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CONTENTS

PHYSIOLOGICAL ASPECTS OF QUALITY IN WHEAT; A REVIEW

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Introduction

During the last decades grain yields of wheat have increased in all agricultural areas of the world, in the industrialized world at rates of 80 - 150 kg ha^{-1} yr^{-1} and in many developing countries until the late sixties at a much slower rate of 5 - 15 kg ha^{-1} yr^{-1}, but in the last decade at about the same rate as in the industrialized world (de Wit et al., 1979). The yield increase can be attributed partly to genetic improvement in dry matter distribution as was found when ancient and modern wheat varieties were compared (Austin et al., 1980, Vos and Sinke, 1981). The major part of the yield increase, however, is the result of improved crop growth conditions through better water management and higher and more timely nitrogen applications in combination with appropriate pest and disease control (Spiertz and Ellen, 1978). As a result of the combined efforts of various disciplines (agronomy, water management, plant nutrition, plant breeding and crop protection) potential yields are closely approached regularly in various farmer's fields in northwestern Europe. These potential yields are dictated by incoming radiation, prevailing temperatures and the physiological, phenological, geometrical and optical characteristics of the crop, and can be calculated on the basis of those characteristics (de Wit, 1965). They are realised under conditions where growth limiting factors such as water or nutrient deficiency are absent and weeds, pests and diseases do not reduce growth and yield. The largest part of agricultural production (> 90%) takes place under circumstances where during part of the growing season water and nutrients are not optimally available and weeds, pests and diseases interfere. Agronomic measures are meant to eliminate growth-limiting and growth-reducing factors. As the gap between potential and actual agricultural production in most agricultural areas of the world including large parts of Europe is still large, this yield increase will continue for the years to come, even under conditons where the market is saturated. This is due to the fact that the efficiency in terms of output per unit of input still increases at higher production levels (de Wit et al., 1987), which provides a strong incentive for higher productivity per unit area.

A detailed study of the agricultural potentials of the European Community has shown considerable scope for increase in production (WRR in prep.; van Lanen et al., 1990). In 1985 the cultivated agricultural area in the EC was about 120.10^6 ha. The area under cereals was about 36.10^6 ha and the production of cereals 162.10^6 tons. The area under wheat was about 15.10^6 ha with a total production of 70.10^6 tons. Potential production of wheat on its present acreage in the EC, taking into account inevitable losses of 15 - 20% due to timeliness etc., is as high as 80.10^6 tons without implementing irrigation or other major changes in water management and 110.10^6 when water limitation is eliminated. Thus a 60% increase in wheat production is still possible. The immense potential may be illustrated by the following data. In the EC-12 about 100.10^6 ha of land is suitable for wheat production and an average yield of 7 t ha^{-1} is not unrealistic, so that 700.10^6 tons of wheat could be produced, or about 10 times the present amount. Taking the present wheat production volume as a maximum, in line with EC and GATT policy, the required area would be about 12.10^6 ha, without major investments in land improvement and irrigation. If improved crop management continues, especially in southern Europe, an area of about 9.10^6 ha would suffice, i.e. considerably less than the area of 15.10^6 ha presently under wheat.

Clearly the potentials for increase in wheat production volume are very large. Most Dutch wheat growers are already at the very top of the European producers in terms of yield and probably also in terms of efficiency. A further increase in production per unit area in Dutch agriculture may not be expected, nor a bigger share in the European market. Stringent environmental regulations, in combination with the aim to minimize the use of external inputs per unit of output, may result in average yield levels somewhat lower than the potential, but not much lower than the present yield levels. The efficiency objective will not automatically lead to lower external inputs, because higher inputs do not necessarily lead to higher losses to the environment, as was illustrated for nitrogen by Addiscot (1988). Therefore, high yields should be aimed at, which would imply the lowest environmental side effects of wheat production at relatively low costs. This should also lead to more attention for quality aspects tailored to the specific needs of the various clients. In a shrinking market, only client-oriented products and producers are likely to survive. In this paper the required quality characteristics are discussed first, then the possibilities to meet these requirements through breeding and agronomic measures and finally the consequences of changing environmental conditions, both abiotic and biotic. The conclusion is that client-oriented specific characteristics can be influenced only marginally by agronomic measures and that the perspectives of breeding are limited. Nevertheless, that seems the only way to go.

Required characteristics of wheat

In an analysis of the demand for various types of wheat Poels (1990) compared the quality requirements of wheat with the present quality of Dutch wheat and indicated the amounts needed for various purposes (Figure 1).

It is shown that annually 900.000 tons of wheat are produced in the Netherlands, of which forty percent (360.000 tons) is used for feed production, thirty percent (270.000 tons) for human consumption, twenty five percent (225.000 tons) is exported and five percent (45.000 ton) is accepted by the European Community intervention (the cereal mountain of the EC). Wheat forms the raw material for five products: animal feed, bread, biscuits and crackers, pastas and starch. The requirement for animal feed is covered by imported cheap grain, soy beans, etc. and only for a small fraction by locally produced grains. The demand for raw material for the various other basic food products for bulk production of 550.000 tons, 60.000 tons, 30.000 tons and 300.000 tons, respectively is not covered by production and this will probably neither be the situation in the near future, as the production costs of wheat for feed outside the Netherlands are lower, in economic, although not in technical terms. Therefore, expanding production within the Netherlands does not pay, rather the contrary, a reason for much political upheaval. There seem to be better prospects for adaptation of the product composition to the demand side. When the supply is tailored to the specific needs of the milling industry and other major high quality markets, this might pay as illustrated recently by the bonus on quality, paid by the big milling industries.

In the bread industry about 550.000 tons of wheat are needed annually. Only about 30 percent of this amount (165.000 tons) is produced in the Netherlands. Production does not suffice either for the other industries: starch, biscuits and pasta production. Overall only 270.000 tons of the 900.000 tons is acquired locally, apparently because the required quality characteristics are not met. This may be due to inherent varietal properties and/or inappropriate agronomic measures. Before evaluating this, better definition of the required characteristics is necessary. Table 1 shows that the characteristics milling quality and early thresh are variable in Dutch wheat. To meet the required quality standards these should be improved. At present, Dutch wheat is suitable for the starch industry and to a lesser extent for the pasta and biscuit industry. However, the latter two markets are only of limited size. The perspectives for increased outlets are best for the bread market. The bread baking quality of the most important Dutch varieties is satisfactory, but the dough quality is poor. In the bread baking industry dough quality is increasingly important for example in deep frozen dough. The baking and processing quality is determined by five characteristics: protein content, protein composition, kernel hardiness, early germination and milling efficiency. Protein content is mainly determined by production conditions, and may be affected by agronomic measures. Protein composition is the major factor determining baking quality. It is mainly a varietal characteristic, hardly affected by environmental conditions and agronomic measures. Kernel hardiness is a varietal characteristic. Hard varieties are normally better suitable for the milling process.

They have a higher fraction mechanically damaged starch kernels which prolongs bread freshness. On the other hand, such damaged kernels are less desirable for the starch industry. Susceptibility to early germination is affected in most varieties equally by varietal properties and environmental conditions. Amylase, produced during early germination, affects baking quality negatively and is a negative factor in the starch industry. Hence, susceptibility to early germination is an undesirable characteristic of a variety. Milling efficiency is predominantly a varietal characteristic. For most of the quality characteristics simple, reliable and efficient selection methods are available, that are now widely used, to develop appropriate varieties. However, an important quality characteristic that seems to have received very little attention in research, is the dough content of the wheat kernels. Varietal differences have not been investigated sufficiently and simple, reliable screening methods are not available. Reological research on dough characteristics of various varieties may lead to such biochemically based screening methods. Especially immunofluorescence methods seem promising for the early detection of gliadines, a group of proteins that determine in combination with the bacaliform glutenines, the dough characteristics of wheat. Clear requirements for quality characteristics can be defined in sufficient detail. Screening techniques to identify the proper traits in a rapid and reliable way are not yet available.

Varietal differences in field experiments

Extensive research on varietal differences in various traits that determine the important quality characteristics, has been carried out during the last decade. Darwinkel (1986, 1987) developed and applied screening methods. Various varieties have been tested at least at seven locations, with 7 to 17 cultivars of very different background, at different nitrogen fertilization regimes. Detailed growth analyses were performed and yield (t ha^{-1}), number of ears (m^{-2}), kernels per ear, 1000 kernel weight and volume weight were determined (Table 2). Differences in yield and various yield components were insignificant. Only three varieties had slightly higher yields than the "standard Dutch" variety. "Quality" varieties such as Camp Rémy, Rektor (not included in Table 2) and Urban had slightly lower yields of up to 10%, while the yield of Iéna was almost 20 % lower than that of average of the other varieties. In the various cultivars the yield was attained by different combinations of yield components, some having a high number of ears per m2, others a high 1000 kernel weight.

The following quality characteristics were examined: kernel hardiness, protein content and sedimentation value (Table 3). Kernel hardiness varied only slightly. Dutch hard wheat cultivars appeared harder than cultivars from abroad. There was no effect of nitrogen fertilization on kernel hardiness. Protein content varied strongly among cultivars.

This difference was highly correlated with yield, high yielding varieties having a lower nitrogen content, as is generally observed in high protein cultivars (Kramer, 1979). The difference in total nitrogen uptake in the kernels is not more than 10%. Sedimentation value varied considerably among cultivars. Dutch cultivars, bred especially for yield, had extremely low values, whereas varieties from abroad had considerably higher values. If nitrogen fertilization increased the sedimentation values of the cultivars, especially those from abroad were affected, on average by 5 units per percent increase in protein content. Various flour characteristics for the different cultivars were determined: milling ratio, the fraction of the kernel found in the flour, fraction ash, water addition possibility and loaf volume (Table 4). Some variation in milling ratio among cultivars was observed. The low yielding, protein-rich cultivar Iéna had the highest milling ratio. There was no relation between nitrogen fertilization and flour yield. The fraction ash was adequate in all cultivars, but varied considerably. However, a clear cultivar effect was absent. Addition of water to the flour to determine the baking quality, depends on kernel hardiness and fraction ash. Soft cultivars, such as Okapi and Kanzler, needed the smallest amount of water, whereas hard kernel cultivars such as Iéna needed the largest amounts. This characteristic may result in sticky dough. There was an effect of nitrogen fertilization on bread volume. Another important characteristic that was screened in the various experiments was elasticity of dough, one of the relevant dough characteristics measured by the extensograph. Dough of the Dutch varieties was extremely flabby, while that of the German cultivars was rigid. Another dough characteristic, elasticity resistance, was also more favourable in the German cultivars. The research of Darwinkel has demonstrated the available range in quality characteristics. It has shown an inverse relation between yield and protein content, however, over a limited range of protein contents. Other quality parameters such as sedimentation value, milling ratio, bread volume and elasticity resistance of dough showed much larger variations. The German cultivars generally showed more favourable values for these quality characteristics. Dutch varieties have much lower values for some of the typical dough parameters, such as elasticity and elasticity resistance and even the Dutch quality varieties still have much lower values. Apparently, quality differences exist among cultivars. Nitrogen fertilization affects nitrogen content of the kernel but this effect is limited. The increase in protein level was also expressed in an increased sedimentation value. This could be due to the experimental conditions.

Effects of environmental conditions on (yield) characteristics

Many experiments have been carried out to determine the consequences of agronomic measures for growth, yield and quality characteristics of wheat. Clear relations between leaf nitrogen content and photosynthesis, growth and production have been demonstrated (Spiertz and Ellen, 1978; Groot, 1989).

Light intensity and temperature have a direct effect on nitrogen content of the kernels. Higher temperatures accelerate protein accumulation in the kernels more than starch accumulation so that the protein fraction increases (van Keulen and Seligman, 1987). Warm summers, such as that of 1976 in the Netherlands, therefore result in high protein levels in the kernels. When sufficient water and nitrogen are available, high radiation levels result in abundant assimilate availability and high grain growth rates. The grain growth rates, however have a maximum, even when assimilates and nitrogen are abundantly available (Sofield et al., 1977). This maximum rate is cultivar-specific, and is a function of ambient temperature (van Keulen and Seligman, 1987). Varietal characteristics may, as indicated above, determine the quality traits of wheat. Agronomic measures, however, determine to what extent the required traits are realized. Environmental conditions, both those that can be managed by man and those that have to be accepted by man, affect growth and production of wheat and have therefore consequences for its yield and quality.
To analyse these dependencies, combined experimental and simulation studies have been carried out by Groot and Spiertz (1990) and van Keulen and Seligman (1987). Experimental analysis by Spiertz and Ellen (1978) has demonstrated the effects of light and temperature on nitrogen content of the kernels and nitrogen uptake and partitioning within the main tiller (Table 5). At lower temperatures the grain filling period, i.e. the period between anthesis and physiological maturity is longer (van Keulen and Seligman, 1987), but the rate of dry matter accumulation in the kernels is lower. As a result of the differential effect of temperature on dry matter and nitrogen accumulation, nitrogen concentration in the grains increases with temperature, even though the nitrogen harvest index decreases, i.e. a smaller proportion of total nitrogen is translocated to the grain.
At lower radiation levels assimilate availability limits the rate of dry matter accumulation in the grain, which again results in higher nitrogen contents in the grain at lower nitrogen harvest indices. In extreme situations, this may lead to physiologically mature kernels with a still green leaf apparatus.
Under unfavourable growing conditions, due to water and/or nutrient limitation or the occurrence of pests and diseases, dry matter production in general is more strongly affected than nitrogen uptake, hence a relatively higher nitrogen content of the kernels results. This was also demonstrated in simulation studies by Groot and Spiertz (1990), using an adapted version of the simple and universal crop growth model of Spitters et al. (1989).

The interactions between carbohydrate and nitrogen metabolism in this model are schematically presented in Fig. 2. Both are strongly affected by external conditions, such as solar radiation, water and nutrient availability. For carbohydrates, the demand of the grains is mainly met by current photosynthesis, about 80%, and only to a limited extent by reallocation of reserves, about 20%. For proteins the grains rely mainly on translocation from the vegetative tissues.

When nitrogen is readily available, leaf nitrogen levels are affected but maximum leaf nitrogen content is only slightly higher (Groot, 1989). Up to anthesis, nitrogen uptake takes readily place. As long as nitrogen content of any plant part is below its maximum possible value corresponding with the current development stage, there is a sink for nitrogen. Values for the maximum nitrogen content are for leaves in the range of 6.7% at emergence to 0.75% at maturity (Groot, 1987). Uptake is thus determined by the demand of the crop, or by availability of nitrogen in the soil, which may be hampered by transport possibilities through the soil particularly in situations of water shortage. After anthesis, nitrogen uptake is considerably lower and most of the nitrogen for the grain is translocated in reduced form from the vegetative parts. In cereals, 40 - 60% of leaf protein consists of Ribulose -1.5 biphosphate carboxylase (RuBPCase), the key enzyme in photosynthesis, so that withdrawal of nitrogen from the leaves ultimately results in so-called self-destruction (Sinclair and de Wit, 1976). Only prolonged nitrogen uptake can counteract self-destruction, but the availability of assimilates to the root system is restricted by the strong sink in the grains and this accelerates root senescence, which hampers root functioning. Often nitrogen transport in the soil is also hampered by drought, so that self-destruction is sooner or later inevitable. The transition between the phase in which CO_2 diffusion limits carbon exchange rate (CER) of individual leaves and the phase in which nitrogen concentration limits CER is gradual, as a result of the translocation of nitrogen towards the strong sink of the kernels (Groot and Spiertz, 1990). The parameter values for the model used in the simulation studies were derived from various experimental sources and the model data were tested against data from independent experiments. In general, total dry matter production and nitrogen uptake were simulated within 10% of the measured values. Simulation experiments with the validated model indicated that, under a given set of weather conditions on a Dutch polder soil (silty loam), grain yield in the absence of nitrogen fertilization would be 5300 kg per ha increasing to 8200 kg per ha under non-limiting nitrogen supply. To realise that situation, application of 120 kg N per ha was sufficient, resulting in a nitrogen yield of 250 kg ha^{-1}. Higher application rates increased grain nitrogen content but not grain yield. These results are in agreement with the observations of Darwinkel (1987), indicating that increased N-application above a threshold increases grain protein content without affecting grain yield. At low nitrogen uptake values the relation between total nitrogen uptake and grain yield is linear; at higher values the yield-uptake curve deviates from the straight line, reflecting an increase in the nitrogen content of grain and straw at harvest, and finally a plateau level is reached where nitrogen no longer is the yield-determining factor. The level of the plateau is determined by genetic traits (nitrogen harvest index and nitrogen content of the grains) and by environmental conditions (radiation, temperature, water availability, pest and disease incidence).

In situations where water is limiting or temperatures are high, nitrogen use efficiency, expressed in kg grain produced per kg N taken up, is low, and grain nitrogen concentrations high (Fig. 3). On sandy soils where water shortage limits growth and yield, the lower grain yield is partly due to a lower nitrogen uptake as a result of restricted nitrogen diffusion towards roots in dry soil. Insufficient moisture availability leads to (partial) stomatal closure with the associated decline in carbon dioxide assimilation.

Changing environmental conditions and quality characteristics of wheat

Experimental and simulation studies have taken place under the prevailing environmental conditions. The results indicate that breeding should lead to the development of cultivars with properties that best approach the demanded quality characteristics. However, this will only be realized under appropriate management practices. The inverse relation between grain protein content and grain yield holds at different levels of nitrogen supply. To attain a high grain protein content which is a requirement for a good baking quality, varieties should be able to accumulate large amounts of nitrogen in the vegetative material before anthesis, that can be easily translocated during grain filling (van Keulen and Seligman, 1987). An alternative would be to extend nitrogen uptake into the grain filling period. That would require maintenance of an active root system after anthesis and sufficient available nitrogen in the root zone. In both cases, nitrogen fertilizer management requires adaptation. The tendency to promote high grain nitrogen levels through very high fertilizer application before anthesis is in many cases ineffective as the storage capacity is inadequate and uptake after anthesis is limited. Moreover, such a strategy leads to a decrease in nitrogen fertilizer recovery and thus to higher nitrogen emissions to the atmosphere and the groundwater, which is undesirable from an environmental point of view. Moreover, very high nitrogen levels in leaf and stem before anthesis promote the development of certain pests and diseases such as powdery mildew (*Erysiphe graminis*), leaf rusts and cereal aphids. Apparently, the possibilities to improve the quality of wheat through crop management are limited and the perspectives for breeding are more promising. It is, however, questionable whether this still holds if environmental conditions change. Both, abiotic and biotic conditions are changing. During the last decades ambient CO_2-concentration has increased considerably due to various activities by man. This affects photosynthesis and growth (Goudriaan, 1990) and may affect efficiency of nitrogen use in terms of dry matter production (van Kraalingen and van Keulen, 1991). In detailed pot experiments by van Kraalingen and van Keulen the consequences of CO_2-enrichment under various levels of N and P availability were evaluated (Figure 4). Only under abundant nitrogen and phosphorus availability dry matter production increased in a CO_2-enriched environment of 700 $\mu l\ l^{-1}$ in comparison to the present 350 $\mu l\ l^{-1}$.

There was a positive effect of CO_2 enrichment on total dry matter production, but proportionally smaller at limited nutrient supply. The effect on straw yield was stronger than on grain yield, hence the harvest index was lower under elevated CO_2 concentrations. CO_2 enrichment did not affect total nutrient uptake, so that the higher dry matter production resulted in lower nutrient concentrations in both grain and straw ('dilution'). Moreover, the nutrient harvest index was lower at higher CO_2 concentrations. Hence, under elevated CO_2 levels grain quality in terms of protein content is likely to be lower as is grain yield. Apparently, at low nitrogen and phosphorus levels CO_2-enrichment hardly affects growth and production, as nitrogen or phosphorus are limiting rather than CO_2. Only when these nutrients are abundantly available CO_2-enrichment has a positive effect. At high nutrient levels the positive CO_2-enrichment effect on yield is partly offset by a negative effect on the quality of the grains.

Biotic effects on growth and yield of wheat may originate from pests, diseases, weeds and environmental pollution, such as acidification. These growth-reducing factors may affect total dry matter production and grain yield, but may also interfere with quality aspects. In a detailed crop physiological analysis, Rossing (1991) has demonstrated the effects of cereal aphids on growth and yield of winter wheat. Aphids extract phloem sap and act as an alternative sink that competes with the grains. Various hypotheses were formulated with respect to partitioning of nitrogen in the phloem sap:

- (i) the total demand equals the sum of the demands of grain and aphids; the supply is distributed in proportion to the respective demands;
- (ii) the total demand equals the sum of the demands of grain and aphids; supply is first utilized by the grains.
- (iii) when present, only the grains determine the total demand; the supply is distributed in proportion to the respective demands;
- (iv) when present, only the grains determine the total demand; the supply is first utilized by the aphids.

To test these hypotheses a simulation model, similar to the one used by Groot (1987), was adapted and parameterized on the basis of results from various detailed experiments (Figure 5). The simulated final grain yield did not differ significantly under the various hypotheses but, the dynamics of grain weight, leaf weight and leaf nitrogen content did. Under hypotheses iii and iv aphids do not affect the size of the sink for nitrogen and carbohydrates. Experimental evidence to support these hypotheses is given by Vereijken (1979). Yield losses and the dynamics of growth and yield reduction agreed with those calculated from the aphid population present in three field trials. Thus, compensation for aphid feeding by increased phloem sap supply to the grains as assumed in hypotheses i and ii, is unlikely to be important.

The accelerated leaf senescence observed in the field, that is simulated under hypotheses i and ii, but not under hypotheses iii and iv, is therefore probably due to other causes. Honeydew, perthotrophic and saprophytic leaf fungi may have caused the decrease in green leaf weight (Rabbinge et al., 1981) and total leaf nitrogen. This decrease in total leaf nitrogen considerably affects the total amount of nitrogen translocated to the kernels. This is compensated by a faster reallocation and as a result photosynthesis at light saturation decreases. These combined effects lead to considerable damage (Figure 6). Cereal aphids cause damage in cereals through the combination of direct and indirect effects. The consequence of this injury mechanism is that at a given level of incidence yield loss is dependent on yield level and production situation. In production situations with high yield expectations, yield reduction increases more than proportional in comparison to low yield levels. The consequences for quality of wheat are less clear. The reduction in nitrogen availability causes a considerable reduction in total biomass and grain yield. The quality of the kernels in terms of protein is, however, hardly affected.

Conclusions

This review of physiological aspects of quality in wheat suggests that the scope for improved quality characteristics of wheat through agronomic measures is very limited. If crop growth conditions are unfavourable, yields are low and the quality of the wheat does not meet the quality requirements of the processing industry. Under optimum growth conditions the nitrogen content of the grain can be increased to a high level but the storage capacity of the kernels is limited. Therefore, agronomic measures alone are not sufficient to reach high quality products. When environmental conditions change, for example if atmospheric CO_2-concentration increases or aphid pests become more frequent the situation does not become more favourable. Agronomic measures may help to improve the production conditions and to reduce negative side effects of production such as over-use of nitrogen fertilizer and pesticides. That is however not the subject of the paper. Breeding seems a more promising way for quality improvement. There is still considerable scope for improvement of the specific characteristics that make Dutch wheat attractive to the processing industry. However, screening and evaluation techniques need further refinement and improvement to arrive at simple and reliable methods that may accelerate that selection process.

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TABLE 1.
QUALITY CHARACTERISTICS OF WHEAT AND QUALITY REQUIREMENTS OF DUTCH WHEAT
(Poels, 1990)

OUTLET MARKET	MILLING QUALITY	BAKING QUALITY	PROTEIN	THRASH	KERNEL HARDINESS	REQUIRED VOLUME IN NETH. IN TONS
BREAD	GOOD	GOOD	HIGH	UNDESIRED	HARD/SOFT	550.000
BISCUIT	GOOD	MODERATE	MODERATE	UNDESIRED	SOFT	60.000
PASTA	GOOD	GOOD	HIGH	UNDESIRED	HARD	30.000
STARCH INDUSTRY	GOOD	NOT RELEVANT	MODERATE	MODERATE	HARD	300.000
NETHERLANDS	VARIABLE	MODERATE	MODERATE	VARIABLE	HARD	900.000

TABLE 2.
KERNEL YIELD, t/ha, EAR NUMBER m^{-2}, KERNELS PER EAR, 1000 KERNEL WEIGHT, HECTOLITRE WEIGHT OF VARIOUS CULTIVARS (AVERAGE VALUES OF VARIOUS LOCATIONS)
(Darwinkel, 1986)

CULTIVARS	YIELD t/ha	EARS PER m^2	KERNELS PER EAR	1000 KERNEL WEIGHT	HECTOLITER WEIGHT
OKAPI	100	100	100	100	100
OBELISK	103	91	123	93	102
GRANTA	101	98	113	92	101
KANZLER	100	84	125	95	100
URBAN	96	102	106	84	103
CAMP REMY	96	87	124	89	101
IENA	83	73	108	108	102
100 =	9.28	505	35.9	52.3	79.1

TABLE 3.
PROTEIN CONTENT AND SEDIMENTATION VALUE OF VARIOUS CULTIVARS (AVERAGE VALUE OF VARIOUS LOCATIONS)
(Darwinkel, 1986)

CULTIVARS	PROTEIN PERCENTAGE	SEDIMENTATION VALUE
OKAPI	100	100
OBELISK	105	150
GRANTA	104	139
KANZLER	107	159
URBAN	108	234
CAMP REMY	110	238
IENA	119	235
100 =	12.2	23

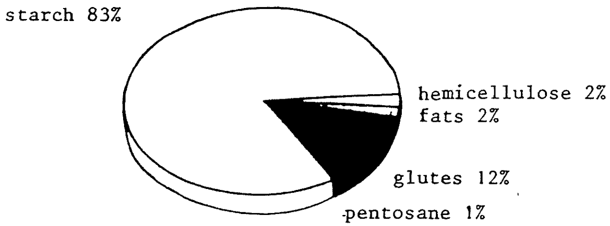
TABLE 4.
MILLING RATIO, FRACTION ASH, WATER ADDITION AND LOAF VOLUME OF VARIOUS CULTIVARS (AVERAGE VALUES OF VARIOUS LOCATIONS)
(Darwinkel, 1986)

CULTIVARS	MILLING RATIO	FRACTION ASH	WATER ADDITION	LOAF VOLUME
OKAPI	100	100	100	100
OBELISK	107	91	108	108
GRANTA	105	96	113	105
KANZLER	103	96	102	103
URBAN	106	94	106	111
CAMP REMY	107	89	105	108
IENA	109	106	114	110
100 =	0.71	0.47	55.4	-

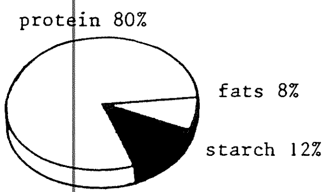
TABLE 5.
EFFECT OF LIGHT AND TEMPERATURE ON NITROGEN CONTENT OF KERNELS AND NITROGEN UPTAKE AND PARTITIONING WITHIN THE MAIN STEM
(Spiertz and Ellen, 1979)

LIGHT INTENSITY $W m^{-2}$	TEMPERATURE ^oC	mg N in STRAW PER TILLER	mg N in KERNELS PER TILLER	NITROGEN FRACTION OF KERNEL
188	10	11.3	42.2	1.65
	15	12.5	38.3	1.78
	20	13.1	40.3	2.20
	25	13.7	38.1	2.68
118	10	11.1	45.4	1.86
	15	12.3	40.8	1.98
	20	13.7	38.4	2.74
	25	14.7	34.6	3.06
64	10	13.1	38.4	2.16
	15	14.4	36.6	2.69
	20	15.1	38.9	3.60
	25	16.9	31.2	3.95

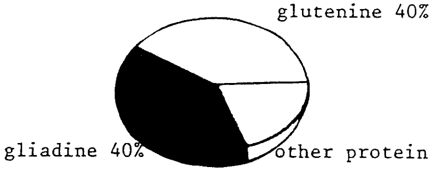
Figure 1: Wheat kernels consist for 75 percent out of flour and 25 percent bran, germ etc. The composition of flour, proteins and glutes is given (Poels, 1990).



Composition of flour



Composition of glutes



Composition of protein in glutes

Figure 2: Relational diagram of the major processes and their interactions during grain filling of cereals. Rectangles represent state variables, valves represent rate variables, solid lines are material flows, broken lines are information flows (Groot and Spiertz, 1990).

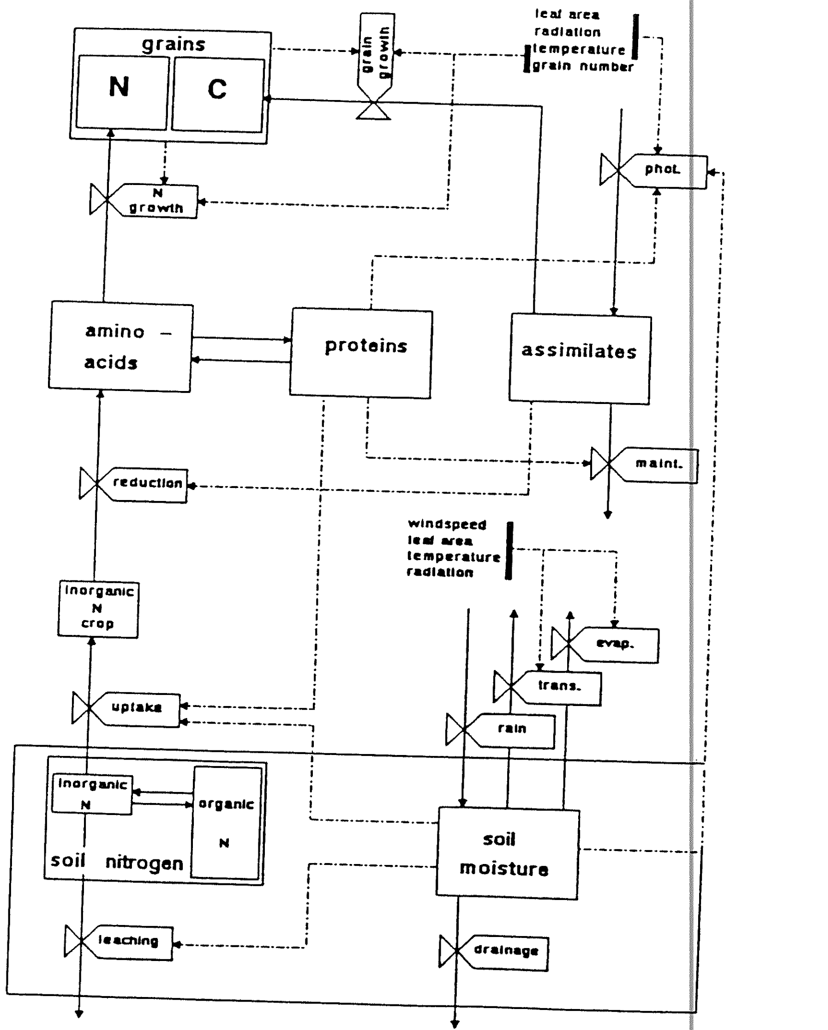


Figure 3: Simulated grain yield for a clay soil (———) and for a sandy soil (—·—), and simulated nitrogen uptake by the crop for a clay soil (— —) and for a sandy soil (- - - -) at different rates of nitrogen application, (Groot and Spiertz, 1990).

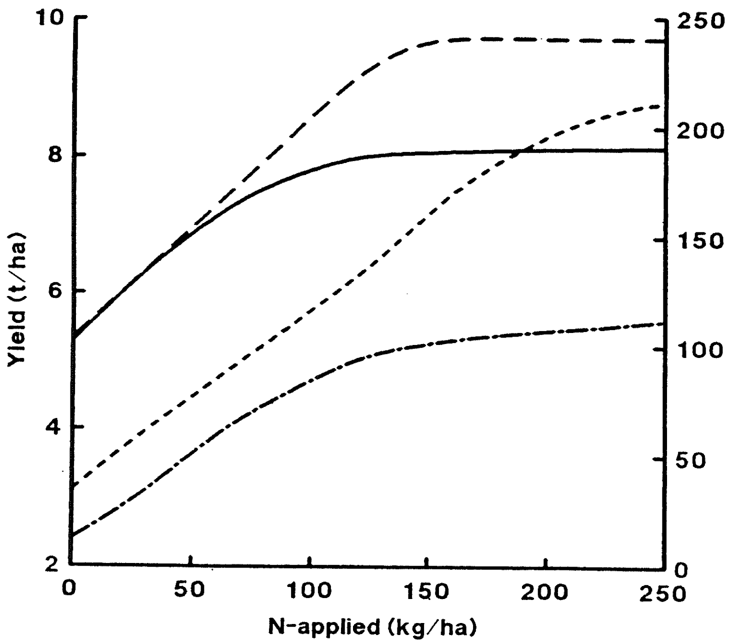


Figure 4: Dry matter production for various combinations of nitrogen and phosphorus availability and two levels of carbon dioxide supply (Van Kraalingen and Van Keulen), 1991). Phosphorus supply (as P_2O_5 per pot of 5.5 l): P_1: 0.035 g; P_2: 0.23 g; P_3: 0.42 g.
Carbon dioxide supply: -: 350 ± 50 μl l^{-1};
+: 700 ± 30 μl l^{-1}.

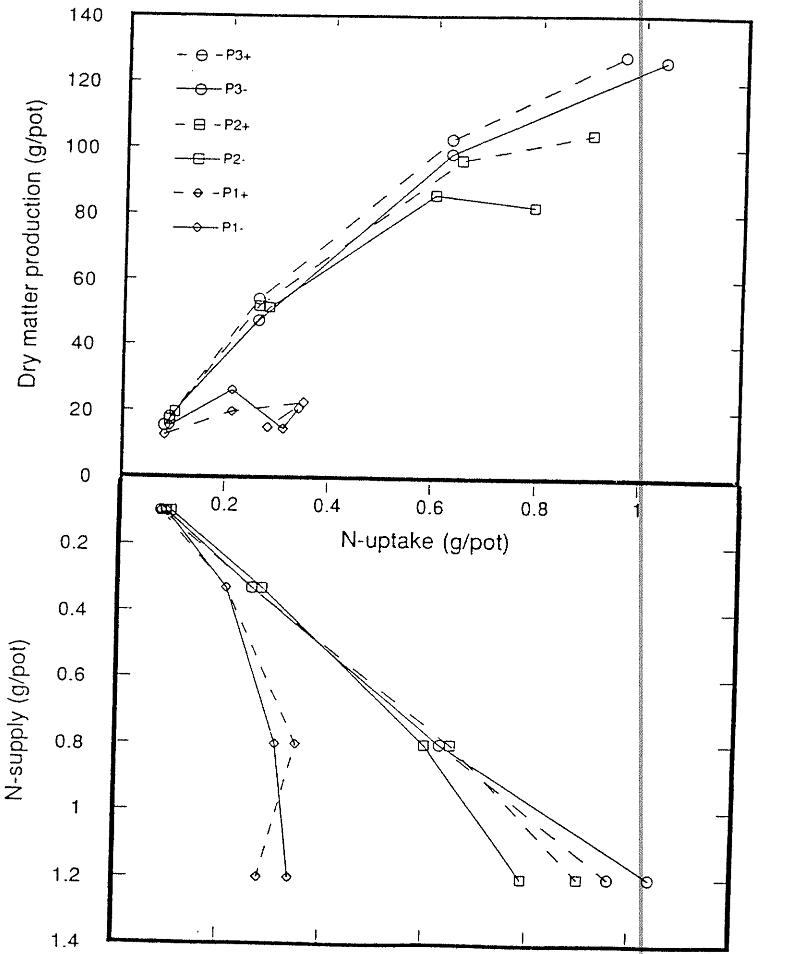


Figure 5: Observed grain yield in two field experiments, Bouwing 84 and EEST 84, and simulated grain yield based on hypothesis IV. Observed grain yield of the control (●) and the most severely infested treatment (o). Simulated grain yield without aphids (———), with an aphid infestation as observed in the control treatment (- - -) and in the most severely infested treatment (--------), respectively. The size of the aphid infestations is shown for the control (—■—) and the most severe infestation (—□—). Leaf area index is simulated (Rossing, 1991).

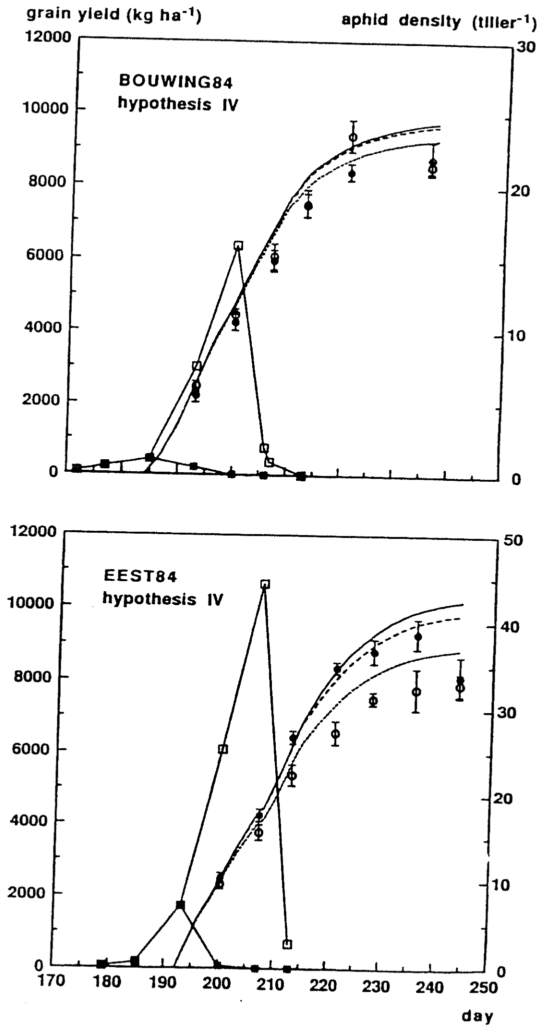


Figure 6: Simulated total damage (kg ha^{-1}) and damage components for EEST 84, the most severe aphid infestation. Simulation runs are based on hypothesis IV.

1. carbohydrate uptake
2. carbohydrate and nitrogen uptake
3. carbohydrate and nitrogen uptake + increased maintenance respiration
4. carbohydrate and nitrogen uptake + increased maintenance respiration + decreased CO_2 assimilation at light saturation (Rossing, 1991).