. The cost of decarboxylation are estimated to amount to 0.59 g CO_2 mole organic acid (Penning de Vries, 1975a). Export of carboxylates out of leaves requires 0.06 g CO_2 per mole.

Translocation cost Most of the proteins present at anthesis are relocated to the grains. Penning de Vries & van Laar (1977) estimated the cost of protein degradation to amount to 0.19 g CO_2 per g protein.

Most of the carbohydrates have to be relocated from the site of synthesis (green cells) to the sites of utilization. Only vein loading and unloading - and not translocation as such - are believed to require energy (Coulson et al., 1972; cf. Wardlaw, 1974). According to estimates of Penning de Vries (1975a) vein loading and unloading gives rise to the evolution of 0.08 and 0.04 g CO_2 per g glucose, respectively.

Uptake of minerals from the soil is estimated to give rise to the evolution of 4.6 g CO_2 per mole; translocation of a mixture of minerals involves the evolution of 0.03 g CO_2 per g.

Maintenance cost According to Penning de Vries (1975b) turnover of proteins consumes 28-53 mg glucose per g protein per day (at 25°C). Conversion of the average value (40.5) to CO_2 units and applying a Q_{10} of 2.0 (cf. the application of the approach of Penning de Vries by de Wit et al., 1978) the cost of maintaining proteins are 0.032 and 0.049 g CO_2 per g protein per day at 16°C and 22°C, respectively. The cost of maintaining ion gradients are estimated to amount to 0.048 g $CO_2 \cdot g^{-1}$ minerals$\cdot d^{-1}$ at 25°C and thus 0.026 and 0.039 $g \cdot g^{-1} \cdot d^{-1}$ at 16°C and 22°C, respectively. The third (correction) term distinguished by these authors is related to the metabolic activity of the plant: it is assumed to consume 0.04 g glucose per g glucose metabolized (cf. de Wit et al., 1978).

Calculations of respiration of vegetative parts and comparisons with measured rates In previous subsections the heterotrophic processes operating in vegetative parts and their carbon-dioxide production coefficients were listed. These coefficients will be used to calculate the respiration rates of constituent organs of plants studied in the present experiments. Calculated rates will subsequently be compared with actually measured rates. However, not all of the data necessary for these calculations have been measured. Therefore additional assumptions are required. These assumptions are:

- one-third of the nitrate is reduced in the roots,
- two-third of all carboxylates are decarboxylated in the roots,
- the uptake rate of minerals other than KNO_3 equals 0.2 times the additional protein production rate (on a weight basis),
- the fractions of gross photosynthate loaded on veins are: 0.6 in leaf blades, 0.2 in stems and sheaths and 0.2 in ears,
- the 'tax on metabolic activity' (the third component of maintenance respiration) is assumed to be paid for 40% by leaf blades and ears and for 10% by stems and sheaths and roots; the total daily metabolic activity or glucose use is set equal to the increment in dry matter (about 40% C, as in glucose), plus the net change (positive or negative) in non-structural carbohydrates, plus the amount of glucose respired.

NB. The last two assumptions are not critical as the total amount of carbon released per plant does not change when different fractions of loading of gross photosynthates and for contribution to the total 'tax on metabolic activity' are assumed for the distinguished groups of organs.

- in each vegetative organ, the minimum amount of unloaded carbohydrates is equivalent to the amount of glucose actually respired. In roots, the metabolites formed through decarboxylation of organic acid ions (equivalent to 0.51 g glucose per gram-ion decarboxylated) can be substracted from this unloaded amount.
- the mineral concentrations in the dry matter of roots, stems and sheaths and leaf blades are 40 $mg \cdot g^{-1}$, 25 $mg \cdot g^{-1}$ and 80 $mg \cdot g^{-1}$ of the dry matter, respectively.

A summary of the heterotrophic processes and their carbon-dioxide production coefficients is given below. Coefficients of sequences of processes have been summed and all coefficients have been transformed into units that allow rapid calculations of respiration rates; the effects of the assumptions have been accounted for in the values of the coefficients. The processes and coefficients are:

Process		*CO_2-evolution coefficients*
1	uptake of KNO_3 and other minerals in root xylem	0.051 g CO_2 per g protein ultimately produced

2	uptake of nitrate in cell, reduction of nitrate, formation of primary nitrogenous organic compounds and their excretion into the phloem	0.60 g CO_2 per g protein ultimately produced
3	transport of carboxylates out of the leaves (2/3 × 2/3 of total quantity produced)	0.03 g CO_2 per g protein ultimately produced
4	decarboxylation of organic acids in roots	0.3 g CO_2 per g per g protein ultimately produced
5	vein loading of carbohydrates	0.08 g CO_2 per g glucose involved
6	unloading carbohydrates	0.04 g CO_2 per g glucose involved
7	degradation of proteins	0.19 g CO_2 per g protein hydrolysed
8	maintenance cost:	
8.1	related to protein turnover	0.059 g CO_2 per g protein per day at 25°C with a Q_{10} of 2.0
8.2	related to maintaining ion gradients	0.048 g CO_2 per g minerals per day at 25°C with a Q_{10} of 2.0
8.3	related to metabolic activity	0.059 g CO_2 per g glucose involved in metabolic activity; shares of organs as indicated above

Table 30 shows an example of a calculation of respiration rates in roots, stems and sheaths, and leaf blades, respectively, using knowledge of the carbohydrate and nitrogen economies of the plants and applying the carbon dioxide evolution coefficients presented above. The data were drawn from Expt VI N2 (plants grown in pots in the phytotron at 16°C) and refer to the period between 18 and 25 days after anthesis. All respiratory terms are expressed in mg $CO_2 \cdot organ^{-1} \cdot d^{-1}$. The increment in total dry matter was 52 mg per plant (culm) per day. The mean total respiration rate amounted to 60 mg CO_2 per plant per day; additional protein was produced at a rate of 1.7 mg per plant per day. Multiplication of all figures with 0.466 results in rates in $g \cdot m^{-2} \cdot d^{-1}$. Table 30 shows that the calculated rate of respiration was similar to the actually measured rate for leaf blades; for stems and sheaths, and especially for roots, calculated rates were much smaller than observed rates.

Similar calculations were performed on other data sets, Table 31 summarizes the results. All respiration rates were expressed in mg glucose per g

Table 30. Example of the calculation of respiration in vegetative organs by applying the coefficients listed in section 4.5.3; data from Expt VI N2 (16°C) for the period 18-25 days after anthesis.

Organs	Activity	Calculated respiration (mg $CO_2 \cdot organ^{-1} \cdot d^{-1}$)
roots	uptake minerals (1)[a]	0.09
	nitrate reduction, etc (2)	0.33
	decarboxylation of organic acids (4)	0.50
	unloading carbohydrates (6)	0.44
	break down of proteins (7)	0.16
	maintenance:	
	related to protein content (8.1)	1.58
	related to mineral content (8.2)	0.59
	related to metabolic activity (8.3)	0.55
		+
	calculated total repiration rate =	4.54
	measured total respiration rate = (both in mg CO_2 per root per day)	16.10
stems and sheaths	loading carbohydrates (5)	1.49
	unloading carbohydrates (6)	0.32
	protein break down (7)	0.20
	maintenance:	
	(8.1)	3.97
	(8.2)	1.11
	(8.3)	0.55
		+
	calculated total respiration rate =	7.64
	measured total respiration rate = (both in mg CO_2 per stem and sheaths per day)	11.76
leaf blades	transport organic acids (3)	0.03
	loading carbohydrates (5)	4.46
	protein break down (7)	0.09
	maintenance:	
	(8.1)	3.02
	(8.2)	1.28
	(8.3)	2.19
		+
	calculated total respiration rate =	11.07
	measured total respiration rate = (both in mg CO_2 per total mass of leaf blades per culm per day)	11.76

a Bracketed numbers refer to process numbers given in Section 4.5.3.

Table 31. Calculated and measured respiration rates in vegetative organs of wheat during the kernel-filling stage; all rates in mg glucose per gram dry weight per day.

Experiment and treatment, period in days after anthesis	Temperature (°C)	Roots			Stems and sheaths			Leaf blades		
		measured total	calculated total	calculated maintenance	measured total	calculated total	calculated maintenance	measured total	calculated total	calculated maintenance
III N1-16										
9-16	16	-	-	-	5.6	2.8	1.8	16.6	10.1	6.7
IV A16										
10-19	16	38.2	6.3	3.9	5.4	2.6	2.0	16.4	17.9	8.5
VA N1										
8-22	16	15.1	5.0	3.0	6.3	2.9	1.7	25.5	17.6	9.2
VB										
13-23	15	-	-	-	6.0	2.8	1.8	20.5	13.6	7.8
VI N2										
18-25	16	19.6	5.2	3.3	4.7	3.1	2.2	13.0	12.3	7.2
IV B22										
9-18	22	37.7	6.5	4.0	5.4	4.8	3.5	18.9	21.5	11.7
mean	16	24.3	5.5	3.4	5.6	2.8	1.9	18.4	14.3	7.9

dry weight per day. The calculated maintenance respiration rates are given separately. According to Table 31 agreement between calculated and observed respiration rates is the exception rather than the rule; for 16°C treatments, calculated and observed rates were equal for the leaf blades of Expt VI N2 (already mentioned above) and for the leaf blades of Expt IV A16. In the 22°C equivalent of the latter treatment (Expt IV B22) calculated leaf blade respiration exceeded the observed rate, whilst a good agreement between the calculated and measured value was found for stems and sheaths at 22°C.

Generally speaking the measured respiration rates were much greater than the calculated rates; at 16°C the ratio between these figures was about 3-6 for roots, rather consistently about 2 for stems and sheaths, and 1.4-1.0 for leaf blades. On average the calculated maintenance respiration rate amounted to 62%, 68% and 55% of the calculated total respiration rate for roots, stems and sheaths, and leaf blades, respectively (16°C cases).

Since the carbon fractions of the dry matter were about 430 mg $C \cdot g^{-1}_{DM}$, respiration rates expressed in mg glucose $g^{-1}_{DM} \cdot d^{-1}$ are numerically about equal to rates expressed in mg C or CO_2 per g C or CO_2 equivalents per day. Thus it follows that the measured total respiration rates were not high even compared to maintenance coefficients, M, generally found. This consideration, plus the fact that measured rates are unlikely to be systematically wrong by a factor of 1.5-2, leads to the inference that the lack of correspondence between calculated and measured rates is due to two possible causes, or a combination of both:

- The coefficients used to calculate respiration associated with translocation and maintenance processes are not adequate for the estimation of respiration of non-growing organs where these activities are the predominant ones.
- respiration of micro-organisms constituted also part of the recorded carbon-dioxide efflux from plant organs.

In spite of intensive spraying with fungicides, plants can generally not be considered to be completely sterile. Thus, measurements of plant respiration will always be biassed to some extent by carbon efflux from various micro-organisms. However, the importance of this respiratory term, relative to true respiration of visually healthy looking plants, is virtually unknown. Considering the magnitude of the difference between observed and calculated respiration it seems justified to assign a heavier weight to the first possibility mentioned. However, in the case of roots there is an alternative explanation, which will be dealt with in the next section.

4.5.4 Specific features of carbohydrate metabolism in roots

More workers reported relatively high respiratory activities in roots, for instance in *Lolium multiflorum* (Hansen & Jensen, 1977; Hansen, 1978,

1979) in rice and maize (Yamaguchi, 1978). Lambers & Steingröver (1978) measured root respiration rates in *Senecio* species, and found higher rates than could be explained considering growth and transport activities. These workers proposed an 'overflow-model'; surplus ATP can be hydrolysed uselessly and excessive amounts of $NADH_2$ can be oxidized wastefully via the cyanide resistant ('alternative') respiratory pathway (cf. Lambers, 1979). Without going into detail, it is of importance to note that these workers do not simply imply 'leaks' in the system, which would always give rise to a low efficiency of root respiration.

The high root respiration rates observed around anthesis in Expts II and IV might be explained as a useless combustion of excessively produced carbohydrates. In these experiments the plants were rather widely spaced (Table 1), whilst 'sink strength' is rather small around anthesis. Thus carbohydrate production exceeded 'demand' and the fraction that could not be stored in aerial organs might have been discarded through the roots.

During grain filling, root respiration declined steadily in all experiments (Fig. 17) while the amount of water-soluble carbohydrates in roots increased as time progressed (Figs 9a-d). The carbohydrates accumulated in the roots might act as osmotic agents, replacing minerals translocated to the tops (Pitman et al., 1971). However, it is not sure whether the tremendous storage of carbohydrates in roots in Expt IV (Section 3.4) can be explained in this way.

4.5.5 Overall efficiency of growth

A suitable measure to express the overall efficiency of growth is Thornley's Y (Thornley, 1976). This parameter is defined as (net C gain)/(net C gain + C respired in growth and maintenance processes).

Analyses of figures on respiration and growth (e.g. Tanaka & Yamaguchi, 1968; Robson, 1973; Yamaguchi, 1978) and analyses of retention of assimilated ^{14}C (e.g. Lian & Tanaka, 1967; Ryle et al., 1976) lead to the inference that in vegetative crops the fraction of assimilated carbon, that remains fixed in plant tissue, is unlikely to exceed 0.65. In the generative phase, Y and Y_g ('true growth efficiency') were generally smaller than in the vegetative phase: first because expensive products like lipids are synthesized in certain crops, and second, due to the relocation of nitrogenous compounds from the vegetative to the generative organs. This transport and the resynthesis of proteins represents an energy expenditure on already present material, or in other words: energy is spent without resulting in a net increase in dry matter. Relocation of nitrogenous compounds occurs also in vegetative, expanding crops, but compared to additional protein formation it is than of less importance.

Ear respiration tied to increment in dry matter (0.16 g glucose per g grain produced) constituted a comparatively small fraction of total plant

respiration. An example of the time course of this variabele, taken from data of Expt VA N1, is depicted in Fig. 28. The highest values of the growth linked proportion of total plant respiration were observed around mid-kernel filling, which coincides with the highest grain growth rates. At that stage of development the highest overall efficiencies were found as well, ranging between 0.55 and 0.65 g $C \cdot g^{-1}C$. As efficiencies were smaller at earlier, and especially at later stages of grain filling, Y values bearing on the whole post-floral period ranged between about 0.45 and 0.55; no systematic effects of temperature or nitrogen treatments were apparent (data not presented). Thus, overall efficiency was much smaller than the 'true growth efficiency' Y_g for grain growth, which amounted to 0.87.

4.6 FACTORS AFFECTING THE ACCUMULATION RATES OF GRAIN CONSTITUENTS

4.6.1 Outline of the discussion of kernel growth rates

The discussion in the succeeding sections serves several ends; i.e. a critical evaluation of the present data and their interpretation in view of existing literature, and, above all, a justification of the approach followed in the construction of a dynamic simulation model (Chapter 5).

At a fixed temperature the kernel growth rate is not constant between anthesis and maturity. During the first one or two weeks after anthesis, and just prior to maturity, the growth rate is generally small (Fig. 1). For analysis the growth rate can be regarded constant during most of the grain-filling period, when the bulk of the dry matter is accumulated (cf. Sofield et al., 1974; Sofield et al., 1977a; Gallagher et al., 1976).

Some factors affecting the mean kernel growth rate during the linear stage will be discussed first. The word 'mean' refers to the fact that the analysis will be based on the average value for all grains of an inflorescence.

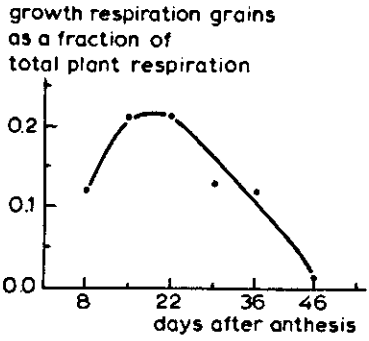

Fig. 28. The change with time in the growth respiration of grains (= 0.24 g CO_2 per g increment in grain dry weight) as a fraction of total plant respiration rate; data taken from Expt VA N1.

The possible differences in (potential) growth rate and/or size between grains, which are associated with their position in a spikelet, or with spikelet position in the spike, will be ignored (e.g. Bremner, 1972; Bremner & Rawson, 1978; Pinthus & Millet, 1978; Ries et al., 1976). Furthermore, grain dry matter will be assumed to be composed of protein and carbohydrates, thus lumping a few percentages of lipids and ash into the latter fraction.

Temperature effects on the accumulation rates of total dry matter and protein will be dealt with separately. The impact of nitrogen dressing on protein accumulation rates will also be discussed. Since the simulation model is intended to cover the whole post-floral period an approach for dealing with protein and carbohydrate accumulation during the periods prior to and after the linear stage will be proposed. A discussion about the determination of the number of kernels will be postponed to Section 4.10.

4.6.2 Genetic differences in mean kernel growth rate during the linear stage

In spite of large differences in experimental conditions, the mean kernel growth rates were about equal within a cultivar, at least when considered at roughly equal temperatures (15°C, 16°C, outdoors). Growth rates of 1.50 and 1.15 mg DM·grain^{-1}·d^{-1} were typical figures for the cultivars Adonis and Bastion, respectively. It needs mentioning that there were only two experiments with cv. Bastion (Expts II and VB), while there were two deviations within cv. Adonis, namely Expt VI and the N2 and N3 treatments of Expt III. Although these deviations need to be explained, it seems justified to conclude that there is a clear genetic difference in mean (potential) kernel growth rates between these two varieties. Unfortunately, an experiment failed to test this hypothesis directly. The description of the cultivars in the Dutch list of recommended varieties (Commissie voor de Samenstelling van de Rassenlijst voor Landbouwgewassen, 1978) provides circumstantial evidence for a genetic difference in kernel growth rate. Both cultivars are classified as early maturing ones, so large differences in post-floral period are not likely. On average their yields are about equal. However, it is stated that cv. Bastion is characterized by relatively small grains and cv. Adonis by relatively large grains. These characteristics combined lead to the inference of a genetic difference in mean kernel growth rate.

It can be proved that there is some association between the dry weight of the vegetative organs and the number of grains (cf. Section 4.10). Whatever the correct interpretation of this association may be, it seems safe to state that, in general, at equal crop dry weight and under equal environmental conditions, varieties differ in the number of kernels set, whilst (among cultivars) the number of kernels and the individual mean kernel growth rate are inversely related to a large extent.

Additional direct evidence in support of the proposition of a genetic determination of the grain growth rate can be found in the literature. For instance, Sofield et al., (1974, 1977a) found equal kernel growth rates within a cultivar in both summer and winter experiments (except at high temperature in combination with low light intensity), whilst these typical rates differed between cultivars. Martinez-Carrasco & Thorne (1979a) suggested that at equal kernel density, the mean (potential) kernel growth rate of cv. Maris Hobbit would be greater than that of cv. Maris Huntsman. Brocklehurst (1977) measured at equal kernel density different kernel growth rates between cv. Maris Huntsman and Val, viz. 1.63 ± 0.09 mg DM·day^{-1} and 1.12 ± 0.07 mg DM·day^{-1}, respectively. Varietal differences in grain growth rates were also reported by Pinthus & Sar-Shalom (1978).

4.6.3 Some possible explanations for genetic differences in kernel growth rates

In Subsection 4.6.2 a view was proposed by which genetic differences in mean potential kernel growth rates can be partly understood (different number of kernels set at equal crop dry weight etc.). Other workers held other physiomorphological factors responsible for genetic differences in growth rate. Brocklehurst (1977) was able to relate the difference in growth rate between cv. M. Huntsman and Val (Subsection 4.6.2) to differences in endosperm cell numbers. Expressed per endosperm cell the growth rates would be about similar in both cultivars indeed.

Within the present framework of discussion it is relevant to quote the work of Jenner & Rathjen (1978). These workers found that differences in kernel growth rates, observed between varieties grown in the field, could be reproduced in cultured ears. They were able to disprove the following postulates, derived from the proposition that genetic variation in rate of dry matter accumulation is due to differences in assimilate supply to the grain:

- that grains of all varieties provided with identical supplies of assimilates all grow at the same rate.
- that the rate of grain growth is positively correlated with levels of assimilates in the developing endosperm.

With respect to the second postulate, it is noted that this tendency was apparent within varieties (cf. Jenner 1970, 1974b); between varieties there was no positive association between these variables and indeed, if any association was indicated, it was an inverse one. In fact, when the increments in ethanol-insoluble residue per grain per week were plotted against the sucrose concent per grain, the regressions were really different between cultivars, suggesting genetic variation in the kinetics of conversion of sucrose into starch.

4.6.4 Effects of carbohydrate supply on the (potential) kernel growth rate

Brocklehurst (1977) reported that kernel growth rates as well as the number of endosperm cells increased on dissecting most of the grains at anthesis. Artificial reduction of kernel numbers at 15 days after anthesis (when the number of endosperm cells was fixed) resulted in no more than small increases in final dry weight per grain. These results give the impression that the mean assimilate supply per grain during the meristimatic stage of endosperm formation may effect the number of endosperm cells formed and so the potential kernel growth rate within a cultivar. Wardlaw (1970) found also fewer endosperm cells at low light intensity than at high light intensity.

It should be mentioned that genetic differences are reported with respect to the extent to which the kernel growth rate and endosperm cell numbers are increased following early dissection of some of the grains. Brocklehurst (1977) found that cv. Maris Huntsman responded less than cv. Val. Similar genetic variation in compensation was described by Pinthus & Millet (1978). Furthermore, Martinez-Carrasco & Thorne (1979a) described and discussed in the light of existing literature the differences in response between cv. Maris Huntsman and cv. Maris Hobbit on dissecting grains at 5 days after anthesis (cf. Martinez-Carrasco & Thorne, 1979b).

Within cv. Adonis (present experiments) the deviating kernel growth rates in Expt VI and in the N2 and N3 treatments of Expt III might be explained by a decreased potential due to a smaller number of endosperm cells, because the amount of available substrate per grain per day was smaller than in other cases. In Expt VI mean daily assimilate supply per grain was small because plants were grown at relatively high density for the level of irradiation, whilst in the N2 and N3 treatments of Expt III ear growth had to compete with regrowing side tillers. An equally well acceptable explanation for the lower kernel growth rate in the Adonis treatments under consideration is that the potential kernel growth rate was not greatly affected, but that such a rate could not be achieved due to lack of substrates. Water-soluble carbohydrate levels were low in the N2 and N3 treatments of Expt III indeed (Fig. 8b). In Expt VI the dry weight of stems and sheaths hardly changed with time. This suggests that carbohydrate levels were low. Furthermore, grain growth responded to short-term changes in irradiation, a response which would not occur if grains grew at their full potential rate (see remainder of this subsection).

A relevant part of the discussion concerns the impact of the carbohydrate level on the kernel growth rate during the linear stage. Jenner (1970, 1974b) and Jenner & Rathjen (1978) reported a fairly direct relationship between the sucrose concentration in the endosperm and the rate of 'structural' tissue formation within a cultivar. Jenner & Rathjen (1972a, 1972b) and Jenner (1974b, 1976) found no simple and direct relationship between the

sucrose concentration in the endosperm and the concentration in the transport system outside the grain. In fact, the movement of sucrose from the end point of the phloem to the endosperm cells is restricted (Jenner 1976) while a saturation of the transport capacity seems to occur at relatively low carbohydrate 'pressures'.

Analyses of growth rates in relation to carbohydrate levels in vegetative organs infer that there is no direct relationship between grain growth and carbohydrate levels (provided the reserve pool is not empty). In the present experiments increases or decreases in the amount of WSC in vegetative parts were not accompanied by concomitant changes in kernel growth rate. A similar picture arises from the data of Spiertz & Ellen (1978) and Spiertz & van de Haar (1978). Additional evidence in support of the proposition that grain growth rate and carbohydrate level (in vegetative parts) are not closely linked originates from the work of Apel (1974). He found that manipulation of carbohydrate supply by varying the CO_2 concentration and/or shading of leaves did not affect grain growth during a period of five days (spring wheat grown indoors). These findings were consolidated in successive papers (Nàtr & Apel, 1974; Apel & Nàtr, 1976; Apel, 1976a). The general picture emerging from these papers is that in wheat and barley, CO_2 enrichment during grain filling increased carbohydrate supply (higher stem dry weight or higher carbohydrate levels, as identified by direct measurements), whilst effects on grain dry weight were marginal.

An other line of evidence disproving a direct relationship between the rate of carbohydrate supply and grain growth can be derived from the work of Sofield et al. (1974). They found no direct relationship between grain growth and radiation when both variables were averaged over intervals of three days. However, a direct relationship was observed in treatments grown at high temperature in combination with a relatively low mean-level of radiation. Under those conditions the potential grain growth rate apparently exceeded the daily rate of carbohydrate production, and reserved were exhausted.

4.6.5 The effect of temperature on mean potential kernel growth rates during the linear stage of grain filling

Between cultivars (and experiments) the mean potential kernel growth rate will often be different, as outlined in previous subsections. Thus it follows that the accelerating effect of temperature on kernel growth rates can only be quantified on a relative scale; it was decided to express it as a Q_{10} for growth rate. Particularly useful sources of information were the papers by Sofield et al. (1974, 1977a). These authors calculated mean kernel growth rates of grains in the central spikelets of wheat. Within a spikelet separate measurements were done on first and second floret grains (1974 paper) and also on third floret grains (1977a paper). After conversion of

differential day/night temperatures to weighted mean daily temperatures values of Q_{10} for kernel growth rates could be calculated straightforwardly from their data of two cultivars for several temperature treatments.

The figures obtained thus, supplemented by those of Spiertz (1974) and some from the present experiments, were used to construct Fig. 29. This figure depicts the relation between the Q_{10} for (potential) kernel growth rate during the linear stage and temperature. The Q_{10} points, calculated for treatments at different temperatures, were placed in the graph at the midpoint of each particular temperature interval. Horizontal bars thus indicate the temperature range for Q_{10} values at the midpoint of the range. Some of the data of Sofield et al., originating from winter experiments at high temperatures, were discarded, since the carbohydrate supply was clearly inadequate to sustain potential growth. The general pattern emerging from Fig. 29 is a decline in Q_{10} for potential kernel growth rate for an increase in temperature. Especially the data from the cultivars Timgalen and Triple

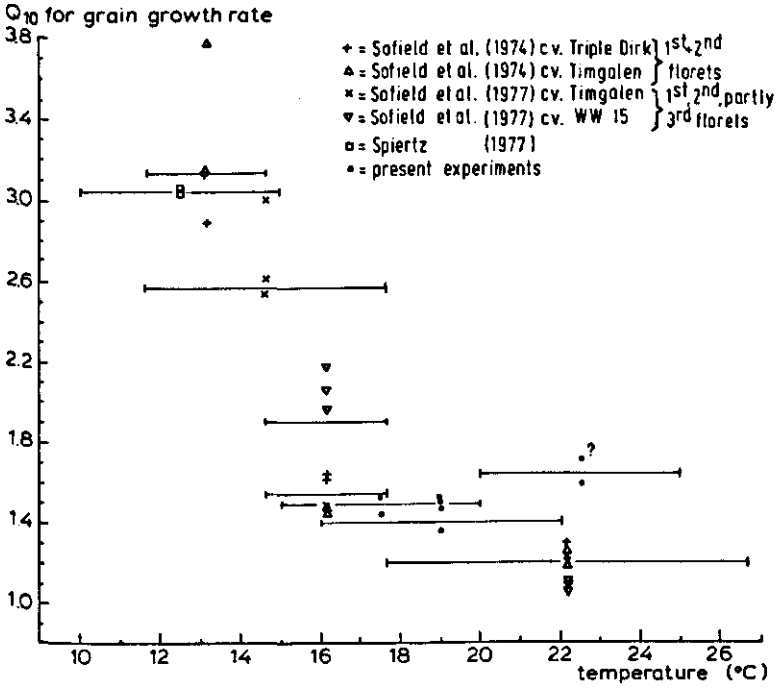

Fig. 29. A family of points indicating the relationship between temperature and the Q_{10} for the potential grain growth rate during the linear stage of grain filling. Horizontal bars indicate the temperature ranges from which the Q_{10} points are derived; for simplicity the Q_{10} values are placed at the mid-point of each range. Data from several sources; experiments were selected where the availability of carbohydrates was not likely to be a growth limiting factor.

Dirk show a considerable extent of consistency. The Q_{10} values for cv. WW15, bearing on the temperature range 14.7°C-17.7°C are actually relatively high, whilst those bearing on the interval 17.7°C-26.7°C are relatively small. Considering the general pattern, the two values for the temperature interval 20°C-25°C (derived from the present Expt II) seem rather high as well.

From Fig 29 the following tabulation can be made of rather representative Q_{10} values for potential growth rate versus temperature:

Temperature range (°C)	Q_{10}
10 - 14	about 3.1
14 - 18	about 1.8
18 - 22	about 1.5
22 - 25	about 1.2
above 25	about 1.0

Incorporation of these figures in an appropriate form into a simulation model will lead presumably to reasonable results.

4.6.6 Temperature effects on the rate of nitrogen deposition in grains during the linear stage of grain filling

It is well established, that the final concentration of nitrogen in the grains is generally higher, the higher the growth temperature (wheat, for example: Sofield et al., 1974, 1977a; Kolderup, 1975; Spiertz, 1977; present experiments; barley, for example: Andersen et al., 1978).

Concerning the causes of higher (final) grain nitrogen concentrations under warmer conditions, it is relevant to recall that within the present experiments the Q_{10} was higher for nitrogen deposition rate than for total dry matter accumulation (Tables 7 and 8). Special cases are the temperature treatments of Expt III and the treatments subsidiary to the main Expt VI: here total dry matter accumulation rate during the linear stage was not affected by temperature, whilst the rate of nitrogen deposition was strongly enhanced. Furthermore, it can be derived from the data of Sofield et al. (1974, their Fig. 1) that an accelerating effect of temperature on the nitrogen accumulation rate in grains was maintained up to higher temperatures than the temperature acceleration of the total dry matter accumulation rate. These results lead to the inference that protein deposition might show a higher optimum temperature than carbohydrate accumulation.

It was intended to construct a plot of Q_{10} values for protein accumulation against temperature, but there were not enough data available. It seems justified to adopt a provisional Q_{10} of 2.0.

In the present Expts III and IV, the temperature acceleration of the nitrogen deposition rate and maturation were so to speak counterbalanced be-

cause final grain nitrogen yields per ear (and per grain) did not differ between temperature treatments. However, cases where there is no such a counterbalance are no exceptions; for instance in the present Expt II as well as in the quoted experiment of Sofield et al. (1974) grain nitrogen yields were considerably smaller at the highest temperatures.

4.6.7 Independent regulation of carbohydrate and protein accumulation in grains

The difference between the temperature effects on accumulation of carbohydrates and protein gives reason to postulate that both processes are regulated by different mechanisms. Direct evidence, supporting this proposition was given by Jenner (1980). At the end of a shading treatment, covering the first ten days after anthesis, the amount of nitrogen in the ethanol-insoluble residue of grain tissue was found to be only slightly smaller than in unshaded plants. The accumulation of (structural) carbohydrates, however, was adversely affected by shading. Trimming ears to four spikelets (at 10 days after anthesis) resulted in an increased supply of sucrose and soluble amino compounds available for distribution to remaining grains. However, more nitrogen entered the grains of trimmed ears than intact ones, but the inflow of sucrose was not increased by trimming the ear, and no more starch was deposited in grains developing in trimmed ears.

The results of the subsidiary treatments of Expt VI are in agreement with Jenner's findings. Variation in daily quantities of incident radiation supplied in ratio's of 1:2:3, were not found to affect the accretion of nitrogen in the grains, whilst carbohydrate accumulation rates responded to radiation (treatments lasting 6 days around mid-grain filling).

The results presented in this subsection (cf. Martinez-Carrasco & Thorne, 1979b) also imply that deposition of nitrogen in grains is even less responsive to short term changes in photosynthesis than carbohydrate accumulation is.

With respect to long term application of differential levels of radiation during grain filling it can be noted that Sofield et al. (1977b) observed smaller final grain dry matter and nitrogen yields the lower the level of radiation (range: 8 100 to 48 400 lux). The final nitrogen concentration was found to be highest at the lowest radiation level. These findings indicate that the nitrogen economy is affected by the availability of carbohydrates in the long term, but they also stress that protein synthesis in grains is more competitive than starch synthesis under conditions of limiting substrate supply.

4.6.8 Physiological and modelling aspects of ontogenetic change in potential accumulation rates of grain constituents

It is generally observed that grain growth enters the linear stage earlier the higher the temperature. Presumably the successive developmental stages in young grains are passed at a faster rate. Wardlaw (1970) for instance observed an accelerating effect of temperature on the rate of endosperm cell production.

An appropriate approach for the description of kernel growth during the lag period seems to consider it as a process of exponential growth, which can be assigned a temperature dependency, as suggested for young maize tissue by de Wit et al. (1970).

Modelling nitrogen accumulation during this particular stage can be achieved by supposing a fixed nitrogen concentration in the new tissue formed. In the present experiments the nitrogen content of young grains ranged between 24 and 28 mg per g dry matter. Spiertz & Ellen (1978) dissected the grains a bit earlier after anthesis and they found initial concentrations of up to 30 mg per g dry matter, with only small differences between nitrogen treatments. So, for the time being, it seems justified to fix the N accumulation rate during the lag phase at 3% of the total DM accumulation rate. From the physiological point of view this solution is not attractive, and not even completely correct if one considers the results of Jenner (1980) quoted earlier, but the amounts of nitrogen involved are small, and therefore the performance of a model will hardly be affected by this assumption.

Near maturity the rate of nitrogen accumulation in the grains may slow down. Two causes, or a combination of both, can be held responsible for this phenomenon. These are:
- an exhaustion of the supply of nitrogenous compounds,
- a decay of enzymes involved in protein assimilation in the grains.

Likewise, a slowing down of the rate of starch accumulation near maturity can be attributed to either a cessation of the supply of carbohydrates or a loss of synthetic capacity of the endosperm, or a combination of both.

In this connection it is relevant to cite the work of Jenner & Rathjen (1977). They measured the rate of ^{14}C incorporation in endosperm cells, cultured for five hours in a ^{14}C-sucrose-containing solution. Field-grown material was used and measurements were extended over the whole post-floral period. The observed time courses of the amount of ^{14}C incorporated into starch, on the one hand, and into other material insoluble in ethanol, on the other, were more-or-less bell-shaped. Since the carbohydrate supply was equally favourable for successive cultured samples, these bell-shaped curves should represent the grain's potential, at least as far as carbohydrate metabolism is concerned. Unfortunately ^{14}C-labelled starch formation ceased earlier in time in vitro, than starch accumulation in the field. This in-

dicates some discrepancy between biosynthesis in intact endosperms and incubation in vitro. Interestingly, the incorporation of ^{14}C in components insoluble in ethanol other than starch (mostly proteins) continued longer than the labelling of starch. A slower rate of decay of enzymes involved in protein metabolism compared to those involved in starch formation might be one of the factors explaining the rather commonly observed increase in grain nitrogen concentration during the terminal stage of grain filling.

The work of Jenner & Rathjen (1977) provides elegant evidence in support of the proposition that the grain itself is actively involved in the regulation of the accumulation of various compounds. Incorporation into a model of the bell-shaped patterns for ontogenetic drift in potential accumulation rates, described by Jenner & Rathjen, is not straightforward, but could be a possibility. However, for the time being the simpler approach is proposed of an exponential initial stage and constant potential rates for the rest of the grain-filling period. In most cases the absence of a decay mechanism of synthetic capacity of grains is not expected to lead to erratic model predictions of grain growth during the terminal stage of grain filling, as the substrate supply will be small anyway. Only in crops rich in nitrogen, where ear maturation may precede senescence of vegetative parts (as for instance in Expt II), the omission of decay of synthetic capacity may lead to higher predicted than observed grain dry weights near maturity.

4.7 UPTAKE AND REDISTRIBUTION OF NITROGEN AFTER ANTHESIS, AS AFFECTED BY NITROGEN FERTILISATION

At any instant during grain filling the rate of nitrogen accumulation in grains is the smaller of two rates, viz. the potential rate of incorporation in the grains (controlled by physiological and genetic factors in the grain) and the rate at which N becomes available either through uptake or remobilization.

The (potential) rate of remobilization can be assumed to be a function of the amount of nitrogen present in vegetative parts. Presumably not all of the nitrogen in vegetative organs can be removed, a fair estimate for 'trapped' nitrogen is 0.4% of the dry weight. For that reason the amount of nitrogen potentially available for relocation is defined by the total amount of nitrogen minus 0.4% of the shoot dry matter.

Table 32 contains data about the amounts of potentially available nitrogen present at anthesis per shoot and per grain, as well as the rates of nitrogen accumulation per grain during the linear stage. Only low temperature treatments were selected (15°C, 16°C, outdoors). It follows readily from this tabulation that there is no simple relationship between the rate of N accumulation per grain and the (initial) amount of nitrogen, potentially available for relocation. First of all it can be noted that the rates of

Table 32. Amounts of nitrogen (N) potentially available for relocation measured at the first sampling after anthesis, and nitrogen accumulation rates per grain during the linear stage from treatments grown at 15°C, 16°C and outdoors.

Experiment and treatment	Amount of N in shoot, potentially available for relocation to the grains (mg)		Rate of N accumulation ($\mu g \cdot grain^{-1} \cdot d^{-1}$)
	per culm	per grain	
II 15 mc	62.08	0.98	17.27
II 15 st	58.72	0.99	19.24?
III N1-16	37.14	0.80	27.64
IV A16 mc	28.20	0.64	26.33
IV A16 st	27.15	0.69	25.17
VA N1	29.55	0.74	22.72
VA N2	36.42	0.91	26.12
VA N3	37.29	0.93	25.41
VB	16.97	0.59	18.23
VI N1	21.95	0.59	18.43
VI N2	43.38	0.96	21.12

mc = main culm; st = side tiller

nitrogen accumulation within a cultivar were rather constant, e.g. a representative figure for cv. Bastion was 18 $\mu g\ N \cdot grain^{-1} \cdot d^{-1}$ (Expts II and VB) and 26 $\mu g\ N \cdot grain^{-1} \cdot d^{-1}$ for cv. Adonis (remaining experiments). Within cv. Adonis the figures from Expt VI were rather small; this was also shown for total dry matter accumulation rate per grain. Even when the data of Expt VI are discarded for a moment, it appears that within a cultivar the rate of nitrogen deposition per grain is not predetermined by the (initial) amount of nitrogen which is potentially available for relocation.

By combining the data in Tables 32 and 12 it can be derived that there is a tendency towards a relatively higher contribution to grain N yield by post-floral uptake in cases where the initial amount of nitrogen, potentially available for relocation, was relatively small per grain. For that reason a plot was constructed with 'gross-root contribution' to grain N yield (= relocation from root tissue plus net uptake) as the ordinate and the weighted mean concentration of nitrogen in shoot dry matter at anthesis as the abscissa (Fig. 30); only low temperature treatments were selected. Fig. 30 indeed corroborates the suggested association between nitrogen concentration at the beginning of grain filling and post-floral uptake. However, three data points drop clearly from an otherwise rather smooth curve, viz. Expt VI N1, VA N1 and Expt III N1-16. It is highly likely that in these cases there was not enough nitrogen available for uptake.

Nitrogen uptake seems to be 'sink' dependent to some extent. This follows from the tendency towards a larger post-anthesis uptake in crops with a relatively low (initial) nitrogen concentration (Fig. 30). Furthermore, an in-

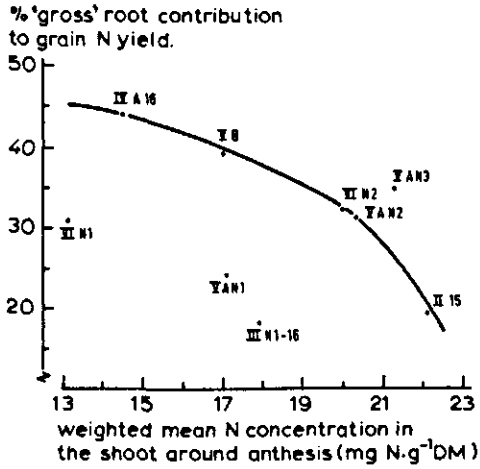

Fig. 30. The relationship between 'gross' root contribution to grain nitrogen yield (consisting of additional net N uptake after anthesis plus N removed from root tissue) and the nitrogen concentration in shoot dry matter at anthesis. Data from experiments and treatments with a moderate temperature regime (15°C, 16°C, outdoors).

creased 'N demand', either due to an enhanced potential nitrogen accumulation rate of the grains at higher temperature (Expt II 20, Expt IV B22), or due to investment of nitrogen in regrowing side tillers (N2 and N3 treatments of Expt III), resulted in an increased nitrogen uptake from the root medium. An increased post-anthesis uptake of nitrogen at warmer temperatures can also be inferred from the data of Spiertz (1977).

The nitrogen economy of a wheat crop in its post-floral stage can be handled in a simulation model on the following simplified basis. The relatively small variation in N accumulation rates within a cultivar gave reason to postulate a genetically-controlled potential N accumulation rate per kernel, which can be regarded as being constant during the linear stage of grain filling, at least at a fixed temperature (Q_{10} = 2.0). The relative contributions to N deposition in grains by N removal from shoot organs, on the one hand, and by N removal from roots plus uptake, on the other, are complementary. The latter can be described as a function of the initial weighted mean nitrogen concentration in shoot dry matter, as proposed above. The relative contribution of individual shoot organs (chaff and rachis, leaf blades, stems and sheaths) to N removal from the total shoot can be taken to be numerically equal to the initial relative distribution of nitrogen over component shoot organs.

4.8 TEMPERATURE EFFECTS ON THE DURATION OF GRAIN GROWTH

First of all it is necessary to comment on the question how the duration of grain growth is measured. In the present experiments duration was defined as the number of days between anthesis and the point where maximum grain dry weight was attained. Anthesis and maximum ear dry weight, especially, are rather difficult to measure uniformly. So the figures from the present experiments, given in Table 9, are approximations. Sofield et al. (1974, 1977a) defined duration in a different manner. They derived duration by extrapolation of the line for linear growth to its intersections with zero and with mature weight. This may be called 'calculated' duration. Obviously, treatment effects on duration can be assessed more sharply by this method, at least, if growth stops rather abruptly. However, because the initial lag is dependent on temperature and because nitrogen accumulation may proceed at an almost constant rate during a longer period than total DM accumulation (cf. Table 7), a function describing the effects of temperature on duration needs to cover the whole post-floral period.

The relationship between temperature and the time lapse required to complete a certain stage of development has been quantified in several ways. Mutsaers (1976) demonstrated that the logarithm of the boll maturation period in cotton was directly (but inversely) related to temperature. Feddes (1971), for instance, observed a direct relationship between the reciprocal of the time lapse required to reach 50% emergence of seeds and temperature. The latter approach is in fact comparable with a degree-days or heat sum concept in which the (mean) daily temperature is diminished with a constant figure (minimum temperature). Bierhuizen & Wagenvoort (1974) and Wagenvoort & Bierhuizen (1977) applied this approach succesfully to quantify temperature effects on germination of seeds, whilst Gallagher (1979) employed it to relate temperature and duration of leaf expansion in cereals. Heat sums and minimum temperatures, describing the temperature dependency of the duration of growth stages of spring wheat before and after heading, were calculated by Kontturi (1979) by means of regression analyses with data of several seasons.

Both approaches will be tested for cereals, using data from the present experiments and from literature. Some of the literature data had to be read from graphs. There are number of differences between the experiments from which the data originate. In most cases, except in the present experiments and in that of Spiertz (1977), differential day and night temperatures were applied. These were converted to weighted mean daily temperatures. Two sets of data bear on weighted mean seasonal temperatures from field experiments, viz. that from Spiertz (1978), and that from Gallagher et al. (1976). The data from Sofield et al. (1974, Fig. 5) and Gallagher et al. (1976) have a bearing on the 'calculated' duration (see above).
Most experiments were done with wheat, one with sorghum (Chowdhury & Wardlaw,

1978) and two with barley (Gallagher et al., 1976; Andersen et al., 1978).

Considering the difficulty in measuring the duration of grain filling exactly and although not all of the lines are straight, Fig. 31 shows that the assumption of an inverse exponential relationship between duration (D, days) and temperature is not clearly disproved. The fact that most lines for wheat (except those from field experiments) run more or less parallel indicates that - if an exponential relationship is assumed - the (negative) exponent can be taken constant. For wheat the numerical value of the slope is about -0.031. A rule of thumb that can be derived from the data reads that the duration of growth is approximately doubled per 10°C drop in temperature.

Lines from different experiments and species differ primarily in intercept. Fig. 31 shows that at any temperature the duration of grain growth was shortest for barley and longest for sorghum. Of course, for wheat the intercept is smaller when the duration of grain growth is calculated as was done by Sofield et al. (1974, 1977a).

Fig. 32 shows a family of points, obtained by plotting 1/D (D = duration in days) against T (T = temperature in °C). From the figure it can be seen that on data from the same source the relationship between 1/D and T is fairly direct. Exceptions are the data derived from Sofield et al. (1974, Fig. 1) and Spiertz (1978), which refer to observations in field crops made in several seasons. From most data depicted in Fig. 32, simple linear regressions were calculated; the results are shown in Table 33. The last column of that table displays the minimum temperature at which there is no progress in development and at which duration becomes infinite (mathematically speaking). For wheat grown in the phytotron, the minimum temperature (T_{min}) appears to be about 6°C, except when duration is established by the method of Sofield; Table 33 indicates an apparently higher minimum temperature for field-grown wheat and a lower one for barley (grown indoors). The reciprocal of the slope b of the regression equation between 1/D and T represents the heat sum above the minimum temperature required to complete the grain-filling stage. Fig. 32 and Table 33 indicate that for wheat grown indoors the minimum temperature and the heat sum are about 6°C and 624 degree-days, respectively.

Considering the fact that the duration of grain-filling period was generally not determined sharply in the experiments from which the data were analyzed, it can be concluded that fitting of 1/D against T is an acceptable tool to quantify the effects of temperature on duration of grain growth. From the mathematical point of view an inverse direct relationship between log D and T and a direct relationship between 1/D and T are mutually exclusive. Based on the gathered material it is hard to decide which of the two appoached should be considered the best. However, a regression equation between 1/D and T has the virtue that it can be incorporated into a dynamic model straightforwardly, as the reciprocal of time (duration) is a rate.

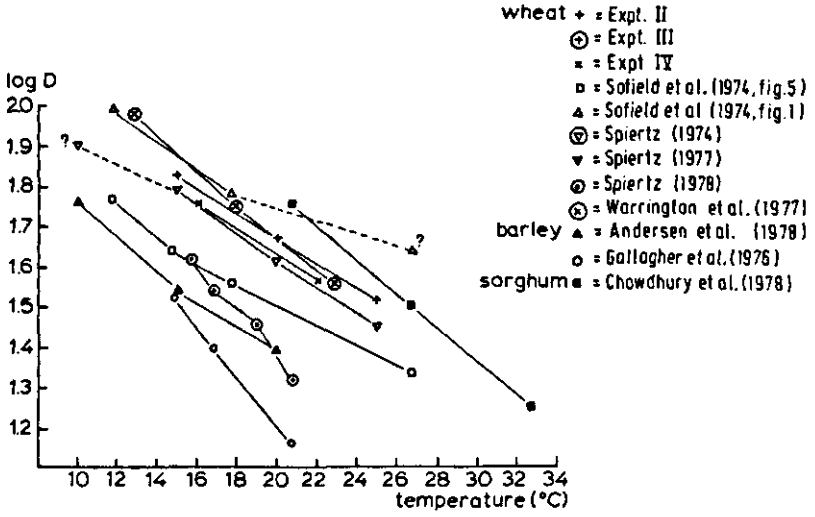

Fig. 31. Relationships between the logarithm of the duration of the grain-filling period (D, in days) and temperature. Data from several sources.

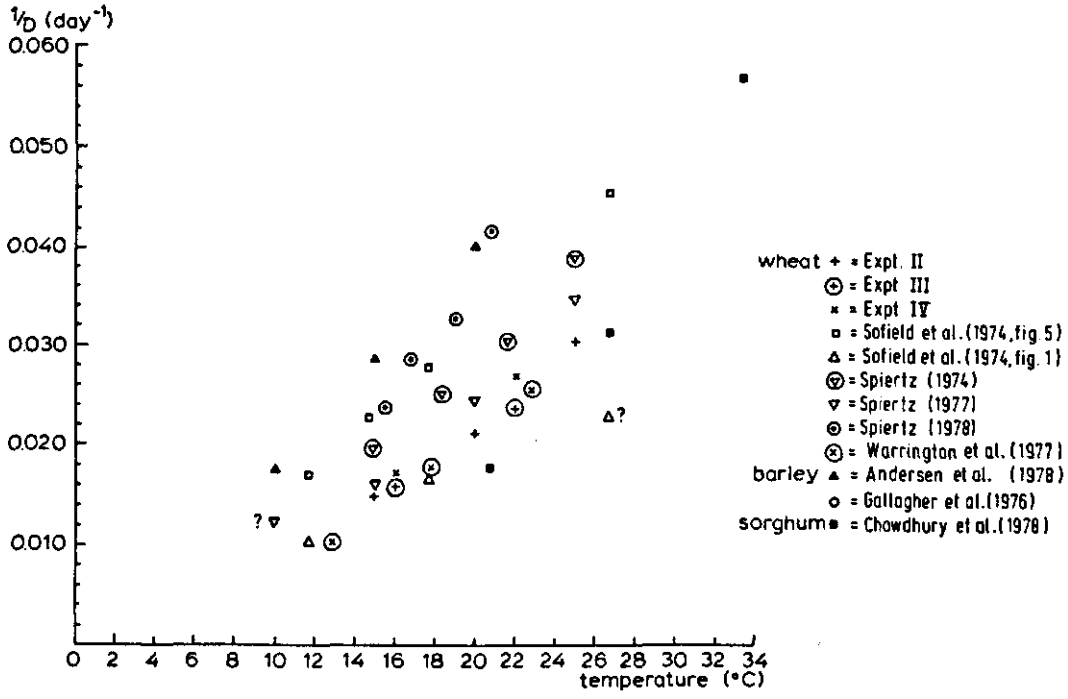

Fig. 32. Relationships between the reciprocal of the duration of the grain-filling period (1/D) and temperature. Data from several sources.

Table 33. Simple linear regressions of the reciprocal of duration of the grain filling period (1/D, D measured in days) against temperature (T, in °C).

Reference	Crop plant	Details 'a'	1/D = a + b T				T_{min} (°C)
			a	b	n	r^2	
Sofield et al. (1974, their Fig. 5)	wheat	c, m, d	-0.00533	0.001897	4	0.99	2.81
Spiertz (1977), present Expts II, III, IV	wheat	-	-0.01006	0.001658	10	0.93	6.06
Warrington et al. (1977)	wheat	m	-0.00930	0.001523	3	0.99	6.10
Spiertz (1974)	wheat	d	-0.01012	0.001913	3	0.99	5.29
Spiertz (1978)	wheat	f	-0.02770	0.003280	4	0.97	8.45
Andersen et al. (1978)	barley	m, d	-0.00505	0.002250	3	0.99	2.25

'a' c = 'calculated duration', see Section 4.8.
d = differential day/night temperatures, converted to weighted mean daily temperatures.
f = regression of duration in the field on mean temperatures during grain filling taken over several years; all other experiments were executed under controlled conditions.
m = each indivudal data point represents a mean of several replicates or cultivars.

In the above analyses it was assumed implicitly that temperature is the principal factor determining the duration of grain growth within species. The fact that for various sources of data duration could be described as a function of temperature, suggests strongly that this assumption is indeed justified for a given crop. But possible impacts of other environmental or (morpho) genetic factors on duration should not be ignored. Sofield et al. (1977a) mentioned little effect of a six-fold range in level of irradiation on duration. Direct effects of nitrogen on duration seem small (Expts III, VA and VI; and Ellen & Spiertz, 1980), in spite of a considerable impact of nitrogen on leaf senescence. Some genetic determination of duration seems likely; cultivars are usually classified in categories according to their relative date of maturity (of course, differences in dates of anthesis should be accounted for as well). Fig. 32 indicates that genetic and possible pre-anthesis history impacts on duration alter primarily the slope of the regression of 1/D against T.

Grain size can be suspected to physically limit the acceptance of carbohydrates. Again, the fact that in wheat, barley and sorghum 1/D and T could be fitted by a simple linear regression, suggests that the physical limit of the grain size does not control the duration of grain growth in these species in practice. Accumulation of dry matter in rice may be restricted by limits on the physical size of the hull (van Keulen, 1977). This can be illustrated further by data of Chowdhury & Wardlaw (1978). These workers

reported that in an indica and in a japonica rice type the mean kernel dry weight at maturity responded little to temperature treatment in the range of 21°C/16°C to 30°C/25°C (day/night temperatures). The fact that it is impossible to fit 1/D against T, especially for indica rice, suggests indeed that some factor other than temperature controlled the cessation of dry matter accumulation in the grains.

4.9 THE DISTRIBUTION OF DRY MATTER AND NITROGEN AT ANTHESIS

In Subsection 3.1.2 and 3.3.2 it was found that the amounts of dry matter and nitrogen were distributed in fairly fixed proportions over ear structures (chaff and rachis), leaf blades and stems and sheaths around anthesis. This rather stable pattern was observed in spite of a wide range in mean shoot dry weights and in nitrogen concentrations between experiments. This section sets out to confirm this finding using data from other sources. Original data from field experiments were supplied by Dr Thorne of Rothamsted Experimental Research Station (Harpenden, U.K.) and by Ing. J. Ellen and Dr Spiertz of the Agricultural University of Wageningen and of the Centre for Agrobiological Research, Wageningen, respectively. The data supplied by Dr Thorne were the basis of articles written by Pearman, Thomas & Thorne (1977, 1978a). These workers investigated the effect of 8 or 9 nitrogen dressings on crop performance during several seasons and with several cultivars and/or genotypes. Table 34 provides some information about those crops and treatments; for more details the reader should consult the papers written by Pearman et al. (1977, 1978a) about these studies. Data from Austin et al. (1977; 47 genotypes) and Kramer (1978; comparison of the old cultivar Juliana with the modern cultivar Lely) were evaluated as well.

From the sources mentioned above Table 35 contains data about the crop dry weights, the distribution of dry matter, the specific leaf area, as well as the total amounts, the distribution and the concentrations of nitrogen at anthesis. The total amount of above-ground dry matter, present around anthe-

Table 34. Some features of crops and treatments of the experiments described by Pearman et al. (1977, 1978a).

Wheat type	Cultivar	Seasons	N treatments
spring wheat	Kleiber	1972, 1973, 1974	0-200 $kg \cdot ha^{-1}$ in 25 kg steps[a]
tall winter wheat	Capelle -Desprez	1975, 1976	0-210 $kg \cdot ha^{-1}$ in 30 kg steps
	Maris Huntsman	1975, 1976	0-210 $kg \cdot ha^{-1}$ in 30 kg steps
semi-dwarf winter wheat	Maris Fundin	1975	0-210 $kg \cdot ha^{-1}$ in 30 kg steps
	Maris Hobbit	1976	0-210 $kg \cdot ha^{-1}$ in 30 kg steps

a Dressings given in one dosing in spring

Table 35. A compilation of some data about the distribution of dry matter and nitrogen, as well as about specific leaf areas in wheat around anthesis.

	References					
	Expts II-VI	Pearman et al. 1977, 1978	Austin et al. 1977	Ellen & Spiertz pers.comm.	Kramer 1978	Kramer 1978
seasons :	-	1972-1976	1975	1978	1976	1976
wheat type [a] :	spring wh.	w+spr. wh.	winter wh.	w+spr. wh	winter wh. cv.Lely	w wh. cv. Juliana
% of total DM in:						
ears	17.2	17.2	16.0	16.5	14.9	12.4
leaf blades	23.2	16.2	22.4	17.5	20.0	23.4
stems and sheaths	59.6	66.6	61.6	66.0	65.1	64.1
total DM $g \cdot m^{-2}$	720-1250	450-1200	448-1646	1100-1400	1090	1025
spec.leaf area $dm^2 \cdot g^{-1}$; range	1.5-2.8	1.4-2.2		ca 1.90	-	-
mean	2.0	1.87(±0.02)				
% of total N in:						
ears	15		19		18	14
leaf blades	39		30		42	45
stems and sheaths	46		51		40	40
weighted mean N content of shoot ($mg \cdot g^{-1}$)	14.5-26.4	6.8-24.9	13.9		16.6	17.2
g $N \cdot m^{-2}$; range	11.9-23.0	2.7-21.9	6.1-21.8			
mean	17.5		17.4		18.1	17.6
N contents (mg $N \cdot g^{-1}$ DM)						
ears	18	15-17	17		20	20
leaf blades	33		28		35	33
stems and sheaths	16		8		10	11

a wh. = wheat, w = winter, spr. = spring.

sis, varies considerably, depending on season, treatment, and wheat type. Representative figures for a rather 'average' season under Dutch and English conditions are about 8 tonnes$\cdot$ha^{-1} for spring wheat and 11 tonnes$\cdot$ha^{-1} for winter wheat.

The specific leaf area cannot be considered a 'natural constant' (cf. Aase, 1978), but especially based on the figure derived from the Rothamsted data (Table 35) it is fair to assume a SLA (specific leaf area) in the order of 1.9 dm^2 green area per gram leaf dry weight for field conditions. We could not find an effect of nitrogen treatment on the SLA in the Rothamsted data. According to Aase's data (1978) the SLA ranged between 1.8 and 2.0 dm^2 green

area·g^{-1} leaf dry weight around anthesis in winter wheat (several seasons and cultivars, Montana, U.S.A.).

Table 35 reveals that the relative distribution of dry matter over ears, leaf blades and stems and sheaths is rather fixed indeed, despite considerable variation in total crop dry weight at anthesis; fair figures are: 16% in ears, 18% in leaf blades and 66% in stems and sheaths.

An attribute of dry matter distribution, not specified in Table 35, concerns the shoot/root ratio (S/R). A well documented example of the changes with time in the dry weights of shoots and roots of a winter wheat crop is given by Gregory et al. (1978). According to their results it is reasonable to assume a S/R of about 10 at anthesis. This figure is in line with data given by Welbank et al. (1974).

The amount of nitrogen, present in above-ground organs at anthesis is subject to considerable variation, depending mainly on fertilizer management, season and wheat type. Assuming a weighted mean mass fraction of nitrogen in dry matter of 14 mg N·g^{-1}DM, the amount of nitrogen taken up at anthesis by average crops (specified above) is 110 kg·ha^{-1} in spring wheat and 150 kg·ha^{-1} for winter wheat.

The data in Table 35 do not indicate narrow ranges for the relative distribution of nitrogen over aerial organs at anthesis; the proportion of shoot nitrogen located in ears is about 15%, the proportions in leaf blades and in stems and sheaths range between about 30-45% and 40-50%, respectively. In the present experiments the proportion of nitrogen in stems and sheaths tended to increase with more nitrogen at the expense of the proportions of nitrogen in leaf blades and in ears (Table 11). This might hold in general.

Helpful alternative attributes to describe the nitrogen distribution at anthesis are the mass fractions (concentrations) of nitrogen the dry matter. It appears from the data given in Table 35, supplemented by those of Spiertz & Ellen (1978) and Gregory et al. (1979), that the initial mass fractions of nitrogen around anthesis are in the order of 17-20 mg N·g^{-1}DM in ears, 26-35 mg N·g^{-1}DM in leaf blades and 6-11 mg N·g^{-1}DM in stems and sheaths. Initial nitrogen concentrations in root tissue are about equal to or slightly higher than those in stems and sheaths.

The vast body of data supplied by Dr Thorne (cf. Table 34) made it possible to establish the relationships between various crop attributes. Table 36 shows that the dry weights of individual shoot organs (ears, leaf blades, and stems and sheaths) could be described satisfactorily as linear functions of the total shoot dry weight around anthesis. An interesting detail is that the semi-dwarf winter wheats invested relatively more dry matter in ears than the other wheat types. It can be derived from data in Table 36 that leaf dry weight constitutes a somewhat greater proportion of shoot dry weight the heavier the crop. The leaf area index (LAI) was closely associated with shoot dry weight. It appeared, however, that the direct relationship broke down at LAI values greater than 4.0, indicating that this LAI

Table 36. Relationships between crop attributes at anthesis, derived from the Rothamsted experiments[a].

Crop plants[b]	Dependent variable Y	Independent variable X	Y = a + b X				Range in X
			a	b	n	r^2	
s wh	ear dw[c]	shoot dw	42.1	0.116	27	0.78	570- 939
t w wh	ear dw	shoot dw	18.4	0.131	32	0.92	370-1207
sd w wh	ear dw	shoot dw	3.2	0.197	16	0.97	416-1185
all	ear dw	shoot dw	17.5	0.147	75	0.79	370-1207
all	dw leaves	shoot dw	-32.6	0.209	75	0.89	370-1207
all	dw stems and sheaths	shoot dw	15.2	0.644	75	0.98	370-1207
all	dw leaves	dw stems and sheaths	-27.5	0.300	75	0.80	253- 779
all	LAI leaves	shoot dw	-0.67	0.004	75	0.89	370-1207
all	LAI leaves < 4	shoot dw	-0.31	0.003	69	0.91	370-1185
all	LAI leaves	dw leaves	0.13	0.017	75	0.89	53- 254
all	N content	shoot dw	-2.19	0.016	75	0.61	370-1207

a Raw data obtained from Dr Thorne; experiments described by Pearman et al. (1977, 1978a), see also Table 34.
b s wh = spring wheat crops only; t w wh = tall winter wheat crops only; all = all data bulked
c dw = dry weight, in $g \cdot m^{-2}$.

value was the limit above which additional green area was less efficiently employed in dry matter accumulation. When the green area of stems and sheaths was included in the LAI a basically similar strong association with shoot dry weight was obtained, at least up to LAI 9.0. It is interesting to note that this limit on 'productive' total LAI was mentioned by Thorne already in 1974 (Thorne, 1974). In contrast with the present results, Aase (1978) reported a breakdown of the direct association between green area and crop dry weight past growth stage F5 (field grown wheat in Montana, U.S.A., for several cultivars and seasons).

The total amount of nitrogen present at anthesis (expressed in $g \cdot m^{-2}$) was correlated with total shoot dry weight as well, although the coefficient of determination, r^2, was rather small compared to those found for most other regressions. It is worthwhile to mention that in the Rothamsted experiments the nitrogen concentrations in the shoot dry matter at anthesis increased only slightly with crop dry weight. Averaged over all crops the average nitrogen fractions amounted to 10.5, 12.9 and 13.8 mg $N \cdot g^{-1}$DM at 400, 700 and 1000 $g \cdot m^{-2}$ shoot dry weight, respectively. Considered for the winter wheat crops separately the nitrogen fractions at the specified crop dry weights were on average: 97, 115 and 123 mg $N \cdot g^{-1}$DM. Without going into detail, it seems that in several treatments of the Rothamsted experiments the nitrogen in the dry matter was diluted to the maximum limit possible;

looking at it from the other side one can say that the poor availability of nitrogen restricted dry matter accumulation in several cases. Especially in 1976, the unusual drought is likely to have affected the nitrogen regime of the crops as well.

What matters here is that the level of nitrogen nutrition as such does not seem to greatly affect the relative distribution of dry matter over aerial organs at anthesis (Table 35, Expts III, VA and VI).

4.10 CONSIDERATIONS ON CROP DEVELOPMENT AND GRAIN YIELD

4.10.1 The determination of kernel numbers

There appeared to be an association between the number of kernels per square metre and the crop dry weight at anthesis in the Rothamsted experiments, but the r^2 values were not extremely high (Table 37). Darwinkel (1978; personal communication 1979) examined crop performance in winter wheat at several planting densities. Different shoot dry weights (expressed in $g \cdot m^{-2}$) and kernel numbers were thus obtained. Because crop dry weights at anthesis were not available the relationships between the number of kernels per square metre and straw dry weight (leaves plus stems) at maturity were calculated from his data. To allow a comparison with Darwinkel's figures to be made a regression was worked out on Rothamsted data with straw plus chaff dry weight at maturity as the independent variable (Table 37). It can be seen that the parameters of the regression equations show some variation between individual data sets. This indicates that there are more determinants of the number of kernels than just the mass of vegetative organs; the rather high intercepts (2 500 till 4 500 kernels$\cdot m^{-2}$ at zero shoot or straw dry weight) point in the same direction. In spite of this, it seems to be justified to state that on average high kernel numbers can only be obtained with sturdy vegetative development.

At any crop dry weight, the semi-dwarf winter wheats tended to produce more grains than the other wheat types used in the Rothamsted experiments. Thus a genetic effect may be involved in the determination of the number of kernels. Furthermore, kernel numbers per ear were found to be smaller the higher the temperature and/or the lower the level of irradiance around anthesis (Wardlaw, 1970; Spiertz, 1977; Warrington et al., 1977; Sofield et al., 1977a). After about 5 days after anthesis the number of kernels is not affected any more by changes in temperature, except possibly at extremely high temperatures (Wardlaw, 1970; Ford & Thorne, 1975; Ford et al., 1976; Chowdhury & Wardlaw, 1978; Expts II, III and IV).

It seems that for modelling purposes the effects of temperature and light intensity around anthesis on grain set can be interpreted as an adaptation of the plant to prevailing assimilate supply. In order to survive a grain in statu nascendi needs to receive its daily portion of assimilates. As

Table 37. Associations between the number of kernels per square metre and the dry weight of the vegetative mass.

Reference[a]	Crops[b]	Dependent variable Y	Independent variable X	Y = a + b X				Range in X
				a	b	n	r^2	
A	s wh	number of kernels·m^{-2}	shoot dw[c] at anthesis	3384	10.3	27	0.57	570- 939
	t w wh	number of kernels·m^{-2}	shoot dw at anthesis	4141	7.2	32	0.82	370-1207
	sd w wh	number of kernels·m^{-2}	shoot dw at anthesis	3929	10.2	16	0.72	416-1185
	all	number of kernels·m^{-2}	shoot dw at anthesis	4114	8.6	75	0.64	370-1207
A	s wh	number of kernels·m^{-2}	non-grain shoot dw at maturity	3710	11.6	27	0.66	518- 831
	t w wh	number of kernels·m^{-2}	non-grain shoot dw at maturity	3503	11.3	32	0.86	274- 845
	sd w wh	number of kernels·m^{-2}	non-grain shoot dw at maturity	2401	19.4	16	0.84	245- 765
	all	number of kernels·m^{-2}	non-grain shoot dw at maturity	4334	11.1	75	0.63	245- 845
B	1977	number of kernels·m^{-2}	straw dw at maturity	2344	17.1	8	0.96	349-1260
	1979	number of kernels·m^{-2}	straw dw at maturity	4671	19.0	12	0.93	742-1096

a A = data from the Rothamsted experiments (see Table 34)
B = data from Darwinkel (1978, personal communication 1979).

b s wh = spring wheat crops only; t w wh = tall winter wheat crops only; sd w wh = semi-dwarf winter wheat crops only; all = all data bulked. 1977 = winter wheat crop grown in 1977 described by Darwinkel (1978); 1979 = winter wheat crop grown in 1979, studied by Darwinkel

c dw = dry weight, in g·m^{-2}.

temperature speeds up physiological processes, this daily ration is temperature dependent. If the daily rate of assimilate supply is too small to meet the requirements of all grains, as many are aborted as necessary to restore the balance between requirement and supply. This manner of interpretation can be extended to both earlier and later events in development: tillering and tiller death, floret initiation and the number of endosperm cells formed can all be thought to be governed by a balance between requirement and supply of assimilates.

Gifford (1977) and Darwinkel (1978) described tillering responses when the mean daily rate of assimilate supply per plant was varied by variation in CO_2 concentration or planting density, respectively. In those two studies it

is clearly shown that adaptation or compensation is accomplished in such a way, that a rather stable final individual kernel dry weight results. In several other studies with wheat, where crop morphology was varied by nitrogen nutrition, or where cultivars were grown in different seasons, the final mean kernel dry weight turned out to be the most stable component of yield (Langer & Liew, 1973; Ellen & Spiertz, 1975; Spiertz & Ellen, 1978; Spiertz & van de Haar, 1978; Pinthus & Sar-shalom, 1978). The stability of mean kernel dry weight in barley was described and discussed by Gallagher et al. (1975).

It seems that the prediction of a relatively stable final grain dry weight can be used as a test criterion for any model or formalism describing the effects of environmental factors, exerted up to one week after anthesis, on the determination of yield components in wheat and barley.

Although adjustment of the number and the size of sinks to the balance of requirement and supply at several stages of development is a view that overlooks genetic and physiological details of the determination of the structure of a crop, the concept may prove to be powerful enough to give good agreement between simulated and observed plant responses to environmental factors. Van Keulen (1977) adopted such an approach in modelling the growth of rice, and application in wheat is in progress (van Keulen, personal communication, 1981).

It is highly relevant to quote results obtained by Rawson & Bagga (1979). Their findings support several of the points made above. They found that the grain number of the main ear was closely correlated with the amount of dry matter in stem, ear structures and in the four uppermost leaves of the main shoot; the partial correlation coefficients demonstrated than leaf weight was best related to grain number. Furthermore they inferred from the experiments with temperature treatments in three cultivars that dry matter is distributed to various plant organs before anthesis is in a fixed proportion, irrespective of the availability of assimilates. A similar conclusion was draw in the previous section in this report with respect to the effect of nitrogen on the distribution of dry matter. Rawson & Bagga (1979) found a good correlation between the number of grains per main ear and the ratio of the sum of total short wave radiation : sum of day degrees above 7°C between sowing and anthesis.

4.10.2 Pre-anthesis development, kernel numbers and grain yield

In a number of studies a direct relationship was found between yield (expressed in $g \cdot m^{-2}$) and the number of grains per square metre, at least up to certain kernel densities. Under Dutch conditions the relationship was found to be direct up to 18 000 kernels$\cdot m^{-2}$ by Darwinkel (1978) and to more than 21 000 kernels$\cdot m^{-2}$ by Spiertz (1978). This difference in upper limit of kernel numbers might depend on season or cultivar (for instance,

Table 38. Associations between grain yield ($g \cdot m^{-2}$) and the number of kernels per square metre, and between grain yield and the dry weight (= dw, in $g \cdot m^{-2}$) of the vegetative mass.

Reference	Crop[a] plant	Dependent variable Y	Independent variable X	Y = a + b X				Range in X
				a	b	n	r^2	
A	all	grain yield	number of kernels	61	0.036	75	0.90	5711-17156
A	all	grain yield	shoot dw at anthesis	171	0.363	75	0.78	370- 1207
B	1977	grain yield	straw dw at maturity	134	0.630	8	0.88	349- 1260
	1979	grain yield	straw dw at maturity	312	0.710	12	0.81	742- 1096

a See legend to Table 37.

because cultivars differ in grain number under comparable conditions (see previous sections)). The paper by Spiertz (1978) provides a detailed account of literature data for wheat.

Table 38 shows the association between grain yield and the number of grains averaged over all Rothamsted data. Examples of a close relationship between grain yield and kernel number in barley were also presented by Gallagher et al. (1975) and Dyson (1977). One can conclude that on average higher cereal yields can be expected the more kernels are set.

Because the number of grains per square metre was shown to be related to the vegetative mass at anthesis, the relationships between yield and shoot dry weight at anthesis were examined in the data sets from Thorne and Darwinkel. Straw dry weight at maturity replaced shoot dry weight at anthesis in the data set from Darwinkel because the latter data were not available. This replacement is not of vital importance because a strong correlation between straw dry weight at maturity and shoot dry weight at anthesis can be envisaged. The results of the regression calculations (Table 38) indicate a rather strong correlation between the variables under consideration. This reinforces the proposition that on average high yields can only be obtained with expansive vegetative development.

In areas with a stable climate during grain filling, yield predictions can in principle be derived from regression equations relating shoot dry weight at anthesis to final grain yield. In areas with unstable, variable weather conditions during grain filling, the amount of uncertainty will be too large. When the number of endosperm cells has been fixed the plant has run out of compensation mechanisms and yield will indeed be affected by the climatic conditions that happen to occur. The vital elements for a dynamic model, which were developed during the course of the preceding chapters and

which will summarized and applied in the next chapter, will hopefully allow progress to be made in attempts to quantify the impacts of radiation and temperature on crop performance during grain filling, given a certain crop structure at anthesis.

5 Simulation of post-floral growth in wheat

5.1 OUTLINE OF THE STRUCTURE OF THE MODEL

A CSMP simulation model was constructed of the grain-filling stage of wheat. The model describes and interrelates gross photosynthesis, respiration, the accumulation of carbohydrates and proteins in the grains, additional uptake and redistribution of nitrogen and leaf senescence as affected by the state of the crop at anthesis and radiation and temperature during the grain-filling period. The model is designed to run with time steps of one day, whilst weights of various constituents and ultimate dimensions of rates of processes are expressed per square metre of land. A good deal of the justification of the approach has been presented already in Chapter 4, and many of the generalizations arrived at will be summarized implicitly in the following treatment of the basic sections of the model.

The model lacks provisions enabling evapotranspiration to be computed. Therefore, water stress cannot be accounted for. This precludes the direct application of the model for conditions where the limited availability of water is an overruling factor. However, it should be possible to extend the model to incorporate the factors of water status of plant and soil. Furthermore, modifying effects of pests and diseases are not dealt with, nor is it possible to compute the amount of soil nitrogen available for uptake by the plant.

Computation of the daily gross photosynthesis rate A procedure for the calculation of daily totals of gross photosynthesis, described by Goudriaan & van Laar (1978), was incorporated into the simulation of grain growth. In this sub-model the relationship between gross photosynthesis per unit green area and absorbed radiation is represented by an asymptotic exponential equation, which is completely defined by two parameters. These are the photosynthetic capacity at saturating radiation, AMAX, and the slope of the curve at the origin, EFFE. A typical value for EFFE is 0.4 (kg $CO_2 \cdot ha^{-1} \cdot h^{-1}$)/ $J \cdot cm^{-2} \cdot s^{-1}$) (Goudriaan, personal communication, 1980). The extinction of light in the canopy proceeds exponentially with leaf area index, calculated from the top. Both incoming photosynthetically active radiation (PhAR) and gross photosynthesis are calculated as averages over the day, accounting for differences in light distribution between clear and overcast skies.

In this sub-model no account can be taken of differences in AMAX between leaves of various age or between tissues of various nature (leaf blades, leaf sheaths, peduncle, ear). Therefore the value inserted for AMAX re-

presents an average for all types and ages of green tissue. In Subsection 4.3.3 it was discussed that AMAX may decline in a senescing leaf. Based on results of Expt I, AMAX was assumed to decline in proportion to the decline in green area index, which is expressed by the formula AMAX = AMAXI × RELLAI, where AMAXI is the value for AMAX of the foliage at anthesis and RELLAI the ratio between the remaining green area index at a point in time and the value at anthesis. Possible impacts of temperature and of (initial) nitrogen concentration on AMAX and on EFFE were not considered in the model.

Computation of respiration rates (in glucose units) Growth respiration in grains was calculated by applying the coefficients of Penning de Vries (1975a). Ear growth-respiration rates thus totalled 0.116 times the carbohydrate accumulation rate, and 0.505 times the protein accumulation rate. The 'cost' of synthesis of other compounds was ignored.

Computation of respiration of vegetative parts from basic biochemical data turned out to be difficult (Subsection 4.5.3). Therefore empirical coefficients were employed. The (maintenance) respiration of ear structures was related to the initial ear dry weight and was programmed as a hyperbolic decline with developmental stage, starting with a coefficient of 22 mg glucose·g^{-1} dry weight at anthesis and attaining half that value at maturity (i.e. if respiration at that time was not restricted because of lack of substrates). The coefficients adopted for respiration of stems and sheaths, and roots were 5.6 and 10 mg glucose·g^{-1} dry weight·d^{-1}. Leaf laminar respiration was linked to green area by adopting a value of 1.11 gram glucose per unit LAI (m^2) per day. The above mentioned coefficients hold at 16°C but were (except for roots) temperature dependent, with a Q_{10} of 2.0. Actually achieved respiration rates decreased as substrates became limiting. Furthermore, respiration rates were multiplied by the reduction coefficients for export of nitrogen. These coefficients will be defined in the discussion of the nitrogen economy.

Test runs showed values for the efficiency of growth, GE, ranging between 0.55 and 0.65 when potential growth was achieved and smaller values near maturity (the term GE is mostly used in literature of Japanese origin; it is defined as: increment in dry weight/(increment in dry weight plus respiration in glucose units)). The obtained GE values are in accordance with published values (e.g. Yamaguchi, 1978; Hodges & Kanemasu, 1977, and references cited therein) as well as with values calculated from the present series of experiments. Thus it seems justified to conclude that predicted respiration rates are in the correct order of magnitude.

Computation of the accumulation of carbohydrates and proteins in grains Grain dry matter was assumed to consist of protein and carbohydrates, thus lumping a few percentages of ash and lipids into the latter fraction. During the 'lag phase' (the first week or so after anthesis) carbohydrate accumula-

tion in grains was assumed to proceed exponentially, with a rate constant of 0.3 $g \cdot g^{-1} \cdot d^{-1}$ at 16°C, which was assigned a Q_{10} of 2.0. During this stage of grain filling, protein accumulation in grains was fixed at 0.17 times the carbohydrate accumulation rate. Grain dry weight at anthesis was estimated to amount to about 7.5 $g \cdot m^{-2}$. Grain growth was programmed to switch from the exponential stage to the linear stage when the exponential growth rate becomes equal to the potential growth rate in the linear stage.

Beyond the lag phase the potential accumulation rates per grain for carbohydrates and for protein (POTRCH and POTRPR, respectively) were considered constant at a fixed temperature. POTRCH and POTRPR were assigned Q_{10} values of 1.5 and 2.0 respectively. The model requires the specification of values for these variables at a reference temperature. Accumulation rates per square metre were obtained by multiplication of rates per grain with the number of kernels per square metre, NOKER. Provisionally the number of kernels was related to the crop dry weight at anthesis, CRDWAN, as follows:

NOKER = 3 500 + 14 CRDWAN

At moderate temperatures the ratio between POTRCH and POTRPR varies between about 7.0 and 9.0. Test runs revealed that the model results were rather strongly affected by the potential accumulation rates per square metre (potential rates per grain times number of grains), in particular because the removal of nitrogen from vegetative parts and leaf senescence (and thus photosynthesis) are linked in the model. This aspect is discussed in more detail in the treatment of the calculation of the leaf area index. No decay of synthetic capacity of grains at the end of the grain-filling phase was built in, so a slowing of the accumulation rates at that stage of development can arise from exhaustion of substrate supplies only.

The carbohydrate economy At each day the amount of carbohydrates, available for growth and respiration, consisted of gross photosynthesis plus reserves (if present). Carbohydrate consumption proceeded at its potential (temperature dependent) rate when there were enough available substrates. If the potential demand exceeded the available amount of substrates the accumulation of carbohydrates in the grains was the first process to suffer. It was slowed down to the level required to bring consumption of carbohydrates into equilibrium with the available amount. If the latter was still too small to meet the glucose demand of grain-protein-growth respiration plus respiration of non-grain parts (while carbohydrate accumulation in grains was reduced to zero already), the deposition of proteins in the grains and the respiratory processes were slowed down in equal proportions.

Feed-back between the level of non-structural carbohydrates and either production or utilization of carbohydrates was not regarded necessary (Section 4.2). To trace possible errors in programming a kind of 'double book-

keeping' of the carbohydrate economy was built in.

Nitrogen uptake and redistribution Daily nitrogen demands of the grains were met by removal of nitrogen from ear structures (chaff and rachis), leaf blades, stems and leaf sheaths, and by removal from roots plus uptake from the soil. The maximum relative contribution by roots and soil (uptake) to daily accretion of grain protein was treated as one variable, designated MXRCRS. MXRCSR was assumed to be related to the weighted mean initial nitrogen concentration in shoot dry matter at anthesis, as shown in Fig. 33 (cf. Subsection 4.6.9). Ear structures, leaf blades and stems and sheaths filled up the fraction of the daily demand still left (=1-MXRCRS) in strict proportion to the amount of nitrogen present in these organs (Subsections 3.3.3 and 4.7). This situation only holds when the nitrogen concentration in the specified organs exceeds a minimum value. No restriction on the export of nitrogen was assumed when the nitrogen concentrations were greater than 5, 6 and 3.5 $mg \cdot g^{-1}$ in ear structures, leaf blades and stems and sheaths, respectively. Between these values and 3.5, 4.0 and 2.5 mg $N \cdot g^{-1}$ DM, respectively, the reduction coefficients on export of nitrogen declined linearly from 1.0 to 0.0. Arbitrarily, the MXRCRS was multiplied by the reduction coefficient for export of nitrogen from stems and sheaths. Potential uptake of nitrogen from the soil was thus slowed down as the amounts of relocatable nitrogen in stems and sheaths and in roots were becoming exhausted. The underlying assumption is that metabolic activity of organs is restricted in this stage of nitrogen depletion. For this reason the respiration rates of ear structures, stems and sheaths, and roots were also multiplied by the reduction coefficients on nitrogen redistribution.

Potential nitrogen accumulation rates in grains could not be achieved anymore when the reduction coefficients dropped below 1.0. Apart from exhaustion, nitrogen redistribution and uptake could also be restricted due

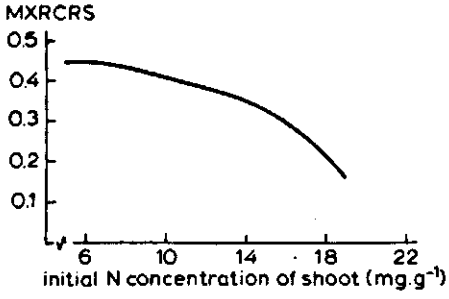

Fig. 33. The relation used in the model between the variable MXRCRS (maximum relative contribution to accretion of the amount of N in grains by net uptake from the soil plus N removed from root tissue) and the weighted mean initial nitrogen concentration in shoot dry matter at anthesis.

to limiting availability of carbohydrates (energy), as discussed in the treatment of the carbohydrate economy.

Calculation of the leaf area index The decline of the green area index of leaf blades (LAIL) was made dependent of the removal of nitrogen from the leaf blades (Subsection 3.5.4). Before explaining the mechanism some variables have to be defined. The relative nitrogen content of leaf blades, RNCLB, is given by NCLB/NCLBI, where NCLB and NCLBI denote the actual and initial amounts of nitrogen in the leaf blades, respectively. The relationship between the relative green area index of leaves, RELLAI, and the relative amount of nitrogen in leaf blades is shown in Fig. 34. For any point in time the absolute value for the green area index of leaf blades can be obtained by multiplying RELLAI by LAILI, where LAILI stands for the initial green area index of leaf blades at anthesis, which has to be given as an input. The total green area index, LAI, was obtained from the green area index of leaves, LAIL, by multiplying with 2.2. This conversion coefficient was derived from data from experiments, conducted at the Rothamsted Experimental Station, U.K. (Pearman et al., 1977, 1978; Section 4.9). The conversion coefficient between green area of leaf blades and total green area was actually obtained from measurements around anthesis (n=75; intercept close to zero, r^2=0.94), but it seems fair to assume a proportional decline for both variables during the grain-filling period, which in turn means the coefficient is assumed to be constant.

Computation of the duration of the grain-filling period Basically, the duration of the grain-filling period was calculated by defining a minimum temperature for development, TMIN, and a heat sum above TMIN, HSUM (Section 4.8). For use in the model these parameters were transformed into a regression equation that relates the rate of development, DVR, to the average

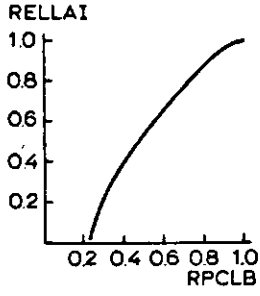

Fig. 34. The relation used in the model between the variables RELLAI and RPCLB. The latter is defined as the ratio between the actual amount and the initial amount of N in leaves; RELLAI is the reduction coefficient by which the initial leaf area index is multiplied to obtain the actual value of LAI on any day.

daily temperature, T (in °C). The form of the regression equation is:

$$DVR = -a + b\,T.$$

The coefficients a and b can be derived straightforwardly from TMIN and HSUM, since b=1/HSUM and a=TMIN×b. The stage of development, assigned the value 0.0 at anthesis was augmented by DVR daily until the value 1.0, and thus maturity, was reached. Appropriate values for TMIN and HSUM are 6°C and about 500 degree-days, respectively.

Test runs showed that the performance of the model was not greatly affected by an accurate assessment of HSUM. This is because the removal of nitrogen from vegetative parts is also temperature dependent via the Q_{10} of 2.0 for the potential rate of protein deposition in grains. Through this mechanism the model also predicts an earlier senescence of vegetative parts and an earlier cessation of grain growth at higher temperatures.

Input requirements of the model The main input data required to initialize and subsequently run the model are:

- the latitude of the location;
- the day number in the year of the date of anthesis;
- the dry weights ($g \cdot m^{-2}$) and nitrogen contents of ear structures, leaf blades and stem and sheaths at anthesis. Root mass is estimated assuming a shoot/root ratio of 10 (Section 4.9); whilst the nitrogen content of roots is not required;
- the green area index of leaf blades at anthesis;
- the amount of non-structural carbohydrates (reserves) at anthesis;
- a value for the photosynthetic capacity at saturating radiation (AMAXI) at anthesis;
- values for the potential rates of accumulation of carbohydrates and of proteins per grain during the linear stage (POTRCH and POTRPR, respectively);
- daily records of daily (gross) radiation and daily mean temperature from the date of anthesis onwards.

If the distribution of dry matter at anthesis is not known it can be derived from the (estimated) total crop dry weight at anthesis as pointed out in Section 4.9. An estimate for the initial green area index of leaves can be obtained by assuming a specific leaf area of 1.9 $dm^2 \cdot g^{-1}$. Simulations can also be started at a date later in the grain-filling stage.

5.2 TESTING OF THE MODEL

The simulation model was to reproduce the pattern of grain growth of some of the winter wheat crops, described by Ellen & Spiertz (1980). The crops were grown on a location at Wageningen in the season 1977/1978. Three crops

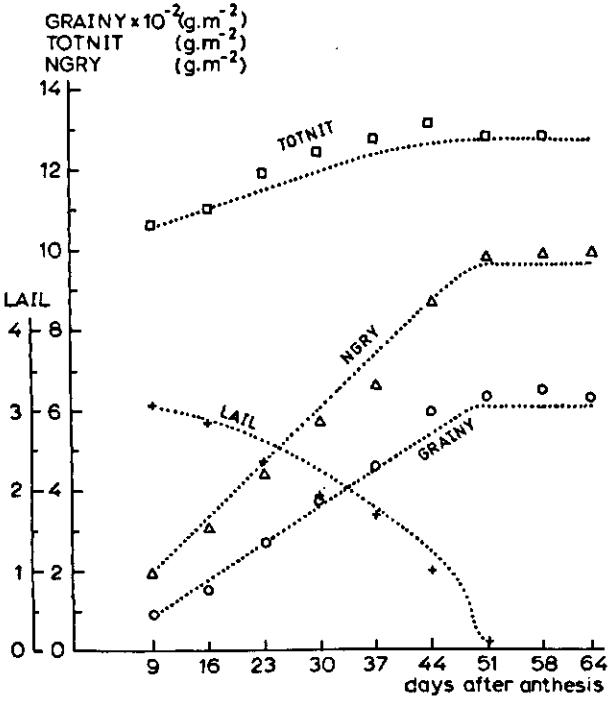

Fig. 35. Observed (□, Δ, 0, +) and simulated (.....) crop performance during the grain-filling stage of winter wheat. Measurements from treatment 0+40+40 kg N·ha^{-1}, season 1977/1978, Wageningen (Ellen & Spiertz, 1980). 0, GRAINY (grain dry matter weight (g·m^{-2}·10^{-2})); Δ, NGRY (amount of nitrogen in grains (g·m^{-2})); □, TOTNIT (total amount of nitrogen in aerial organs (g·m^{-2})); +, LAIL (green area index of leaf blades).

were selected, differing in time and amount of nitrogen supply, viz. the nitrogen treatments were 0+0+0 kg·ha^{-1}, 0+40+40 kg·ha^{-1} and 40+40+40 kg·ha^{-1}, dressings being applied in autumn, early spring and late spring, respectively. The only reason for selecting these crops was that sufficiently detailed analyses of growth (DM, N, LAI) were available.

First a simulation of treatment 0+40+40 was attempted. Good agreement between observed and simulated crop performance was obtained when AMAXI was assigned the value 1.5 g CO_2·m^{-2}·h^{-1}, and the potential accumulation rates of carbohydrates and proteins per grain values of 0.8 mg·grain^{-1}·d^{-1} and 0.1 mg·grain^{-1}·d^{-1}, respectively at 16°C. Figure 35 shows the correspondence between observed (discrete symbols) and simulated (dotted lines) time courses of grain dry matter yield (GRAINY), grain nitrogen yield (NGRY), total uptake of nitrogen by above-ground parts (TOTNIT), and of green leaf laminar area (LAIL).

Next, the initial conditions of treatments 0+0+0 and 40+40+40 kg N/ha were used in simulation runs, without change in other parameters. Observed

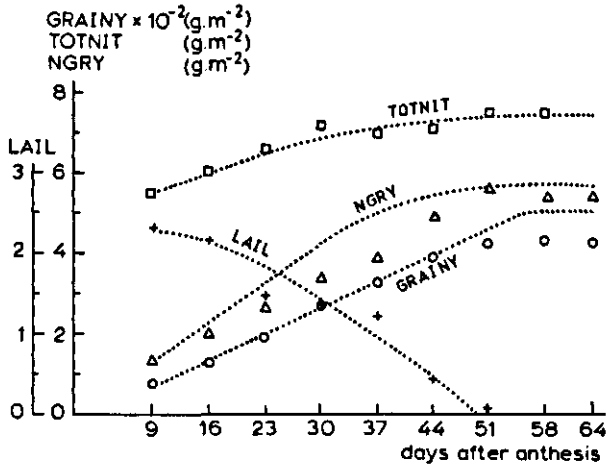

Fig. 36. Observed (□, Δ, 0, +) and simulated (.....) crop performance during the grain-filling stage in winter wheat. Data from treatment 0+0+0 kg N·ha^{-1}, Wageningen, season 1977/1978 (Ellen & Spiertz, 1980). See legend of Fig. 35 for abbreviations and symbols.

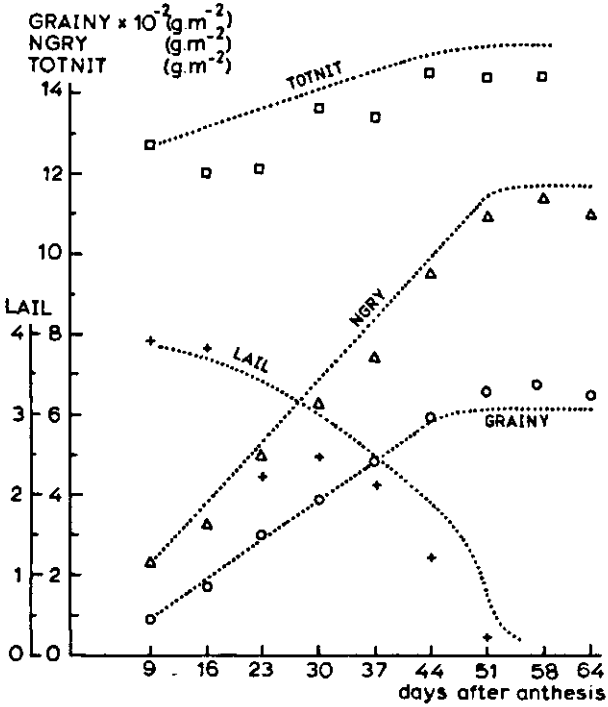

Fig. 37. Observed (□, Δ, 0, +) and simulated (.....) crop performance during the grain-filling stage of winter wheat. Data from treatment 40+40+40 kg N·ha^{-1}, Wageningen, season 1977/1978 (Ellen & Spiertz, 1980). See legend of Fig. 35 for symbols and abbreviations.

and simulated crop performances were in reasonable agreement, as shown by Figs 36 and 37. It is noted that simulated grain dry matter yield exceeded observed yield beyond 50 days after anthesis for the nitrogen treatment 0+0+0 kg·ha^{-1}, whilst the accumulation of protein in grains was also transiently overestimated. In the treatment 40+40+40 kg·ha^{-1}, predicted nitrogen uptake was generally higher than observed values (TOTNIT), but the initial measured nitrogen content of the crop may have been over-estimated, considering the data of subsequent samplings.

Lastly, simulations were undertaken of a spring wheat crop grown at a location in Wageningen in the season 1977. This crop is described in previous chapters under the notation Expt VB. The simulations were begun at 7 days after anthesis. Good agreement between observed and simulated crop performance (Fig. 38) was obtained after adjustment of AMAXI to 2.25 g $CO_2 \cdot m^{-2} \cdot h^{-1}$ and of POTRCH and POTRPR to 0.9 and 0.13 mg·grain^{-1}·d^{-1}, respectively. Fig. 38 also displays the effect of changes in the value inserted for AMAXI. The sensitivity of the model for the values of AMAXI, POTRCH and POTRPR will be discussed later.

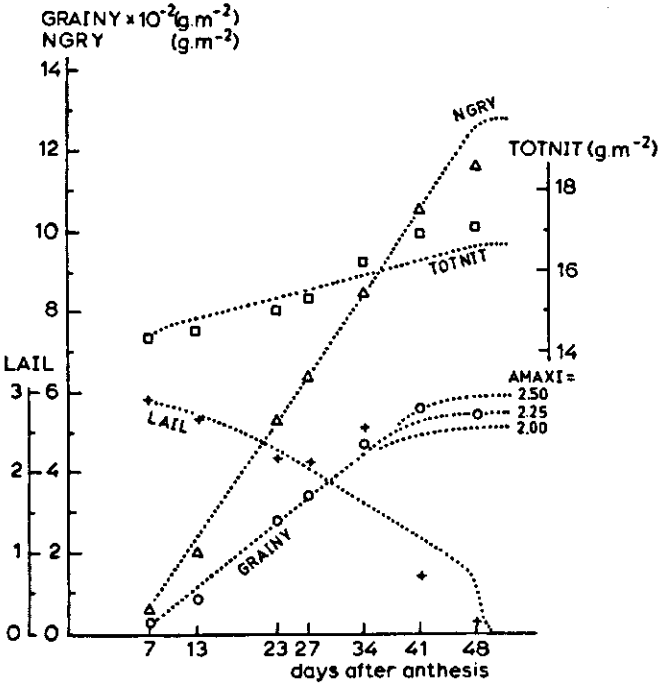

Fig. 38. Observed (□, Δ, 0, +, data from Expt VB) and simulated (.....) crop performance during the grain-filling stage of a spring wheat crop, grown in Wageningen in the season 1977. See legend of Fig. 35 for abbreviations and symbols; AMAXI = initial photosynthetic capacity per unit green area at light saturation (g $CO_2 \cdot m^{-2} \cdot h^{-1}$).

The correspondence between simulated and observed changes in the amount of water-soluble carbohydrates (WSC) is an other suitable feature to test the performance of the model. It can be seen from Fig. 39 that observed and simulated quantities of WSC matched reasonably well for the 1977 spring wheat crop (AMAXI=2.25), except for the last weeks of the grain-filling period. According to model predictions the reserve pool was empty beyond 38 days after anthesis, whilst there was still an appreciable amount of WSC measured at ear maturity in the real crop. Possibly this discrepancy arises from the assumption in the model, that all WSC are readily available for metabolism. In a real plant, however, the situation is presumably more complex, for instance because of spatial separation of sites of 'demand' and of presence of carbohydrates. On the other hand, an underestimation of gross photosynthesis or an overestimation of respiration during the terminal stage of grain filling are also obvious reasons for smaller computed than observed quantities of WSC near maturity.

Carbohydrate analyses were not available from the 1978 winter wheat crops. However, for the nitrogen treatments 0+40+40 $kg \cdot ha^{-1}$ and 40+40+40 $kg \cdot ha^{-1}$ the patterns and the amount of change of the dry weight of stems and leaf sheaths (Ellen & Spiertz, 1980) corresponded reasonably well with the computed change in reserve levels (data not shown). In the nitrogen treatment 0+0+0 $kg \cdot ha^{-1}$, simulated temporarily storage of carbohydrates was somewhat greater than could be inferred from the changes in stem dry weight. This overestimation of carbohydrate accumulation during the first half of the grain-filling stage resulted in the overestimation of grain growth near maturity (Fig. 36).

Apparently the goodness of fit between simulated and observed crop performance depends among other things on the value inserted for the initial photosynthetic capacity, AMAXI, since appropriate values were different for

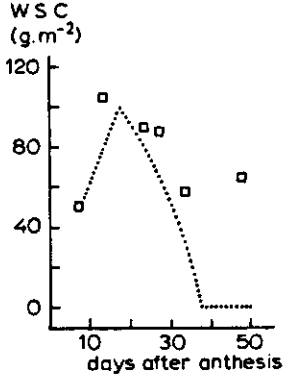

Fig. 39. Observed (□) and simulated (.....) amounts of water-soluble carbohydrates ($g \cdot m^{-2}$) in the 1977 spring wheat crop (Expt VB).

both years. To illustrate the sensitivity of the model for the value assigned to AMAXI, results of runs were incorporated in Fig. 38 with AMAXI equal to 2.0 and 2.5 g $CO_2 \cdot m^{-2} \cdot h^{-1}$, respectively. It appeared that no crop attributes were affected by these changes in AMAXI except the accumulation of carbohydrates in the grains during the last two weeks of the grain-filling period. Altering the value of AMAXI by 10% led to a change in the grain dry matter yield of about 7%.

If in simulations the choice of a value for AMAXI is limited to the range 2.0-2.5 g $CO_2 \cdot m^{-2} \cdot h^{-1}$ model predictions will generally be satisfactory, since the difference between computed grain dry matter yield for these two extreme values for AMAXI hardly exceeds the error of yield measurements. However, the range of possible values for AMAXI seems to be wider, as a value of 1.5 g $CO_2 \cdot m^{-2} \cdot h^{-1}$ was appropriate for the 1978 winter wheat crops. This figure led to an unacceptable underestimation of grain dry matter yield by 23%, when applied in a simulation of the 1977 spring wheat crop (data not shown).

The difference in appropriate values for AMAXI between the 1977 spring wheat crop and the 1978 winter wheat crops can be made plausible to some extent when the following facts are considered: The fraction leaf blades of the initial crop dry weight was 0.20 in the spring wheat crop and close to 0.15 for all winter wheat crops (with no clear differences in specific leaf area). If typical AMAX values were higher for leaf blades than for other green parts (and if leaf blades intercept on average more radiation per unit area than other green tissue) a higher value for the mean photosynthetic capacity of all green tissue seems not unreasonable for the 1977 crop. Some indication for different AMAX values for different green parts of the wheat plant at anthesis can be derived from the work of Puckridge (1972; see also Austin et al., 1976).

The regression equation relating the number of kernels per square metre to crop dry weight at anthesis gave rise to an accurate assessment of the number of kernels per square meter of all four crops tested (data not shown). The results of simulations apparently depend on the values assigned to the potential accumulation rates of carbohydrates and proteins per grain, as appropriate values differed between the 1977 spring wheat crop and the 1978 winter wheat crops. The values of these parameters are affected by genotype and possibly by environmental factors during the period of formation of generative structures, as shown and discussed in previous chapters. To indicate the sensitivity of the model for the values assigned to the potential accumulation rates per grain of carbohydrates and proteins (POTRCH and POTRPR, respectively) it is noted that an increase in the values of these parameters by 10% led to a decrease in computed grain dry matter yield of about 6%, whilst the decreases in the total amount of nitrogen and grain nitrogen yield were less than 1%. Computed attributes were increased to the same extent when the values of POTRCH and POTRPR were diminished with 10%.

However at mid-kernel filling, grain dry matter and nitrogen yields were higher with higher values of the accumulation rates. Moderate changes in the values assigned to the potential accumulation rates thus primarily affect the pattern of growth, rather than the final result, especially with respect to attributes of the nitrogen economy.

In conclusion it can be stated that the simulation model enabled the carbohydrate and nitrogen economies of several crops to be satisfactorily reproduced. In order to arrive at a good agreement between observed and computed patterns of growth, only three parameters of the model needed adjustment between the two seasons, viz. the (initial) photosynthetic capacity per unit green area at saturating irradiance and the potential accumulation rates per grain for carbohydrates and proteins. Although the latter two parameters are determined to some extent by genotype and pre-floral history, it is felt that for prospective applications the precision of the model would benefit from a more detailed or more reliable treatment of the potential accumulation rates per square metre (as composed of rates per grain times number of grains per square metre). Some refinement in the determination of gross photosynthesis rates seems desirable as well.

5.3 APPLICATIONS OF THE SIMULATION MODEL

5.3.1 Effects of temperature and radiation on grain yield

Grain yield is affected by conditions of temperature and radiation (Chapters 3 and 4). The simulation model was employed to quantify and further illustrate these effects for two crops, of which post-floral performance was simulated well. The first crop selected was a winter wheat crop grown at Wageningen in the season 1977/1978: viz. treatment 0+40+40 kg nitrogen supplied per ha, described by Ellen & Spiertz (1980) (see also Section 5.2). The second reference crop selected was a spring wheat crop grown at Wageningen in 1977; this crop is described in previous chapters as Expt VB. Simulation runs were made supposing that on each day during the grain-filling period mean daily temperature was lower than recorded values by 1°C, equal to recorded values and higher than recorded values by 1°C, 2°C and 3°C. Likewise, the daily quantity of incident photosynthetically active radiation (PhAR) was assumed to have been smaller than recorded values by 100 $J \cdot cm^{-2}$, equal to recorded values, and greater than recorded values by 100, 200 and 300 $J \cdot cm^{-2} \cdot day^{-1}$. Simulations were made for all combinations of the five radiation and temperature 'levels'. The computed grain dry matter yields and the nitrogen concentrations in the grains at maturity are shown for all combinations of temperature and radiation by Figs 40a and 40b, respectively; the winter wheat crop 0+40+40 kg $N \cdot ha^{-1}$ is the reference crop.

Grain yields increased in response to increase in daily radiation and decreased with rise in temperature. Interactions in the statistical sense be-

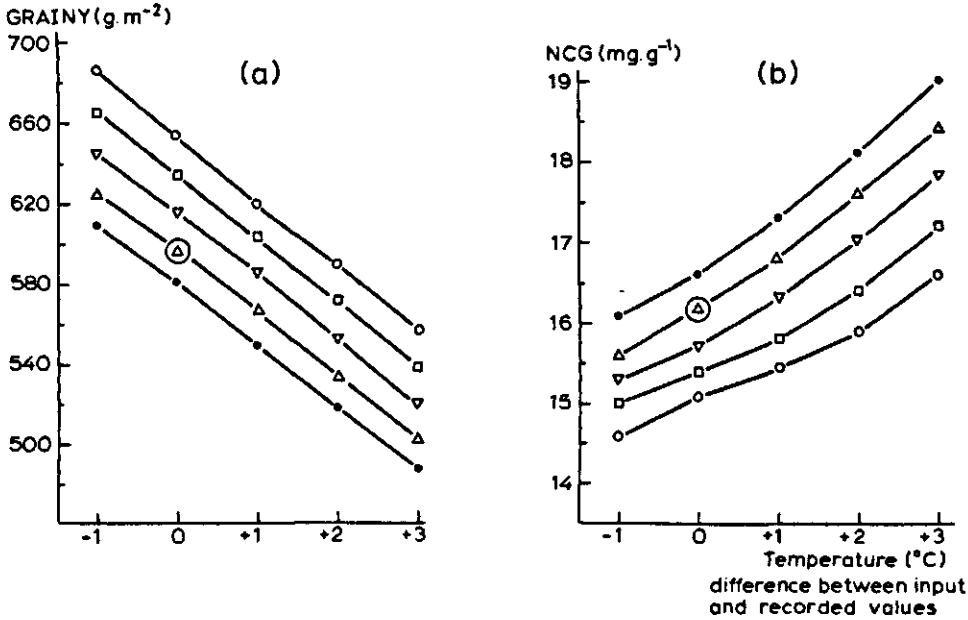

Fig. 40. Computed effects of changes in temperature and radiation on: (a) grain dry-matter yield, GRAINY ($g \cdot m^{-2}$) and (b) nitrogen concentration of grain dry-matter at maturity, NCG, (mg $N \cdot g^{-1}$DM). Crop characteristics at 9 days after anthesis of winter wheat treatment 0+40+40 kg $N \cdot ha^{-1}$ (Ellen & Spiertz, 1980) were used as input plus 1978 records of daily mean temperature and daily radiation totals. Twenty-five simulation runs were made in which daily temperature and radiation inputs were altered as follows: mean daily temperatures were assumed to be smaller than recorded values by 1°C, equal to recorded values, and greater than recorded values by 1, 2 and 3°C; daily radiation totals were assumed to be smaller than recorded values by 100 $J \cdot cm^{-1} \cdot d^{-1}$ (PhAR) (·), equal to recorded values (Δ), greater than recorded values by 100 $J \cdot cm^{-2} \cdot d^{-1}$ (∇), by 200 $J \cdot cm^{-2} \cdot d^{-1}$ (□) and by 300 $J \cdot cm^{-2} \cdot d^{-1}$ (0). Values for GRAINY and NCG for actually recorded temperatures and radiation are encircled.

tween 'levels' of radiation and temperature were absent. At each 'level' of radiation the average yield reduction per degree centigrade rise in temperature was 30 $g \cdot m^{-2}$. Simulations with the 1977 spring wheat crop as a reference crop revealed a yield reduction per degree rise in mean daily temperature of 35 $g \cdot m^{-2}$ when daily PhAR would have been smaller than actually recorded values by 100 $J \cdot cm^{-2}$, and 42 $g \cdot m^{-2}$ when 300 $J \cdot cm^{-2}$ was added to each recorded value for the daily radiation total. These figures compare favourably with results of the phytotron experiments II and IV of the present series: yield reduction per degree rise in temperature amounted to between 35 and 45 $g \cdot m^{-2}$ in Expt II (treatments grown at 15°C, 20°C and 25°C during

grain filling) and to 20 $g \cdot m^{-2}$ in Expt IV (treatments at 16°C and 22°C). Expressed as a percentage, grain yield can be expected to drop by 4-8% per degree rise in temperature if radiation remains unaltered.

Increase in radiation counteracted the adverse effect of rise in temperature on grain yield. In order to maintain a certain yield level, an increase in daily PhAR by 150-180 $J \cdot cm^{-2}$ would seem to be required per degree centigrade rise in temperature for the 1978 winter wheat crop (Fig. 40a). The corresponding figure for the 1977 spring wheat crop is 125-135 $J \cdot cm^{-2} \cdot d^{-1}$. At each temperature 'level' final grain yield of the winter wheat crop increased by about 18 $g \cdot m^{-2}$ per 100 $J \cdot cm^{-2} \cdot d^{-1}$ additional PhAR; for the spring wheat crop the increase was 28 $g \cdot m^{-2}$. It is worthwhile noting that the higher yields with more radiation were achieved during the last weeks of grain filling. During that stage, crops ran earlier out of carbohydrates the lower the radiation 'level'. The behaviour of the model in response to change in daily radiation totals was in fact similar to its behaviour in response to change in the value inserted for the photosynthetic capacity (Fig. 38).

Effects of changes in temperature and radiation on the nitrogen economy were very small. Simulated values for grain nitrogen yield, NGRY, and the total amount of nitrogen in the shoot at maturity, TOTNIT, declined somewhat in response to increase in temperature for the 1978 winter wheat reference crop. Changes in radiation did not affect TOTNIT at all, whilst NGRY was slightly enhanced by radiation at the lowest temperature 'level'. Consequently, values for the harvest index for nitrogen, HIN, were rather stable. The smallest and greatest values of the array of 25 combinations of temperature and radiation conditions were: 12.37 and 12.91 g $N \cdot m^{-2}$ respectively for TOTNIT, 9.27 and 10.05 g $N \cdot m^{-2}$ for NGRY, and 0.779 and 0.749 for HIN. Since NGRY was hardly affected by changes in temperature and radiation the variation in the concentration of nitrogen grains at maturity, shown in Fig. 40b, was mainly brought about by the effects of these environmental factors on carbohydrate accumulation in the grains. Simulated responses of the nitrogen regime of the 1977 spring wheat crop to changes in temperature and radiation were basically similar to, but even smaller than, those described for the 1978 winter wheat crop.

In order to underline the computed effects of temperature and radiation on grain yield it is noted that simulations with fixed temperatures (ranging between 13°C and 21°C) in combination with fixed radiation levels (650-1050 $J \cdot cm^{-2} \cdot d^{-1}$ PhAR) gave similar values for the yield reduction per degree centigrade rise in temperature and for the amount of extra radiation required to compensate for the adverse effects of rise in temperature. Lastly, it is interesting to note that a picture essentially similar to Fig. 40a can be constructed from the data of Spiertz (1977, Table 3) on the effects of temperature and radiation on final grain yield per ear.

5.3.2 Effects of the nitrogen content at the beginning of grain filling on post-floral growth

Simulation runs were made to study the effects on crop performance of varying the amount of nitrogen present in the shoot at the beginning of grain filling. Crop characteristics of nitrogen treatment 0+40+40 kg·ha^{-1} (Ellen & Spiertz, 1980) at 9 days after anthesis were given as input plus recorded conditions of temperature and radiation in 1978. However the amount of nitrogen present in ear structures (chaff and rachis), leaf blades and stems and sheaths at the beginning of grain filling (=NCNTI) was varied, covering the range 6.6 to 15.6 g N·m^{-2}. The value of NCNTI for the reference crop was 8.6 g N·m^{-2}. The amount of dry matter initially present was not varied and thus the weighted mean initial nitrogen concentration in the dry matter of shoot organs (=NCSI) varied between 7.3 and 17.4 mg·g^{-1}.

Computed effects on crop performance are summarized by Fig. 41, showing grain dry matter yield (GRAINY), the final concentration of nitrogen in the grains (NCG), the harvest index for nitrogen (HIN) and the total amount of nitrogen in the shoot at maturity (including grains) (TOTNIT) as functions of NCNTI and NCSI. At small values for NCNTI grain yield responded markedly to additional nitrogen. As initial amounts of nitrogen were higher grain yield increased about proportionally: between 8.6 and 12.6 g N·m^{-2} grain yield increased by about 22 g·m^{-2} per unit additional initial nitrogen. At very high values of NCNTI the response levelled off. Grain yield of this particular reference crop might have been higher by one tonne per ha if its initial nitrogen content would have been twice the value actually measured. Yield advantage due to more nitrogen was achieved during the last week of the grain-filling period and was the result of delayed leaf senescence.

The nitrogen concentration in the grains at maturity was more or less curvilinearly related to the initial nitrogen content of the shoot. The total amount of nitrogen taken up by the above-ground crop at maturity, TOTNIT, was fairly directly related to the initial amount of nitrogen. The simulated value for the amount of nitrogen taken up after anthesis was 3.38 g N·m^{-2} for NCNTI equal to 6.6 g·m^{-2}; this figure increased to 4.86 for NCNTI equal to 12.6 g N·m^{-2} and declined at still higher initial nitrogen contents.

The computed total amount of residual nitrogen in ear structures, leaf blades, and stems and sheaths increased with more initial nitrogen. At nitrogen levels of 6.6 g·m^{-2} the amount of residual nitrogen was 2.86 g·m^{-2}; this figure increased to 3.20 g·m^{-2} for NCNTI equal to 10.6 g·m^{-2}, and rose rapidly with more initial nitrogen, attaining a value of 5.21 g·m^{-2} for NCNTI equal to 15.6 g·m^{-2}.

The harvest index for nitrogen was parabolically related to the initial amount of nitrogen. For small NCNTI the harvest index increased because grain nitrogen yield rose more than the amount of residual nitrogen in non-

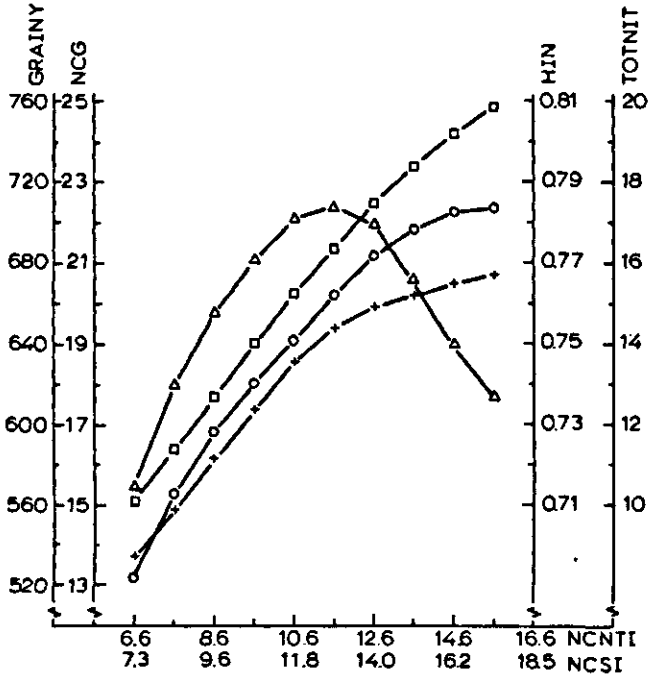

Fig. 41. Computed effects of the initial amount and concentration of nitrogen in the shoots at the beginning of grain filling (NCNTI in g $N \cdot m^{-2}$ and NSCI in mg $N \cdot g^{-1}DM$, respectively) on: grain dry matter yield, GRAINY (0, $g \cdot m^{-2}$), the nitrogen concentration in grain dry matter at maturity, NCG (+, mg $N \cdot g^{-1}DM$), the harvest index for nitrogen, HIN (Δ), and the amount of N present in the shoot at maturity, TOTNIT (□, g $N \cdot m^{-2}$). Initial crop dry weight and weather data (treatment 0+40+40 kg $N \cdot ha^{-1}$, season 1977/1978, Wageningen; data from Ellen & Spiertz, 1980) remained constant in all simulation runs.

grain shoot organs at maturity. As the initial amount of nitrogen further increased, this situation reversed, leading to a decline in HIN above 11.6 $g \cdot m^{-2}$ initial nitrogen.

5.3.3 Growth efficiency for absorbed radiation

In a third application the simulation model was employed to calculate the growth efficiency for adsorbed photosynthetically active radiation (PhAR). The method, described by Gallagher & Biscoe (1978) was used to derive the required values. These authors derived absorbed PhAR from incident PhAR by multiplication with a reduction coefficient (FP) related to the total green area index (LAI):

$$FP = (1-EXP(0.9\times k\times LAI))/1.11$$

where k is an extinction coefficient equal to 0.44 for temperate cereals. For wheat and barley these workers reported a typical value of 3 gram dry matter produced per megaJoule absorbed PhAR during the period between seedling emergence and ear emergence. Averaged over the whole growing season (thus including the post-floral stage) this figure dropped to values of about 2.2 g $DM \cdot MJ^{-1}$.

For the 1978 winter wheat crop (treatment 0+40+40 kg $N \cdot ha^{-1}$, Ellen & Spiertz, 1980) and for the 1977 spring wheat crop (Expt VB of the present series) growth efficiency for absorbed radiation ranged between 1.8 and 3.0 g $DM \cdot MJ^{-1}$ during most of the grain-filling period when computed on a daily basis. Averaged over the whole grain-filling period 1.50 and 1.75 g $DM \cdot MJ^{-1}$ absorbed PhAR were produced by the winter wheat crop and the spring wheat crop, respectively. It should be remembered that these figures also apply to the actual crops, since observed and simulated patterns of growth matched well. With both reference crops, growth efficiency for absorbed radiation decreased somewhat at increasing 'levels' of radiation and temperature (Subsection 5.3.2). Growth efficiencies for absorbed PhAR between about 1.4 and 1.9 g $DM \cdot MJ^{-1}$ for the grain-filling stage alone are not unlikely, considering the figures quoted from Gallagher & Biscoe (1978).

Summary

Effects of temperature and of nitrogen supply on post-floral growth of wheat (*Triticum aestivum* L.) were studied in a series of experiments. Different temperature treatments were applied in three experiments from one week after anthesis onwards. In two of these experiments, plants were grown on nutrient culture (hydroponics) in a phytotron. In a third experiment with temperature treatments plants were raised in pots in a greenhouse; three levels of nitrogen supply were imposed in this experiment. In two other experiments on variation in nitrogen supply, plants were also grown in pots; in one experiment pots were placed outdoors, while the other experiment was conducted under controlled environmental conditions in a phytotron. Variations in nitrogen dressings were started at growth stages Feekes 6 to 7. One experiment consisted of observations in a field crop under normal agricultural management.

Observations included analyses of growth and recordings of respiration rates per organ and of apparent photosynthesis per plant. Furthermore, the mass fractions of total nitrogen, water-soluble carbohydrates, starch (grains only), and cell wall constituents were determined.

Temperature enhanced the transition from the lag stage to the linear stage of grain growth. The grain growth rate during the linear stage was generally enhanced by higher temperature, but warmth shortened the duration of the grain-filling period. Analyses of the present data and that of the literature revealed a continuous decline in Q_{10} for potential grain growth rate during the linear stage against increase in temperature. Computations with data from various sources indicated that the impact of temperature on the duration of the grain-filling period in cereals can be approximated by both a log-linear relationship between duration and temperature and by a heat sum above a minimum temperature. In two of the three experiments grain nitrogen yield was similar between temperature treatments. This implies that in these cases the shorter duration of deposition of grain proteins was fully compensated by a faster rate at higher temperatures. In the other experiment, grain nitrogen yield decreased for an increase in temperature.

In two of the three experiments variation in nitrogen dressings did not lead to differences at anthesis in dry weight per plant, and it gave only small yield differences. The nitrogen contents of vegetative organs and leaf area durations increased with increase of nitrogen in dressings. In the third experiment, dry weights per organ, as well as nitrogen contents and final yield, were higher for higher nitrogen dressing rates. Nitrogen treatments did not affect the duration of grain filling.

Temperature drastically influenced the carbohydrate economy. Water-soluble carbohydrates (WSC) did not accumulate in stems at high temperatures, or they metabolized rapidly if present in plants subjected to higher temperatures. There was a tendency towards higher WSC concentrations at lower levels of nitrogen nutrition. As the experiments progressed, WSC accumulated in roots, especially in nutrient culture experiments; in an extreme case the WSC content amounted to 380 $mg \cdot g^{-1}$ root dry matter at ear maturity.

The relative contribution of component shoot parts to the total amount of nitrogen removed from the shoot during the grain-filling period was predetermined by the initial distribution of nitrogen over these organs at anthesis. Post-floral uptake of nitrogen tended to be greater in crops with a smaller weighted-mean concentration of nitrogen in shoot dry matter at anthesis.

Shoot dry matter at anthesis was distributed in fairly fixed proportions over ear structures (chaff and rachis), leaf blades, and stems and sheaths. Regression equations on plant attributes, measured around anthesis, were calculated from data of experiments conducted at the Rothamsted Experimental Station Harpenden. Analyses of these and other data revealed a rather strong association between the number of grains per square metre and the aeric mass of the vegetation. Furthermore, grain yield was associated with the dry weight of the crop at anthesis and with the number of grains per square metre.

Respiration rates per organ (ears, leaf blades, stems and leaf sheaths, and roots) followed distinct patterns of change in time. Leaf blade respiration was closely associated with green area. Averaged over all observations, leaf blade respiration was 68 mg $CO_2 \cdot m^{-2}$ green area$\cdot h^{-1}$ at 16°C. During most of the grain-filling period respiration rates of stems and sheaths were rather stable and amounted to 0.47 mg $CO_2 \cdot g^{-1}$(DM-WSC)$\cdot h^{-1}$ at 16°C when averaged over all observations. Shortly after anthesis, root respiration rates for pot-grown plants amounted to 1.16 mg $CO_2 \cdot g^{-1}$DM$\cdot h^{-1}$ at 16°C. Specific root respiration rates were about twice as high in plants grown on nutrient culture (hydroponics). Ear respiration rate was linearly related to ear growth rate: each additional gram of grain dry matter produced involved the release of 0.24 gram carbon dioxide. Related to ear dry weight at the beginning of grain filling, maintenance respiration of ears amounted to 10-19 mg $CO_2 \cdot g^{-1}$ initial DM$\cdot d^{-1}$; this figure held for most of the grain-filling period, except shortly after anthesis when rates were about twice as high.

The temperature coefficient for respiration, Q_{10}, was about 2.2 on the short term, and tended to drop to about 1.4 on the long term when calculated between treatments at different, but constant temperature. In those experiments where variation in nitrogen supply had no impact on dry weight and green area per plant at anthesis, total plant respiration rates started to diverge when nitrogen treatments began to affect the amount of green leaf area.

Comparisons were made between observed respiration rates and rates calculated by applying the respiration coefficients for various processes estimated from biochemical data by Penning de Vries and others (Penning de Vries et al., 1974; Penning de Vries, 1975a,b; de Wit et al., 1978). Observed and calculated growth respiration rates of ears matched closely. In non-growing vegetative organs, the ratios between observed and calculated respiration (predominantly due to transport and maintenance) ranged from 1.3 to 1.0 for leaf blades, from 6 to 3 for roots, and were rather consistently 2 for stems and sheaths.

Apparent photosynthesis was not clearly affected by rise in temperature in the range 15-22°C. Differences between temperature treatments in apparent photosynthesis, which emerged in the long term, were attributable to treatment effects on the rate of leaf senescence. Nitrogen effects on photosynthesis per plant were due to treatment effects on foliar senescence.

A dynamic simulation model was constructed of the grain-filling phase of wheat. The model describes and interrelates gross photosynthesis, respiration, the accumulation of carbohydrates and proteins in the grains, redistribution and additional uptake of nitrogen, and leaf senescence, all of which depend on the state of the crop at anthesis and conditions of radiation and temperature afterwards. The model was able to reproduce satisfactorily attributes of post-floral growth of the four crops tested. The sensitivity of the model for the values of some parameters is discussed. Under otherwise similar conditions, grain dry-matter yield was predicted to be smaller by 30-40 $g \cdot m^{-2}$ per degree centigrade rise in temperature during the grain-filling period. A concomitant increase in radiation by 130-180 $J \cdot cm^{-2} \cdot d^{-1}$ (PhAR) could nullify this adverse effect of temperature. Model calculations showed little effects of changes in temperature and radiation on grain nitrogen yield. A saturation type of response curve was predicted for grain dry-matter yield and for final grain nitrogen concentration versus initial nitrogen content of the crop at anthesis.

Samenvatting

Deze studie behandelt de effecten van de temperatuur en van stikstofvoorziening op de groei van tarwe (*Triticum aestivum* L.) na de bloei. In drie proeven werden verschillende temperaturen ingesteld vanaf een week na de bloei. In twee van deze proeven werden de planten in een fytotron gekweekt op voedingsoplossing. Bij een derde proef met variatie in temperatuur werden de planten in potten in een kas gekweekt; in deze proef werden eveneens drie niveaus van stikstofbemesting aangebracht. Bij twee andere proeven met variatie in stikstofvoorziening werden de planten eveneens in potten gekweekt; bij de ene proef werden de potten buiten opgesteld, bij de andere in een fytotron. In de laatstgenoemde proef werden tijdens de korrelvullingsperiode gedurende korte periodes variaties aangebracht in de temperatuur en in het lichtniveau. In alle proeven met verschillen in de stikstofbemesting werden de behandelingen begonnen bij groeistadium Feekes 6 tot 7. Eén proef bestond uit het verrichten van waarnemingen in een veldgewas met een gangbare teeltverzorging.

Met regelmatige tijdsintervallen werden gewasanalyses uitgevoerd, met name bepalingen van vers- en drooggewicht per orgaan en van het groene bladoppervlak. Ook werden ademhalingssnelheden per orgaan en netto fotosynthesesnelheden per plant gemeten. Daarnaast werden de concentraties in de droge stof bepaald van totaal-stikstof, wateroplosbare koolhydraten, zetmeel (alleen in korrelmateriaal) en van celwandbestanddelen.

De overgang van de aanloopfase met geringe korrelgroeisnelheid naar de fase met nagenoeg constante korrelgroeisnelheid (de lineaire fase) vond bij hogere temperaturen vervroegd plaats. De korrelgroeisnelheid gedurende de lineaire fase was in het algemeen groter bij hogere temperatuur, terwijl warmte de lengte van de korrelvullingsperiode bekortte. Uit analyses van de huidige gegevens en van literatuurgegevens bleek, dat de temperatuursversnelling van de hoogst bereikbare korrelgroeisnelheid voortdurend afneemt bij stijging van temperatuur. Uit berekeningen met gegevens van verscheidene auteurs bleek tevens, dat bij granen het temperatuurseffect op de duur van de korrelvullingsperiode beschreven kan worden door een log-lineair verband tussen de duur en de temperatuur alsook door een warmtesom boven een minimumtemperatuur.

In twee van de drie proeven met verschillende temperatuursbehandelingen werd de eindopbrengst aan stikstof in de korrels niet door de temperatuur beïnvloed; dit houdt in, dat in deze proeven bij hogere temperatuur het nadelige effect van een kortere groeiduur op de stikstofopbrengst werd goedgemaakt door een hogere snelheid van stikstofophoping in de korrels. Echter,

in een derde proef nam de stikstofopbrengst in de korrels af naarmate de temperatuur hoger was.

In twee van de drie proeven met verschil in stikstofbemesting leidden deze behandelingen niet tot verschillen in drooggewicht per plant bij de bloei en tot slechts geringe verschillen in opbrengst, terwijl de stikstofinhoud van de plant en het produkt van groen oppervlak en tijd groter waren bij hogere stikstofgift. In een derde experiment met stikstoftrappen waren echter bij de bloei en ook later de drooggewichten van de diverse organen zwaarder en waren hun stikstofinhouden en de opbrengst groter bij meer stikstof. Verschillen in stikstofbemesting hadden geen invloed op de duur van de korrelvullingsperiode.

De koolhydraathuishouding werd drastisch door de temperatuur beïnvloed bij alle proeven met variatie in temperatuur. Bij hogere temperatuur vond geen ophoping plaats van in water oplosbare koolhydraten (WOK), terwijl de op het moment van verhoging van de temperatuur eventueel reeds aanwezige koolhydraten met grote snelheid werden verbruikt.

Bij proeven met verschillende stikstofgift was er een tendens waarneembaar naar hogere WOK-concentraties bij lagere stikstofgift. Naarmate planten ouder werden namen de WOK-concentraties in de wortels toe, vooral bij planten die op een waterculture gekweekt werden. De hoogste waarde bedroeg 380 mg WOK per g droogwortelgewicht bij rijpheid van de plant.

Van de stikstof, die bij rijpheid in de bovengrondse delen werd aangetroffen, was reeds 60 tot 85% in de plant aanwezig bij de bloei. De stikstofopname van de plant na de bloei bleek relatief groter te zijn naarmate de gewogen gemiddelde stikstofconcentratie in de droge-stof van de halm bij de bloei lager was. Van alle stikstof in de bovengrondse delen bevond zich bij rijpheid 60 tot 80% in de korrels. Gedurende de korrelvullingsfase vond er dus in belangrijke mate herverdeling van stikstof plaats. De relatieve bijdrage die de samenstellende delen van de halm (kaf plus aarspil, bladschijven en stengels plus bladscheden) leverden aan de hoeveelheid stikstof, die uit de halm als totaal naar de korrels werd getransporteerd, bleek numeriek gelijk te zijn aan de relatieve stikstofverdeling over deze organen bij de bloei.

De verdeling van de droge-stof bij de bloei over kaf plus aarspil, bladschijven en stengels plus bladscheden bleek bij de verschillende proeven en behandelingen nagenoeg constant te zijn. De betrekkingen tussen gewichten en andere kenmerken van samenstellende delen van de plant bij de bloei werden berekend uit gegevens van proeven die zijn uitgevoerd op het Rothamsted Experimental Station te Harpenden in Engeland (dr. G.N. Thorne, pers. meded.; zie ook Pearman et al., 1977 en 1978a). Uit analyses van gegevens van verschillende door anderen uitgevoerde proeven bleek een vrij sterke samenhang te bestaan tussen het aantal korrels per m^2 en het drooggewicht van het gewas bij de bloei (in $g \cdot m^2$). De korrelopbrengst bleek in sterke mate samen te hangen met het aantal korrels per m^2; ook waren de kor-

relopbrengst en het drooggewicht van het gewas bij de bloei in vrij sterke mate gecorreleerd. Een en ander leidt tot de slotsom, dat een goede ontwikkeling van het gewas bij de bloei nodig is om hoge opbrengstverwachtingen te rechtvaardigen.

Met regelmatige intervallen werden de ademhalingssnelheden van aren, bladschijven, bladscheden plus stengels en van wortels apart gemeten. In alle organen bleek de verandering van de ademhalingssnelheid in de tijd volgens een vrij vast patroon te verlopen. De ademhaling van bladeren bleek nauw samen te hangen met hun groene oppervlak. Gemiddeld over alle waarnemingen bedroeg de ademhalingssnelheid van bladschijven bij 16°C 68 mg $CO_2 \cdot m^{-2}$ groen oppervlak$\cdot h^{-1}$. Gedurende het grootste deel van de korrelvullingsperiode was de ademhalingssnelheid van stengels plus bladscheden vrij stabiel en bedroeg gemiddeld 0,47 mg $CO_2 \cdot g^{-1}$ DS minus WOK per uur bij 16°C (DS = droge-stof). Kort na de bloei bedroeg de ademhalingssnelheid van wortels van planten die in potten werden gekweekt bij 16°C gemiddeld 1,16 mg $CO_2 \cdot g^{-1}$ DS$\cdot h^{-1}$: bij wortels van planten die op een waterculture werden gekweekt lag dit cijfer ongeveer tweemaal zo hoog. De ademhalingssnelheid van de aar nam toe met zijn groeisnelheid; per gram toename in korrelgewicht ontwijkt er 0,24 g CO_2. Betrokken op het droge aargewicht bij het begin van de korrelvulling bedroeg de onderhoudsademhaling van aren 15-19 mg $CO_2 \cdot g^{-1}$ aanvankelijk drooggewicht per dag. Dit cijfer heeft betrekking op het grootste deel van de korrelvullingsperiode; gedurende een korte periode na de bloei werd een ongeveer tweemaal zo hoge waarde gevonden.

De temperatuurscoëfficiënt van de ademhaling, de Q_{10}, bedroeg gemiddeld 2,2. Bij berekening van de Q_{10} tussen behandelingen met constante, doch verschillende temperatuur, werd op langere termijn in bladeren en stengels plus bladscheden een waarde van 1,4 gevonden. In proeven met verschillende stikstofbemestingen, waar deze behandelingen niet tot verschillen leidden in drooggewicht per plant bij de bloei, werden de verschillen in ademhalingssnelheid van de totale plant pas van betekenis nadat een stikstofeffect op de afstervingssnelheid van de bladeren was opgetreden.

Penning de Vries en medewerkers (Penning de Vries et al., 1974; Penning de Vries, 1975a, b; Penning de Vries & van Laar, 1977; de Wit et al., 1978) maakten berekeningen van de koolzuurontwikkeling die optreedt bij de opbouw, de afbraak en het transport van plantaardige bestanddelen per eenheid van gewicht; ook gaven zij schattingen van coëfficiënten ter berekening van de onderhoudsademhaling van de plant. Met behulp van deze coëfficiënten werden berekeningen gemaakt van de te verwachten ademhalingssnelheden in de huidige proeven. Vergelijkingen met gemeten waarden leerde dat de gemeten- en de berekende groeiademhaling van de aren nauw overeen kwamen. In niet-groeiende vegetatieve organen bewoog het verhoudingsgetal tussen gemeten en berekende ademhalingsnelheid zich tussen 1,3 en 1,0 bij bladschijven en tussen 6 en 3 bij wortels, terwijl de gemeten ademhalingssnelheid van stengels en bladscheden meestal tweemaal zo groot was als de berekende snelheid.

De netto fotosynthesesnelheid per plant werd niet duidelijk beïnvloed door verhoging van de temperatuur in het traject tussen ongeveer 15°C en 22°C. De verschillen in fotosynthesesnelheid, die op den duur optraden tussen planten met verschillend temperatuursregime, konden worden toegeschreven aan het effect van de temperatuur op de bladveroudering. Stikstofeffecten op de fotosynthesesnelheid per plant traden eveneens pas op toen behandelingseffecten op de bladafsterving zichtbaar werden.

Er werd een dynamisch simulatiemodel gemaakt van de korrelvullingsfase van tarwe. Het model beschrijft in hun onderlinge samenhang de bruto fotosynthese, de ademhaling, de ophoping van koolhydraten en van eiwitten in de korrels, de herverdeling en de opname van stikstof en de bladveroudering in afhankelijkheid van de staat van het gewas bij de bloei en van de dagelijkse hoeveelheid straling en de dagelijkse gemiddelde temperatuur daarna. Het model bleek in staat te zijn het groeiverloop gedurende de korrelvullingsfase van vier gewassen, waarvan metingen bekend waren, op bevredigende wijze na te kunnen rekenen. Volgens berekeningen met het model neemt onder overigens gelijke omstandigheden de korrelopbrengst met 30-40 $g \cdot m^{-2}$ af bij stijging van de temperatuur met 1°C gedurende de korrelvullingsfase. Dit nadelige effect van de temperatuur kan worden opgeheven wanneer tegelijkertijd de fotosynthetisch actieve straling met 130-180 $J \cdot cm^{-2} \cdot d^{-1}$ toeneemt. Volgens modelberekeningen wordt de stikstofopbrengst van de korrels weinig beïnvloed door schommelingen in temperatuur en straling. Onder overigens gelijke omstandigheden neemt de berekende korrelopbrengst eerst evenredig toe bij toename van de stikstofconcentratie in de plant bij de bloei, doch bij hoge aanvankelijke stikstofconcentratie neemt de berekende respons van de korrelopbrengst sterk af; eenzelfde afnemende respons werd berekend voor de stikstofconcentratie in de korrels bij rijpheid.

Appendix A, Expt II. Dry weights (DM), amounts of nitrogen (N), water-soluble carbohydrates (WSC) and starch in mg per organ.

Experiment and treatment	Days after anthesis	Grains								Chaff and rachis					
		Main culm				Side tiller				Main culm			Side tiller		
		DM	N	WSC	starch	DM	N	WSC	starch	DM	N	WSC	DM	N	WSC
II 15	-3[a]	530	10.28	72.6		340	7.99	58.5							
	4[a]	760	9.89	115.2		510	10.81	55.1							
	10	280	7.78	127.7	36	160	4.48	77.9	15	610	9.85	79	610	11.44	71
	18	660	15.84	178.2	225	340	8.91	128.7	73	640	9.78	94	570	11.03	106
	26	1515	33.84	170.4	760	964	22.08	167.1	419	640	7.09	40	640	8.35	62
	38	2180	45.34	106.8	1241	1770	35.75	102.1	983	620	6.17	31	610	6.53	35
	53	2560	56.03	104.2	1648	2350	55.93	99.9	1471	620	3.91	15	590	4.49	17
	68	2760	65.09	102.1	1650	2560	57.60	92.2	1627	610	3.93	13	620	3.85	14
II 20	11	330	9.11	131.3	62	180	4.88	78.2	26	550	8.08	65	530	9.26	61
	17	835	20.92	94.8	394	530	13.62	98.2	196	520	6.74	35	420	7.83	40
	25	1435	30.14	81.8	759	1160	27.49	67.3	591	530	5.92	23	530	6.37	26
	37	1950	53.82	113.1	997	1850	47.55	119.7	986	570	4.65	21	590	5.19	24
	47	2010	56.05	182.1	866	1850	53.28	141.0	894	550	4.39	18	520	4.45	17
II 25	12	420	12.81	99.3	143	220	7.11	67.5	54	560	8.02	47	670	12.21	97
	16	860	18.85	68.6	419	507	14.30	59.2	230	570	8.06	36	630	10.86	50
	19	1110	30.30	63.5	562	850	23.80	47.9	414	560	6.67	26	550	7.52	25
	24	1410	40.20	66.3	725	1131	30.70	52.0	667	590	6.79	21	490	6.22	21
	33	1580	48.66	116.1	717	1400	43.26	118.4	637	490	4.61	16	590	5.19	24

Appendix A, Expt II continued.

Experiment and treatment	Days after anthesis	Leaf blades						Stem and sheaths						Root		
		Main culm			Side tiller			Main culm			Side tiller					
		DM	N	WSC	DM	N	WSC	DM	N	WSC	DM	N	WSC	DM	N	WSC
II 15	-3	800	30.92	58	580	24.07	46	1770	34.59	84	1310	28.68	59	800	31.20	19
	4	840	31.23	63	630	25.20	52	2090	35.36	212	1830	34.59	161	980	36.46	16
	10	810	30.50	59	610	24.10	48	2440	41.64	433	2000	35.40	282	900	33.51	18
	18	810	27.21	69	610	22.20	55	2330	37.42	385	1880	30.64	312	950	28.79	17
	26	740	21.44	49	550	17.55	38	2370	31.60	356	1870	26.18	271	920	27.60	19
	38	770	20.47	69	600	17.82	58	2260	28.51	296	1830	23.42	254	890	22.25	17
	53	700	16.11	68	550	13.86	61	2290	20.72	396	1900	16.53	330	970	20.10	62
	68	760	11.59	50	560	9.07	67	2330	15.18	406	1930	12.35	387	1080	16.35	181
II 20	11	810	30.53	45	710	29.61	41	2180	39.79	318	1770	31.33	290	860	29.98	15
	17	760	25.62	45	580	20.79	35	2070	33.82	230	1660	27.89	163	870	29.23	13
	25	710	19.64	41	690	21.60	39	1920	25.50	121	1610	22.40	109	950	26.45	19
	37	780	19.53	60	580	15.72	52	2030	24.75	168	1710	19.67	148	950	23.87	36
	47	790	17.77	70	600	14.58	68	2220	20.78	300	1870	16.47	277	1060	26.12	143
II 25	12	770	26.42	43	600	22.80	33	2270	38.92	272	1920	34.18	206	940	30.73	15
	16	740	24.64	40	580	20.65	30	2160	34.91	195	1760	29.04	141	930	32.89	16
	19	770	22.97	41	570	19.27	28	2100	31.93	112	1710	26.16	82	820	24.52	12
	24	710	20.15	38	530	15.53	21	2000	26.75	90	1640	22.14	75	990	27.72	18
	33	770	17.23	64	600	14.70	70	1970	21.13	106	1640	18.20	104	840	21.84	38

a. complete ear

Appendix A, Expt III. Dry weights (DM), amounts of nitrogen (N), water-soluble carbohydrates (WSC) and starch in mg per organ.

Experiment and treatment	Days after anthesis	Grains				Chaff and rachis			Leaf blades			Stems and sheaths			Roots			Side tillers cumulative	
		DM	N	WSC	starch	DM	N	WSC	DM	N	WSC	DM	N	WSC	DM	N	WSC	DM	N
III N1-16	-3[a]	361	9.06	40					658	21.83	24	1366	19.85	117	781	11.24	23		
	3[a]	420	9.62	44					579?	19.91	24	1502	18.43	202	828	10.67	42		
	9[a]	612	13.04	132					676	19.03	41	1809	17.99	443	1063	12.28	59		
	16	340	8.57	115	97	500	8.20	50	647	18.44	38	1858	15.70	508	675	6.81	65		
	30	1320	26.53	79	829	470	5.08	30	625	10.80	37	1833	10.82	546	720	6.86	104		
	44	1970	41.37	120	1238	430	3.53	16	545	5.05	17	1573	7.50	177	670	6.48	96		
	64	2120	43.88	199	1229	440	2.38	19	538	4.44	16	1374	5.22	107	592	6.10	58		
III N2-16	-3[a]	342	9.30	42					633	25.91	15	1196	27.31	28	689	15.03	14		
	3[a]	381	9.22	35					588	23.20	18	1278	27.78	60	659	14.35	14		
	9[a]	564	12.58	114					722	27.06	23	1499	28.22	180	871	17.02	14	88	3.38
	16	370	9.66	107	113	450	7.88	39	657	23.70	15	1430	22.86	186	674	12.29	17	210	7.88
	30	1240	28.64	82	734	440	6.03	23	647	19.93	30	1489	17.05	289	643	9.64	39	350	11.20
	44	2075	49.59	95	1281	320	3.07	11	626	13.02	39	1618	11.75	182	793	8.59	98	420	12.60
	64	2390	51.15	196	1369	480	4.51	15	544	4.87	15	1455	7.95	223	631	7.12	98	420	12.60
III N3-16	-3[a]	352	9.33	35					609	25.54	13	1169	30.12	21	758	17.51	11		
	3[a]	412	8.94	38					636	24.80	22	1311	29.02	66	774	16.94	16		
	9[a]	568	13.29	114					702	28.06	28	1508	32.12	149	981	19.74	15	113	4.58
	16	330	8.81	98	108	480	9.26	52	666	25.20	39	1412	26.99	167	705	13.46	11	310	12.62
	30	1190	28.32	74	698	430	6.97	19	685	23.33	32	1334	21.02	127	590	10.60	13	587	17.49
	44	1910	47.37	82	1155	440	4.75	16	630	16.14	31	1320	16.04	96	681	10.54	26	746	27.01
	64	2230	49.28	124	1275	470	4.79	19	589	9.38	35	1420	10.93	210	661	9.50	69	949	30.65

a. complete ear

Appendix A, Expt III continued

Experiment and treatment	Days after anthesis	Grains				Chaff and rachis			Leaf blades			Stems and sheaths			Roots			Side tillers cumulative	
		DM	N	WSC	starch	DM	N	WSC	DM	N	WSC	DM	N	WSC	DM	N	WSC	DM	N
III N1-22	10	130	3.74	54	23	530	10.28	67	663	18.68	29	1811	16.01	441	1102	11.73	87		
	17	630	14.99	55	336	440	6.29	31	643	16.67	28	1644	12.75	367	614	6.77	43		
	31	1530	34.27	97	915	430	3.57	13	604	8.34	27	1492	7.70	208	597	6.23	59		
	38	1660	43.99	128	958	410	3.44	9	507	4.38	13	1295	6.43	103	588	5.91	59		
	45	1740	46.11	98	1003	430	3.53	11	569	4.80	14	1341	6.44	43	560	5.83	41		
	65	1690	45.93	126	956	420	2.86	9	484	4.02	13	1329	6.70	45	341	4.10	5		
III N2-22	10[a]	674	14.56	142					672	25.86	30	1550	27.37	185	974	17.24	20	130	4.84
	17	540	14.63	50	277	420	6.93	21	630	22.42	36	1316	23.33	92	558	9.17	12	260	9.72
	31	1400	39.34	62	843	420	4.91	10	661	19.00	27	1322	14.75	71	562	8.87	22	296	10.48
	38	1750	52.50	93	970	440	5.06	13	657	16.49	42	1347	12.25	94	645	10.24	38	310	11.01
	45	1730	53.80	84	-	440	5.19	16	584	11.75	41	1423	11.74	136	616	9.53	74	333	11.49
	65	1840	54.28	97	1013	490	5.39	16	605	8.31	28	1353	9.03	32	532	8.54	27	459	17.12
III N3-22	10	130	3.71	55	22	520	10.92	77	672	25.98	33	1414	29.16	122	903	16.45	16	169	6.42
	17	520	14.51	49	264	440	7.48	21	678	25.10	43	1308	26.21	82	566	10.72	9	240	9.91
	31	1350	39.15	63	768	450	5.58	13	680	20.89	24	1264	18.34	52	525	9.43	13	347	13.05
	38	1660	48.64	87	919	450	5.13	14	680	18.16	47	1307	16.31	76	586	11.27	22	405	13.45
	45	1650	50.00	81	914	430	4.99	14	626	16.47	42	1359	13.73	135	729	14.79?	73	405	15.00
	65	1770	51.68	80	965	460	5.75	15	596	10.67	28	1256	9.29	26	505	10.39	11	777	33.88

a: complete ear

Appendix A, Expt IV. Dry weights (DM), amounts of nitrogen (N), water-soluble carbohydrates (WSC) and starch in mg per organ.

Experiment and treatment	Days after anthesis	Grains								Chaff and rachis					
		Main culm				Side tiller				Main culm			Side tiller		
		DM	N	WSC	starch	DM	N	WSC	starch	DM	N	WSC	DM	N	WSC
IV A16	5	90	2.50	29		47	2.00	19		430	6.38	36	385	6.43	34
	10	190	5.00	60		160	4.05	78		480	6.94	45	470	7.43	44
	19	810	15.86	99	472	660	13.79	131	347	490	4.97	39	430	4.95	27
	28	1470	25.40	89	1009	1290	22.45	107	861	480	3.89	21	440	4.00	24
	37	2050	38.34	103	1415	1710	31.29	81	1179	450	3.40	15	420	3.44	19
	46	2360	46.14	154	1585	2170	40.15	132	1350	450	2.42	10	420	2.44	12
	58	2470	53.25	276	1417	2260	48.95	210	1357	470	1.96	8	420	1.68	7
IV B22	9	230	6.35	62		190	5.19	84		470	6.26	36	420	6.47	30
	18	990	20.29	48	602	820	16.81	60	497	470	4.28	20	420	4.58	25
	27	1730	36.86	96	1070	1480	30.78	60	918	440	3.02	16	420	3.96	20
	40	2050	52.02	140	1187	1860	46.87	113	1088	450	2.64	8	410	2.34	8
IV C22	20	890	18.94	98	530	700	14.28	96	402	470	4.37	22	420	4.62	25
	29	1720	33.83	71	1167	1510	29.45	71	1058	480	3.45	13	420	3.61	17
	44	2120	50.53	107	1351	1920	44.16	90	1241	450	2.11	8	410	1.92	7
IV D22	27	1470	27.65	101	960	1190	22.13	80	780	470	3.69	19	420	3.78	23
	37	2110	43.95	99	1462	1940	39.19	96	1317	460	2.73	12	440	3.21	19
	48	2290	52.63	107	1489	2100	46.20	101	1400	460	2.18	7	420	1.97	7

Appendix A, Expt IV continued

Experiment and treatment	Days after anthesis	Leaf blades						Stem and sheaths						Root		
		Main culm			Side tiller			Main culm			Side tiller					
		DM	N	WSC	DM	N	WSC	DM	N	WSC	DM	N	WSC	DM	N	WSC
IV A16	5	670	15.22	39	530	14.34	24	1670	15.57	127	1430	14.02	111	1760	39.05	30
	10	620	15.41	28	580	16.41	24	1770	15.88	219	1550	15.50	197	1980	38.08	54
	19	650	14.22	28	570	15.90	23	1960	14.83	305	1650	13.70	308	1940	36.28	77
	28	660	13.93	44	530	13.14	31	2050	12.71	432	1830	11.16	425	1990	30.25	362
	37	620	10.01	44	520	9.10	38	2120	10.32	609	1800	7.74	510	2280	25.27	595
	46	540	5.79	25	480	5.18	23	1970	7.56	421	1740	6.61	411	2620	24.92	895
	58	570	3.72	12	410	2.83	14	1780	5.68	223	1540	4.62	200	2690	25.02	1020
IV B22	9	640	15.85	25	620	16.93	22	1750	15.32	175	1580	14.69	175	2020	39.46	36
	18	660	14.66	25	600	15.90	21	1810	14.12	177	1530	13.01	161	1860	37.20	30
	27	650	11.36	40	520	11.60	32	1720	9.30	161	1480	9.03	148	1800	26.87	136
	40	560	5.27	22	480	4.70	17	1710	7.51	95	1450	5.22	89	2300	27.87	603
IV C22	20	640	14.47	28	560	15.51	20	1970	15.61	316	1640	13.45	274	1890	36.41	59
	29	570	11.46	32	510	11.78	26	1760	10.79	203	1550	9.61	202	1820	25.89	124
	44	530	3.97	11	430	3.40	10	1630	6.57	64	1440	5.47	62	2080	23.50	446
IV D22	27	630	12.61	37	520	13.00	28	1950	11.83	355	1690	11.15	340	1860	29.07	125
	37	560	7.75	30	550	7.87	35	1900	8.88	301	1650	7.43	292	2140	25.89	404
	48	560	3.85	10	420	2.90	9	1660	5.65	78	1440	5.04	70	2300	23.72	660

Appendix A, Expt. VA. Dry weights (DM), amounts of nitrogen (N), water-soluble carbohydrates (WSC) and starch in mg per organ.

Experiment and treatment	Days after anthesis	Grains				Chaff and rachis			Leaf blades			Stem and sheaths			Root		
		DM	N	WSC	starch	DM	N	WSC	DM	N	WSC	DM	N	WSC	DM	N	WSC
VA N1	1[a]	311	5.56	32					444	15.62	30	1498	17.37	157	462	6.10	8
	8	140	3.33	70	28	343	5.04	32	433	13.25	35	1775	15.86	394	494	5.38	30
	15	447	9.30	102	193	339	4.14	24	429	11.70	37	1807	13.02	476	469	4.91	26
	22	1009	17.25	72	643	357	3.64	21	424	11.05	37	1776	11.35	435	450	4.04	31
	29	1364	22.64	62	930	341	2.93	15	377	8.41	31	1624	10.88	380	409	3.46	45
	36	1684	29.47	51	1141	346	2.84	11	350	4.93	19	1614	8.34	318	429	3.10	43
	46	1879	37.39	62	1259	321	2.05	5	271	3.07	4	1364	6.46	98	298	2.16	20
	53	1914	37.71	74	1248	302	1.90	3	218	2.38	2	1358	5.63	93	346	2.56	27
VA N2	1[a]	314	5.85	32					462	16.32	32	1466	23.21	109	435	8.57	10
	8	118	2.75	60	17	344	5.54	37	470	16.97	31	1745	22.82	299	391	6.88	17
	15	465	9.63	132	188	360	4.90	31	480	15.77	49	1749	19.82	358	399	6.39	14
	22	975	18.43	72	634	357	4.06	23	458	14.60	37	1695	16.54	325	452	6.00	23
	29	1356	23.46	65	896	350	3.61	18	466	14.38	41	1600	16.55	268	352	4.92	22
	36	1627	31.89	70	1085	359	3.23	12	382	9.01	21	1519	13.85	141	330	4.49	13
	46	1948	45.19	64	1249	362	2.75	5	293	3.93	5	1492	10.03	83	282	3.19	12
	53	1862	42.83	54	1179	316	2.40	2	236	3.35	3	1376	10.82	64	250	3.01	11
VA N3	1[a]	326	6.10	39					471	18.05	35	1469	24.22	122	557	10.14	9
	8	129	2.97	65	21	342	5.54	32	483	18.26	29	1678	25,68	225	404	7.72	13
	15	477	10.06	119		355	4.93	28	491	17.57	40	1754	21.93	355	409	7.32	11
	22	981	18.44	69	626	356	4.38	23	470	16.50	33	1687	19.21	270	459	7.63	11
	29	1327	25.35	61	868	330	3.40	15	454	14.66	31	1512	18.45	205	351	5.99	15
	36	1493	30.46	53	967	330	3.14	10	402	10.63	21	1384	16.70	92	340	5.81	11
	46	1936	41.43	66	1250	355	3.34	6	341	6.51	12	1555	14.09	164	323	4.79	23
	53	1851	44.05	42	1156	319	2.78	2	268	4.67	4	1454	13.75	117	276	4.26	22

a. complete ear

Appendix A, Expts VB and VI. Dry weights (DM), amounts of nitrogen (N), water soluble carbohydrates (WSC) and starch in mg per organ.

Experiment and treatment	Days after anthesis	Grains				Chaff and rachis			Leaf blades			Stem and sheaths			Root	
		DM	N	WSC	starch	DM	N	WSC	DM	N	WSC	DM	N	WSC	DM	N
VB	7	44	1.17	22	5	203	3.49	17	272	8.79	11	783	8.76	71		
	13	157	3.76	68	34	249	3.74	24	332	9.71	14	1004	10.01	155		
	23	524	9.93	48	314	248	2.89	13	295	7.80	16	911	7.55	131		
	27	643	12.06	29	413	245	2.53	8	282	7.00	11	891	7.14	139		
	34	870	15.99	36	549	246	2.02	5	274	6.14	11	851	6.36	88		
	41	1045	19.77	40	680	266	1.90	7	259	4.64	11	922	5.44	130		
	48	1016	21.69	38	634	264	2.17	4	227	3.52	4	909	4.58	110		
VI N1	4[a]	376	6.58						552	10.95		1471	14.02		704	7.11
	11	187	4.34			340	4.79		539	11.20		1547	12.15		576	5.76
	18	404	7.76			310	3.72		527	9.61		1558	9.98		537	4.46
	25	737	12.60			338	3.01		515	8.32		1483	10.36		522	5.17
	32	1016	16.97			326	2.64		508	7.64		1443	8.73		499	4.84
	48	1478	29.26			332	1.49		422	3.65		1297	4.62		676	5.27
VI N2	4[a]	451	9.74						644	19.15		1595	25.33		728	11.50
	11	186	4.52			440	6.64		628	17.64		1721	21.62		611	7.94
	18	437	8.57			442	6.06		631	15.41		1689	16.09?		560	8.40
	25	809	15.86			435	4.65		594	14.88		1707	19.25		559	7.43
	32	1178	22.38			423	3.93		591	12.53		1613	17.64		561	6.00
	48	1771	39.14			428	2.74		546	9.48		1560	12.35		789	7.65

a. complete ear

Appendix B. Green leaf areas in $cm^2 . culm^{-1}$ of all experiments and treatments.

Experiment and treatment	Days after anthesis	Main culm	Side tiller	Total plant	Experiment and treatment	Days after anthesis	Main culm	Side tiller	Total plant
II 15	4	143							
	10	128	103	230	IV A16	5	99	86	185
	18	113	77	190		10	105	93	198
	26	89	81	170		19	104	93	197
	38	75	61	136		28	93	87	180
	53	76	55	131		37	74	71	146
	68	32	11	43		46	23	20	43
						58	1	1	1
II 20	11	118	91	209					
	17	120	100	220	IV B22	9	105	93	198
	25	92	82	174		18	104	86	190
	37	68	66	134		27	87	78	165
	47	75	63	139		40	16	11	27
II 25	12	110	78	188	IV C22	20	103	78	181
	16	105	97	202		29	84	81	165
	19	87	72	159		44	2	3	5
	24	81	80	161					
	33	64	69	133	IV D22	27	88	89	177
						37	61	61	122
						48	1	1	1

Appendix B, continued

Days after anthesis	Experiment and treatment			Days after anthesis	Experiment and treatment		
	III N1-16	III N2-16	III N3-16		III N1-22	III N2-22	III N3-22
-3	132	147	135				
3	105	116	115				
9	99	115	115	10	93	116	108
16	89	104	105	17	82	102	101
30	51	97	100	31	32	87	95
				38	1	78	81
44	2	64	65	45	0	43	79
64	0	1	33	65	0	0	9

Days after anthesis	Experiment and treatment			Days after anthesis	Experiment VB	Days after anthesis	Experiment VI N1	Experiment VI N2
	VA N1	VA N2	VA N3					
1	122	127	123	7	56	4	62	101
8	117	121	120	13	48	11	59	93
15	98	111	106	23	39	18	57	87
22	91	111	107	27	38	25	40	83
29	70	103	104	34	46?	32	37	66
36	30	63	67	41	13	48	1	39
46	2	3	26	48	2			
53	0	1	4					

Appendix C. Photosynthetic rates measured in Expts II, IV and VA

Experiment and treatment	Days after anthesis	Relative apparent photosynthesis rates	Experiment and treatment	Days after anthesis	Apparent photosynthesis mg CO_2. (plant.h^{-1})	Experiment and treatment	Days after anthesis	Apparent photosynthesis mg CO_2. (plant^{-1}.h^{-1})
II 15	4	100	IV A16	12	16.4?	VA N1	1	9.6
	10			19	19.2		7	10.7
	18	69		24	19.1		14	9.8
	26	58		28	20.4		21	8.4
	38	48		37	13.8		28	7.7
	53	38		41	7.3		35	3.4
	68	0		46	-2.0		42	-0.4
				48	-0.3		49	-2.0
II 20	11	88						
	17	70	IV B22	11	19.7	VA N2	1	9.7
	25	57		18	18.4		7	10.5
	37	42		25	17.3		14	9.0
	47	33		27	15.1		21	9.5
				32	12.6		28	10.1
II 25	12	68					35	4.2
	16	66	IV C22	20	18.5		42	3.6
	19	63		23	16.3		49	-1.7
	24	48		29	16.5			
	33	29		38	2.3	VA N3	1	9.5
							7	10.0
			IV D22	26	19.3		14	9.7
				27	17.1		21	8.2
				33	13.2		28	9.4
				36	8.1		35	5.5
				38	4.7		42	2.8
							49	-0.5

Appendix D. Respiration rates from all experiments and treatments.

Experiment and treatment	Days after anthesis	Respiration rates of separate organs and of total plant (mg $CO_2.h^{-1}$)					
		Ear	Leaf blades	Stem and sheaths	Side tiller	Root	Total plant
II 15	4						8.26
	10	1.17		0.99		1.89	9.52
	18	1.62		1.32		1.07	9.59
	26	1.48		0.87		1.42	7.92
	38	1.17		1.25		0.65	7.96
	53	0.42		0.78		1.58	6.05
	68	0.00		0.95		1.29	4.92
II 20	11	1.73		1.71		1.44	12.88
	17	2.20		0.97		1.53	10.99
	25	1.53		0.86		1.60	9.65
	37	0.66		1.35		0.78	8.29
	47	0.00		0.98		1.82	6.60
II 25	12	2.55		1.81		1.01	15.17
	16	2.46		1.13		1.13	11.70
	19	1.76		1.65		0.84	11.36
	24	1.61		1.17		1.10	8.63
	33	0.35		1.66		0.56	7.58
IV A16	5	0.83	0.81	0.88	2.23	5.10	9.85
	10	0.94	0.69	0.63	2.13	5.11	9.50
	19	1.05	0.61	0.55	2.16	3.99	8.36
	28	0.83	0.51	0.58	2.04	3.16	7.12
	37	0.67	0.43	0.64	1.78	2.87	6.39
	46	0.47	0.25	0.48	1.40	2.29	4.89
	58	0.12	0.07	0.35	0.46	1.97	2.97
IV B22	9	1.60	1.10	1.06	3.41	5.39	12.56
	18	1.28	0.81	0.77	2.86	3.59	9.31
	27	0.92	0.63	0.76	2.38	2.83	7.52
	40	0.01	0.30	0.55	1.00	2.58	4.44
IV C22	20	1.28	0.83	0.82	3.11	3.43	9.47
	29	1.01	0.70	0.84	2.67	2.44	7.66
	44	0.02	0.20	0.51	0.82	1.83	3.38
IV D22	27	1.15	0.66	0.87	2.79	2.94	8.41
	37	0.99	0.66	0.96	2.52	2.59	7.72
	48	0.02	0.10	0.41	0.44	1.91	2.88

Appendix D, continued.

Experiment and treatment	Days after anthesis	Respiration rates per organ and total plant					Experiment and treatment	Days after anthesis	Respiration rates per organd and total plant				
		Ear	Leaf blades	Stem and sheaths	Root	Total plant			Ear	Leaf blades	Stem and sheaths	Root	Total plant
III N1-16	9	0.64	0.71	0.59			III N1-22	10	1.10	0.69	0.95		
	16	1.25	0.63	0.66				17	1.16	0.73	0.65		
	44	0.67	0.11	0.58				38	0.42	0.12	0.62		
	64	0.00	0.00	0.00				45	0.04	0.00	0.22		
III N2-16	9	0.85?	0.70	0.65			III N2-22	10	1.09	0.75	0.95		
	16	1.13	0.74	0.50				17	1.31	0.84	0.73		
	44	0.87	0.36	0.58				38	0.65	0.72	0.95		
	64	0.22	0.09	0.53				45	0.04	0.69	0.81		
								65	0.03	0.07	0.10		
III N3-16	9	0.65	-	0.68			III N3-22	10	1.07	0.88	0.92		
	16	1.06	0.62	0.46				17	1.18	0.77	0.64		
	44	0.90	0.55	0.70				38	0.65	0.74	0.88		
	64	0.16	0.34	0.75				45	0.03	0.69	0.91		
								65	0.00	0.20	0.15		
VA N1	1	0.64	0.81	1.06	0.54	3.04	VB	7	0.49	0.55	0.40		1.43
	8	0.83	0.76	0.72	0.52	2.83		13	0.86	0.42	0.40		1.68
	15	1.12	0.71	0.68	0.43	2.94		20	0.82	0.36	0.31		1.49
	22	1.05	0.58	0.58	0.35	2.56		23	0.75	0.35	0.30		1.41
	29	0.82	0.55	0.71	0.32	2.40		27	0.56	0.31	0.32		1.18
	36	0.74	0.33	0.63	0.28	1.98		34	0.39	0.28	0.30		0.97
	46	0.51	0.16	0.65	0.24	1.56		41	0.44?	0.22	0.31		0.98
VA N2	1	0.67	0.93	1.03	0.48	3.11		48	0.26	0.13	0.31		0.70
	8	0.90	0.73	0.78	0.38	2.79	VI N1	4	0.48	0.35	0.51	0.72	2.06
	15	1.28	0.80	0.72	0.41	3.20		11	0.67	0.31	0.33	0.66	1.97
	22	1.04	0.70	0.71	0.44	2.88		18	0.76	0.32	0.38	0.50	1.95
	29	0.82	0.85	0.74	0.32	2.72		25	0.62	0.26	0.36	0.45	1.70
	36	0.80	0.53	0.68	0.29	2.29		32	0.60	0.26	0.38	0.41	1.65
	46	0.50	0.11	0.56	0.25	1.41		48	0.35	0.05	0.30	0.33	1.03
VA N3	1	0.67	0.88	1.10	0.55	3.20							
	8	0.83	0.72	0.72	0.46	2.73	VI N2	4	0.58	0.51	0.65	0.81	2.55
	15	1.18	0.86	0.72	0.39	3.15		11	0.81	0.58	0.45	0.79	2.63
	22	0.97	0.72	0.61	0.52	2.81		18	0.85	0.51	0.49	0.69	2.55
	29	0.95	0.79	0.84	0.31	2.89		25	0.89	0.47	0.48	0.65	2.49
	36	0.62	0.55	0.66	0.34	2.17		32	0.82	0.39	0.47	0.54	2.22
	46	0.63	0.49	0.82	0.34	2.27		48	0.58	0.28	0.54	0.54	1.94

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