Grain growth in oats: experimentation and modelling

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Preface

This report is the result of a fellowship of the senior author for the period April - December 1991 at CABO-DLO in the Department of Crop Physiology and Ecology. The fellowship was granted by the International Agricultural Centre (IAC). The reported investigations were carried out in the framework of a project jointly financed by CABO-DLO and the Netherlands Grain Centre (NGC).

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A model for grain growth, based on combined deterministic and stochastic approaches was developed for quantitative description of grain filling and grain weight variability. To simplify and identify the connections between various theories developed for growth and yield formation in field crops, it is suggested to use the term sink equivalent to module or plant subunit and logically sink variability equivalent to module or plant subunit variability and differentiation, respectively.

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1. Introduction

General overview

Oats has been a major crop in the Netherlands, covering a total area of over 150 000 ha in the forties and still about 125 000 ha at the beginning of the sixties (van Keulen et al., 1991, Fig. 1.1). From then on, its importance rapidly declined, as it was largely replaced by silage maize on sandy soils, and by economically more attractive crops, such as wheat on clay soils, and in the middle of the eighties only some 6 000 ha were cultivated. Over the same period, average yields increased from slightly over 3.5 t/ha to 5.4 t/ha, representing an average annual yield increase of 0.06 t/ha (Fig. 1.2), which is much higher than the value of about 0.01 t/ha, reported for the period 1850 - 1950 (Gmelich Meyling, 1976). However, it is substantially lower than that for wheat, for which in the period 1960 - 1975 average yield increased by about 0.08 t/ha annually and from then onwards even with about 0.1 t/ha (Spiertz et al., 1992). Undoubtedly, this difference must be partly attributed to the much greater efforts in plant breeding and crop management research devoted to wheat, while also the EC Common Agricultural Policy (CAP), with its guarantee prices for wheat, has stimulated the use of yield-increasing imputs, like nitrogen fertilizers and pesticides.

In view of the success of the CAP, which has led to surplusses of wheat, and current EC regulations, wheat cultivation has come under pressure and alternative crops and markets are looked for. One of the possibilities suggested is expansion of the area under oats, because of the growing demand for human consumption, for which according to the Netherlands Grain Centre a substantial net import exists in the Netherlands (NGC, 1988). Also from a practical point of view, oats seem to be an attractive alternative as cereal in the crop rotation. The Netherlands Grain Centre (NGC, 1988) estimates that national demand for oats is about 90 000 tons annually, and may increase if "oat bran" would become a successful food item, as in the US.

The prospects for cultivation of oats in the Dutch arable farming systems can be considered from different viewpoints.

An important consideration for these prospects is the yield potential of the crop, which can be estimated on the basis of available energy, a major determinant of crop production under the temperate conditions negative correlation exists between grain yield and grain nitrogen content, as also observed in wheat (Kramer, 1979), so that under drought stress, where grain yield is limited by moisture supply, grain nitrogen contents are high.

The variation in grain characteristics among panicles in the stand is generally greater then that within the panicle (Youngs and Shands, 1974). Within a spikelet, groat weight decreases and groat fraction increases from primary through secondary to tertiary grains. Protein content varies only slightly between primary and secondary groats (mean difference 0.7 % or less), but about 60 % of the total protein content is in the primary groats.

Grain characteristics also vary with position of the grain in the panicle. Correlations between groat distance from the panicle base and grain weight, groat weight, and protein weight were positive and highly significant. Differences in groat characteristics, associated with groat position may be related in part to differences in development pattern of the groats, as florets of spikelets attached at the top of the panicle flower earlier, and grains mature earlier than from those attached more towards the base. As groats develop in different positions in the panicle, probably assimilate availability to the younger groats, located near the panicle base, may be limited, thus resulting in smaller groats. Limited assimilate supply may also be one of the reasons for the absence of tertiary grains in the spikelets near the panicle base.

Seed quality

While ample attention has been paid to thousand grain weight in oats, the available data generally refer to bulk samples, without differentiation between primary and secondary grains. Therefore, while a sample of oats is given a characteristic thousand grain weight, it may contain a very wide range of seed sizes and weights. This variability is undesirable because of the losses of smaller seeds during cleaning and adverse effects of smaller seeds on subsequent plant growth and yield.

The influence of seed size on grain yields has been studied extensively in barley and wheat. At normal seeding rates, plants grown from larger seeds are superior to those from small seeds in seedling growth and grain yield (Boyd et al., 1971; Kaufmann and Guitard, 1967; Frey and Wiggans, 1956). In most instances these higher grain yields have been attributed to increased tillering and higher ear densities, without much effect on other yield components or emergence percentage (Wood et al., 1977; Austenson and Walton, 1970; Demirlicakmak et al., 1963; Kaufmann and McFadden, 1963).

In oats, the influence of seed size on grain yield has not been studied as extensively. Many years ago Kiesselbach (1924) and Zavitz (1927) tested oat cultivars that were low-yielding according to present standards. Zavitz (op. cit.) reported that plants grown from larger seeds produced from 12.7 to 29.4 % more grain than plants grown from medium and small seeds. Kiesselbach (op. cit.) reported a difference in yield of 6.2 % for the cultivar Kherson.

To our knowledge, only Brinkman (1979) investigated the differences between primary and secondary grains. Plots seeded to primary grains yielded 14.5 % more grain and 13.1 % more straw than those seeded to secondary grains. Combinations of primary and secondary grains yielded proportionally to the seed composition, irrespective of genotype, environment or their interaction. However, he limited his observations to the effects of seed type on yield and its components. Since secondary grains are invariably smaller than primary grains, these effects may be a reflection of seed size, irrespective of the origin of the grain, primary or secondary.

This assumption was confirmed by Tibelius and Klick (1986) who found 8-15 % higher grain yields in plots seeded to primary seeds. Yield differences were most strongly associated with the length of the seedling-heading period. No differences were found between the plots seeded to primary and secondary seeds of the same weight.

Aims of the study

The short overview of the literature indicates that for both sowing and industrial processing uniformity of oat grains is an important quality characteristic, i.e. grain size distribution should be as narrow as possible (van Keulen et al., 1991).

Unfortunately, the most commonly used grain size parameters like thousand grain weight, hectolitre weight, or the fractional distribution derived from partitioning over sieves of different mesh size, are only partial characteristics of grain size variability. Although grain uniformity is one of the most important properties for the processing industry, relevant information in the literature is scarce, especially with respect to the factors influencing grain size variability. Moreover, not much attention seems to have been paid to the interactive effects of genetic properties and crop management on this characteristic.

Therefore, our efforts were directed towards filling these gaps in the knowledge. More specifically, the aims of the study were:

1. To analyse grain yield formation in oats.
2. To analyse grain filling and grain weight variability in oats.
3. To analyse the processes underlying this variability.
4. To identify factors influencing these processes.
5. To develop a model describing the process of grain filling, including a description of grain weight distribution.
6. To analyse the effects of genotype x environment interaction on grain weight variability.

Approach

As grain weight variability originates at the morphological level of plant organization, a modular description of plant growth seems a suitable approach (White, 1979; Porter, 1983a, b). Thus, an individual plant, at any instant, may be considered as comprising cohorts of meristems of different age and growth intensity (White, 1979). Plant development is an interactive process and the possession of many cohorts of reproducing growth centres gives plants the potential for repeated and sequential cycles of development and senescence (Leopold, 1961).

The other important feature that must be considered in morphological studies is the hierarchical structure with branching at various levels, which is typical for the majority of plants. Already Arber (1941) stated that plants present the clearest indication that biological systems are hierarchical in design, i.e. built up in a modular way. This is a useful concept, because considering plants as modular systems simplifies description of plant form and architecture. Plants develop as the result of interaction between two parameters of modular growth, (i) the effort (propensity) to produce consecutive modules, which is a dynamic process, and can be expressed therefore in a rate equation, and (ii) the positioning of these modules, which introduces a spatial dimension into the process. Plant form is a direct consequence of these dynamics and they can thus be used to provide a mechanistic description of plant morphology. This concept supports the view that plant form may be either constrained by developmental control of the metapopulation of meristems (modules) or by the carbon economy of the plant.

Oat morphology has not been studied as extensively as that of other small grain cereals, probably because of its complicated inflorescence in the form of a panicle, although some descriptions of its morphological development have been published (Cannon, 1900; Noguchi, 1929; Arber, 1934; Bonnett, 1966).

Several branching processes take place during the development of the oat plant (Fig. 1.3a). As in all small grain cereals, the oat stem passes through two stages of development. In the first stage, the shoot apex remains short, leaf primordia differentiate, leaves grow, and tiller buds develop in the axes of the leaves at the base of the stem. The sequence of tiller cohort formation may be described as illustrated in Fig. 1.4 for wheat (Masle-Meynard and Sebillotte, 1981). In the second stage, the internodes of the stems elongate, and the panicle branches, spikelets and flower parts differentiate and develop.

The oat panicle is defined as a many-branched determinate inflorescence consisting of a main axis from which arise lateral axillary branches which are grouped on alternate sides of the main axis at its nodes (Fig. 1.5). The main axis and each of the lateral branches terminate in a single apical spikelet. The branches within one layer (connected at one node) may be designated as branches of the first, second and third order depending on their point of origin, i.e. whether they arise from the main axis (first order) or the lateral branches (second and third order). The average number of nodes (branch layers) on the panicle may range from 5 to 7 according to Fore and Woodworth (1933). These values, however vary depending on variety and growing conditions.

The sequence of differentiation of the branch primordia of the different orders is in accordance with the hierarchical structure of the oat plant. As the branch primordia of the first order increase in size at nodes with many lateral branches, branch primordia of the second order appear below the apex and on alternate sides of the first. In turn and in the same way, primordia of the branches of the third order arise from the second. Branches elongate between the spikelet and their attachment to the parent axis.

Spikelet differentiation begins first at the tip of the central axis and proceeds basally in succession at the tips of the primordia of the first order branches. At the nodes, the sequence of spikelet differentiation is (1) branches of the first order, (2) branches of the second order, and (3) branches of the third order. To generalize, those branch primordia that differentiate first are the first to show differentiation of spikelets.

Differentiation of the empty glumes is the first sign of spikelet development. Within the spikelet the florets differentiate acropetally. The florets are alternate and attached to a short rachilla. Floret primordia first appear as protuberances below the apex of the shoot above the empty glume primordia. The more basal floret is always more advanced in development than those above it.

In oat the basal floret and the next one above it are usually fertile but the third floret does not often produce a grain (Fig. 1.6), except in some varieties or in especially favourable environments.

Floret parts differentiate in the following order: lemma, stamens, palea, lodicules and pistil. Ovary, styles and stigmas is the order of differentiation of the parts of the pistil.

Grains may be considered as the individual subunits (modules) at the end of the complex branching process during oat plant ontogeny. White (1979) warned that to distinguish subunits that are realistic ecologically, may be sometimes very difficult. He recommended a pragmatic choice, depending on the purpose of the study and the nature of the plant.

Five hierarchical levels of plant organisation, that influence final grain size may be distinguished within the oat plant (Fig. 1.3b). At each level, subunits are formed that can be considered as the modules: tillers, panicle layers, branches within different layers, spikelets within branches, and grains within spikelets. Initiation of those plant organs occurs in time sequences and also growth rates of the same order subunits are not identical. These are the main factors influencing grain size variability analysed in this report.

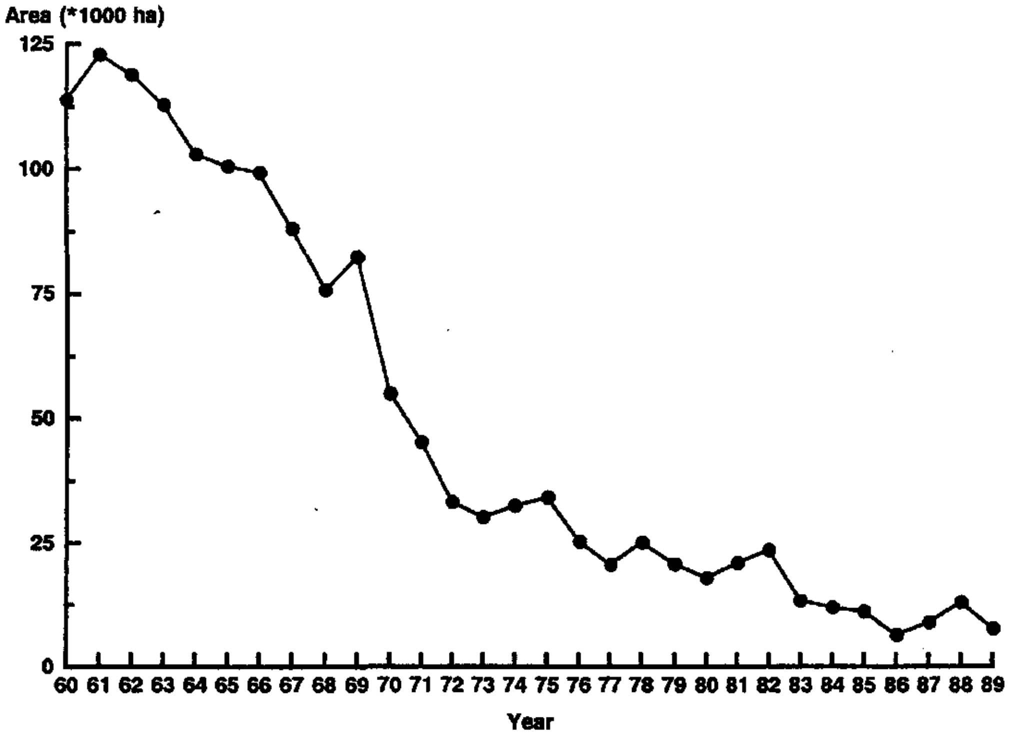


Figure 1.1: The cultivated area of oats in the Netherlands from 1960 till 1989 (van Keulen et al., 1991).

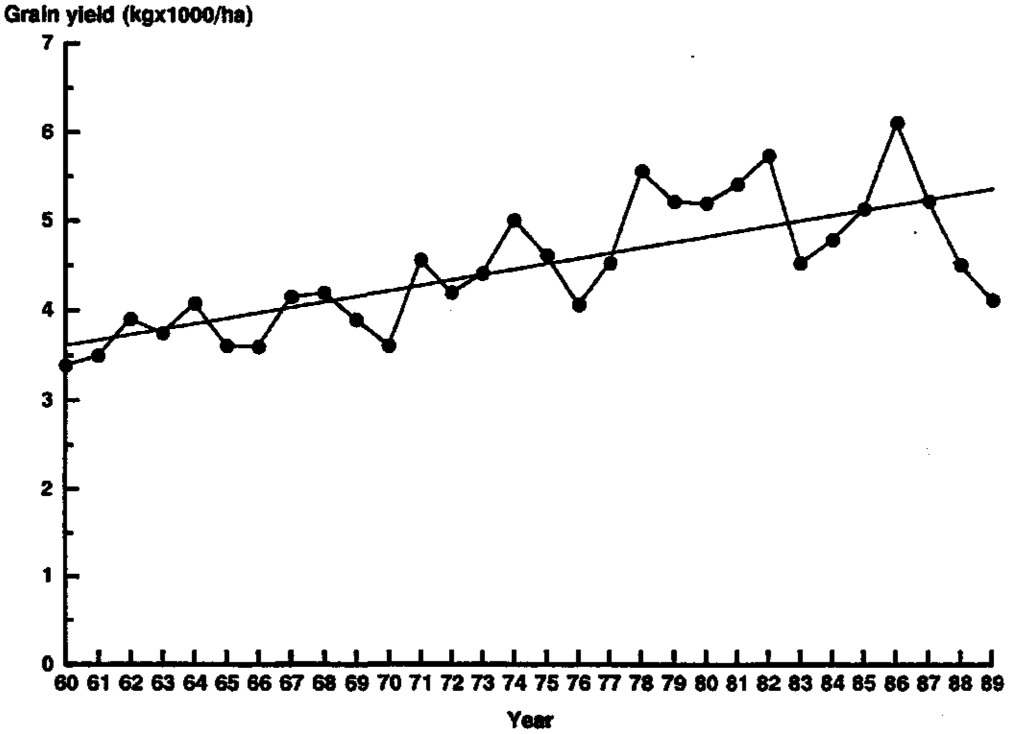


Figure 1.2: Avarage grain yield of oats in the Netherlands from 1960 till 1989 (van Keulen et al., 1991).

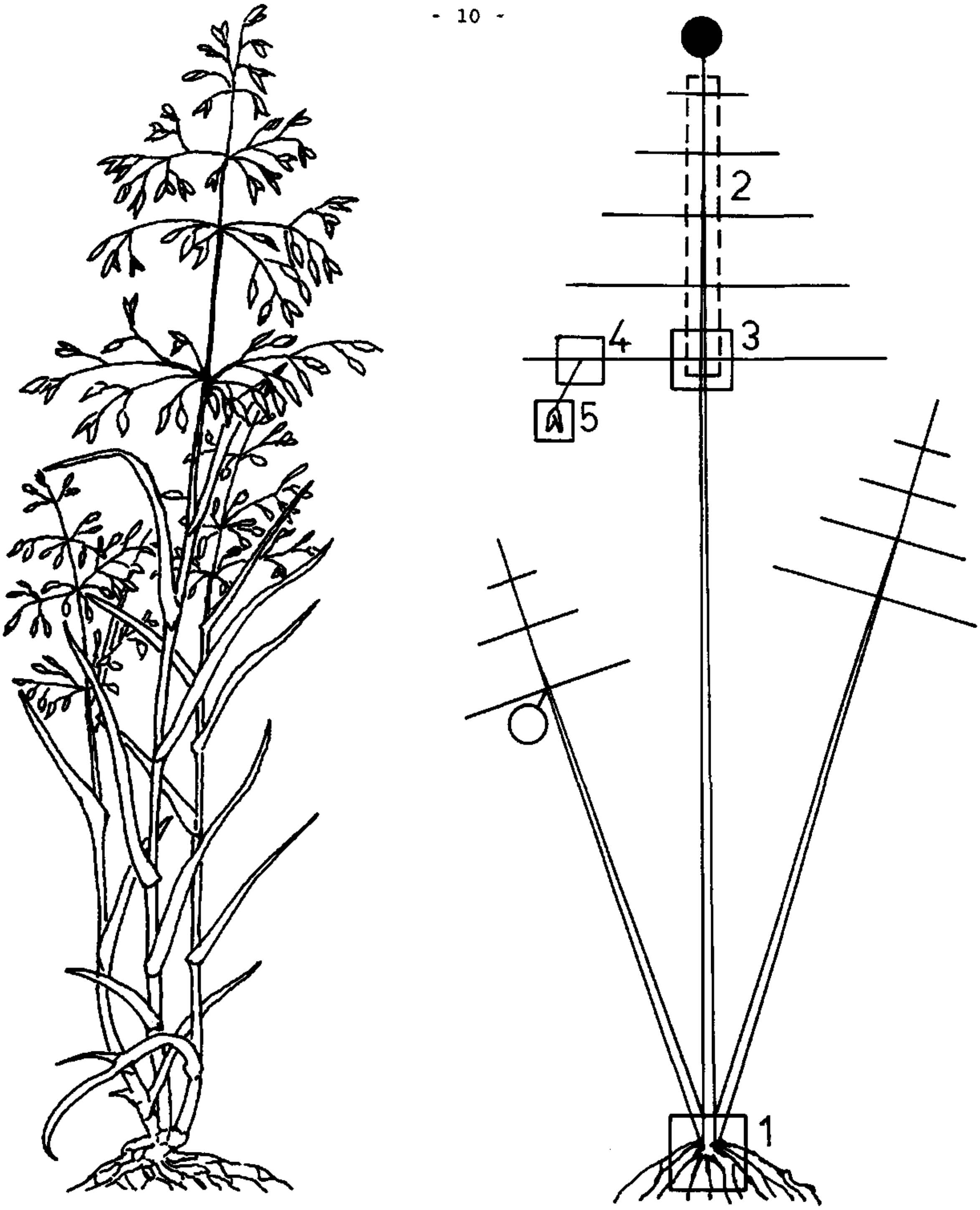


Figure 1.3: Hierarchies in the morphological structure of the oat plant. (a) plant morphology; (b) description of hierarchies in plant organization:

1 - tillering node, 2 - nodes (layers) of the panicle, 3 - branches within the panicle node, 4 - spikelets within branch, 5 - grains within spikelet

the oldest spikelet (usually with the biggest grains)
the youngest spikelet (usually with the smallest grains)

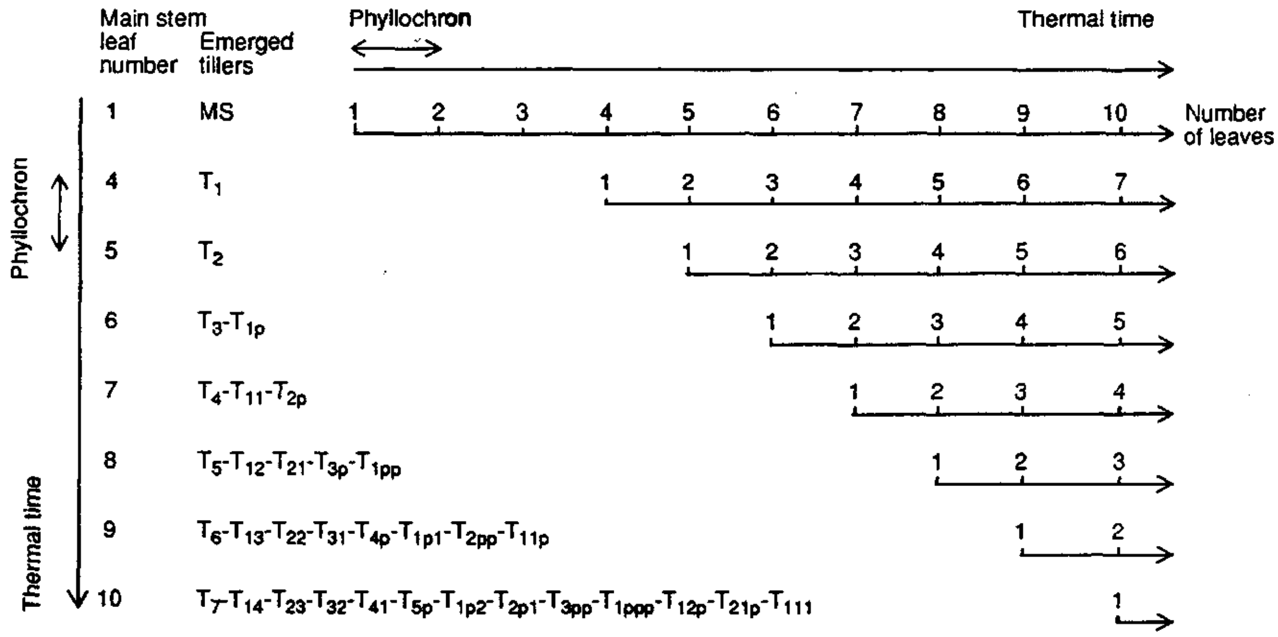


Figure 1.4: Pattern of leaf and tiller appearance for a wheat plant under non-limiting nutrition (Masle-Meynard and Sebillotte, 1981). The coleoptile tiller is not represented because it is rarely observed under experimental conditions and does not have a stable development pattern.

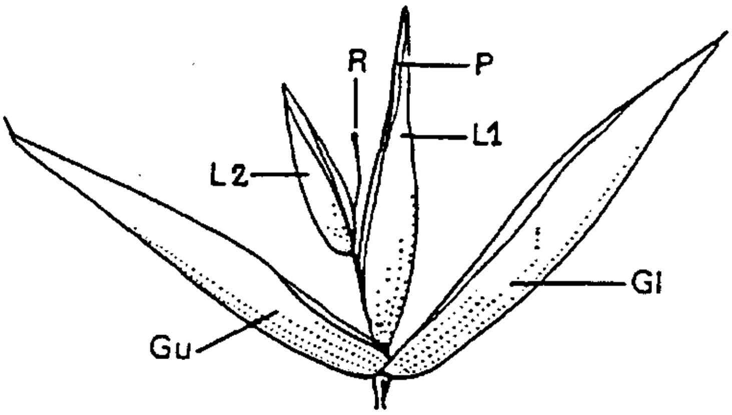


Figure 1.5: Component parts of an oat panicle and the way of spikelet sampling (numbers 1 - 10 show the position of the spikelets in which the weight of grains was measured).

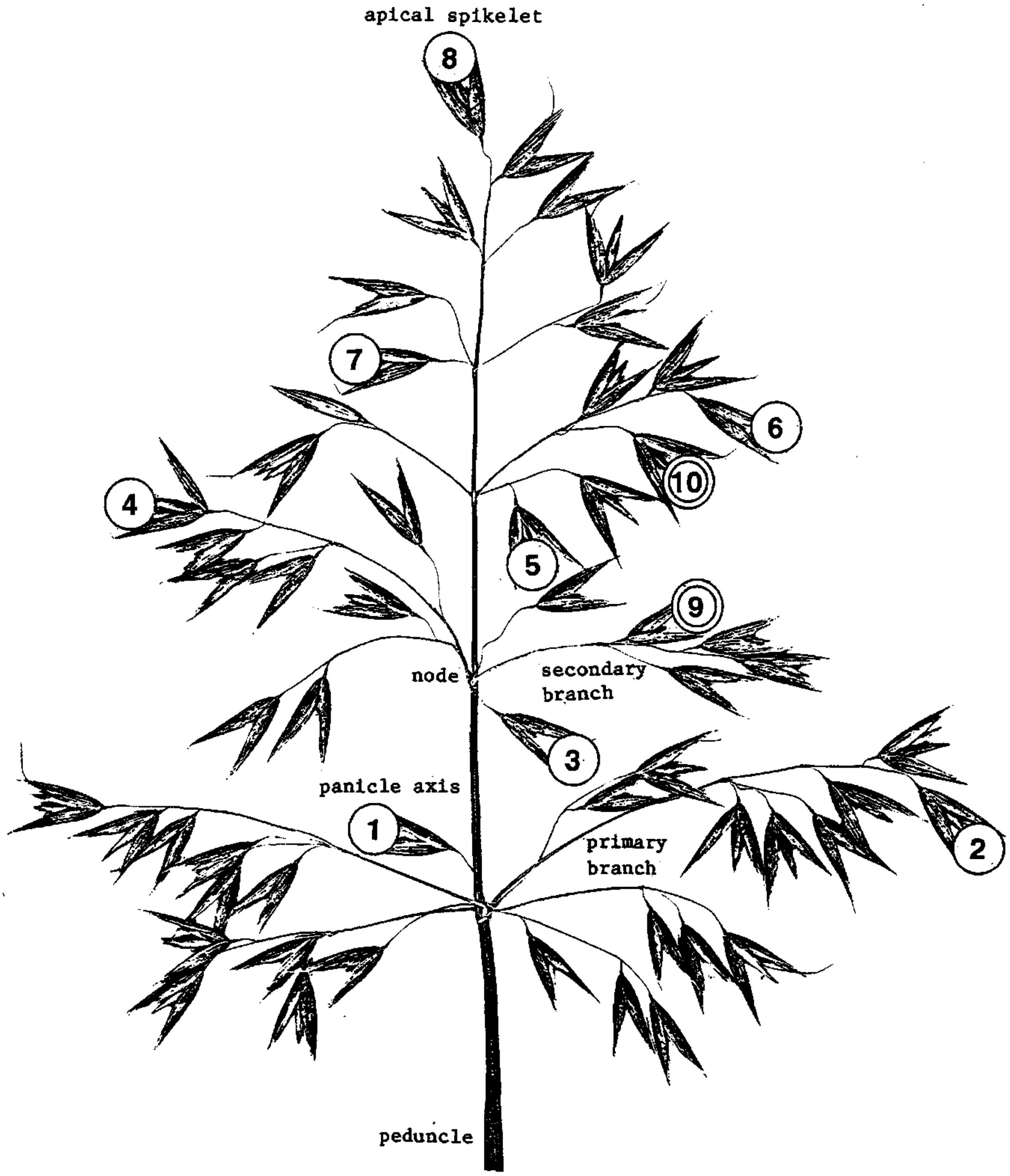


Figure 1.6: Single spikelet (Gl - lower glume, Gu - upper glume, L1 - lemma of the primary grain, L2 - lemma of the secondary grain, P - palea, R - rachilla).

2. MATERIALS AND METHODS

Field conditions

The field experiments were carried out in 1990 and 1991 by the Centre for Agrobiological Research (CABO-DLO) Wageningen at the Droevendaal experimental farm on sandy soil with characteristics as given in Table 1:

Table 1: Characteristics of the soils in the 1990 and 1991 oat experiments.

Characteristic	1990	1991
Organic matter content (%)	4.6	2.6
pH-KCl	5.8	5.4
MgO-NaCl (mg/kg)	70	106
Pw (mg/kg)	41	50
K-number (mg/kg)	12	20
K-HCl (mg/kg)	-	13

The preceding crop was potatoes in both years. Potassium fertilizer, (Kali-zout 60, (containing 60 % potassium) was applied in spring before soil preparation at a dose of 200 kg/ha in 1990 and 100 kg/ha in 1991. Phosphorus fertilizers were not applied, as the phosphorus status of the soil, expressed in the Pw number was considered adequate.

Weather conditions during the experimental periods, in comparison to long-term average conditions, are given in table 2.

Varieties used in experiments

Wilma - variety from the Dutch list of varieties, derived from a cross Kr. Perona x Cebeco 7633 and introduced in 1986. The variety is adapted the Dutch conditions, where it matures rather early and gives good to very good yields; it provides satisfactory ground cover and has rather good lodging resistance, even if the straw is rather long; it has good field resistance against powdery mildew.

Cebeco 8852 - new breeding material derived from a cross (OtB 184 x Gambo) x Cebeco 7858. This material has very short straw, 30 - 40 cm shorter than common oat varieties like Wilma; the much improved straw stiffness entails very good resistance to lodging and shattering; it is susceptible to powdery mildew, and should be sown as early as possible in spring, ripening is fairly late, the yielding capacity is good.

Nitrogen treatments

Three nitrogen treatments were applied (kg/ha): N1, no nitrogen dressing; N2, 100 - v + 40; N3, 100 - v + 40 + 60, with v total mineral nitrogen in the soil layer 0-60 cm just prior to the first dressing. This value was in 1990 24.4 kg/ha (rounded to 20) and in 1991 33.8 kg/ha (rounded to 30). The first dose of nitrogen (100-v) was applied in spring during soil preparation, the second dose (40 kg/ha) at the beginning of stem elongation (DC 30 - 32, Zadoks et al., 1974) and the third one (60 kg/ha) at the flag leaf stage (DC 37 - 39).

Nitrogen was applied in all cases as kalkammon (NH_4NO_3, 26% N).

Experimental design

In both years field experiments were arranged in two parts, each consisting of a randomized block design with four replicates. One part, comprising 24 plots (2 varieties, 3 nitrogen treatments, and 4 replicates) was used for periodic sampling during the vegetation period. The other part of the experiment also comprising 24 plots was retained for the final combine harvest.

Each plot consisted of 20 rows each of 15 m length, with rows 0.14 m apart, i.e. a gross area of 42 m^2. The net area harvested by combine harvester was 10 x 2.25 = 22.5 m^2. Experiments were sown by standard drill machine at a seeding rate of 300 seeds per m^2. Crop management practices are detailed in Table 3.

Table 2: Basic characteristics of weather conditions per decade during the experimental periods (March-August) in comparison to long-term average (1954-1991) conditions (x = average d = difference from long term average, M-month).

Month	Decade	Average air temp. at 1.5 m (°C)				Precipitation (mm)				Cumulative global radiation (J/cm^2)				Vapour preasure at 1.5 m (mb)				Wind speed at ^{2}m (m/s)			
		1990		1991		1990		1991		1990		1991		1990		1991		1990		1991	
		x	d	x	d		d		d		d		d	x	d	x	d	x	d	x	d
3	I	6.9	2.9	8.7	4.7	15.4	-0.3	8.9	- 6.8	5402	-1302	6278	-426	8.7	1.6	9.0	1.9	5.4	2.4	2.9	-0.1
	II	9.7	4.7	10.5	5.5	4.2	-15.1	7.3	-12.0	12017	4503	7531	17	9.0	1.7	10.4	3.1	2.5	-0.7	2.9	-0.3
	III	7.5	1.0	6.8	0.3	13.4	-9.7	1.1	-22.0	11635	2764	14363	5492	8.3	0.5	6.8	-1.0	3.3	-	3.0	-0.3
	M	8.0	2.8	8.6	3.4	33.0	-25.1	17.3	-40.8	29054	5965	28172	5083	8.7	1.3	8.7	1.3	3.7	0.5	2.9	-0.3
4	I	6.6	-0.5	9.5	2.4	8.9	-9.1	9.9	-8.1	17210	6492	13012	2294	6.6	-1.5	8.7	0.6	3.2	0.1	4.2	1.1
	II	7.4	-0.5	8.9	1.0	35.1	18.9	11.1	-5.1	11810	-1127	15946	3009	8.3	-	7.2	-1.1	3.3	0.3	2.6	-0.4
	III	11.6	2.8	6.6	-2.2	6.4	-9.1	15.2	-0.3	17567	2870	14950	253	10.3	1.6	7.0	-1.7	2.6	-0.1	2.6	-0.1
	M	8.5	0.6	8.3	0.4	50.4	0.7	36.2	-13.5	46587	8235	43908	5556	8.4	-	7.6	-0.8	3.1	0.2	3.1	0.2
5	I	17.2	6.1	8.2	-2.9	9.5	-8.6	13.1	-5.0	21741	6506	14049	-1186	11.8	1.8	8.2	-1.8	2.3	-0.5	2.3	-0.5
	II	12.2	-0.2	9.6	-2.8	18.6	0.7	18.4	0.5	14836	-1568	14772	-1632	10.4	-0.5	9.2	-1.7	2.4	-0.3	2.4	-0.3
	III	12.3	-0.6	11.5	-1.4	-	-19.0	0.3	-18.7	26541	9408	19867	2734	8.8	-2.3	10.2	-0.9	1.7	-0.9	2.2	-0.4
	M	13.8	1.6	9.8	2.4	28.1	-26.9	31.8	-24.2	63118	14346	48688	-84	10.3	-0.4	9.2	-1.5	2.1	-0.6	2.3	-0.4
6	I	13.7	-0.9	11.1	-3.5	36.4	-13.1	19.7	-3.6	13142	-4031	13886	-3287	12.3	-0.3	10.1	-2.5	2.6	0.1	2.7	0.2
	II	14.2	-0.9	12.4	-2.7	17.2	-5.8	50.1	27.1	14736	-2903	12585	-5054	12.6	-0.4	11.3	-1.7	1.5	-1.0	3.6	1.1
	III	17.0	1.2	14.7	-1.1	77.4	54.3	63.8	40.7	16532	313	12350	-3869	15.3	1.4	13.5	-0.4	2.9	0.3	3.2	0.6
	M	15.0	-0.1	12.7	-2.4	131.0	61.6	133.6	64.2	44410	-6621	38821	-12210	13.4	0.2	11.6	-1.6	2.3	-0.2	3.2	0.7
7	I	14.2	-2.6	21.0	4.2	32.2	10.2	9.5	-12.5	12631	-4252	21993	5110	13.1	-1.5	16.9	2.3	3.9	1.4	3.0	0.5
	II	17.0	0.2	17.4	0.6	-	-29.8	20.0	-9.8	24090	8576	14125	-1389	13.3	-1.8	15.5	0.4	0.4	-2.1	3.4	0.9
	III	18.4	1.5	18.6	1.7	2.5	-22.6	11.6	-13.5	21856	6593	21385	6122	14.4	-0.8	14.5	-0.7	0.1	-2.4	1.8	-0.7
	M	16.6	-0.2	19.0	2.2	34.7	-42.2	41.1	-35.8	58576	10917	57502	9843	13.6	-1.4	15.6	0.6	1.4	-1.1	2.7	0.2
8	I	19.4	2.1	19.1	1.8	15.1	-4.4	0.1	-19.4	18942	3909	17431	2398	14.7	-0.6	16.2	0.9	1.0	-1.2	1.2	-1.0
	II	17.4	0.5	16.7	-0.2	40.4	13.8	5.4	-21.2	15645	1644	14895	895	14.3	-0.6	13.9	-1.0	3.0	0.5	2.4	-0.1
	III	17.7	1.7	17.7	1.7	11.7	-12.9	0.9	-23.7	13973	712	19434	6173	16.3	1.9	13.1	-1.3	1.5	-0.9	2.3	-0.1
	M	18.2	1.5	17.8	1.1	67.2	-3.5	6.4	-64.3	48561	6265	51760	9465	15.1	0.3	14.3	-0.5	1.8	-0.6	1.9	-0.5

Table 3: Crop management practices during the vegetation periods in 1990 and 1991

a/ Nitrogen dressing	1990	1991
1st dose	10/4	17/4
2nd dose	19/5	5/6
3rd dose	8/6	20/6

b/ Crop protection treatments

Year	Date	Pesticide	Dose per hectare
1990	28/4	Demithoaat	2.0 l
	4/5	MCPA	2.5 l
		MCPP	2.5 l
	21/5	Pirimor	0.3 kg
	23/5	Cycocel	2.0 l
	31/5	Corbel	1.0 l
	28/6	Pirimor	0.5 kg
	26/7	Decis	0.3 l
1991	8/5	MCPA	0.5 l
		MCPP	0.5 l
	1/7	Corbel	1.0 l
	1/7	Pirimor	0.5 l
	12/7	Corbel	1.0 l

Table 4: Timing of crop phenological observations stages for oatsin 1990 and 1991

Phenological data were recorded using the decimal code of Zadoks et al. (1974). The timing of the main phenological stages characterising crop development is given in Table 4.

Phenological stage	DC	1990	1991
Sowing date	-	17/3	20/3
Germination (50 %)	07	30/3	2/4
Beginning of tillering	20 - 21	23/4	1/5
Beginning of stem elongation	30 - 31	18/5	30/5
Flag leaf appearance	37 - 39	8/6	18/6
Heading	53 - 56	23/6	30/6
Anthesis	63 - 66	29/6	4/7
Ripening	91 - 92	5/8	11/8
Combine harvest	-	9/8	19/8

Sampling procedures and measurements

a. Soil sampling

Before sowing, before the second and third nitrogen dressing, and before final harvest the soil layers 0-20, 20-40, 40-60 and 60-100 cm were sampled for determination of mineral nitrogen and water content.

b. Classical growth analysis

In the course of the growing period (8 times in 1990, 25/4, 9/5, 21/5, 5/6, 19/6, 3/7, 17/7, 31/7, and 4 times in 1991, 24/4, 13/5, 8/7, 18/8) plants were sampled (16 times 0.7 m row length in 1990, 8 times 1 m row length in 1991) to determine:

- number of plants and tillers in 5 rows in 1990 and in 3 rows in 1991;
- fresh and dry weight of aboveground biomass in whole samples;
- on subsamples of 25 plants at each harvest: fresh weight, dry weight, nitrogen content, water soluble carbohydrate content, number of live and dead leaves, leaf area, weight of above- and belowground plant

parts, weight of panicles, number of spikelets and grains per panicle.

c. Grain filling measurements

1990

Eight times during the grain filling period (19/6, 27/6, 3/7, 10/7, 17/7, 25/7, 31/7, and 8/8) grains from the 25 main stem panicles were separated, and dried to constant weight at 50-70 °C. The number of spikelets per panicle was also counted.

1991

Starting from anthesis, five randomly selected main stem panicles per plot were sampled periodically during the grain filling period (1/7, 9/7, 16/7, 20/7, 23/7, 27/7, 30/7, 3/8, 6/8, 12/8, and 19/8) for determination of the primary and secondary grain dry weight. Grains were sampled from 10 spikelets in different positions in the panicle (Fig. 1.5), to establish possible effects of spikelet position on grain filling. The panicles were dried to constant weight at temperatures of 50-70 °C before grain separation and weighing.

d. Grain weight variability measurements

Five randomly selected main stem panicles were sampled from each treatment at ripening. The structural parts of the panicle (modules - nodes, branches, and spikelets) were counted and the weight of all primary and secondary grains was measured individually.
A 15 g sample of combine-harvested grain after cleaning was taken from each treatment to measure individual grain weight.

e. Combine harvest

After combine harvest the grain was cleaned and fresh weight per plot determined. Subsamples of about 1 kg of grain were taken for determination of dry weight, thousand grain weight, nitrogen content and grain quality parameters. Grain yields were expressed at standard 16 % water content.

Data processing

Results from the experiments were subjected to analysis of variance according to the model for randomized block design and to linear and non-linear regression analyses. For grain variability analyses common characteristics of variability (mean, maximum and minimum values, range, variance, standard deviation, coefficient of variation, skewness and standard error of skewness) were used.

The data were processed by the GENSTAT 5 program.

3 RESULTS

3.1 GROWTH ANALYSIS

Classical growth analysis (Watson, 1947) considers the plant and crop from the point of view of dry matter accumulation and its partitioning among the various plant parts. For cereals usually six components are distinguished for partitioning of dry matter (stems below ground, stems and sheaths, green leaf, dead leaf, chaff and frame, grain). This type of analysis has been performed for the experiments described in Chapter 2, eight times in 1990 and five times in 1991.

Results for variety Wilma are given in table 5 and figs. 3.1.1 and 3.1.2, those for Cebeco 8852 are in table 6 and figs. 3.1.3 and 3.1.4. A number of characteristics are in agreement with earlier published results of growth analyses of cereals in general and oats in particular (Frey et al., 1967; Brinkman and Frey, 1977; Frey, 1988):

1. Crops without nitrogen dressing (N1) produced significantly lower total aboveground dry matter than those supplied with additional nitrogen (N2 and N3).
2. Differences in total dry matter production between N2 and N3 nitrogen treatments were very small for both varieties and in both years.
3. These differences in dry matter production are also reflected in leaf area indices (figs. 3.1.5 and 3.1.6).
4. The pattern of dry matter partitioning was very stable and neither variety nor year had a significant effect, despite significantly higher biological and grain yields in 1991.
5. At the higher doses of nitrogen (N2 and N3) the partitioning between stems and sheats and green leaf was modified in favour of green leaf. This is also evident in figs. 3.1.5 and 3.1.6, representing the dynamics of leaf area formation.
6. The last dose of nitrogen (60 kg/ha at the flag leaf stage-N3) slightly increased leaf area and the proportion of green leaf dry matter, which is in agreement with common knowledge that high nitrogen availability maintains vegetative growth and reduces the rate of senesence.
7. Between the last two sampling dates (17/7 and 31/7) in 1990, total aboveground dry matter decreased for both varieties under N1 and N3

(figs. 3.1.1 and 3.1.3). In N1 this reduction is associated with a relatively higher decrease in stem and sheath dry matter, in N3 with a decrease in green leaf dry matter.

8. Although the yield in 1991 was significantly higher, the ranking among the varieties and the nitrogen treatments was practically the same in both years (Fig. 3.1.7).

These results may be considered representative for crop growth dynamics and yield formation in field experiments. In this section special attention will be paid to crop and plant structure.

Table 5: Aboveground dry matter accumulation and partitioning for variety Wilma in 1990 and 1991.

Date	Total aboveground dry matter (g/m^2)	Belowground stems*	Partitioning of aboveground dry matter (%)				
			Stems and sheaths	Green leaf	Dead leaf	Chaff and frames	**Grain
1990							
N1							
25/4							
9/5	127	14.6	32.7	67.0	0.3		
21/5	283	9.2	45.5	53.0	1.5		
5/6	569		64.9	30.1	5.0		
19/6	844		61.3	13.2	6.2	6.3	13.0
3/7	755		58.0	6.2	4.5	6.6	24.7
17/7	1137		46.3	2.0	4.6	5.3	41.8
31/7	925		35.9		6.3	5.3	52.5
N2							
25/4	17	26.8	13.8	86.2			
9/5	185	13.0	32.3	67.2	0.5		
21/5	380	6.9	47.1	51.8	1.1		
5/6	753		64.7	29.0	6.3		
19/6	954		57.5	16.2	4.7	7.7	13.9
3/7	1418		53.6	10.2	3.7	7.4	25.1
17/7	1454		42.2	6.1	4.8	5.6	41.3
31/7	1530		35.4	0.1	8.1	5.4	51.0
N3							
19/6	1026		57.7	17.2	4.5	7.4	13.2
3/7	1388		53.6	10.6	3.7	7.6	24.5
17/7	1570		42.3	6.8	3.9	6.2	40.8
31/7	1484		35.5	0.4	8.4	5.3	50.4

1991						
N1						
24/4	13	24.8	17.8	82.2		
13/5	86	20.4	30.5	69.5		
4/6	327	11.7	47.1	50.7	2.2	
8/7	839		59.7	9.7	4.2	26.4
19/8	972		35.6		6.0	58.4
N2						
24/4	12	25.2	18.0	82.0		
13/5	110	19.3	30.5	69.5		
4/6	472	10.3	50.7	46.4	2.9	
8/7	1215		55.7	12.6	4.5	27.2
19/8	1496		36.5		7.5	56.0
N3						
8/7	1237		55.9	13.7	3.2	27.2
19/8	1514		37.3		7.3	55.4

(* - belowground stems are not included in total aboveground dry matter, ** - in 1991 grain includes chaff and frames)

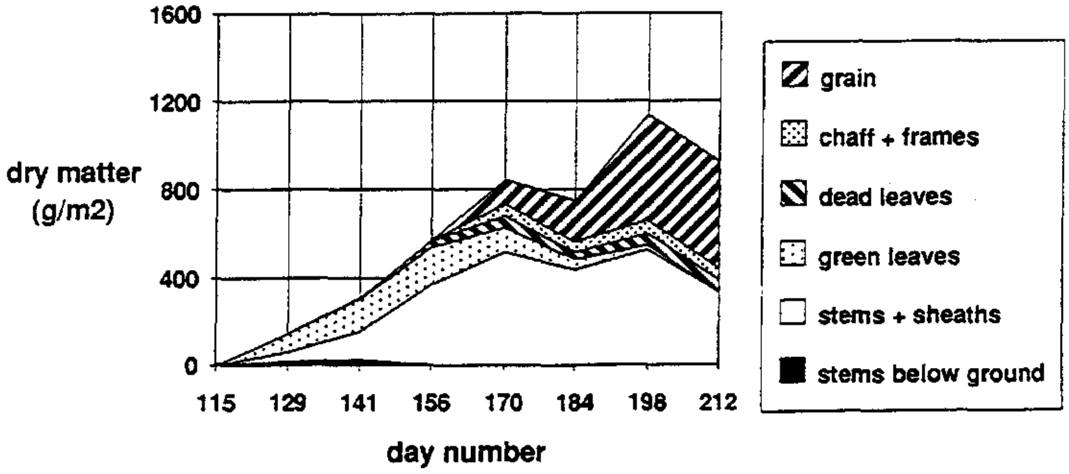
Table 6: Aboveground dry matter acumulation and partitioning for Cebeco 8852 in 1990.

Date	Total above-ground dry matter (g/m^2)		Partitioning of aboveground dry matter (%)				
		Below-ground stems*	Stems and sheaths	Green leaf	Dead leaf	Chaff and frames	**Grain
1990							
N1							
25/4							
9/5	110	16.1	29.0	70.7	0.3		
21/5	260	8.9	43.9	55.0	1.2		
5/6	595		64.3	31.5	4.2		
19/6	805		58.4	16.1	5.3	7.5	12.7
3/7	925		55.9	6.0	6.9	7.1	24.1
17/7	1031		46.3	3.3	4.3	6.0	40.1
31/7	918		34.9	0.1	7.2	6.3	51.5
N2							
25/4	16	25.7	12.3	87.7			
9/5	173	13.6	31.8	67.9	0.3		
21/5	415	6.7	47.9	50.7	1.4		
5/6	772		62.5	31.1	6.5		
19/6	950		53.8	18.1	4.4	9.2	14.5
3/7	1422		51.2	10.8	3.7	8.3	26.0
17/7	1430		39.4	6.4	4.8	6.5	42.9
31/7	1402		32.7		8.4	6.6	52.3
N3							
19/6	1065		54.1	19.1	4.5	8.9	13.4
3/7	1382		49.4	11.4	5.0	8.9	25.3
17/7	1535		39.0	7.4	4.2	6.8	42.6
31/7	1432		33.0	0.2	8.6	6.6	51.6
1991							
N1							
24/4	12	22.7	17.7	82.3			
3/5	92	19.3	28.5	71.5			
4/6	343	11.2	46.5	51.1	2.4		
8/7	860		54.0	11.9	6.0		28.1
19/8	901		30.0		7.4		62.6
N2							
24/4	11	25.0	16.7	83.3			
13/5	102	19.0	28.6	71.4			
4/6	448	10.0	50.8	46.8	2.4		
8/7	1142		50.0	14.0	5.6		30.4
19/8	1411		32.1		9.3		58.6
N3							
8/7	1167		50.3	16.7	4.6		28.4
19/8	1355		31.3		9.1		59.6

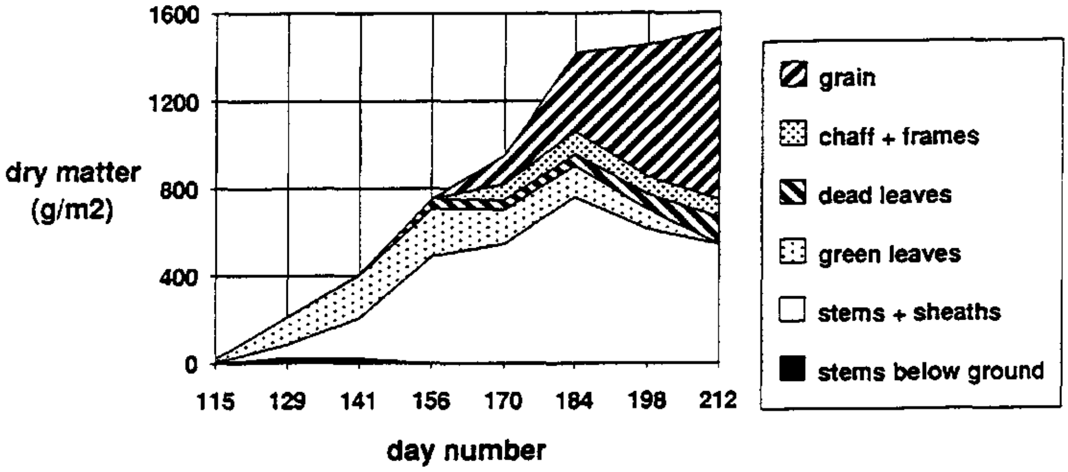
(* - belowground stems are not included in total aboveground dry matter.

** - in 1991 grain includes chaff and frames)

a/ Nitrogen treatment N1



b/ Nitrogen treatment N2



c/ Nitrogen treatment N3

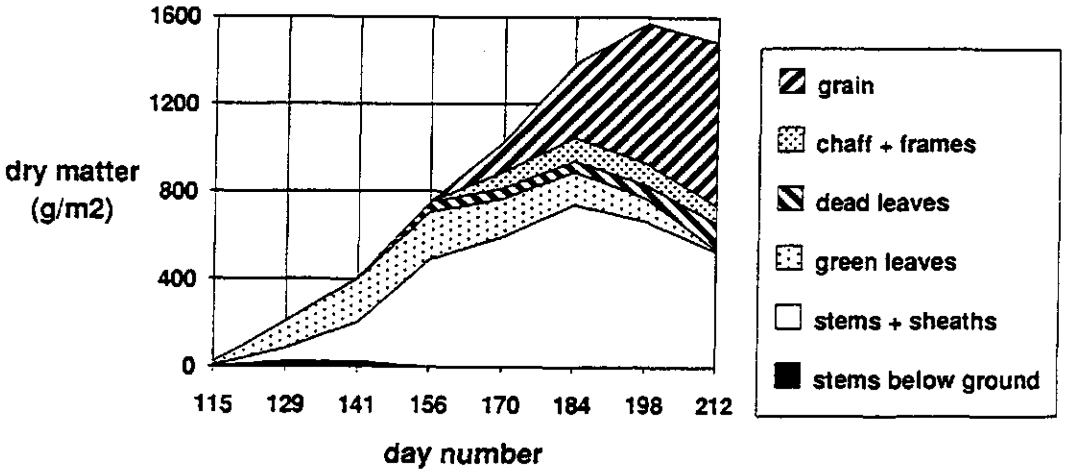
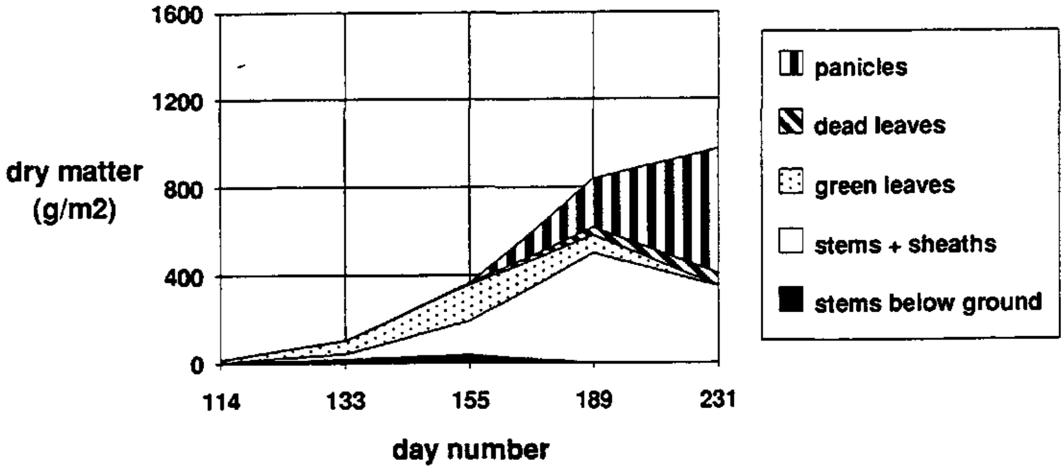
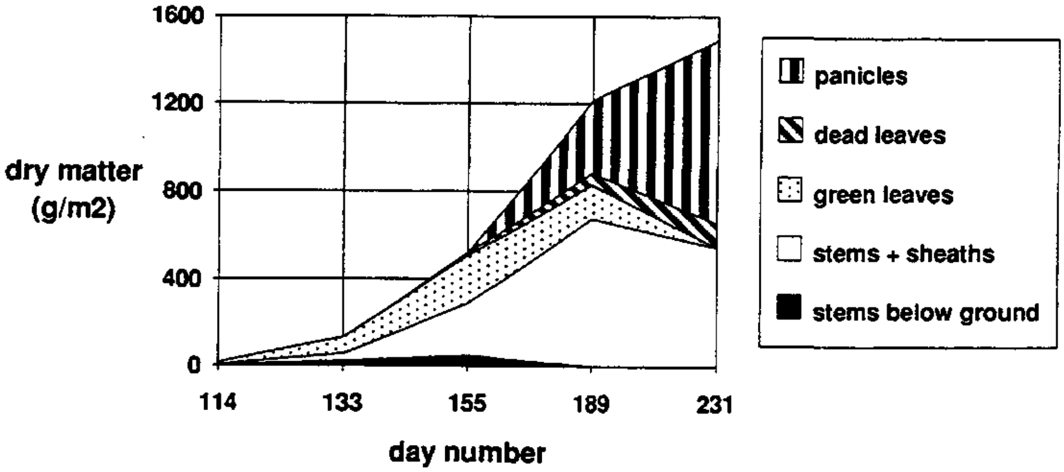


Figure 3.1-1: Dry matter partitioning for variety Wilma in 1990.

a/ Nitrogen treatment N1



b/ Nitrogen treatment N2



c/ Nitrogen treatment N3

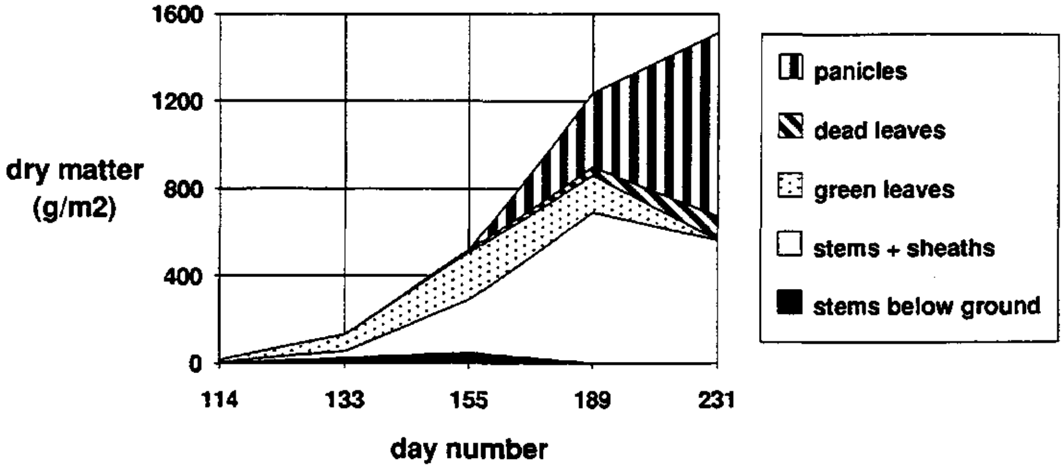
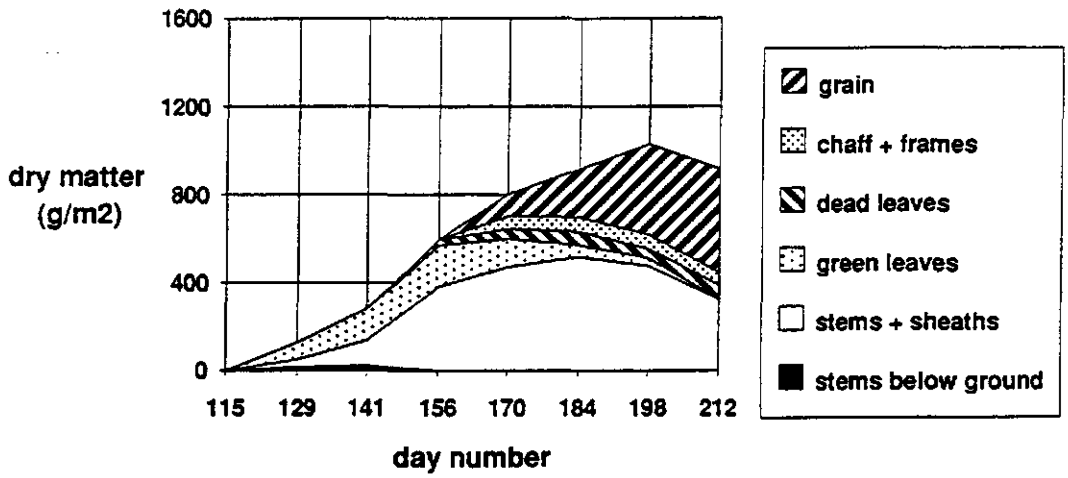
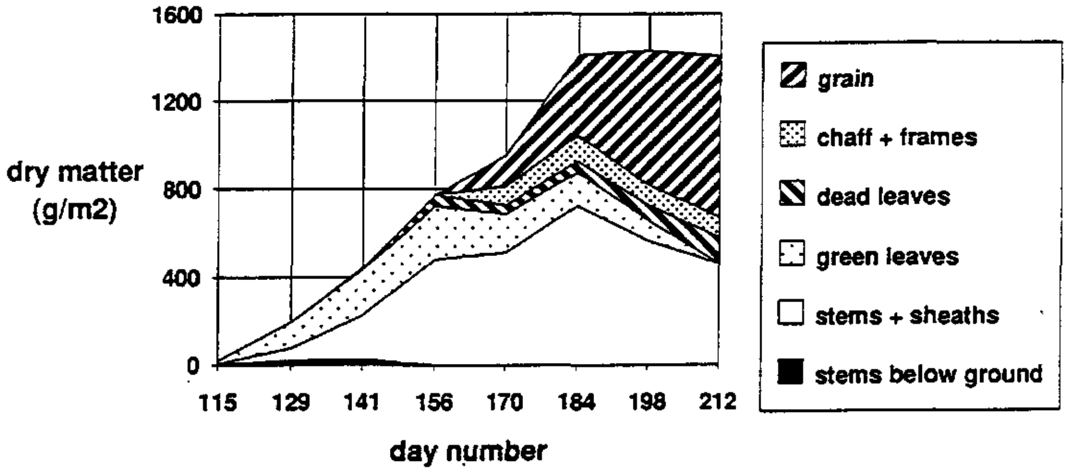


Figure 3.1-2: Dry matter partitioning for variety Wilma in 1991.

a/ Nitrogen treatment N1



b/ Nitrogen treatment N2



c/ Nitrogen treatment N3

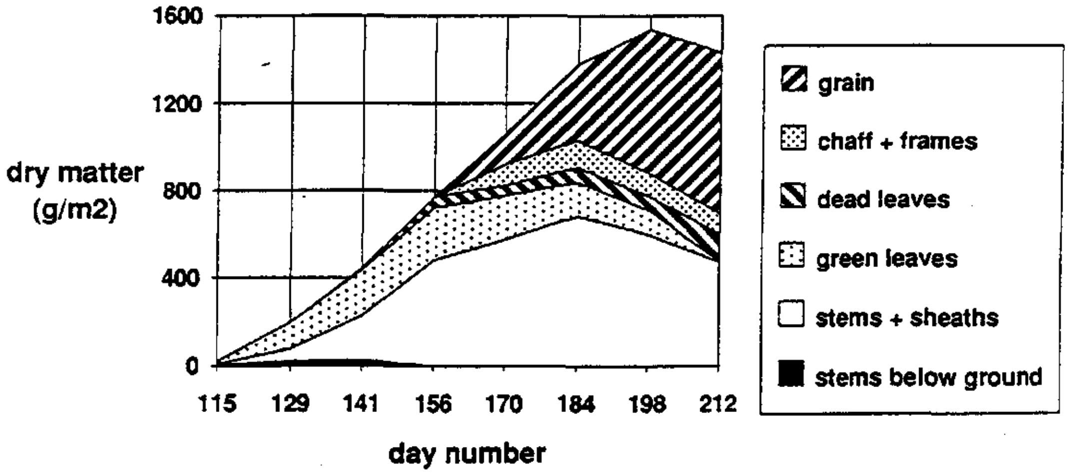
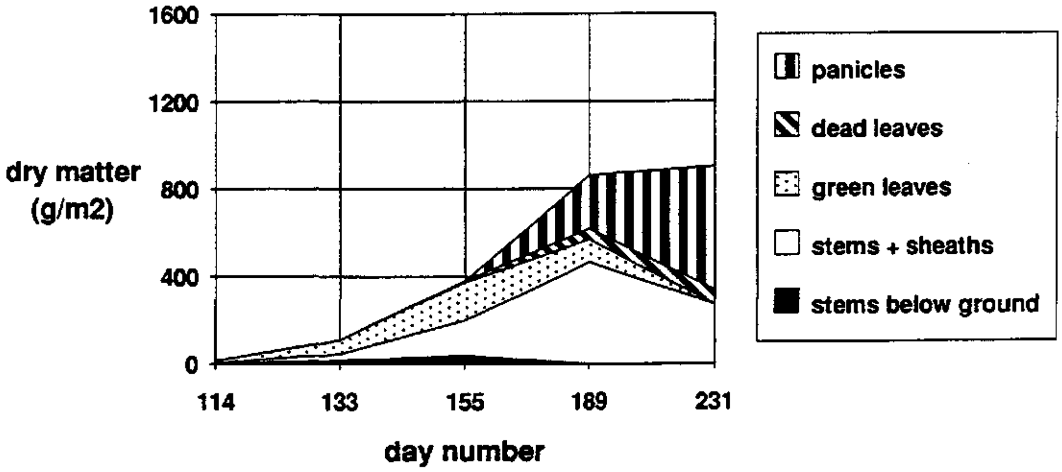
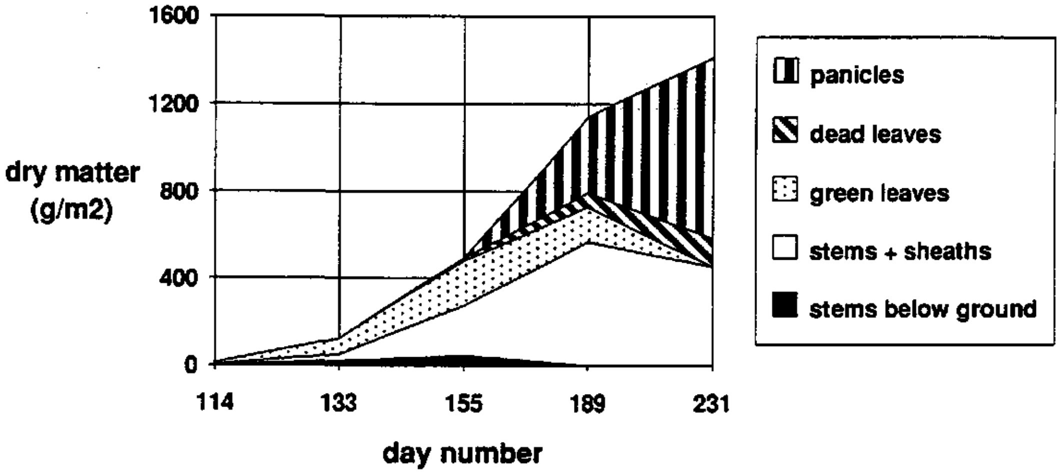


Figure 3.1-3: Dry matter partitioning for Cebeco 8852 on 1990.

a/ Nitrogen treatment N1



b/ Nitrogen treatment N2



c/ Nitrogen treatment N3

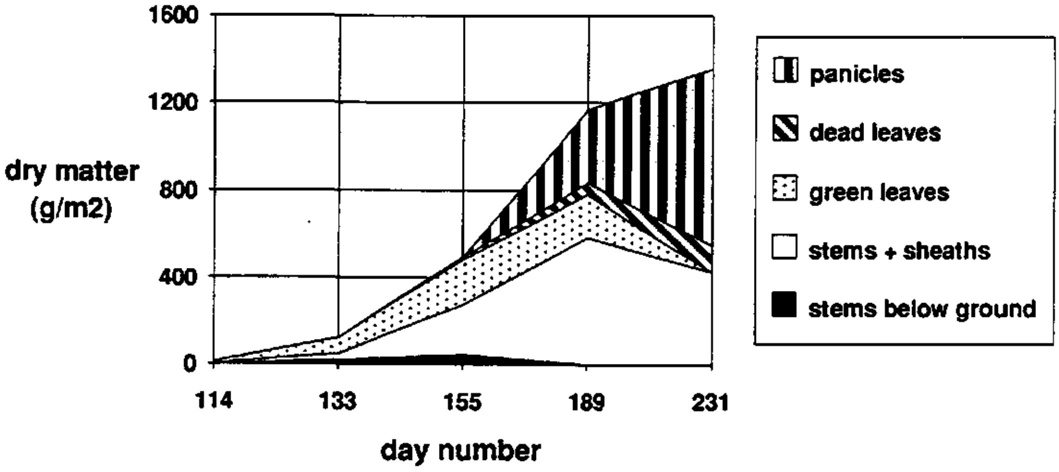
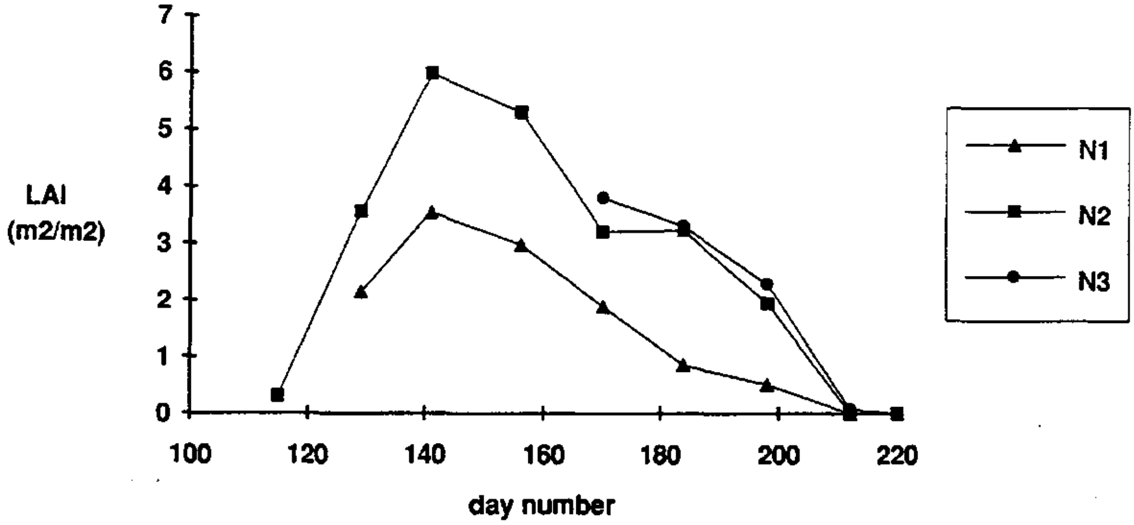


Figure 3.1-4: Dry matter partitioning for Cebeco 8852 in 1991.

a/ Wilma



b/ Cebeco 8852

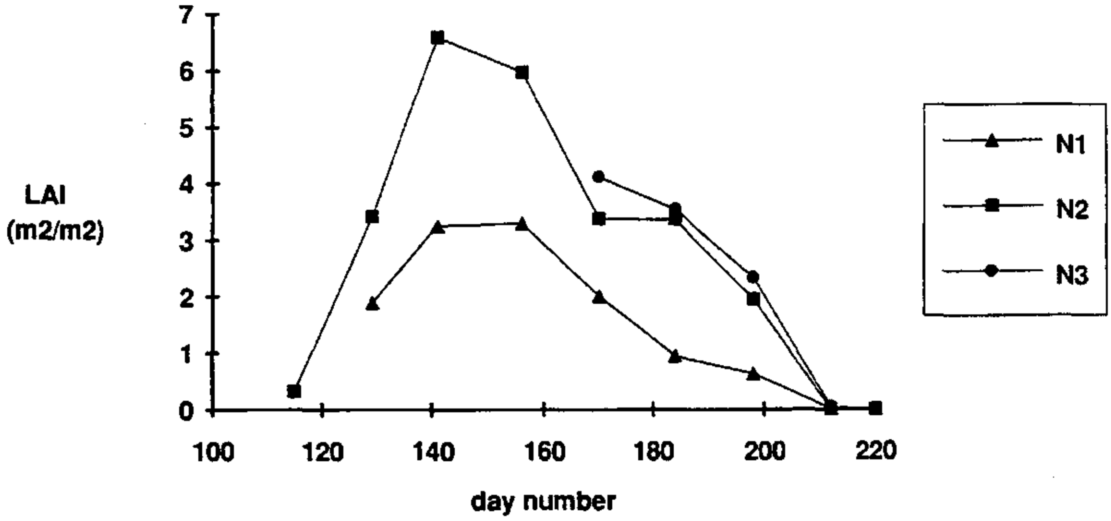
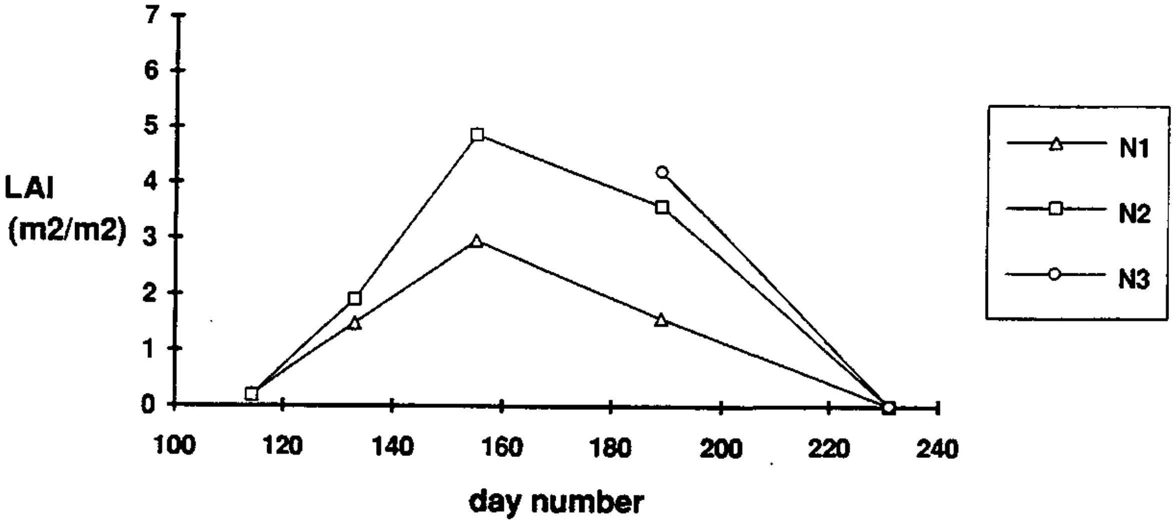


Figure 3.1-5: Leaf area index in 1990.

a/ Wilma



b/ Cebeco 8852

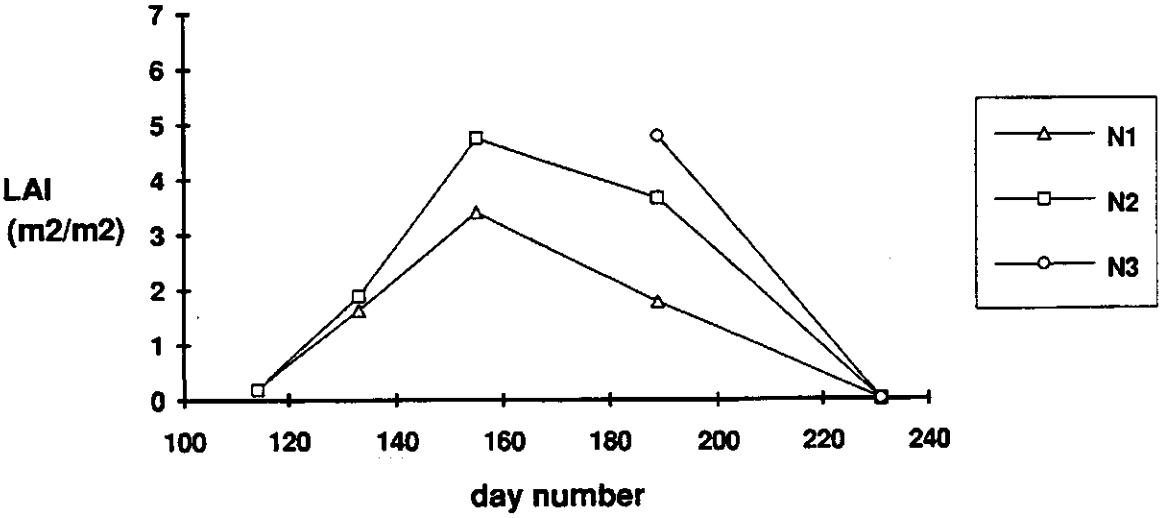


Figure 3.1-6: Leaf area index in 1991.

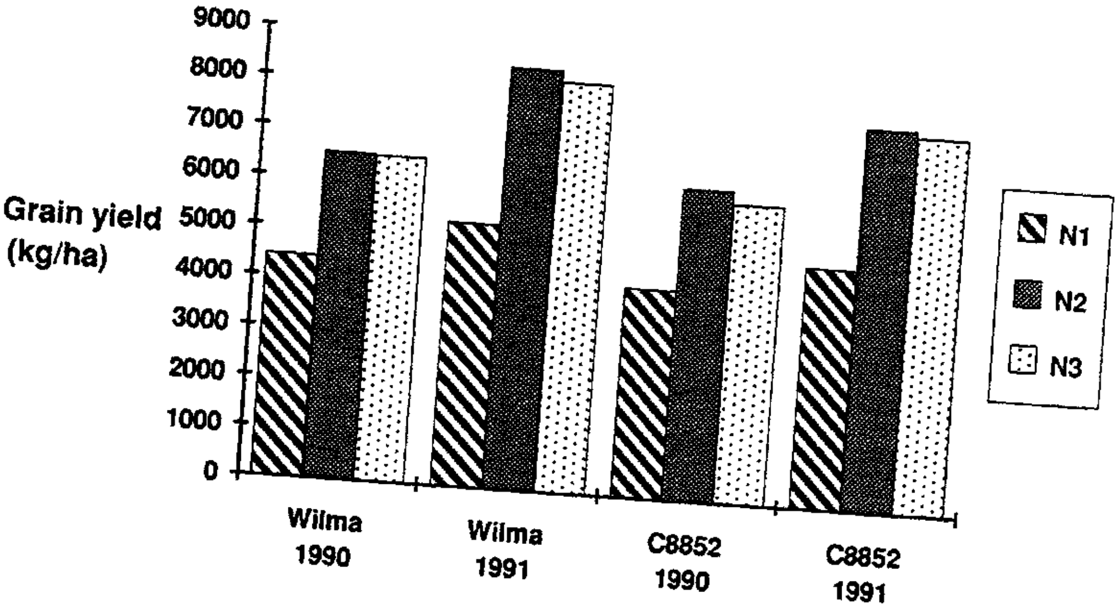


Figure 3.1-7: Grain yield in 1990 and 1991.

3.2 STAND STRUCTURE

Grain yield, thousand grain weight and number of grains per m^2 from the final combine harvest for the various treatments are given in table 7. The differences between years were highly significant and ranged between 12 and 25 %. Wilma showed significantly higher grain yields in both years. The yield under N1 was significantly lower than under N2 and N3 for both varieties in both years (table 7), while that under N3 was slightly lower than under N2, the highest yielding variant in both years for both varieties.

The pattern of grain yield differences is identical to that for the number of grains per m^2, except that differences between varieties are not significant (tables 7 and 8).

Thousand grain weights show an opposite pattern, with the highest values under N1 and those in N2 and N3 significantly lower and similar. Except for Cebeco 8852 in 1991, the values for N3 were slightly lower than for N2. Cebeco 8852 had significantly smaller grains than Wilma. The differences between varieties were larger in 1990 (table 7) and also the thousand grain weights were significantly higher in all experiments in that year (table 8). On the contrary the yield and number of grains per m^2 were significantly higher in 1991.

The explanation is that in 1991 the weather conditions for crop growth and yield formation were more favourable. Crops produced more grains per m^2 as the result of more proliferate panicle branching, but also because more younger and smaller spikelets with smaller grains were produced. The lower values of thousand grain weight under N2 and N3 are from this point of view the result of a higher proportion of "branches" younger in the panicle, containing a higher proportion of smaller grains. Thus, the lower thousand grain weights are the result of developmental delay in later formed spikelets and grains under more favourable growing conditions such abundant nitrogen supply (N2 and N3) or favourable weather conditions (1991).
To confirm these conclusions an analysis of stand structure was made.

As the sowing rate was the same (300 grains/m^2) the number of plants per m^2 was counted for both varieties under N1 and N3. Results in tables 9 and 10 show significant interactions between year and variety. Therefore, average values for individual varieties in both years from table 9 were used in calculating some values given in table 11.

The results given in tables 11-14 may be summarized as follows:

1. Aboveground biomass was higher in 1991 and was significantly influenced by nitrogen treatment in both years and by variety in 1990.
2. The number of stems per plant and per m^2 was significantly influenced by all evaluated factors in the order: year, nitrogen treatment and variety. A significant interaction nitrogen x variety was observed in 1991.
3. The highest total number of stems per m^2 was produced under nitrogen treatment N3.
4. The number of `small' stems was significantly influenced by nitrogen treatment only and the highest numbers were observed under N2.
5. The number of small stems was influenced significantly by nitrogen in both years and by variety in 1990.
6. Cebeco 8852 produced higher numbers of small stems and thus reached higher total numbers of stems.
7. Average weight of big stems was influenced by year, variety and nitrogen treatment. Dry weight of small stems was significantly influenced by year. Both types of stems were bigger in 1991 and bigger in Wilma than in Cebeco 8852.
8. Dry weight of small stems ranged from 16-26 % of big stems in 1990 and from 35-62 % in 1991, respectively. The values for grain dry weight were lower (11-25 % in 1990 and 17-48 % in 1991). Hence, also the harvest index of small stems was lower (table 11).
9. Grain number of small stems was 19 % of that of big stems for Wilma in 1990 and ranged from 30 (N3) to 45 % (N1) in 1991. For Cebeco 8852 these values ranged between 23 (N3) and 32 % (N1) in 1990 and between 32 (N3) and 58 % (N1) in 1991.
10. Average productivity of both big and small stems was highest under N1 and decreased to N3. The difference was significant for small stems only and for big stems there was a significant interaction between nitrogen treatment and year (tables 13 and 14).
11. Average grain weight of both types of stems decreased significantly from N1 to N3 but more pronounced in small stems (table 11b).

Many of these results confirm or support the basic concepts of plant hierarchical structure and modular growth introduced in Chapter 1. This implies that higher growth activity (i.e. higher assimilate supply) in oats results in more profuse branching and consequently in a longer delay for the later formed plant organs and finally in a more extended range for grain weight towards lower values, or in other words lower average thousand grain weights. To quantify the growth modification and the range in delay between the oldest and the youngest grains, special measurements of branching processes as illustrated in Fig. 1.3 are necessary at the level of individual plants.

Table 7: Final yield, thousand grain weight and number of grains per m^2 for two oat varieties in 1990 and 1991.

Characteristic	Year	Wilma			Cebeco 8852		
		N1	N2	N3	N1	N2	N3
Grain yield (t/ha)	1990	4.41	6.49	6.46	4.16	6.20	5.93
	1991	5.10	8.15	7.91	4.65	7.42	7.27
T G W (g)	1990	41.54	35.46	35.32	39.91	34.32	34.14
	1991	40.42	33.63	31.80	36.21	29.51	30.23
Number of grains per m^2	1990	10 620	18 318	18 294	10 476	18 148	17 416
	1991	12 604	24 232	24 862	12 823	25 167	24 095

Table 8: Results of analysis of variance on grain yield, thousand grain weight and number of grains per m^2 from combine harvest (Y = year, V = variety, N = nitrogen treatment, R = replicate, * = significant, ** = highly significant).

Source of variation	d.f.	Grain yield (t/ha)		Thousand grain weight (g)		Number of grains per m^2	
		v.r.	F pr.	v.r.	F pr.	v.r.	F pr.
Stratum Y.R							
Y	1	66.44**	0.001	95.34**	0.001	125.59**	0.001
Residual	6	1.20		0.84		1.24	
Stratum Y.R.N							
N	2	158.17**	0.001	151.14**	0.001	250.38**	0.001
Y.N	2	4.71*	0.031	1.22	0.330	12.80**	0.001
Residual	12	3.17		0.64		2.89	
Stratum Y.R.N.V							
V	1	45.35**	0.001	27.82**	0.001	0.31	0.583
Y.V	1	3.05	0.098	5.14*	0.036	1.20	0.288
N.V	2	0.87	0.437	1.18	0.331	2.22	0.137
Y.N.V	2	0.49	0.622	0.85	0.445	0.39	0.685
Residual	18						
s.e.d. Y		0.1399		0.322		453.8	
N		0.1561		0.430		500.0	
V		0.0715		0.438			
Y.N		0.2281				734.3	
Y.N (x)		0.2207				707.1	
Y.V				0.544			
Y.V (x)				0.619			

(x) - when comparing means with the same level of Y

Table 9: Number of plants per m^2 in 1990 and 1991.

Variant		1990 (9/5)	1991 (13/5)
Wilma	N1	323	281
	N3	328	273
	Mean	326	277
Cebeco 8852	N1	289	303
	N3	295	287
	Mean	292	295

Table 10: Results of analysis of variance on plant number per m^2 (Y = year, V = variety, N = nitrogen treatment, R = replicate).

Source of variation	d.f.	v.r.	F pr.
Stratum Y.R			
Y	1	3.16	0.126
Residual	6	1.28	
Stratum Y.R.N			
N	1	0.08	0.789
Y.N	1	0.58	0.476
Residual	6	0.90	
Stratum Y.R.N.V			
V	1	0.43	0.523
Y.V	1	4.73*	0.050
N.V	1	0.02	0.884
Y.N.V	1	0.04	0.844
Residual	12		
s.e.d.	Y.V	17.29	
Y.V (x)		16.66	

(x) - when comparing means with the same level of Y.

Table 11a: Stand structure in 1990 and 1991 - big stems.

Characteristic	Year	Wilma			Cebeco 8852		
		N1	N2	N3	N1	N2	N3
Number per plant	1990	0.95	1.33	1.34	1.21	1.61	1.52
	1991	0.96	1.04	1.04	0.89	1.23	1.10
Number per m^2	1990	311	433	437	335	447	421
	1991	279	305	303	264	362	324
Weight per stem (g)	1990	2.55	2.60	2.47	2.44	2.65	2.56
	1991	3.56	4.28	4.51	2.55	3.51	3.22
Grain weight per stem (g)	1990	1.24	1.16	1.11	1.21	1.23	1.18
	1991	1.87	2.22	2.30	1.45	1.84	1.75
Grain number per stem	1990	42	43	42	41	48	47
	1991	55	72	77	45	70	62
Weight per grain (mg)	1990	29.85	27.09	26.65	29.78	25.72	24.84
	1991	34.21	31.29	27.91	32.56	25.40	28.90
Harvest index	1990	0.485	0.450	0.445	0.498	0.468	0.462
	1991	0.525	0.520	0.510	0.542	0.522	0.540
Grain number per m^2	1990	13 062	18 619	18 354	13 735	21 456	19 787
	1991	15 345	21 960	23 331	11 880	25 340	20 088
Grain yield per m^2 (g)	1990	386	502	485	405	550	497
	1991	522	677	697	383	666	567

Table 11b: Stand structure in 1990 and 1991 - small stems.

Characteristic	Year	Wilma			Cebeco 8852		
		N1	N2	N3	N1	N2	N3
Number per plant	1990	0.07	0.28	0.41	0.16	0.42	0.65
	1991	0.07	0.13	0.23	0.04	0.23	0.30
Number per m^2	1990	24	92	134	45	116	181
	1991	20	38	67	13	69	88
Weight per stem (g)	1990	0.46	0.44	0.46	0.64	0.46	0.42
	1991	1.64	1.49	1.33	1.57	0.83	1.81
Grain weight per stem (g)	1990	0.20	0.13	0.13	0.30	0.13	0.13
	1991	0.89	0.77	0.58	0.81	0.32	0.70
Grain number per stem	1990	8	8	8	13	12	11
	1991	25	26	23	26	17	23
Weight per grain (mg)	1990	23.81	17.02	16.73	23.29	11.01	11.45
	1991	35.84	29.38	25.20	31.67	17.39	23.96
Harvest index	1990	0.415	0.290	0.288	0.463	0.263	0.300
	1991	0.535	0.520	0.430	0.525	0.377	0.407
Grain number per m^2	1990	192	736	1 072	585	1 392	1 991
	1991	500	988	1 541	338	1 173	2 024
Grain yield per m^2 (g)	1990	5	12	17	14	15	24
	1991	18	29	39	11	22	62

Table 11c: Stand structure in 1990 and 1991 - all stems combined.

Characteristic	Year	Wilma			Cebeco 8852		
		N1	N2	N3	N1	N2	N3
Aboveground	1990	960	1 554	1 394	986	1 483	1 433
biomass (g/m^2)	1991	1 065	1 627	1 648	992	1 546	1 481
Stem number	1990	335	524	571	380	563	602
per m^2	1991	299	343	370	277	431	412
Grain number	1990	13 254	19 355	19 426	14 320	22 848	21 778
per m^2	1991	15 845	22 948	24 872	12 218	26 513	22 112
Grain yield (*)	1990	4.54	5.96	5.82	4.86	6.55	6.04
(t/ha)	1991	6.26	8.19	8.54	4.57	7.98	7.30

(*) - At 16% grain moisture content

Table 12: Results of analysis of variance on the total aboveground biomass and numbers of stems per m^2 (Y = year, V = variety, N = nitrogen, R = replicate, * = significant, ** = highly significant).

Source of variation	d.f.	Biomass (g/m^2) v.r.	F pr.	All stems v.r.	F pr.	Big stems v.r.	F pr.	Small stems v.r.	F pr.
Stratum Y.R									
Y	1	7.79*	0.032	61.81**	0.001	41.82**	0.001	41.38**	0.001
Residual	6	1.42		0.89		1.65		0.39	
Stratum Y.R.N									
N	2	160.45**	0.001	30.18**	0.001	25.70**	0.001	18.64**	0.001
Y.N	2	1.19	0.339	3.88*	0.050	3.36	0.070	2.09	0.166
Residual	12	1.51		4.00		1.03		3.70	
Stratum Y.R.N.V									
V	1	6.00*	0.025	15.40**	0.001	1.75	0.203	12.74**	0.002
Y.V	1	5.52*	0.030	0.01	0.927	0.42	0.525	1.49	0.238
N.V	2	0.50	0.615	2.53	0.107	1.01	0.385	1.58	0.233
Y.N.V	2	1.62	0.225	3.23	0.063	1.51	0.248	0.73	0.496
Residual	18								
s.e.d. Y		32.7		17.88		14.04		7.73	
N		33.7		23.16		13.38		15.13	
V		22.4		9.46				6.42	
Y.N				32.17					
Y.N (x)				32.75					
Y.V		39.7							
Y.V (x)		31.7							

(x) - when comparing means at the same level of Y

Table 13: Results of analysis of variance on mean big stem characteristics in 1990 and 1991 (Y = year, V = variety, N = nitrogen treatment, R = replicate, * = significant, ** = highly significant).

Source of variation	d.f.	Stem dry matter (g) v.r.	F pr.	Grain dry matter (g) v.r.	F pr.	Grain number v.r.	F pr.	Individual grain weight (mg) v.r.	F pr.	Harvest index v.r.	F pr.
Stratum Y.R											
Y	1	84.43**	0.001	219.32**	0.001	88.23**	0.001	24.41**	0.003	48.93**	0.001
Resid.	6	1.61		0.81		1.59		1.55		1.54	
Stratum Y.R.N											
N	2	11.26**	0.002	3.83	0.052	23.49**	0.001	43.48**	0.001	5.04*	0.026
Y.N	2	7.68**	0.007	6.95**	0.010	11.05**	0.002	1.14	0.353	1.58	0.246
Resid.	12	0.61		0.57		0.35		0.68		0.97	
Stratum Y.R.N.V											
V	1	19.03**	0.001	8.61**	0.009	1.07	0.315	9.20**	0.007	5.60*	0.029
Y.V	1	19.67**	0.001	11.90**	0.003	4.98*	0.039	1.04	0.321	0.00	0.952
N.V	2	0.39	0.680	0.12	0.883	0.67	0.526	3.50	0.052	0.34	0.715
Y.N.V	2	0.58	0.572	0.25	0.784	0.65	0.535	3.89*	0.039	0.36	0.705
Resid.	18										
s.e.d. Y			0.115		0.048		2.09		0.551		0.008
N			0.111				2.03		0.542		0.008
V			0.116		0.071				0.538		0.007
Y.N			0.173		0.090		3.14				
Y.N (x)			0.157		0.093		2.87				
Y.V			0.164		0.086		3.48				
Y.V (x)			0.164		0.100		3.93				
Y.N.V									1.251		

(x) - when comparing means at the same level of Y

Table 14: Results of analysis of variance on mean small stem characteristics in 1990 and 1991
(Y = year, V = variety, N = nitrogen treatment, R = replicate, * = significant, ** = highly significant).

Source of variation	d.f.	Stem dry matter (g) v.r.	Stem dry matter (g) F pr.	Grain dry matter (g) v.r.	Grain dry matter (g) F pr.	Grain number v.r.	Grain number F pr.	Individual grain weight (mg) v.r.	Individual grain weight (mg) F pr.	Harvest index v.r.	Harvest index F pr.
Stratum Y.R											
Y	1	100.25**	0.001	110.16**	0.001	77.57**	0.001	78.81**	0.001	68.84**	0.001
Resid.	6	0.67		1.17		1.13		0.62		0.56	
Stratum YRN		1.94	0.186	8.53**	0.005	1.12	0.357	19.99**	0.001	15.92**	0.001
N	2	1.16	0.347	1.51	0.261	0.46	0.643	0.05	0.948	1.27	0.316
Y.N	2	1.17		0.91		1.03		1.32		0.90	
Resid.	12										
Stratum Y.R.N.V											
V	1	0.02	0.902	1.30	0.270	0.61	0.445	15.15**	0.001	1.16	0.296
Y.V	1	0.43	0.521	3.06	0.097	5.77*	0.027	0.56	0.464	2.45	0.135
N.V	2	2.18	0.142	3.61*	0.048	1.19	0.327	2.77	0.089	2.02	0.162
Y.N.V	2	2.57	0.104	3.15	0.067	1.41	0.269	1.46	0.258	0.29	0.751
Resid.	18										
s.e.d. Y			0.096		0.048		1.50		1.13		0.016
N					0.055				1.76		0.026
V							1.25				
Y.V							2.04				
Y.V (x)							1.96				
N.V					0.079						
N.V (x)					0.081						

(x) - when comparing means at the same level of Y and N respectively

3.3 GRAIN FILLING

Grain filling in 1990

Grain growth was not followed at individual positions within the spikelet and the panicle, hence the values of grain dry matter accumulation refer to total weight per unit area (Fig. 3.3.1) or an `average' grain (Fig. 3.3.2). Growth curves for average grains are different per variety and nitrogen treatment. From Fig. 3.3.2 it may be concluded:

- Wilma forms larger grains than Cebeco 8852
- the largest average grains were produced under nitrogen treatment N1, those under N2 and N3 were smaller and differed only slightly.

The differences per unit area between N1 and N2 or N3 are bigger for both varieties (Fig. 3.3.1). The higher growth rate for N2 and N3 especially between the last two measurements is probably associated with growth of later formed grains.

Grain filling in 1991

Destructive measurements of grain weight preclude continuous measurement of the weight increments of the same grains. Differences in weight between individual grains located at the same position in the panicle were often very large and this was a major source of variability in experimental data.

To evaluate the influence of other factors on grain weight variability, an analysis of variance has been performed on each of the eleven samplings during the grain filling period. Sources of variation included 2 varieties, 3 nitrogen treatments, 10 spikelet positions in the panicle and 2 grain orders in the spikelet. The block structure was designed in three strata as illustrated in table 15.

The analysis showed that all evaluated factors had a highly significant influence on grain weight from the onset till the end of the grain filling period. Grain order (primary versus secondary grains) was the most important source of variation. The second most important factor was the spikelet position in the panicle. Differences between varieties were much smaller, but greater than those between nitrogen treatments.

Highly significant interactions variety x spikelet position and nitrogen treatment x grain order showed up during the `linear' growth phase of grains. The significant interactions nitrogen treatment x spikelet position and nitrogen treatment x grain order showed up in the first two samplings only. Table 15 also shows two significant interactions which appeared spurious: (1/7 and 3/8) variety x spikelet position x grain order, and (6/8) spikelet position x grain order.

The weight of secondary grains was on average about 55 % of that of the primary grains at the first sampling, and about 57 % at ripening. The largest differences among the spikelets in the panicle (Fig. 1.5) were between the apical spikelet (No. 8) and that at the bottom of the panicle (No. 1), i.e. between the oldest and the youngest (table 16). The ranking of the other spikelets also corresponded to the time sequence of branch and spikelet differentiation, which starts at the tip of the central axis and proceeds basally in succession at the tips of the spikelets of the first order branches (Chapter 1). Therefore, in both varieties, the spikelets at positions No. 8, 6 and 4 had the largest grains and those close to the panicle nodes at positions No. 1, 3 and 5 had the smallest grains (table 17). The ranking of the grains in the spikelets at the positions No. 2, 7, 9 and 10 changed in the middle of grain filling.

Within the panicle nodes the largest differences were observed at the first (basal) node between the smallest spikelet attached to the node (No. 1) and that at the tip of the primary branch (No. 2). This difference decreased proceeding acropetally to the top of the panicle in both varieties. This pattern, resulting from the time sequence of the panicle part formation was very stable.

The significant interactions observed, occurred during the first part of the grain filling period, indicating that the evaluated factors influenced the pattern of grain growth. Therefore, to analyze grain growth, the grain growth curves were represented by analytical functions. A generalized logistic growth curve: `y = A+C/(1+T*EXP(-B(x-M)))**1/T` with four parameters (B, M, T, C; with constraint A = 0) was found most suitable for description of the growth curves of the various grain cohorts. The results of the analysis of variance on its four parameters are given in table 18.

At this point it should be recalled that the results from the destructive samplings were highly variable. Out of the 600 possible cases, in 70 cases it was impossible to calculate parameters for a generalized logistic curve with the Genstat program. Some of the curves, calculated for each combination of all factor levels and replicates were unrealistic.

Therefore, the maximum value of parameter C (upper asymptote) was set at 80 mg, and the analysis of variance on this parameter was calculated from 487 growth curves only (table 18).

The value of parameter B which is associated with the slope of the curve is influenced by spikelet position and by the interaction spikelet position x grain order (table 18). The averages in table 19 show that the grains in the older spikelets at the tip of the primary branches exhibited higher growth rates than in the younger ones close to the bottom of the panicle nodes. This especially held for the secondary grains in these spikelets. The primary grains show higher growth rates in the lower parts of the panicles.

The value of parameter M, representing the point of inflection, is influenced by spikelet position, grain order and strongly by their interaction. Also the interactions variety x grain order and nitrogen treatment x spikelet position x grain order were significant. The growth rate of the primary grains, especially of those at the tips of primary branches declined relatively early in the grain filling period, as expressed by low values of the parameter M in table 20.
This also is a consequence of their earlier initiation. On the other hand, the extremely high values for spikelet No. 1 (at the bottom of the panicle) result from the fact that in most of these spikelets either the secondary grain or both grains were lacking. The differences between the varieties were probably associated with different times of ripening, C8852 being a few days later than Wilma. The three-way significant interaction nitrogen treatment x spikelet position x grain order is difficult to interpret.

The value of parameter T is significantly influenced by spikelet position and by the interaction grain order x spikelet position. The average values in table 21 only permit some general conclusions. The negative values of this parameter correspond to cessation of grain growth in the bottom spikelets (No. 1). The values exceeding 1, characterizing higher growth rates during the first part of the grain filling period, are typical for the grains in the top spikelets of the primary branches or in the middle of the panicle. The observed variation was larger in the secondary grains than in the primary ones, i.e. differences among spikelet positions within the panicle were expressed more pronounced in the secondary grains.

Finally, parameter C represents the upper asymptote of the growth curve, i.e. final grain weight. In accordance with the previous analysis of variance on grain weight (table 15), significant effects were found for all evaluated factors, except nitrogen treatment. In addition, some significant interactions showed up, i.e. variety x nitrogen treatment, nitrogen treatment x spikelet position, variety x nitrogen treatment x spikelet position, spikelet position x grain order, variety x spikelet position x grain order, nitrogen treatment x spikelet position x grain order. These were not found in the analysis of variance of final grain weight. The explanation may be that the calculated growth curves more strongly express differences in growth which were registered by analysis of variance on the grain weight in the first part of grain filling period, where these interactions were also significant.

For a more complete illustration of the effects of the evaluated factors on grain growth pattern and the growth curve parameters several growth curves representing the basic factors and their combinations are shown in figs. 3.3.3-3.3.6. The parameter values and the percentage of variance accounted for are presented in table 22.

The overall conclusion may thus be:

All types of growth curves can be observed between that of the largest grain (which is usually the primary grain at the apical spikelet) and the x-axis (which represents zero growth). Within these boundary conditions also grain weight variability is expressed.

Table 15: Results of the analysis of variance on grain weight during the grain filling period in 1991 (in the columns only the variation ratio is presented, * = significant , ** = highly significant, V = variety, N = nitrogen treatment, P = spikelet position in the panicle, G = grain order, R = replicate).

Source of variation	d.f.	Date of grain weight measurement variation 1/7	9/7	16/7	23/7	20/7	27/7	30/7	3/8	6/8	12/8	19/8
Stratum V.N.R												
V	1	26,19**	13.23**	14.48**	59.04**	38.53**	49.21**	16.85**	16.17**	12.27**	13.97**	19.54**
N	2	17.27**	14.10**	11.08**	11.99**	4.38*	13.97**	5.48**	7.51**	2.02**	7.01**	12.09**
V.N	2	1.28	0.19	2.75	1.91	1.13	0.13	0.88	0.02	1.98	1.62	2.00
Residual (v.r.)	24	5.38	5.33	3.98	2.06	2.10	1.60	1.97	2.35	2.53	3.00	2.00
Stratum V.N.R.P												
P	9	175.95**	163.72**	113.30**	79.36**	82.57**	83.39**	49.95**	47.73**	27.63**	29.09**	36.63**
V.P	9	3.94**	1.79	3.69**	3.40**	4.00**	0.69	0.82	0.89	1.45	1.37	0.74
N.P	18	2.20**	1.78*	1.57	1.65	0.67	0.91	1.18	1.19	1.46	1.45	0.94
V.N.P	24	1.13	1.09	1.00	0.98	1.25	0.89	1.22	0.91	1.25	1.55	0.46
Residual (v.r.)	216	1.76	1.60	1.21	1.37	1.04	1.09	1.12	1.07	0.84	1.19	1.11
Stratum V.N.R.P.G												
G	1	2607.20**	2449.51**	923.74**	887.93**	740.59**	759.03**	665.14**	683.48**	390.47**	672.25**	710.24**
V.G	1	2.96	0.02	0.44	4.60*	1.23	1.12	0.67	1.09	0.20	1.75	2.06
N.G	2	42.72**	12.66**	5.03**	5.84**	1.07	2.77	1.02	1.08	1.64	0.76	0.81
P.G	9	4.03**	3.71**	1.27	1.35	0.90	0.93	1.79	1.97	2.48**	1.20	2.34
V.N.G	2	0.60	1.54	1.73	0.84	1.80	1.61	0.97	0.97	0.02	1.68	1.35
V.P.G	9	1.94*	1.20	1.08	0.93	0.76	1.42	0.79	2.99**	1.14	1.89	0.97
N.P.G	18	1.24	1.05	0.50	1.24	1.02	0.91	1.09	1.17	0.89	1.36	1.90
Residual (m.s.)	258	0.69	2.89	15.08	21.38	39.96	45.94	57.04	64.35	88.48	76.75	70.29

Table 16: Mean grain weight (mg) as a function of the evaluated factors at the first and the last measurement date.

Factor	Level	First 1/7	Last 19/8
Grain order (primary)	1	6.320	42.67
(secondary)	2	2.857	24.43
	s.e.d.	0.068	0.68
Spikelet position (No.)	1	1.500	19.93
	2	4.550	37.47
	3	2.220	24.87
	4	6.067	39.63
	5	3.683	28.15
	6	6.800	37.63
	7	4.783	35.75
	8	7.483	40.95
	9	3.900	34.53
	10	4.917	36.60
	s.e.d.	0.202	1.61
Variety (Wilma)	1	5.123	35.81
(Cebeco 8852)	2	4.053	31.30
	s.e.d.	0.209	1.02
Nitrogen treatment (N1)	1	5.420	36.01
(N2)	2	4.390	30.01
(N3)	3	3.955	34.54
	s.e.d.	0.256	1.25

Table 17: Ranking of evaluated spikelets (No. 1 - 10; Fig. 1.5) in the set according to mean grain weight (1 is largest grain) in the course of grain filling (variety No 1 = Wilma, No 2 = Cebeco 8852).

Order in grain weight	Date of measurement																					
	1/7		9/7		16/7		20/7		23/7		27/7		30/7		3/8		6/8		12/8		19/8	
	Variety																					
	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
	Spikelet position number																					
1	8	8	8	8	8	8	8	6	8	8	8	8	8	8	8	8	8	8	8	8	8	8
2	6	6	6	6	6	6	6	8	6	6	6	6	4	6	6	6	6	2	4	6	4	4
3	4	4	4	4	4	4	4	4	4	4	4	4	6	4	4	4	4	4	6	4	2	7
4	7	10	10	2	10	2	2	10	2	7	2	2	10	7	2	10	2	6	10	10	6	10
5	10	2	7	10	7	7	7	2	10	2	10	10	7	10	7	2	7	10	2	9	9	6
6	2	7	2	7	2	10	10	7	7	10	9	7	2	2	10	5	10	9	5	7	10	2
7	5	9	9	9	9	9	9	9	9	9	7	9	9	9	9	7	9	7	7	2	7	9
8	8	5	5	5	5	5	5	5	5	5	5	5	5	5	5	9	5	5	9	5	5	5
9	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
10	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 18: Results of the analysis of variance on the parameters of the generalised logistic grain growth curve in 1991 (in the culms there is set up the variation ratio, * = significant, ** = highly significant, V = variety, N = nitrogen treatment, P = spikelet position in the panicle, G = grain order, R = replicate).

Source of variation	d.f.(m.v.)	Parameter			d.f.(m.v.)	
		B	M	T		C
Stratum V.N.R						
V	1	0.14	4.08	1.85	1	28.70 **
N	2	0.35	1.04	0.02	2	0.74
V.N	2	0.29	0.85	0.02	2	8.99 **
Residual (v.r.)	24	1.22	0.79	1.47	24	1.55
Stratum V.N.R.P						
P	9	5.59 *	510.10 **	5.24 **	9	12.92 **
V.P	9	1.12	0.75	0.42	9	0.76
N.P	18	0.74	0.76	1.49	18	2.69 **
V.N.P	18	0.50	1.02	0.68	18	4.00 **
Residual (v.r.)	213 (3	1.16	2.25	1.69	200 (16)	1.96
Stratum V.N.R.P.G						
G	1	0.04	934.02 **	0.11	1	680.38 **
V.G	1	1.60	3.90 *	1.41	1	0.66
N.G	2	0.76	0.60	0.37	2	1.08
P.G	9	5.81**	1085.15 **	8.67 **	8 (1)	3.44 **
V.N.G	2	2.48	0.77	0.26	2	0.88
V.P.G	8 (1)	1.30	1.20	1.20	8 (1)	2.37 *
N.P.G	16 (2)	0.64	1.73 *	1.20	16 (2)	2.88 **
Residual (m.s.)	194 (64)	1.98	24144.00	73.97	165 (93)	65.24

Table 19: Mean values of parameter B according to spikelet position and interaction spikelet position x grain order.

Spikelet No	Mean of B	Primary grains	Secondary grains
1	- 0.509	0.544	- 1.562
2	0.681	0.790	0.572
3	0.945	0.713	1.177
4	1.088	1.233	0.943
5	0.638	0.462	0.814
6	0.896	0.637	1.154
7	0.708	0.664	0.753
8	1.143	0.496	1.790
9	0.653	0.682	0.625
10	0.645	0.558	0.731
s.e.d.	0.276	0.377	

Table 20: Mean values of parameter M as a function of spikelet position and the interactions spikelet position x grain order and variety x grain order.

Spikelet No	Mean	Primary grains	Secondary grains
1	2177.8	104.5	4251.0
2	28.1	13.1	43.1
3	10.0	70.2	- 50.2
4	45.3	74.8	15.9
5	25.3	29.8	20.5
6	19.4	18.6	20.3
7	22.3	23.2	21.4
8	16.4	16.4	16.5
9	29.2	31.2	27.1
10	74.2	127.3	21.0
s.e.d.	42.54	51.13	
Variety	Wilma	21.3	434.1
	Cebeco 8852	80.3	444.2
	s.e.d.	21.13	
Grain order		50.9	438.7
	s.e.d	12.69	

Table 21: Mean values of parameter T as a function of spikelet position and the interaction spikelet position x grain order.

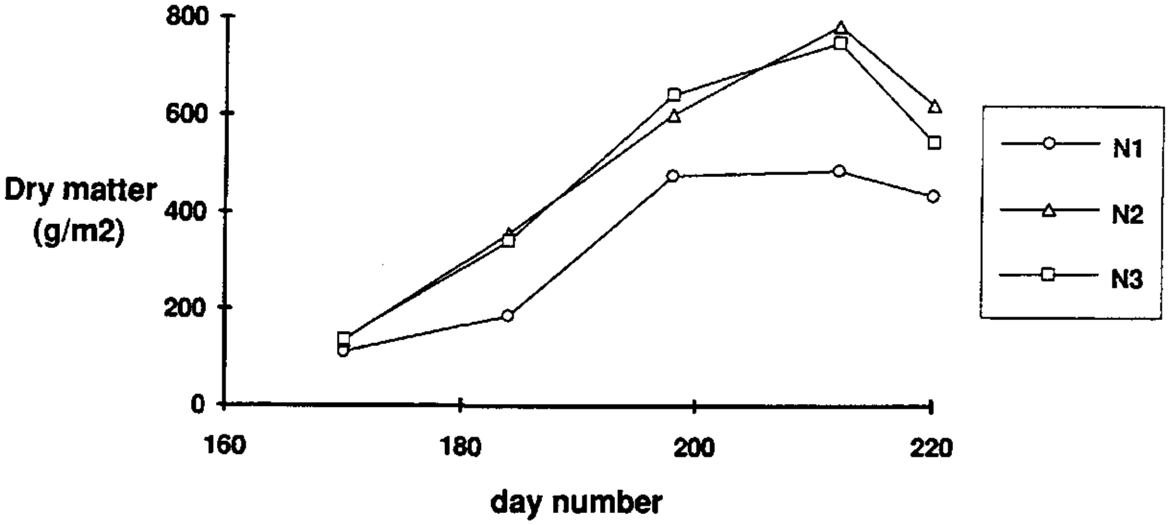
Spikelet No	Mean	Primary grains	Secondary grains
1	- 1.64	7.18	- 10.46
2	6.60	6.63	6.57
3	10.32	8.95	11.69
4	8.33	9.81	6.85
5	6.91	5.35	8.47
6	9.60	8.02	11.17
7	8.17	7.30	9.04
8	8.40	5.55	11.25
9	7.46	7.32	7.59
10	7.91	7.11	8.71
s.e.d.	2.041	2.575	

Table 22: Values of the parameters and the percentage of variance accounted for for the growth curves presented in the figures 16-19.

Curve identification		Curve number	Parameters				Accounted percentage
			B	M	T	C	of variance
Figure 3.3.3							
Maximum values		1	0.2033	12.81	1.82	60.85	98.7
Overall mean		2	0.2253	17.69	2.53	33.32	99.3
Primary grains		3	0.2020	17.37	2.31	42.29	99.0
Secondary grains		4	0.2610	18.01	2.79	24.45	99.5
Wilma		5	0.2346	17.38	2.59	35.45	99.3
Cebeco 8852		6	0.2266	18.35	2.66	31.14	99.1
Nitrogen	N1	7	0.1794	16.04	1.84	35.75	97.4
treatments	N2	8	0.2950	18.77	3.64	32.25	98.4
	N3	9	0.1572	16.40	1.33	32.91	97.8
Figure 3.3.4							
V1 N1 G1		1	0.3810	16.05	4.69	54.30	90.1
V1 N2 G1		2	0.2830	16.03	3.54	53.92	98.6
V1 N3 G1		3	0.3320	15.26	3.64	49.78	96.1
V2 N1 G1		4	0.2183	14.93	2.63	52.58	97.6
V2 N2 G1		5	1.1180	21.81	19.00	45.41	79.1
V2 N3 G1		6	1.5290	21.78	19.00	44.10	82.5
V1 N1 G2		7	0.1446	8.82	0.49	35.69	63.1
V1 N2 G2		8	1.4310	20.90	19.00	33.81	81.8
V1 N3 G2		9	0.2190	15.18	2.09	37.15	96.8
V2 N1 G2		10	1.2420	20.61	19.00	30.97	92.6
V2 N2 G2		11	0.2920	14.27	2.53	31.60	95.8
V2 N3 G2		12	0.5190	21.27	6.98	31.87	98.8
Figure 3.3.5							
V1 N1 G1		1	0.0952	11.22	0.33	46.96	89.5
V1 N2 G1		2	0.3286	19.54	4.02	44.64	99.2
V1 N3 G1		3	0.0702	14.46	0.08	53.60	97.4
V2 N1 G1		4	0.1274	18.81	1.40	48.01	94.6
V2 N2 G1		5	0.1064	13.26	0.33	43.52	93.0

V2 N3 G1	6	0.2620	19.09	2.87	35.34	87.0
V1 N1 G2	7	1.4840	23.22	19.00	28.38	89.8
V1 N2 G2	8	0.5600	20.32	5.87	26.27	95.3
V1 N3 G2	9	0.1010	14.40	0.42	26.28	79.7
V2 N1 G2	10	0.3730	23.65	5.09	26.76	98.3
V2 N2 G2	11	0.3450	22.03	4.27	22.70	90.1
V2 N3 G2	12	0.2290	20.77	2.35	22.25	95.1
Figure 3.3.6						
P1 G1	1	0.1140	21.48	1.10	41.46	95.6
P1 G2	2	0.9947	38.11	19.00	12.76	43.0
P2 G1	3	1.3240	22.41	19.00	17.61	94.5
P2 G2	4	0.1700	15.90	1.30	33.87	92.5
P3 G1	5	0.1167	19.36	1.30	43.44	94.9
P3 G2	6	0.0790	13.90	0.04	20.05	69.7
P4 G1	7	1.0300	21.34	15.40	50.04	98.1
P4 G2	8	0.2120	15.59	2.04	35.90	92.5
P5 G1	9	1.1810	23.23	19.00	41.62	88.5
P5 G2	10	0.1200	13.97	0.72	28.38	87.2
P6 G1	11	0.1054	8.96	0.37	53.44	95.9
P6 G2	12	0.4420	15.14	4.90	31.39	82.1
P7 G1	13	0.2860	17.80	3.91	46.11	86.6
P7 G2	14	0.1790	17.41	1.85	33.68	92.8
P8 G1	15	0.3810	16.05	4.69	54.30	90.1
P8 G2	16	0.1446	8.82	0.49	35.69	63.1
P9 G1	17	0.0952	11.22	0.33	46.96	89.5
P9 G2	18	1.4850	23.20	19.00	28.34	89.9
P10 G1	19	0.0961	12.61	0.47	53.27	93.1
P10 G2	20	1.2340	24.38	19.00	31.63	90.0

a/ Wilma



b/ Cebeco 8852

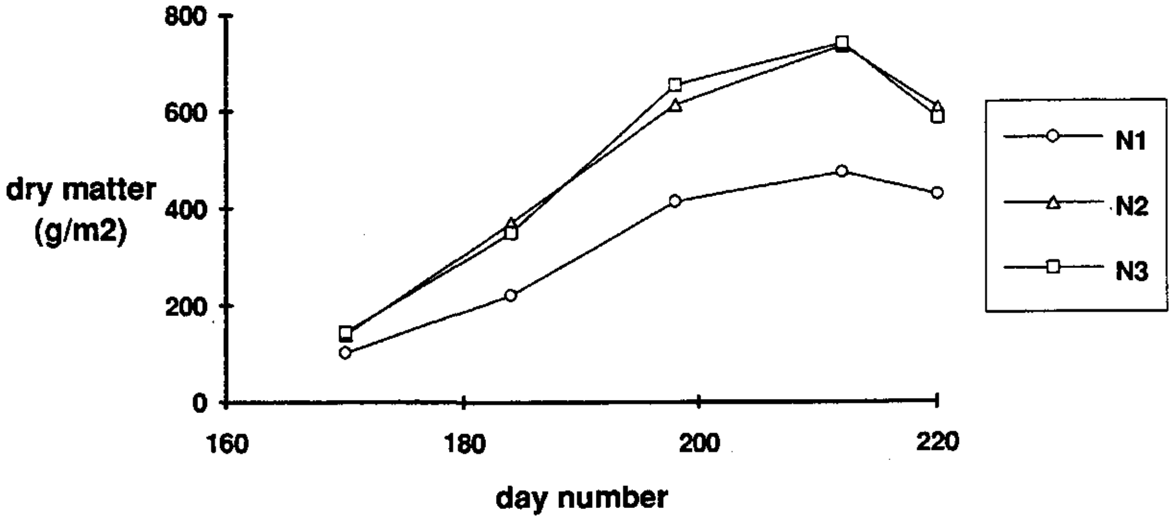
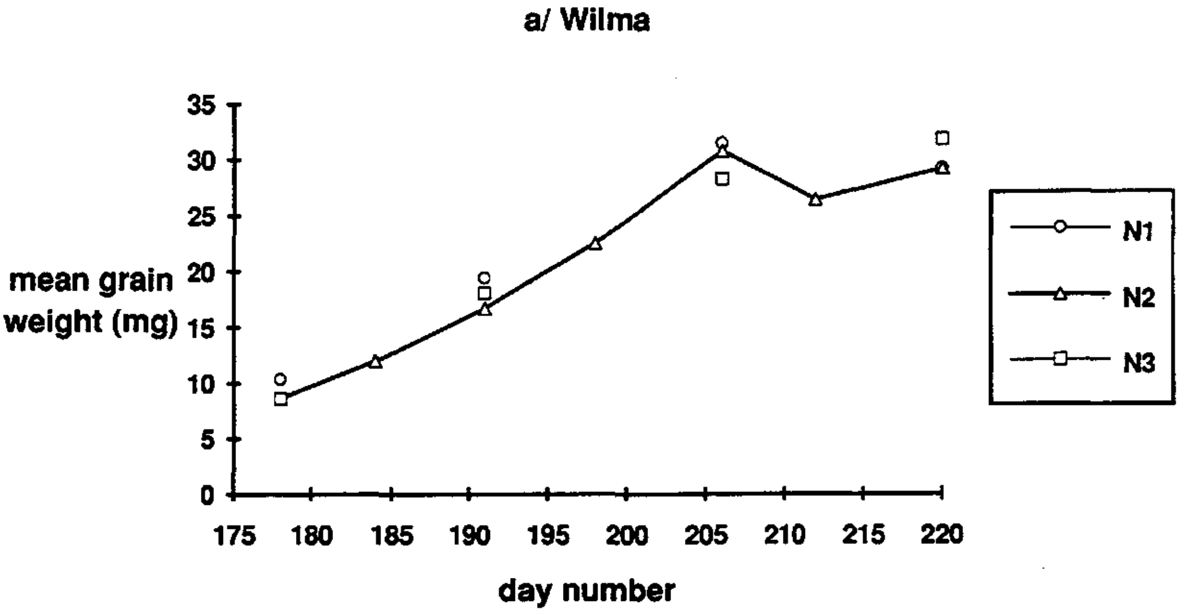


Figure 3.3-1: Grain dry matter acumulation in 1990.



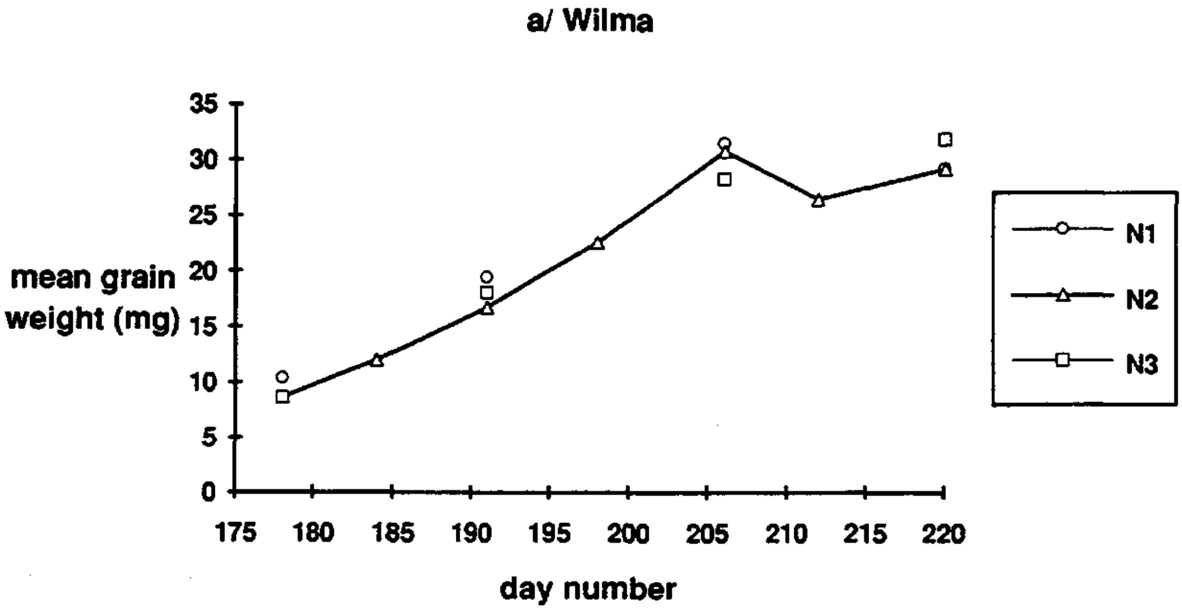


Figure 3.3-2: Mean grain filling in 1990.

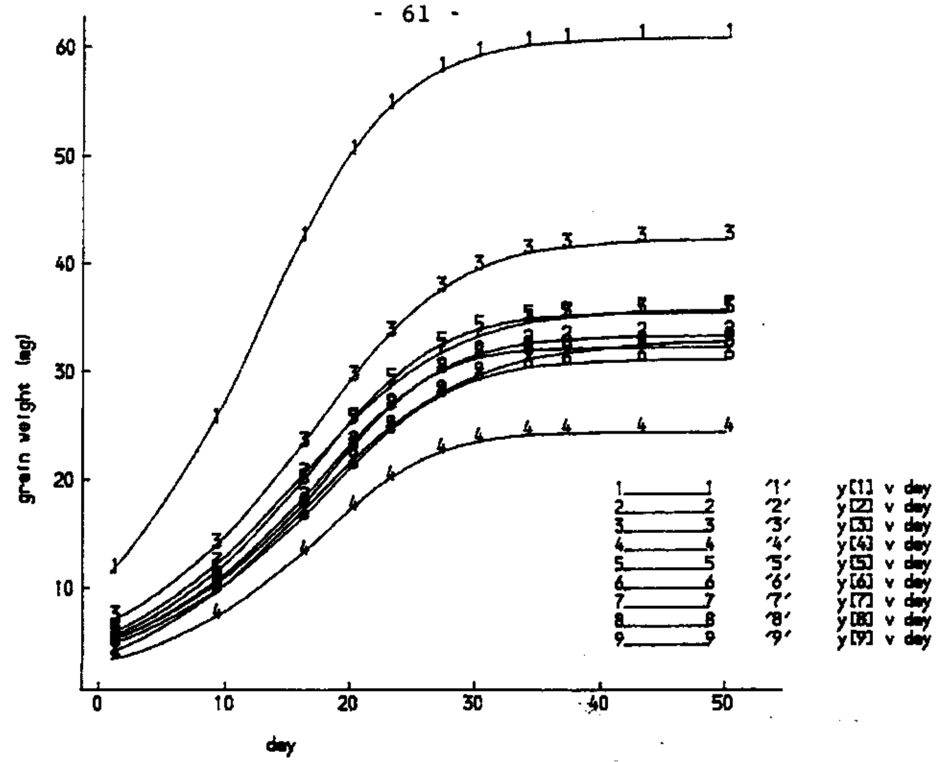


Figure 3.3.3: Grain growth curves representing: 1 - maximum grain weight, 2 - overall mean, 3 - primary grains, 4 - secondary grains, 5 - Wilma, 6 - Cebeco 8852, 7 - N1, 8 - N2, 9 - N3.

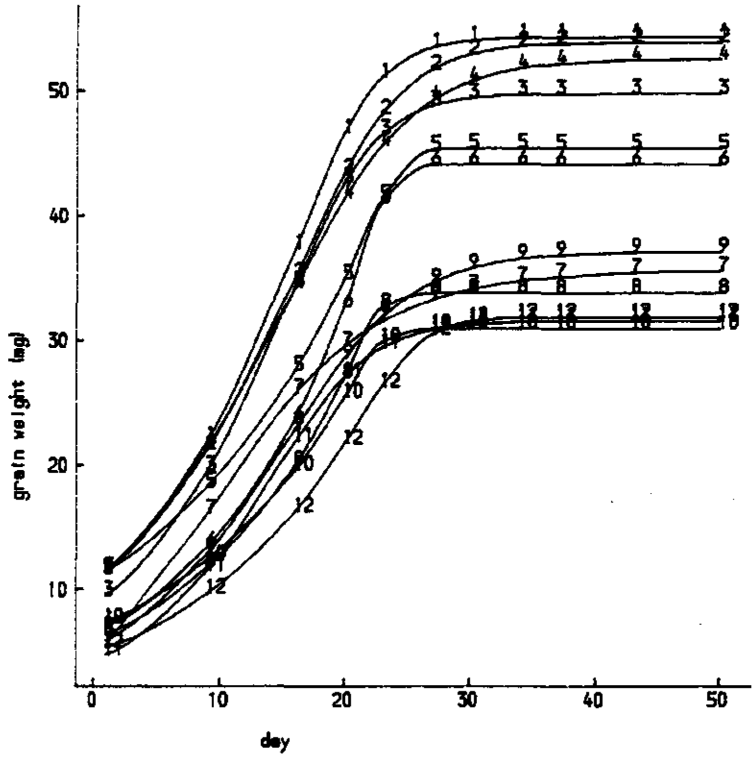


Figure 3.3.4: Curves representing the influence of variety and nitrogen treatment on the growth of the primary and the secondary grains in the apical spikelet No. 8 (1 - V1N1G1, 2 - V1N2G1, 3 - V1N3G1, 4 - V2N1G1, 5 - V2N2G1, 6 - V2N3G1, 7 - V1N1G2, 8 - V1N2G2, 9 - V2N3G2, 10 - V2N1G2, 11 - V2N2G2, 12 - V2N3G2).

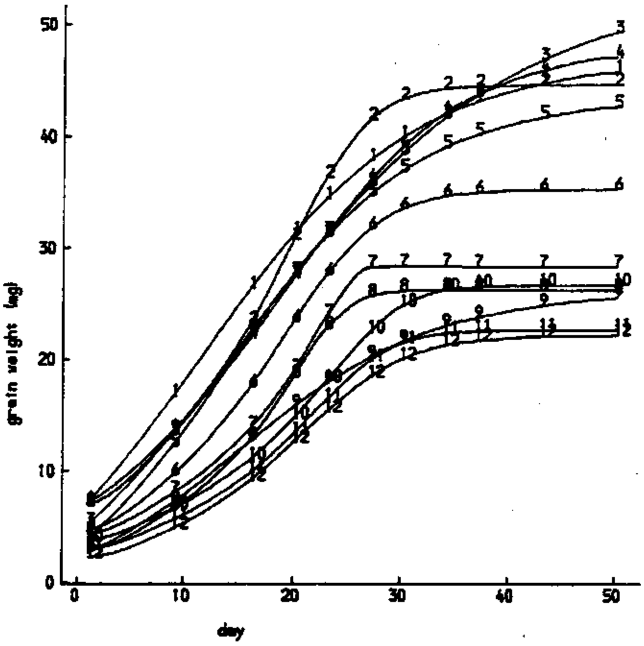


Figure 3.3.5: Curves representing the influence of variety and nitrogen treatment on the growth of the primary and secondary grains in spikelet No. 9 in the middle of the panicle (1 - V1N1G1, 2 - V1N2G1, 3 - V1N3G1, 4 - V2N1G1, 5 - V2N2G1, 6 - V2N3G1, 7 - V1N1G2, 8 - V1N2G2, 9 - V1N3G2, 10 - V2N1G2, 11 - V2N2G1, 12 - V2N3G2).

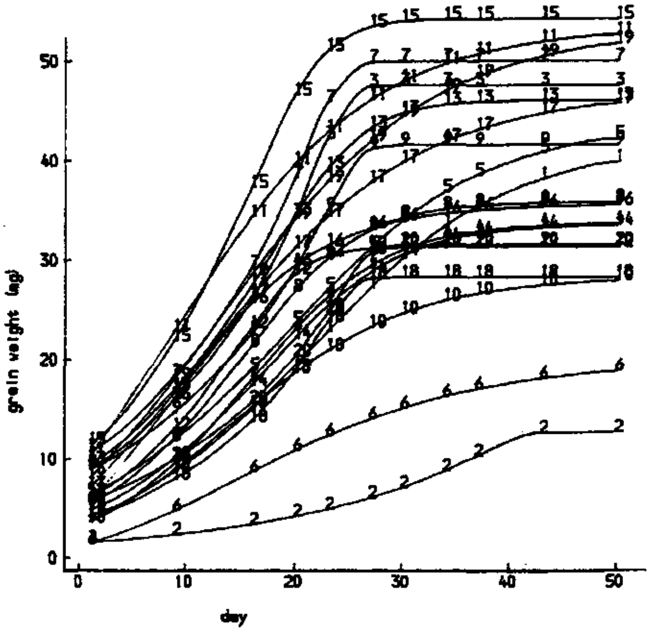


Figure 3.3.6: Curves representing the growth of the primary and secondary grains in all 10 measured spikelet positions within the panicle for variety Wilma and nitrogen treatment N1 (1 - P1G1, 2 - P1G2, 3 - P2G1, 4 - P2G2, 5 - P3G1, 6 - P3G2, 7 - P4G1, 8 - P4G2, 9 - P5G1, 10 - P5G2, 11 - P6G1, 12 - P6G2, 13 - P7G1, 14 - P7G2, 15 - P8G1, 16 - P8G2, 17 - P9G1, 18 - P9G2, 19 - P10G1, 20 - P10G2).

3.4 GRAIN WEIGHT DISTRIBUTION

Grain weight distribution was calculated from individual grain weights determined in larger samples harvested at the dead-ripe stage. Grain weight was determined in two ways for each of the 6 variants of the experiment (2 varieties x 3 nitrogen treatments):

1. Individual grain weight was determined in approximately 15 g samples per variant from the grain cleaned after combine harvest.
2. Individual grain weight, combined with identification of the grain position within all spikelets (primary and secondary grains) was measured on 10 randomly selected main stem panicles in 1990 and on 4 in 1991.

Histograms of grain weight distribution and common statistics of variability referring to the overall grain weight distribution are given in figs. 3.4.1 and 3.4.2. The abbreviations used for the statistics are explained in table 23. A number of typical characteristics can be observed:

1. A bimodal grain weight distribution is typical for nitrogen treatment N1. The pattern is identical for both varieties in both years. Grain weight distribution in nitrogen treatments N2 and N3 shows a similar pattern in both varieties: a monomodal distribution, left-side skewed in 1990 and of variable skewness in 1991.
2. Left skewed (skewness > 0) grain weight distributions are characteristic for all combinations of variety x nitrogen treatment in 1990 (Fig. 3.4.1).
   On the other hand, grain weight distributions in treatments N2 and N3 in 1991 (Fig. 3.4.2) are characterized by a symmetrical shape or right skewness (skewness < 0).
3. A significant difference between varieties was observed in treaments N2 and N3 in 1991. In Wilma the distribution varied from symmetrical to significantly left-side skewed; in Cebeco 8852 it varied from insignificantly left-side skewed to bimodal.
4. Average grain weight in nitrogen treatment N1 is essentially higher (by 3.1 - 16.3 %) than in N2 and N3. Differences in average grain weight between the latter two nitrogen treatments are small.

Results from the second method of grain weight determination are shown in figs. 3.4.3 - 3.4.14. Additional information on the grain position allowed evaluation of the relationship between the weight of primary and secondary grains and the variability within the groups of primary and secondary grains separately. Therefore, three histograms and the corresponding statistics of variability (for secondary grains, primary grains and all grains combined, respectively) are given in figs. 3.4.3 - 3.4.14. At the top of these figures graphs are presented of the correlation between the weight of the primary (x-axis) and that of the secondary (y-axis) grains. The points represent individual spikelets with two grains whose weight has been determined separately. The information from figs. 3.4.3 - 3.4.14 allows a more detailed analysis of grain weight variability within the panicle.

In general, within the graphs three clusters can be distinguished. The larger one, situated approximately in the middle between the axes, represents the spikelets with both well-developed primary and secondary grains. Within this cluster, points more distant from the origin represent spikelets at an advanced stage of development ("older") with consequently larger grains, and points closer to the origin "younger" spikelets with smaller grains. The two other clusters, each situated closer to one of the axes represent spikelets in which one of the two grains is under-developed or aborted. The cluster situated close to the x-axis represents spikelets with well-developed primary grains but under-developed or missing secondary grains. The cluster situated close to the y-axis represents the usually smaller group of spikelets in which the primary grains have been aborted or are less-developed but the secondary grains are developed.

For nitrogen treatment N1 the picture typically consists of three very compact clusters, sharply distinguished and fairly distant from the origin. For both the primary and the secondary grains the variation in grain weight is relatively small, their histograms are therefore rather narrow, and the overall histogram of grain weight distribution shows a typical bimodal pattern (figs. 3.4.3, 3.4.6, 3.4.9, 3.4.12). In reality, however, it comprises three peaks. The first one from the left represents aborted grains (i.e. empty husks) with very low weights (0 - 10 mg). That fraction, however, is missing in the samples from the combine harvest, as it has been removed during cleaning. Therefore, it has not been considered in interpreting the histograms.

Nitrogen application at the beginning of stem elongation (N2) results in protraction of the central cluster aslant downwards to the origin and in a shift of both smaller clusters from the axes towards the central cluster (figs. 3.4.4, 3.4.7, 3.4.10, 3.4.13). This trend continues with the third nitrogen dressing (N3) applied at the flag leaf stage (figs. 3.4.5, 3.4.8, 3.4.11, 3.4.14). Generally, this results in greater variability in grain weight of both the primary and the secondary grains, particularly through extending the columns representing the lower grain weight classes (< 40 mg for primary grains and < 25 mg for secondary grains). However, differences between varieties and years were found.

In 1990, Wilma produced in N2 and especially in N3 practically one cluster of points with the bottom at the x-axis (in the position 10 - 15 mg) and extending diagonally to the right (figs. 3.4.4 and 3.4.5). Histograms of both the primary and the secondary grains are more extended in width. Relatively higher columns of higher secondary and lower primary grain weight classes (between 30 - 40 mg) filled in the gap in the bimodal distribution of all grains combined. Thus the histogram representing nitrogen treatment N3 has one peak only and is almost symmetrical, if the fraction of grains under 5 mg is not considered. The explanation for these results may be that in 1990 in nitrogen treatment N2 and especially in N3 Wilma proportionally extended the weight range of both the primary and the secondary grains.

This pattern is in general reproduced.in 1991. However, the extension is not proportional in the primary and the secondary grain weight range (figs. 3.4.6 - 3.4.8). A more narrow distribution, with higher frequencies in classes representing the larger grains (between 40 - 60 mg) is characteristic for primary grains in all nitrogen treatments. The frequency of the primary grain weight classes between 50 - 60 mg decreases and that between 40 - 50 mg increases from nitrogen treatment N1 to N3. On the contrary, the histograms of the secondary grains for N2 and N3 (figs. 3.4.7 and 3.4.8) show higher frequencies in the lower weight classes (between 5 - 30 mg). The graphs consist of two separate clusters, with the central cluster tailing off towards the x-axis. This represents a narrower grain weight distribution of the primary grains and a wider distribution of the secondary grains. The smaller cluster, representing spikelets with small primary grains and more developed secondary grains is distinct in both N2 and N3 (figs. 3.4.7 and 3.4.8). The overall distribution changes from bimodal in N1 to monomodal in N3 as in 1990, but it is more narrow with relatively higher frequencies in the larger grain classes. The frequency of the smallest grains is lower in all nitrogen treatments in comparison to 1990.

The transition in overall grain weight distribution from bimodal in N1 to monomodal in N3, characteristic for Wilma, is not visible in Cebeco

8852. In both N2 and N3 the bimodal distribution is maintained in both years (figs. 3.4.10, 3.4.11 and 3.4.13, 3.4.14). The behaviour of Cebeco 8852 also differs in the two years. In 1990 it is characterised by greater variability within the clusters. In both the N2 and N3 treatments the central cluster tails off towards the y-axis and is practically connected to the cluster representing the spikelets with empty primary and larger secondary grains. Thus, the graph shows a large cloud of points starting from the y-axis and extending parallelly along the x-axis at a distance of about 15 mg. The third cluster, representing the spikelets with either small or without secondary grains, is situated very close to the x-axis with only a few points a little farther removed. This results in narrow and tall histograms for the secondary grains, covering the grain weight classes from 15 till 35 mg (figs. 3.4.9 - 3.4.11). On the other hand, the histograms of the primary grains have reduced height and extended width, with relatively higher frequencies in the lower grain weight classes. The histograms of all grains combined therefore, have one high and one low peak. This leads to the conclusion that the response of Cebeco 8852 in 1990 to increased nitrogen application was largely expressed in the primary grains.

In 1991, similarly to Wilma, the graph representing the relation between the weight of the primary grain and that of the secondary grain for treatment N1 consists of three very compact and distinct clusters (Fig. 3.4.12). Therefore, all histograms in this figure are very narrow. The lowest grain weight classes (< 20 mg) virtually only comprise secondary grains. The reaction to increased nitrogen application (N2 and N3) is expressed in extended and diluted central clusters, perpendicular to the x- and y-axes. Also two smaller clusters, close to the axes, representing incomplete spikelets, can be identified. This results in greater width of the histograms of both the primary and secondary grains in approximately the same proportion (figs. 3.4.13 and 3.4.14). Contrary to 1990, there is hardly any difference in height for these histograms in N1 and N3 (figs. 3.4.12 and 3.4.14) and it is much smaller for N2 (Fig. 3.4.13). Summarizing, it implies that in 1991 Cebeco 8852 responded to increased N application (N2 and N3) by a proportional increase in weight of both the primary and the secondary grains.

To quantify the described differences, the statistics of grain weight variability presented below each histogram can be used. It should be kept in mind, however, that the fraction smallest grains (< 15 mg) is included in the calculations, which strongly influences the values of variance, standard deviation, coefficient of variation and skewness. This fraction represents mostly empty husks, which are included in the first two weight classes (0 - 10 mg) for secondary grains and in the interval between 5 -15 mg for primary grains. For instance, 12 mg grain weight can either represent the empty husk of a primary grain or a small, partially filled, secondary grain. Empty husks are removed by grain cleaning and small grains remain. Therefore, in the histograms representing cleaned grain, the lowest class (0 - 5 mg) is practically absent, but there are some grains in the classes 5 - 10 and 10 - 15 mg. Figs. 3.4.3. - 3.4.14 indicate that these are mostly secondary grains.

Transition from the bimodal to the monomodal distribution is associated with a modification in canopy structure. The crop without nitrogen dressing consists mainly of main stem panicles, which, however, have lower numbers of spikelets and grains than those from the crop supplied with nitrogen. At the level of main stems, the mean differences between N2 and N1 and between N3 and N1 are practically identical, at 9.9 and 8.6 spikelets per panicle representing 20.4 and 17.8 %, respectively of the number of spikelets per panicle in treatment N2 (table 24). Much larger differences may be expected at the level of tillers. Higher tiller numbers per plant and larger numbers of spikelets per main stem and per first order tiller, typical for nitrogen treatments N2 and N3, result in substantially higher numbers of grains per unit area (Section 3.2).

In these larger cohorts the time differences in initialization are also larger, i.e. additional tillers and spikelets show delayed development and are therefore smaller than those initiated earlier. Thus, in the histograms pertaining to all grains combined for N2 and N3, differences between primary and secondary grains may be masked by differences at the preceding hierarchical levels, i.e. due to the time delay in tiller and spikelet formation. The result is a monomodal distribution for all grains. The bimodal grain weight distribution of Cebeco 8852 in N3 (Fig. 3.4.2) indicates that differences may exist between varieties with respect to the rate of tiller and spikelet initialization and development.

Modification of the position of the clusters in the graph depicting the relation between the weights of primary and secondary grains and deviations from the pattern of histograms described above, therefore, can be considered as a result of genotype x environment interactions. The intensity of branching at each hierarchical level (i.e. at particular stages of crop development, Fig. 1.3) is very sensitive to environmental conditions and guarantees plasticity in plant morphogenesis. In the course of crop development continuous interaction exists with environmental conditions (`sources') using these adaptation mechanisms successively as dictated by plant hierarchical structure.

It should be noted, that the source for grain growth consists of assimilates produced and directly incorporated and reserves translocated from the vegetative parts of the plant. The interaction is therefore realized at two levels:

1. Between environmental conditions and vegetative parts of plants.
2. Between these vegetative parts (source) and reproductive parts (grains, representing sinks).

With respect to grain formation, the delay in tiller, spikelet and grain initialization is mostly affected by interactions at the first level. Interactions at the second level influence mostly grain growth rate. For illustration of the differences in initialization patterns the results from Section 3.2 can be used. For a complete picture of grain filling an analysis of assimilate supply is necessary. Following that, the modifications in grain weight distribution may be explained in more detail.

Table 23: Explanation of abbreviations of used statistics.

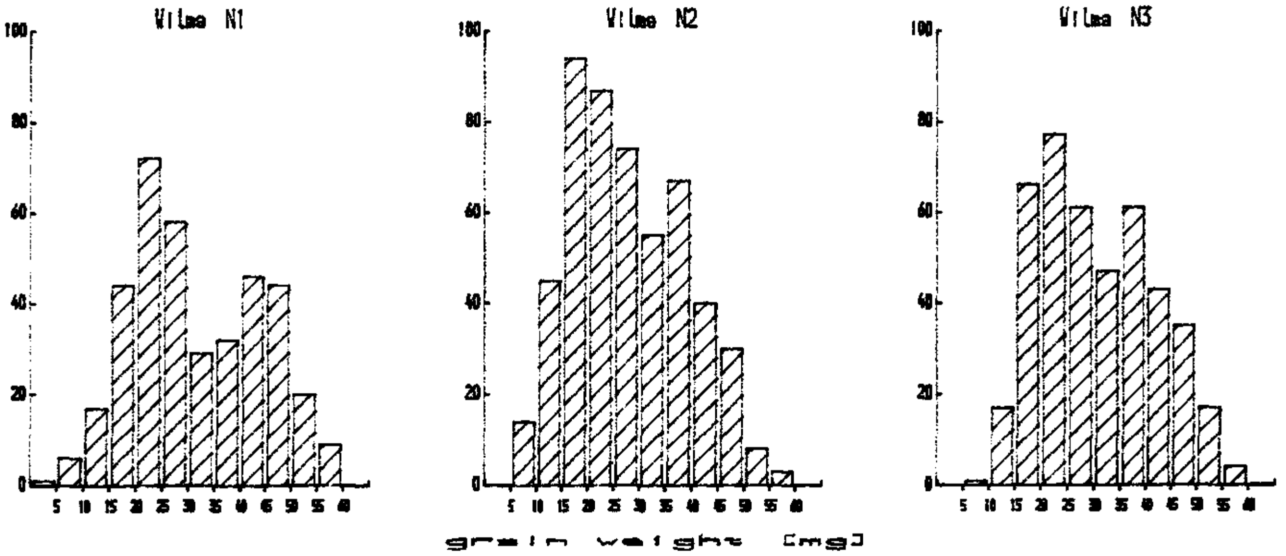
nobs - number of observations [n]
mean - arithmetic mean [x]
min - minimum value
max - maximum value
range - difference between maximum and minimum values
var - variance [ ]
sdev - standard deviation [s]
cv % - coefficient of variation [s/x 100]
sum - sum of values [xi]
skew - skewness [b = g = m3/(m2 m2)]
sesk - standard error of skewness [6/(n+3)]

Table 24: Differences between nitrogen treatments in number of spikelets per mean main stem panicle.

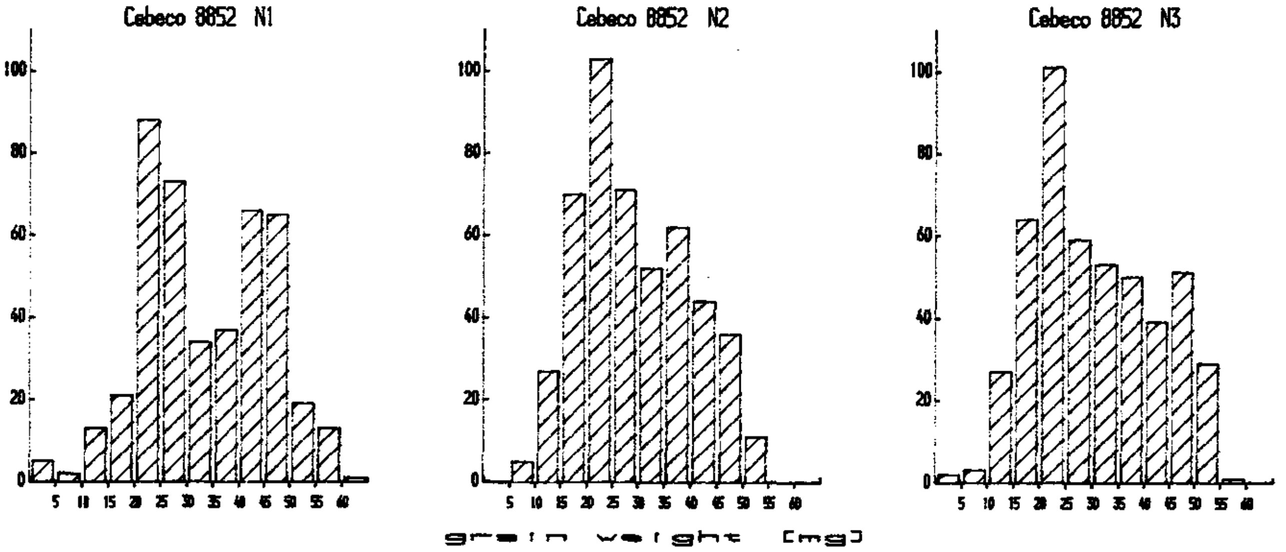
Variety	Year	N2 - N1		N3 - N1		N3 - N2	
		Number	% N2*	Number	% N2*	Number	% N2*
Wilma	1990	18.2	42.4	13.1	30.5	- 5.1	11.9
	1991	9.2	16.2	8.8	15.5	- 0.5	0.9
Cebeco 8852	1990	4.3	10.2	6.7	15.9	2.4	5.7
	1991	8.0	12.6	6.0	9.4	- 2.0	3.1
	Mean	9.9	20.4	8.6	17.8	- 1.3	5.4

Differences between nitrogen treatments

% N2* = expression of differences (values in left column) as percentage

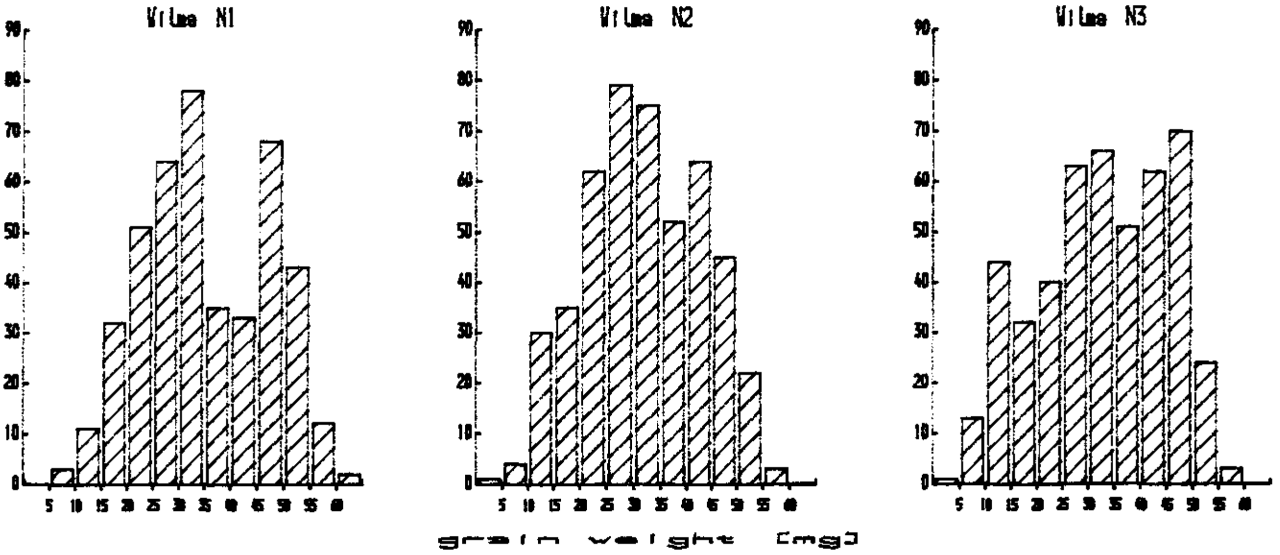


nobs	378.00	517.00	429.00
mean	32.42	28.35	31.27
min	5.00	8.00	9.00
max	60.00	59.00	60.00
range	55.00	51.00	51.00
var	154.16	120.11	122.23
sdev	12.42	10.96	11.06
cv %	38.29	38.66	35.35
sum	12256.00	14655.00	13415.00
skew	0.20	0.35	0.32
sesk	0.13	0.11	0.12

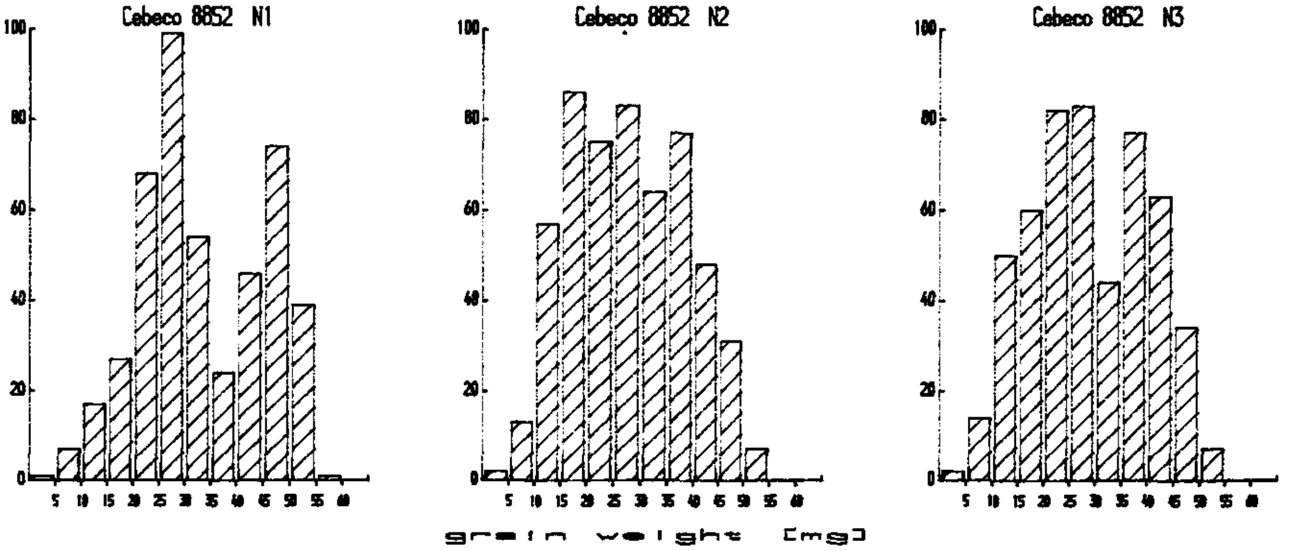


nobs	437.00	481.00	479.00
mean	34.24	29.77	30.95
min	3.00	8.00	2.00
max	61.00	55.00	57.00
range	58.00	47.00	55.00
var	146.94	113.41	140.36
sdev	12.12	10.65	11.85
cv %	35.40	35.77	38.28
sum	14965.00	14320.00	14824.00
skew	0.00	0.33	0.26
sesk	0.12	0.11	0.11

Figure 3.4.1: Histograms of grain weight distribution and statistics of grain weight variability from combine harvest for two varieties and three nitrogen treatments in 1990.

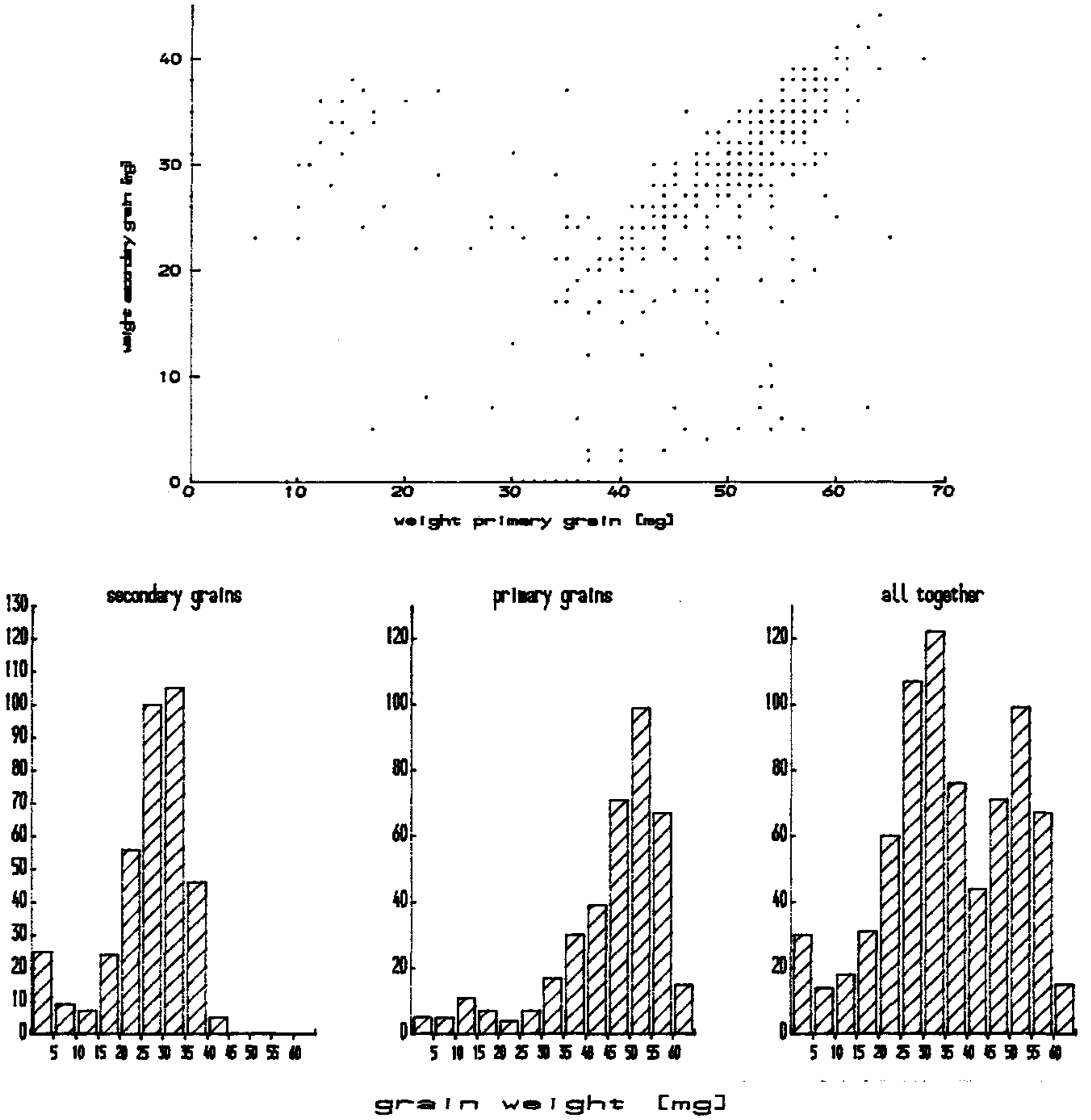


nobs	432.00	472.00	469.00
mean	35.71	32.59	33.10
min	8.00	2.00	5.00
max	62.00	57.00	58.00
range	54.00	55.00	53.00
var	143.80	126.28	158.74
sdev	11.99	11.24	12.60
cv %	33.58	34.48	38.06
sum	15426.00	15381.00	15525.00
skew	0.06	-0.01	-0.23
sesk	0.12	0.11	0.11



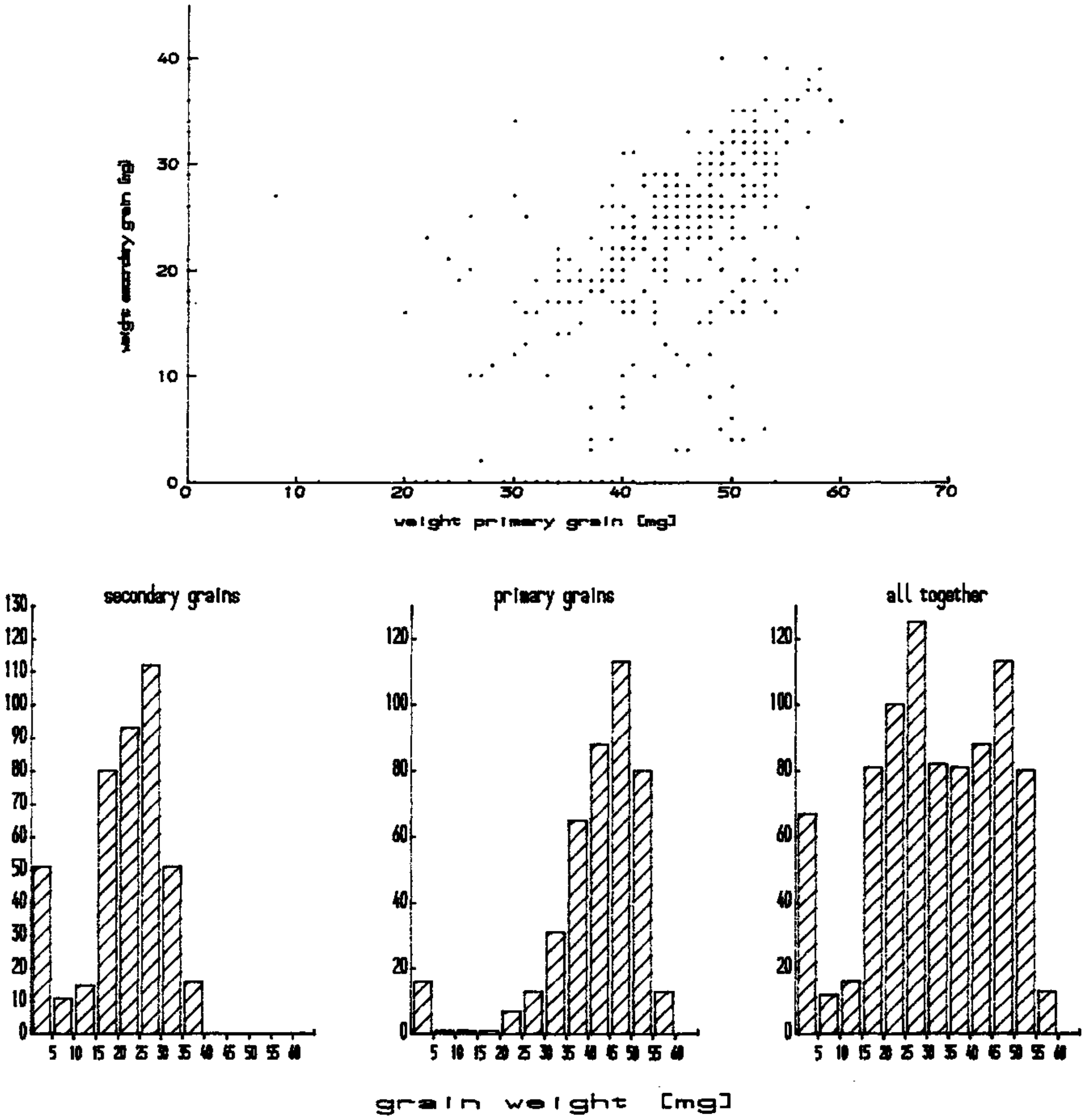
nobs	457.00	543.00	516.00
mean	33.88	28.36	29.39
min	5.00	3.00	4.00
max	58.00	54.00	54.00
range	53.00	51.00	50.00
var	137.34	120.32	126.09
sdev	11.72	10.97	11.23
cv %	34.59	38.68	38.21
sum	15485.00	15398.00	15164.00
skew	0.05	0.14	0.04
sesk	0.11	0.10	0.11

Figure 3.4.2: Histograms of grain weight distribution and statistics of grain weight variability from combine harvest for two varieties and three nitrogen treatments.



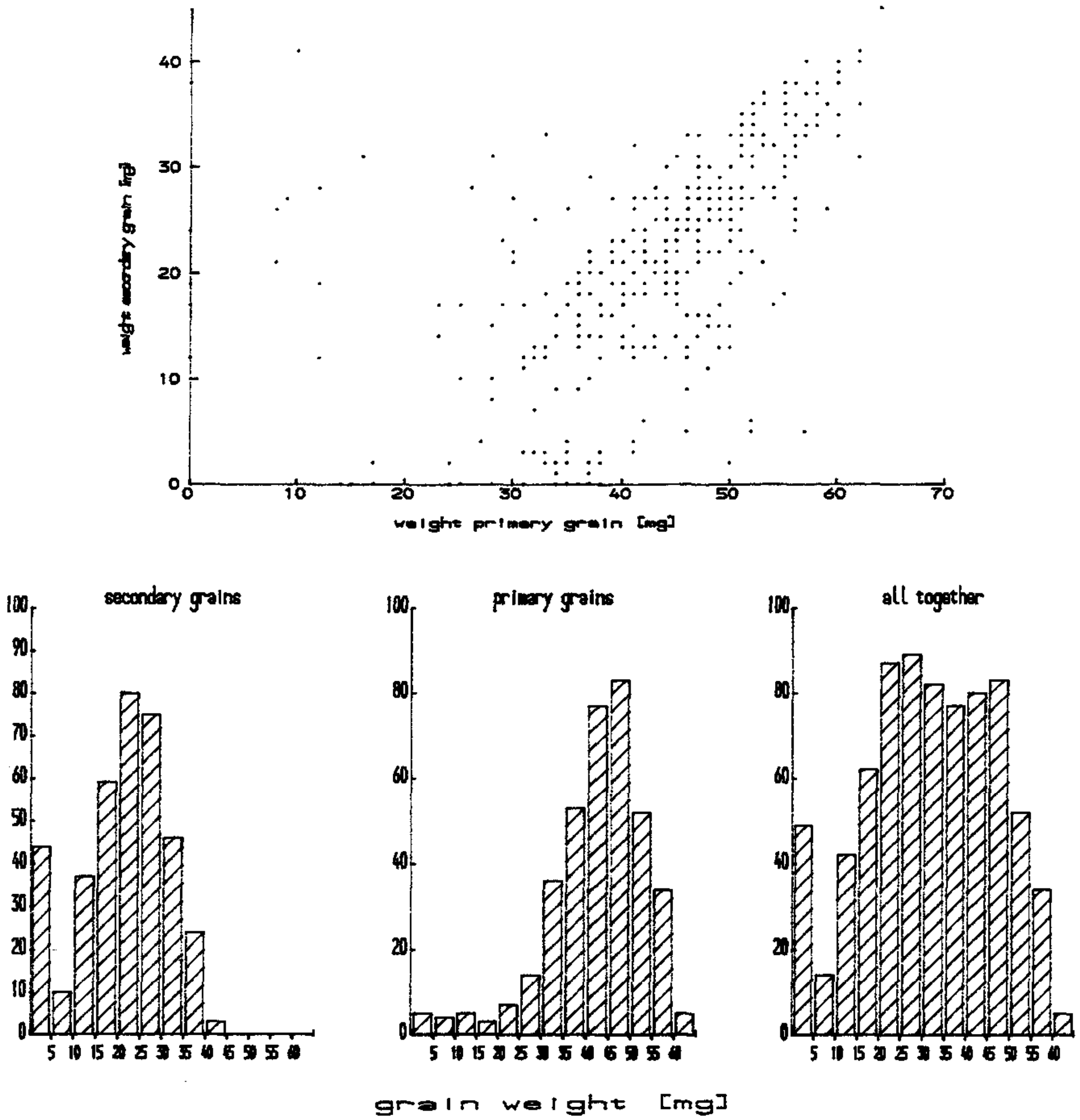
nobs	377.00	377.00	754.00
mean	27.02	46.34	36.68
min	0.00	0.00	0.00
max	44.00	68.00	68.00
range	44.00	68.00	68.00
var	91.30	167.12	222.46
sdev	9.56	12.93	14.92
cv %	35.36	27.90	40.66
sum	10188.00	17471.00	27659.00
skew	-1.28	-1.60	-0.36
sesk	0.13	0.13	0.09

Figure 3.4.3: Characteristics of primary - secondary grain weight relationships, grain weight distribution and grain weight variability for variety Wilma under nitrogen treatment N1 in 1990.



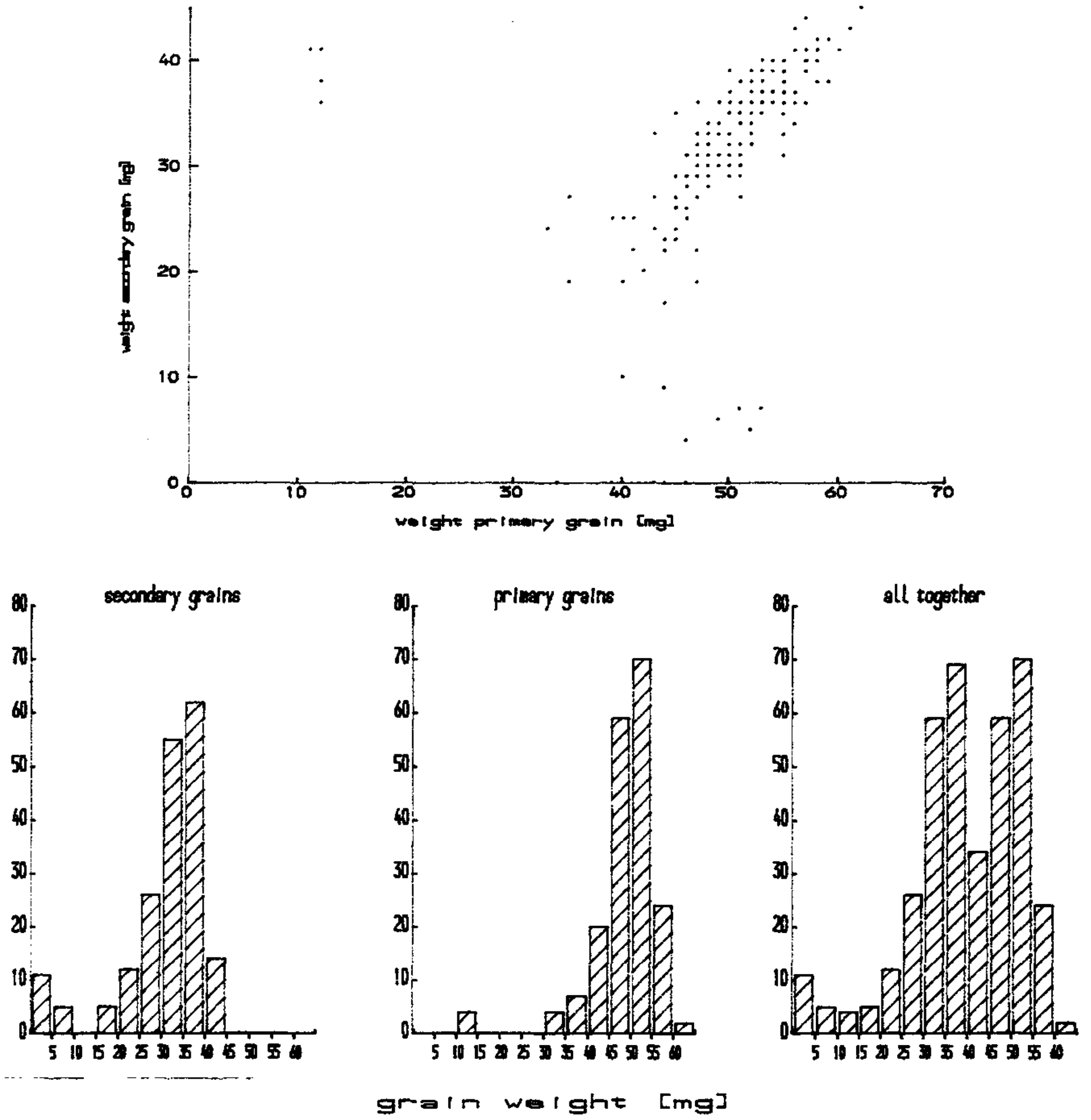
nobs	429.00	429.00	858.00
mean	21.68	42.57	32.13
min	0.00	0.00	0.00
max	40.00	60.00	60.00
range	40.00	60.00	60.00
var	96.35	129.75	222.15
sdev	9.82	11.39	14.90
cv %	45.27	26.76	46.39
sum	9301.00	18263.00	27564.00
skew	-0.88	-2.05	-0.42
sesk	0.12	0.12	0.08

Figure 3.4.4: Characteristics of primary - secondary grain weight relationships, grain weight distribution and grain weight variability for variety Wilma under nitrogen treatment N2 in 1990.



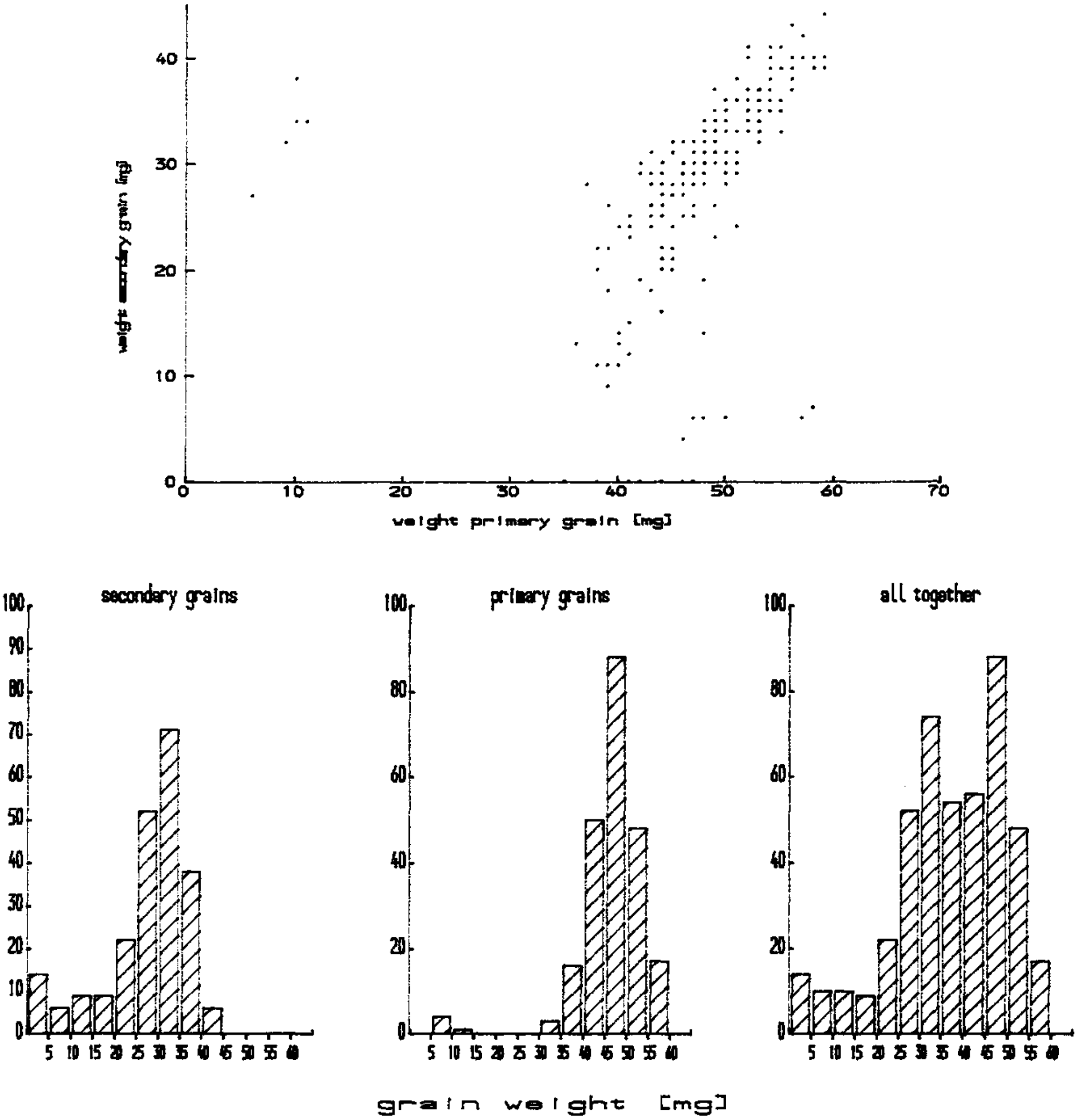
nobs	378.00	378.00	756.00
mean	21.57	42.93	32.25
min	0.00	0.00	0.00
max	45.00	64.00	64.00
range	45.00	64.00	64.00
var	104.99	126.15	229.54
sdev	10.25	11.23	15.15
cv %	47.50	26.17	46.98
sum	8155.00	16226.00	24381.00
skew	-0.48	-1.25	-0.23
sesk	0.13	0.13	0.09

Figure 3.4.5: Characteristics of primary - secondary grain weight relationships, grain weight distribution and grain weight variability for variety Wilma under nitrogen treatment N1 in 1991.



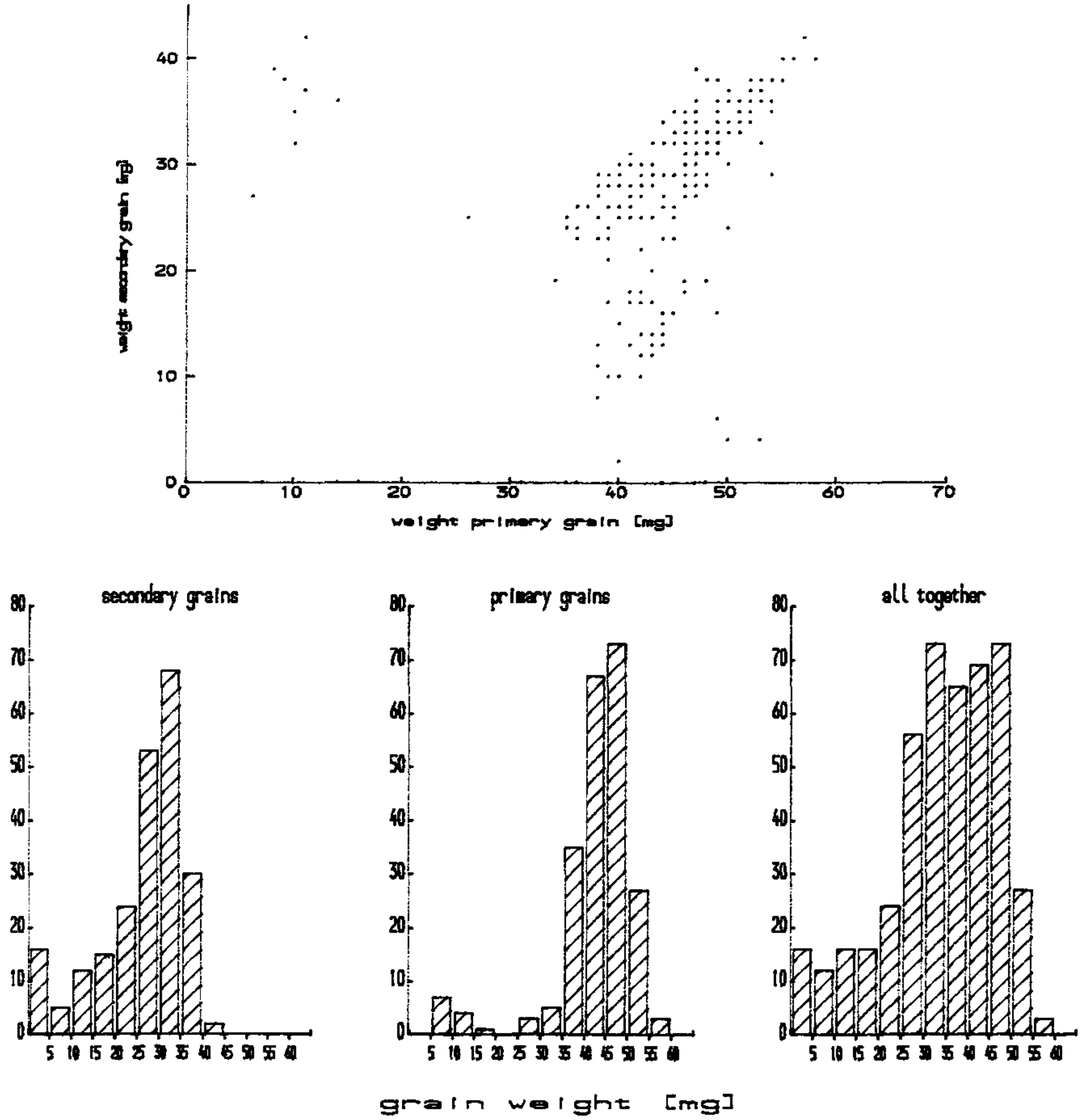
nobs	190.00	190.00	380.00
mean	31.02	49.39	40.21
min	0.00	11.00	0.00
max	45.00	62.00	62.00
range	45.00	51.00	62.00
var	101.78	58.87	164.69
sdev	10.09	7.67	12.83
cv %	32.52	15.54	31.92
sum	5894.00	9384.00	15278.00
skew	-1.78	-2.54	-0.98
sesk	0.18	0.18	0.13

Figure 3.4.6: Characteristics of primary - secondary grain weight relationships, grain weight distribution and grain weight variability for Cebeco 8852 under nitrogen treatment N2 in 1991.



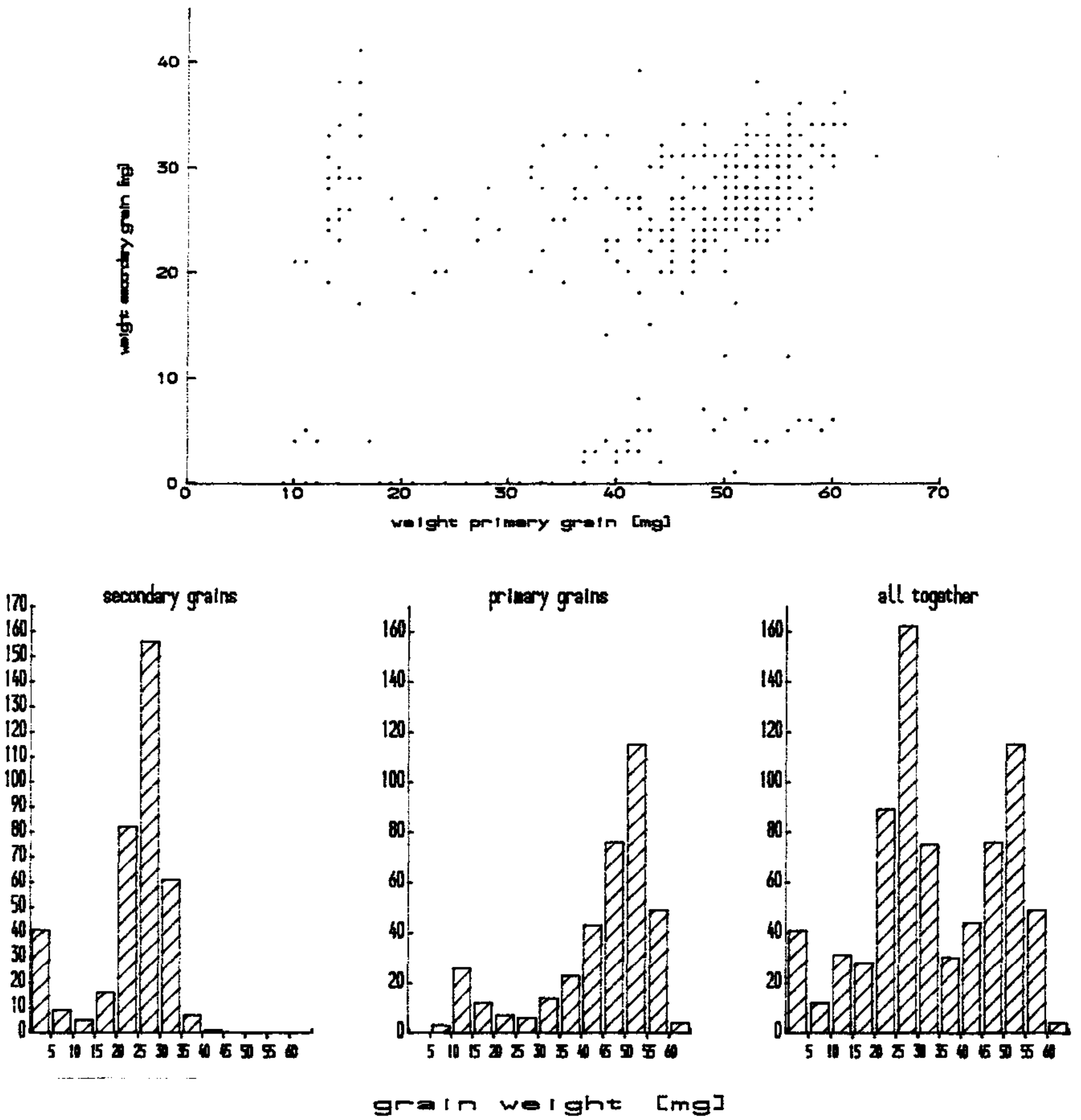
nobs	227.00	227.00	454.00
mean	27.92	47.08	37.50
min	0.00	6.00	0.00
max	44.00	59.00	59.00
range	44.00	53.00	59.00
var	105.29	59.01	173.98
sdev	10.26	7.68	13.19
cv %	36.75	16.31	35.17
sum	6338.00	10688.00	17026.00
skew	-1.36	-2.58	-0.86
sesk	0.16	0.16	0.11

Figure 3.4.7: Characteristics of primary - secondary grain weight relationships, grain weight distribution and grain weight variability for Cebeco 8852 under nitrogen treatment N3 in 1991.



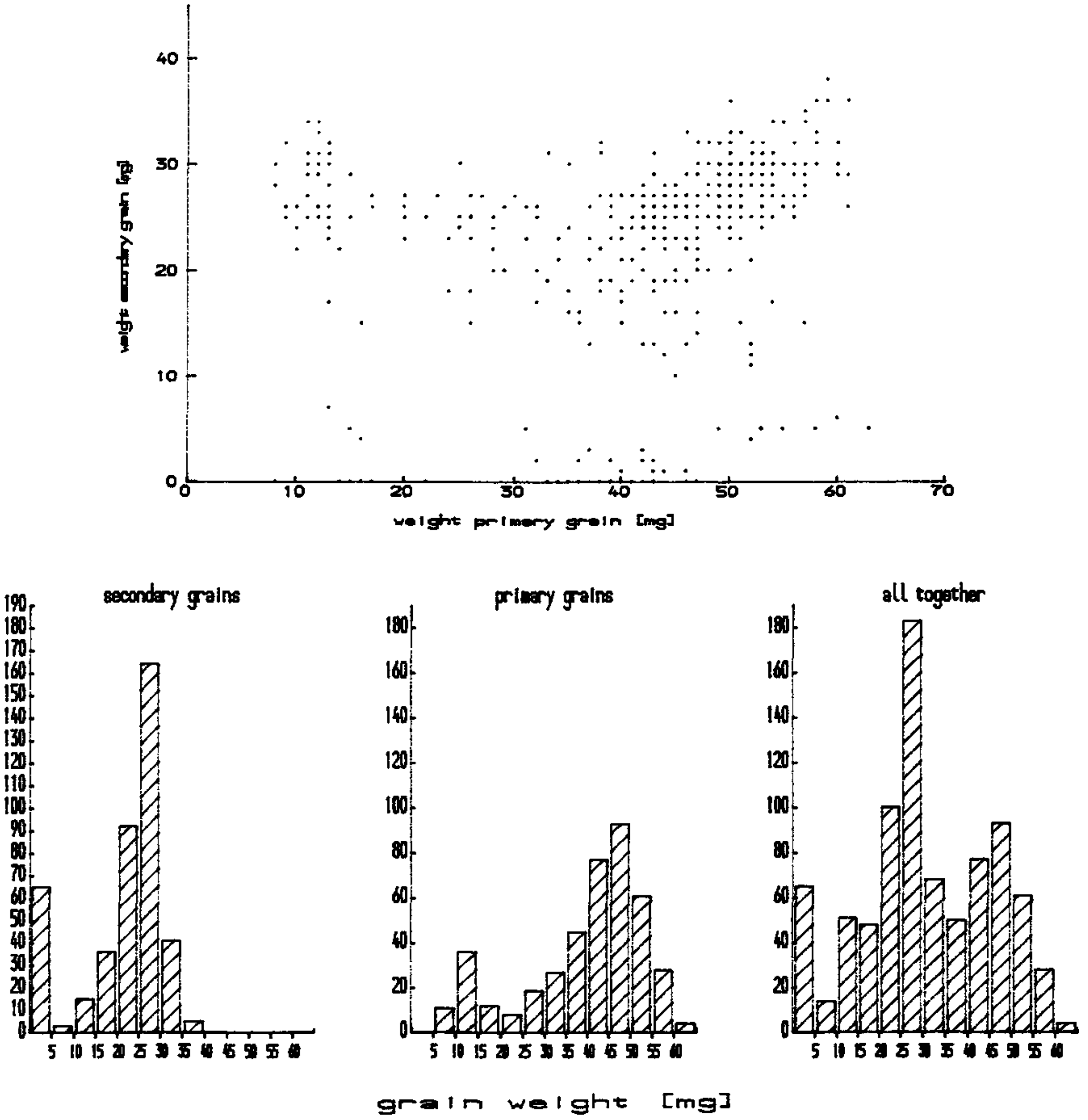
nobs	225.00	225.00	450.00
mean	26.66	43.04	34.85
min	0.00	6.00	0.00
max	42.00	58.00	58.00
range	42.00	52.00	58.00
var	103.24	87.71	162.47
sdev	10.16	9.37	12.75
cv %	38.11	21.76	36.58
sum	5998.00	9683.00	15681.00
skew	-1.23	-2.20	-0.84
sesk	0.16	0.16	0.12

Figure 3.4.8: Characteristics of primary - secondary grain weight relationships, grain weight distribution and grain weight variability for variety Wilma under nitrogen treatment N3 in 1991.



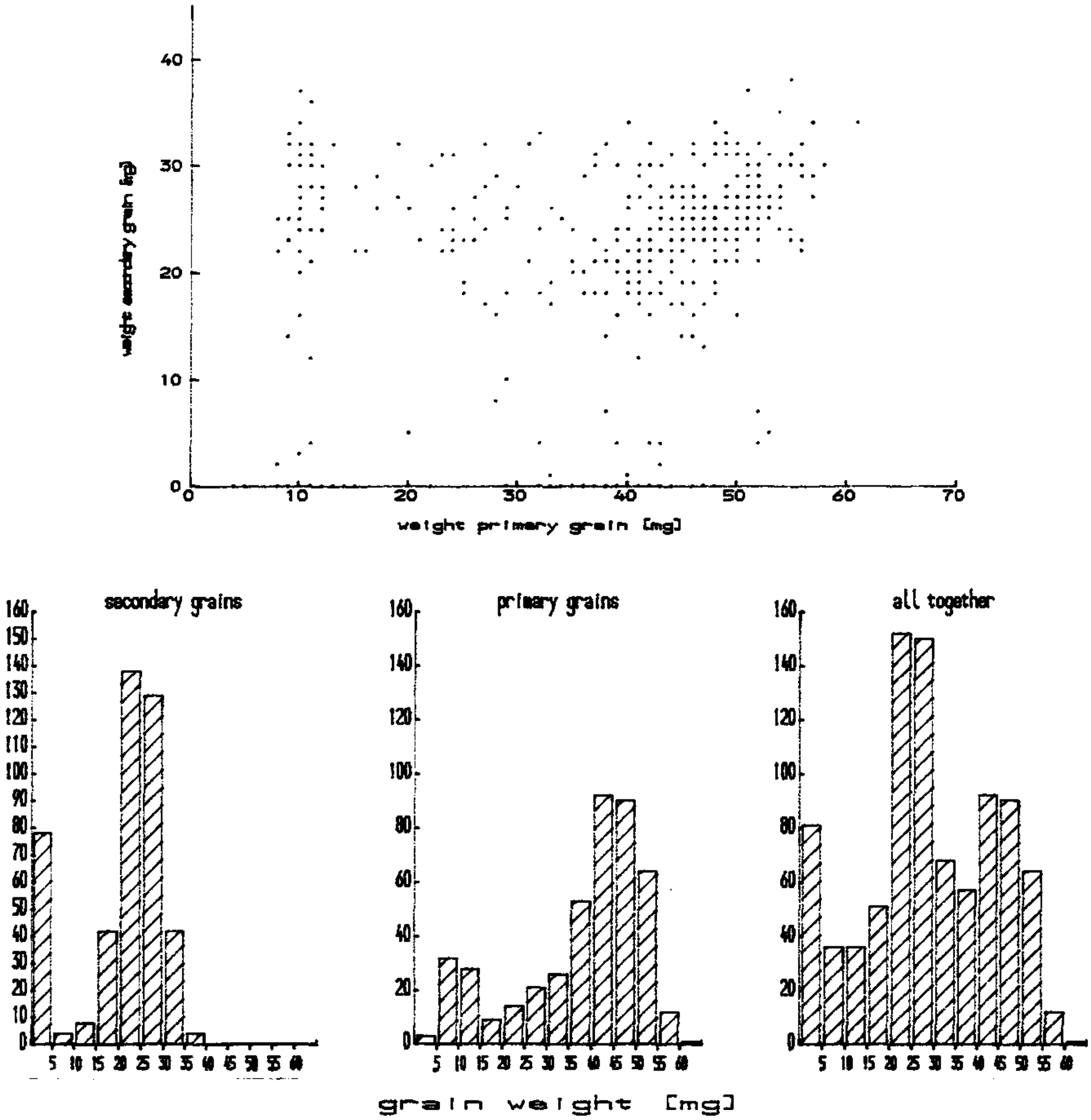
nobs	378.00	378.00	756.00
mean	24.06	44.73	34.39
min	0.00	9.00	0.00
max	41.00	64.00	64.00
range	41.00	55.00	64.00
var	85.54	172.11	235.69
sdev	9.25	13.12	15.35
cv %	38.45	29.33	44.64
sum	9093.00	16909.00	26002.00
skew	-1.43	-1.34	-0.20
sesk	0.13	0.13	0.09

Figure 3.4.9: Characteristics of primary - secondary grain weight relationships, grain weight distribution and grain weight variability for Cebeco 8852 under nitrogen treatment N1 in 1990.



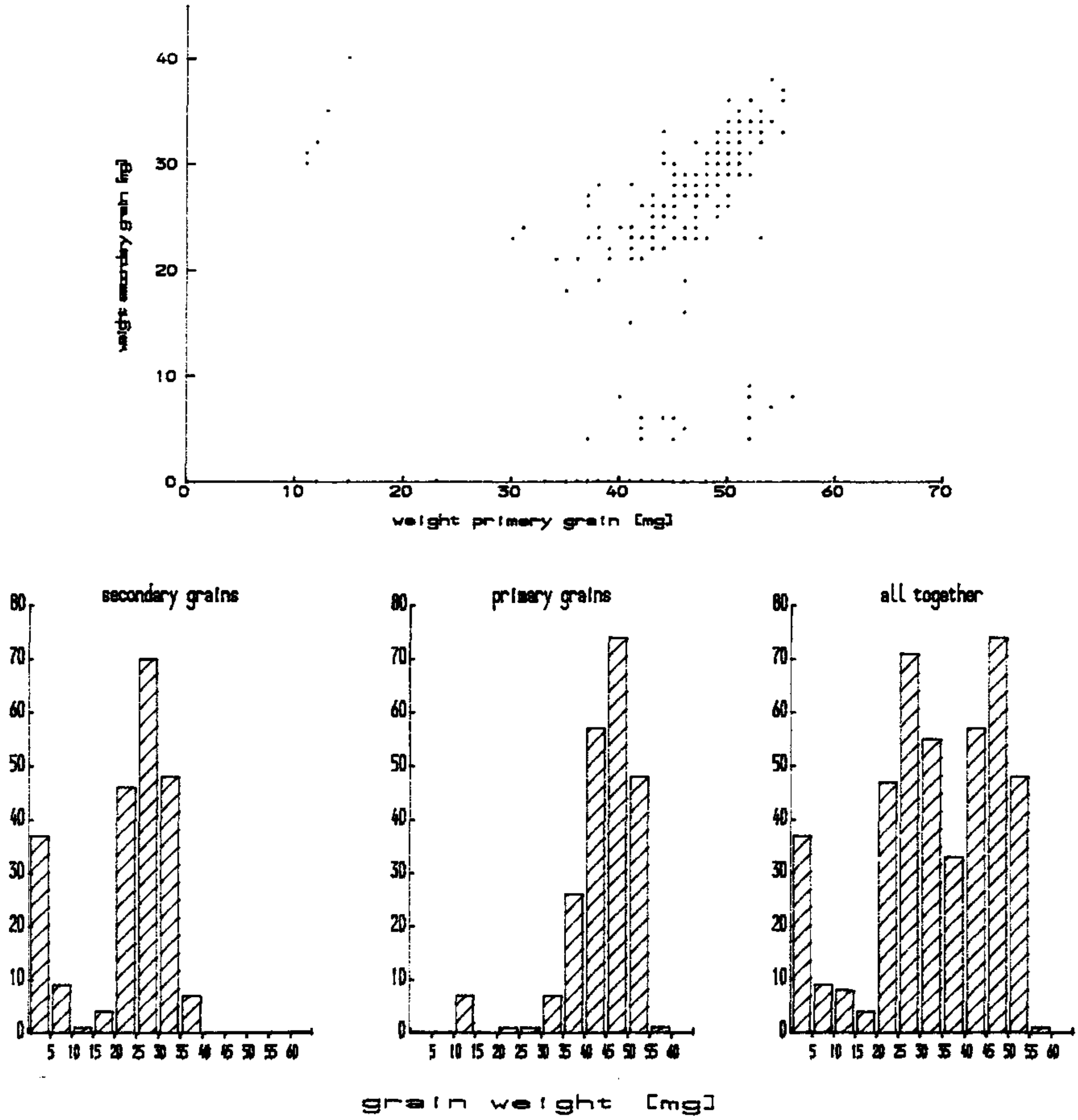
nobs	421.00	421.00	842.00
mean	21.79	40.35	31.07
min	0.00	8.00	0.00
max	38.00	63.00	63.00
range	38.00	55.00	63.00
var	100.70	186.24	229.53
sdev	10.04	13.65	15.15
cv %	46.05	33.82	48.76
sum	9174.00	16988.00	26162.00
skew	-1.20	-0.93	-0.17
sesk	0.12	0.12	0.08

Figure 3.4.10: Characteristics of primary - secondary grain weight relationships, grain weight distribution and grain weight variability for Cebeco 8852 under nitrogen treatment N2 in 1990.



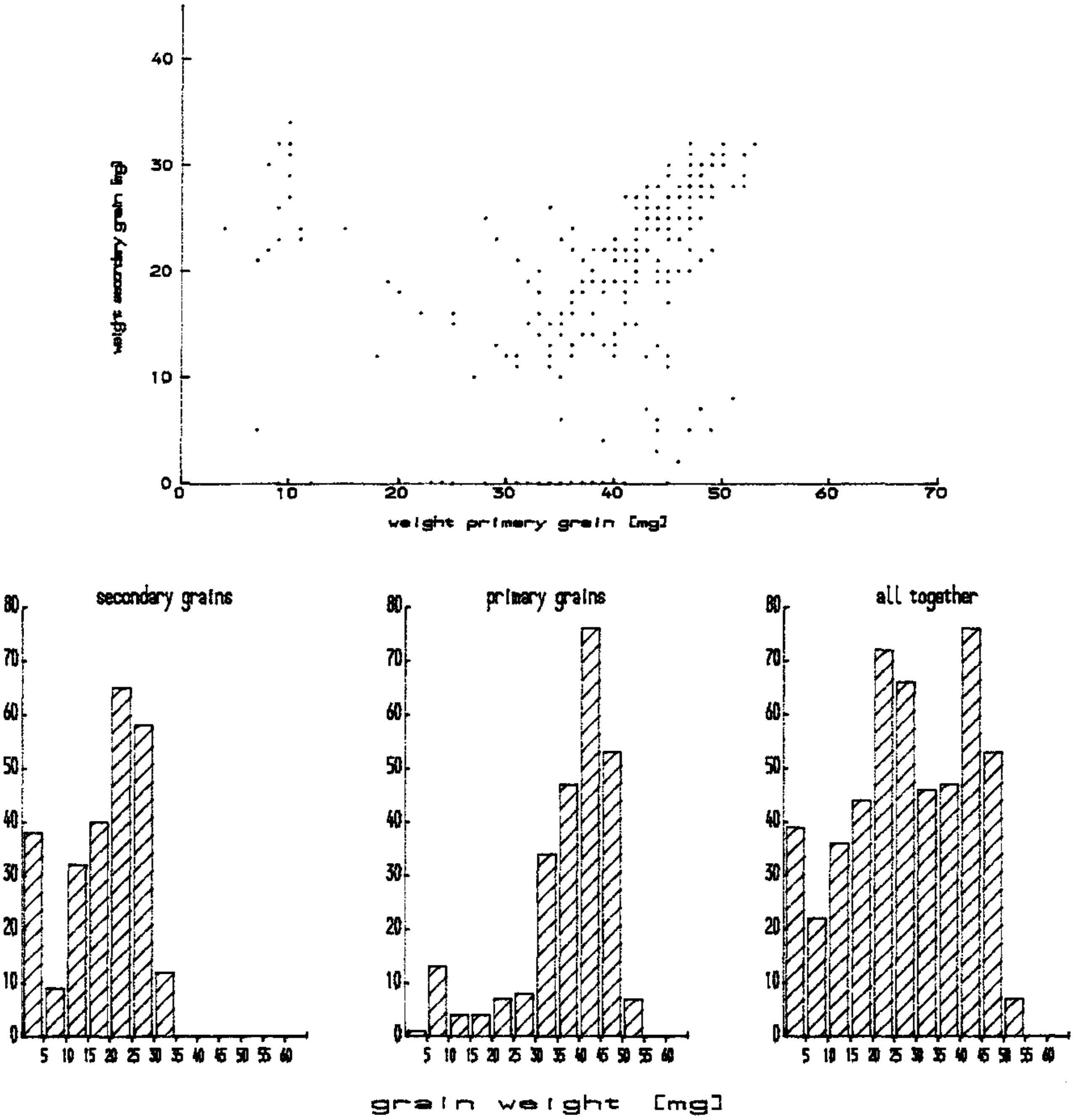
nobs	445.00	445.00	890.00
mean	20.68	38.17	29.42
min	0.00	4.00	0.00
max	38.00	61.00	61.00
range	38.00	57.00	61.00
var	106.58	196.97	228.20
sdev	10.32	14.03	15.11
cv %	49.93	36.77	51.34
sum	9201.00	16986.00	26187.00
skew	-1.07	-0.93	-0.20
sesk	0.12	0.12	0.08

Figure 3.4.11: Characteristics of primary - secondary grain weight relationships, grain weight distribution and grain weight variability for Cebeco 8852 under nitrogen treatment N3 in 1990.



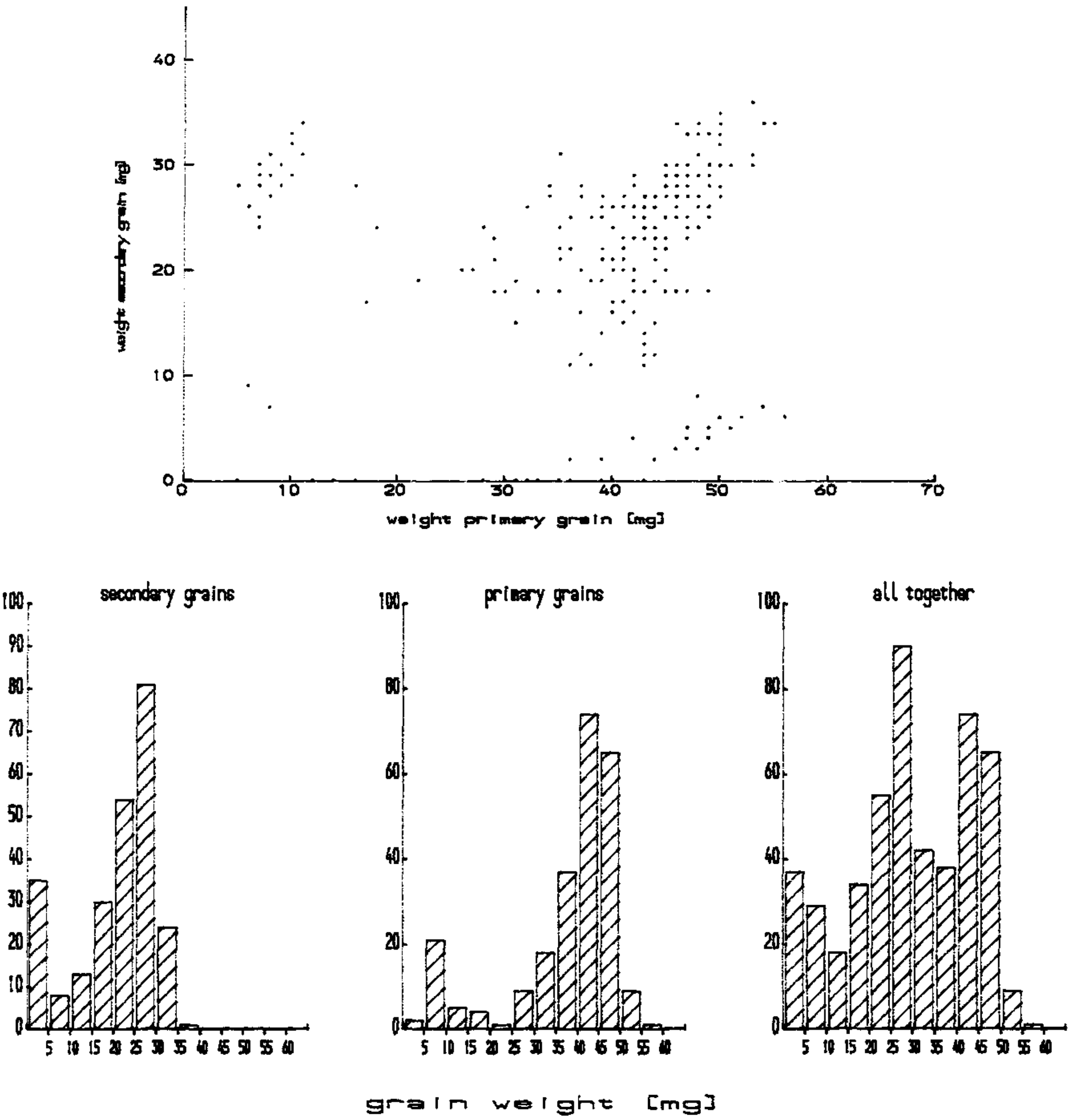
nobs	222.00	222.00	444.00
mean	22.62	44.72	33.67
min	0.00	11.00	0.00
max	40.00	56.00	56.00
range	40.00	45.00	56.00
var	129.65	63.42	218.74
sdev	11.39	7.96	14.79
cv %	50.34	17.81	43.93
sum	5021.00	9928.00	14949.00
skew	-1.07	-2.12	-0.75
sesk	0.16	0.16	0.12

Figure 3.4.12: Characteristics of primary - secondary grain weight relationships, grain weight distribution and grain weight variability for Cebeco 8852 under nitrogen treatment N1 in 1991.



nobs	254.00	254.00	508.00
mean	18.69	38.33	28.51
min	0.00	4.00	0.00
max	34.00	53.00	53.00
range	34.00	49.00	53.00
var	90.88	109.04	196.36
sdev	9.53	10.44	14.01
cv %	51.01	27.25	49.15
sum	4747.00	9735.00	14482.00
skew	-0.73	-1.51	-0.33
sesk	0.15	0.15	0.11

Figure 3.4.13: Characteristics of primary - secondary grain weight relationships, grain weight distribution and grain weight variability for Cebeco 8852 under nitrogen treatment N2 in 1991.



nobs	246.00	246.00	492.00
mean	20.91	38.36	29.63
min	0.00	5.00	0.00
max	36.00	56.00	56.00
range	36.00	51.00	56.00
var	97.69	159.15	204.48
sdev	9.88	12.62	14.30
cv %	47.28	32.89	48.25
sum	5143.00	9437.00	14580.00
skew	-0.95	-1.47	-0.38
sesk	0.16	0.16	0.11

Figure 3.4.14: Characteristics of primary - secondary grain weight relationships, grain weight distribution and grain weight variability for Cebeco 8852 under nitrogen treatment N3 in 1991.

4. DESCRIPTION OF THE MODEL OF GRAIN GROWTH

As shown in the preceding chapter, the weight increase of single grains may be described by a logistic curve. This refers to the average weight increase of a large number of grains. However, the growth of an individual grain in the grain cohort may show a different pattern in the course of the grain filling period, i.e. its growth can be delayed or terminated.

We can assume, that the weight increase of a grain per unit time at a given point in time is affected only by the state of the grain at that time and that the state of the grain follows a Markov transition matrix. Such a model has been used by Miyagawa (1983) for the description of the compound frequency distribution of single seed weight in soybean and for explanation of the positive correlation between weights of seeds within a pod.

This concept appeared attractive and the model was therefore adapted for description of grain filling in oats, having mostly two grains per spikelet.

To describe changes in growth rate, the model distinguishes three stages in the state of the grain (Fig. 4.1). When the grain is in the first stage, F (an ideal condition), the weight increase from time t to time $t+\Delta t$ equals ΔW, represented by the function $f(W)$ during the time interval Δt. When the grain makes the transition from the first stage F to the second stage S, the weight increase during the time interval Δt equals $c\Delta W$, with c a positive constant. Transition from the first stage F to the third stage T represents cessation of grain growth, which is considered an irreversible step. Figure 4.2 shows the possible states of a grain after two time steps Δt.

The probabilities for a given transition of a single grain between states in the time interval between t and $t+t\Delta$ are given in table 25. The probability that a grain is at stage F at time t and at stage S at time $t+\Delta t$ is $p1$. The probability of a transition from stage S to stage F during that time interval is $p2$, that from S to T $p3$ and that from F to T $p1p3$. These probabilities are independent of time t.

When yt is a probability variate that shows the stage of the grains at $t = 1$, it holds:

$$P(yt+1 = i|yt = j, yt-1 = k,...,y0 = 1) = P(yt+1 = i|yt = j).$$

These variates i,j,k, and l represent one of the grain growth stages F, S, or T. Using this, we can describe the probabilities p1, p2 and p3 as:

$$p1 = P(y_{t+1} = S|y_t = F)$$
$$p2 = P(y_{t+1} = F|y_t = S)$$
$$p3 = P(y_{t+1} = T|y_t = S).$$

The probability of a transition from the first stage F to the third stage T is:

$$p1p3 = P(y_{t+1} = T|y_t = F).$$

For a full description of two grains growing within a spikelet, we need $3^2 = 9$ stages. These nine stages characterize the state of the spikelet and are designated E1,..., E9 (table 26). For instance, E1 represents the situation where both the primary grain and the secondary grain are in the first stage (F), E2 that where the primary grain is in the first stage (F) and the secondary grain in the second stage (S), etc.

When Xt is a probability variate that represents the stage of the spikelet and $t = 1$, it holds that:

$$P(X_{t+1} = i|X_t = j, X_{t-1} = k, \ldots, X_0 = l) = P(X_{t=1} = i|X_t = j).$$

The variates i,j,k and l represent one of the stages from E1 to E9. The probabilities of transition of the spikelet stages are given in table 26. When $y^p(t)$ is the probability variate of the primary grain at time t and $y^s(t)$ that of the secondary grain, we can formulate the following hypothesis for the probabilities of transition:

$$P(X_{t+1}) = E_j|X_t = E_i$$
$$= P(y_{t+1} = k, y_{t+1} = l|y_t = m, y_t = n)$$
$$= P(y_{t+1} = k|y_t = m).P(y_{t+1} = l|y_t = n). (k,l,m,n).$$

The variates k,l,m, and n represent one of the stages F, S, or T in this equation.

The difference of (k,l,m,n) from 1 represents the gap from independence.

For practical purposes, however, description of the transition from stage F to stage S and from S to T has been based on the following assumptions:

1. The probabilities for transition of both the primary and the secondary grain are symmetrical. Hence, when the transition FF - FS can be presented by $P(yt+1 = F, yt+1 = S|yt = F, yt = F)$, the probability of the transition FF - SF is identical.
2. When one of the grains remains in stage F, the probability of transition of the other grain from stage F to stage S is a-fold and that from stage S to stage F 1/a-fold, compared to the probabilities for the situation that the growth of both grains within the spikelet is independent.
3. When one of the grains remains in stage S, the growth of both grains in the spikelet is independent.
4. When one of the grains remains in stage T, the probability of transition of the other grain from stage F to stage S is a-fold and that from stage S to stage F 1/a-fold, compared to the probabilities for the situation that the growth of both grains within the spikelet is independent.
5. If for a spikelet holds that $(Xt+1 = Xt)$, the sum of transition probabilities is set to 1.

The primary and the secondary grain within the oat spikelet are not identical in size and growth rate. To take these differences into account, in the model, two grain growth curves are introduced with different parameter values for the primary and secondary grains and different values for the modification of growth rate, c1 for the primary and c2 for the secondary grain.

Table 25: Matrix of probabilities for description of growth of an individual grain.

Stage at time t	Stage at time $t + \Delta t$		
	F	S	T
F	1 - p1 - p1p3	p1	p1p3
S	p2	1 - p2 - p3	p3
T	-	-	1

Table 26: Matrix of probabilities for description of growth of two grains within a spikelet.

Stage at time	t	Stage at time t + Δt								
		FF	FS	FT	SF	SS	ST	TF	TS	TT
E1	FF	q1	(1-p1-p1p3)p1a	(1-p1-p1p3)p1p3	(1-p1-p1p3)p1a	p1	p1p3	(1-p1-p1p3)p1p3	p1p3	p1p3
E2	FS	(1-p1-p1p3)p2/a	q2	(1-p1-p1p3)p3	p1p2	p1(1-p2p3)	p1p3	p1p2p3	(1-p2-p3)p1p3	p1p3
E3	FT	-	-	q3	-	-	p1a	-	-	p1p3
E4	SF	(1-p1-p1p3)p2/a	p1p2	p1p2p3	q4	p1(1-p2-p3)	p1p3(1-p2-p3)	p3(1-p1-p1p3)	p1p3	p1p3
E5	SS	p2	(1-p2-p3)p2	p2p3	(1-p2-p3)p2	q5	(1-p2-p3)p3	p2p3	(1-p2-p3)p3	p3
E6	ST	-	-	p2/a	-	q6	-	-	-	p3
E7	TF	-	-	-	-	-	q7	q7	p1a	p1p3
E8	TS	-	-	-	-	-	p2/a	p2/a	q8	p3
E9	TT	-	-	-	-	-	-	-	-	1

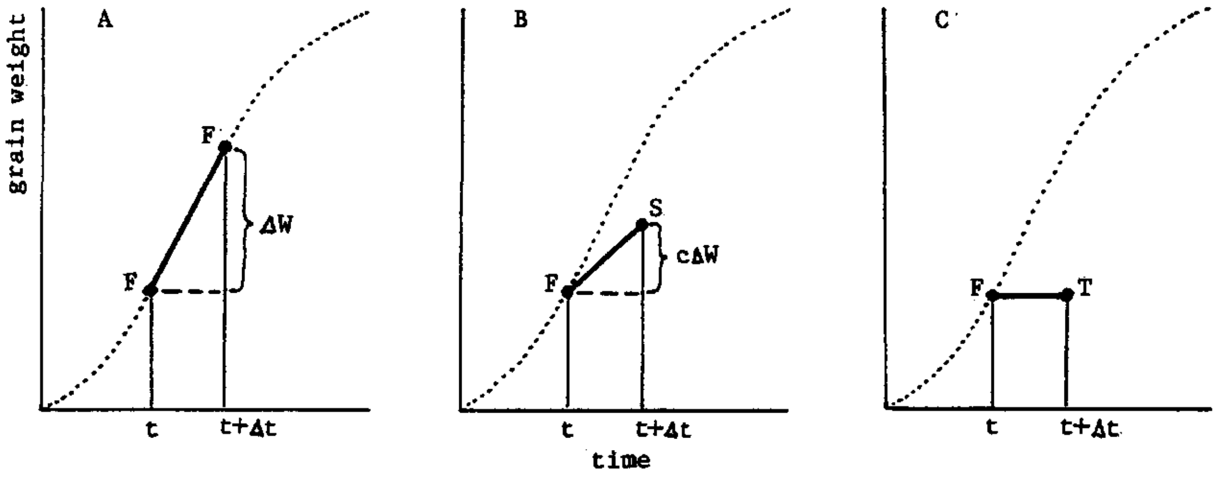


Figure 4.1: The model of grain growth. The y-axis represents grain weight and the x-axis time. The dotted curve shows continuous growth and the solid lines various stage transitions. The graph shows the changes in grain growth stage after time Δ t; A - the grain remained in stage F, B - the grain moved from stage F to stage S, and C - the grain moved from stage F to stage T.

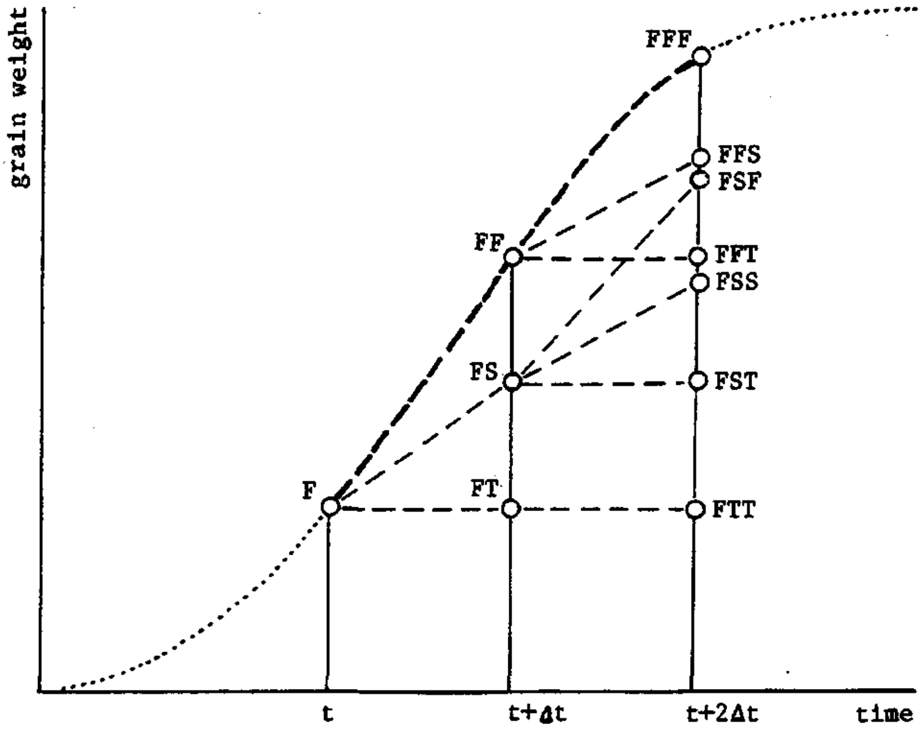


Figure 4.2: The possibilities of grain stage transitions from stage F after two time steps Δt.

5. RESULTS OF SIMULATIONS

Based on the model described in Chapter 4, the calculation procedure in 11 steps is shown in table 27. The actual program in Turbo Pascal is given in Appendix 1.

The program has general applicability in describing variability within plant organs. It has the option to select a specific group of random numbers, while two types of growth curves for individual grains may be introduced.

Random numbers can be generated for each simulation run individually, or can be retained for a set of simulation runs. The second option allows more accurate comparison of simulated and empirical results. When working interactively with the model, a starting number has to be defined for each generation of random numbers and by using the identical number for the various runs, identical sets of random numbers are generated.

Two types of logistic growth curves for individual grains can be introduced in the model:

1. The generalized logistic growth curve with four parameters (Payne at al., 1987), which can be calculated by GENSTAT directly from empirical data.
2. The modified equation for a logistic growth curve used by Miyagawa (1983), characterized by two parameters. Before these can be calculated, the parameters t0 (starting time for growth curve calculations) and W0 (weight of grain at time t0) must be specified.

As shown in table 27 the model has seven sets of parameters:

- parameters characterizing the growth curves for individual grains
- time parameters
- the number of spikelets considered
- grain weight range at the start of the calculations
- growth rate modification factors
- probabilities for grain stage transitions
- degree of competition.

Growth curve parameters

The time course of dry matter accumulation in all primary and secondary grains is derived from two curves only. These curves should represent the potential grain growth rates, i.e. those realized in the absence of any source limitation. Therefore, the data pertaining to the largest primary and secondary grains should be used to derive the growth curve parameters. In oats those refers to the grains in the top spikelet of the main stem panicles. These growth curves can be considered to represent the grain filling potential under ideal conditions with unlimited source supply.

Parameters of the generalized logistic growth curve have been analysed in Section 3.3. As in the model also other parameters are used, i.e. c and t, the designation of parameters used by GENSTAT was changed as follows: B = f, M =m, T = 1, C = g. Parameters for Miyagawa's curve are described in his paper (Miyagawa, 1983).

Time parameters (in days)

t0 - used for Miyagawa's curve only, where it indicates the time corresponding to W0 (initial grain weight in the model)

tmax - finish time of the calculation procedure; for Miyagawa's growth curve tmax is defined relative to t0; for the generalized logistic growth curve relative to t = 0

t - time determining the starting point of the calculations

t_stop - time at which the calculation procedure can be temporarily halted to reset calculation parameters (c1, c2; p1, p2, p3; a).

Number of spikelets considered

The number that can be handled by the model is practically unlimited. As the number of spikelets and grains per unit area is an important stand characteristic, it is most convenient to apply the calculation procedure to a certain stand area. For a clear graphical presentation of results an area of about 0.15 m^2 is most suitable, corresponding to about 300 - 1000 spikelets, depending on stand density.

Grain weight range

This range at the start of the calculations is one of the important parameters. For the primary grains it can be specified by the weights of the smallest and the largest individual grain, characterizing the length of the period of grain formation, which depends on the branching processes. The degree of branching depends on assimilate availability, and more profuse branching may be the result of a longer period of branching or a higher rate of branching. Crops growing under limited source availability, therefore exhibit a narrower range in primary grain weight. Crops growing under conditions of more abundant assimilate availability exhibit a wider interval of initial grain weights, especially in the lower weight range (more extended period of grain formation). The weight of the secondary grain within the spikelet is usually around 50 % of that of the primary grain. In the program, allowance is made to specify the proportional weight either as a fixed value or as a range.

Growth rate modification

These parameters can also be specified as a fixed number or as a range. Quantitative estimates of these parameters should be made in relation to the probabilities for the differential transition of grain weights between stages, because both are used for modification of the grain growth trajectories. Some general rules can be formulated:

1. Crops having spikelet cohorts formed over a longer period of time exhibit more extended ranges of grain growth trajectories, i.e. more trajectories are situated close to the x-axis.
2. Lack of assimilates reduces grain growth rate. Under such conditions, the growth rate of the secondary grains is more strongly affected than that of the primary grains.
3. The growth rate depends on the current supply of assimilates. To mimick a variable supply, the program contains the option to halt the calculation procedure (using t_stop) to reset parameters of growth rate modifications (c1 and c2), probabilities for stage transitions (p1, p2 and p3) and degree of competition (a), respectively.

Probabilities for stage transitions

The function of these parameters has been described in Chapter 4. Note that p1 and p2 refer to growing grains and p3 determines grain growth cessation and has a higher value therefore in crops with limited assimilate supply, where higher numbers of aborted grains and lower grain numbers per unit area are usually observed (for instance treatment N1). The value of p3 is usually one or two orders of magnitude smaller than that of p1 and p2.

Degree of competition (a)

This parameter influences the relationship between growth of the grains within the spikelet. Its value ranges between 0 and 1. When a = 1, growth of the grains is independent. Lower values, representing competition for limited resources, contribute to formation of the three clusters of points in the graphical presentation of grain weights, typical for crops with limited assimilate supply.

The program has two options for presentation of results:

1a Graphs depicting the relation between the weights of the primary and the secondary grains (for example Fig. 44). Below each graph actual values of some characteristics at the time of interruption of the calculation procedure are presented:

t - time at interruption of the calculations
dw1 - slope of the primary grain growth curve at time t (mg/d)
dw2 - slope of the secondary grain growth curve at time t (mg/d)
wt1 - primary grain weight at time t (mg)
wt2 - secondary grain weight at time t (mg)
n - number of spikelets considered.

1b Histograms of grain weight distribution with common statistics of variability, arranged similarly to the experimental results (Section 3.4), with the addition of a histogram and statistics of differences between primary and secondary grain weights.

2a Isolation of the central cluster and presentation of the parameters of the linear regression between primary and secondary grain weights (cf. Fig. 45).

These parameters are presented below the graph:

bpg - boundary value for selection of primary grains (mg)
bsg - boundary value for selection of secondary grains (mg)
t - time of interruption of the calculation procedure
n-2 - number of selected spikelets reduced by 2 (d.f. for calculation of the correlation coefficient)
r - correlation coefficient
a - constant of linear regression
b - regression coefficient
(for the equation $Ws = a + b.Wp$, where Wp is the weight of primary grains and Ws is the weight of secondary grains within the spikelets).

2b Histograms of the selected grain weight distributions and common statistics of variability arranged as under 1b (Fig. 5.9).

The dynamics of the results of the calculation procedure after 5, 10, 15, 20, 30 and 50 days are shown in figs. 5.4 - 5.9. These figures refer to the metapopulation of spikelets for variety Wilma under nitrogen treatment N1 in 1990. Simulation parameters are given in Fig. 3.4.7.

Although most of the parameters have a real biological meaning, the model as a whole must be characterized as descriptive. The values of the parameters can be established interactively by successive calculations, comparing the results with experimental values.

As an illustration six examples from the experiments described in Section 3.4 were treated, as specified in table 28.

One single growth curve was specified for the primary grains and one for the secondary grains for all six cases (figs. 5.1 and 5.2). All time parameters were also identical. The value tmax = 50 corresponds to the length of the grain filling period of 50 days observed in 1991.

The number of spikelets specified refers to about 0.15 m^2 of the stand area. The values of n for the individual variants were estimated from measured grain densities (see Section 3.2).

The range in primary grain weights at the start of the calculations was also derived from experimental results. The average weight is higher and the range narrower in crops under limited nitrogen supply (N1). In nitrogen treatment N3 initial average grain weight is lower and the range wider towards the lower values. The initial weight of the secondary grains, as a fraction of that of the primary grains is the same (0.3 - 0.6) in all cases, as derived from measurements at the start of grain filling.

The values of the probabilities of transition vary among varieties and nitrogen treatments (except p2 which has the same value in all situations). Variety Wilma has larger grains, therefore p1, representing the probability of transition from the first to the second grain stage (Table 25), has relatively lower values, i.e. 0.15 to 0.20 (Fig. 5.1). For Cebeco 8852, with smaller grains, the value is logically higher and 0.5 is used in all three cases (Fig. 5.2). Values of p3 were specified according to nitrogen treatment. Higher values are used for N1 (p3 = 0.02 for Wilma and 0.015 for Cebeco 8852) and lower values for N3 (p3 = 0.004 for Wilma in both 1990 and 1991 and p3 = 0.005 for Cebeco 8852 in 1991). As an exception, a value of p3 = 0.015 for Cebeco 8852 for N3 in 1990 had to be specified to reproduce the observed grain weight distribution, which is affected by gradual cessation of growth in the primary grains (Fig. 3.4.11).

The degree of competition (a) was specified on the basis of the assumption that in crops under limited nitrogen supply (source limitation) competition between the grains within the spikelets is stronger. Therefore, lower values of a (0.15 and 0.10) were used for crops under nitrogen treatment N1 and higher values (0.35 and 0.25) for crops under N3 (figs. 5.1 and 5.2). Lower values result in a more condensed central cluster, higher maximum weights for both the primary and the secondary grains and extension of the clusters towards both axes (figs. 5.9 and 5.14). Therefore, in that situation the smaller clusters are further from the origin and close to the axes, representing spikelets with either dominant primary grains (close to the x-axis) or secondary grains (close to the y-axis). On the other hand higher values of a result in a more dispersed central cluster (figs. 5.11, 5.12, 5.14, 5.15), in agreement with the experimental results in figs. 3.4.5, 3.4.8, 3.4.11, 3.4.14.

Values of the growth rate modification factors were generally specified as intervals, with different values for c1 and c2 in all situations (figs. 5.1 and 5.2).

The option to adjust the growth rate in intervals and separately for primary and secondary grains, makes the model more flexible than that published by Miyagawa (1983) and allows independent modification of the primary and the secondary grain weight distribution. Attempts to attain patterns of grain weight distribution similar to the observed ones result in different c1 and c2 values per variety, year and nitrogen treatment (figs. 5.1 and 5.2). To attain more even and extended primary grain weight distributions (with higher frequencies of low values) for Cebebo 8852 under N1 and N3 in 1990, wider ranges for c1, including values > 1 had to be applied (0.1 - 1.5 and 0.1 - 1.4, respectively, Fig. 5.2). This implies that the growth rate is partly reduced (c1 < 1) and partly increased (c1 > 1). On the other hand, a single value (c2 = 0.6) or a very narrow interval (c2 = 0.5 - 0.6) are required to reproduce the very narrow distribution of the secondary grains in these cases (Fig. 5.2).

This may seem to complicate parametrization of the calculation procedure, but on the other hand illustrates the possibilities of the model to describe different situations of variety x treatment interaction, especially the differential response of spikelets and grains in different positions within the panicle to the actual assimilate supply.

The option to interrupt the calculation procedure at a certain moment, to reset the parameters for modification of the grain growth trajectories, can be used for description of dynamic reactions of primary and secondary grain growth to environmental conditions. This option can also be used to describe grain embryo abortion, which occurs mostly at pollination and fertilization, i.e. during the first days of the grain filling period. That is probably the reason that in figs. 3.4.3 and 3.4.9, presenting the experimental results of treatment N1, the clusters are more sharply distinguished than in the simulated patterns (figs. 5.15 and 5.16). There, the higher value of p3 was operational during the full grain filling period.

For an illustration of parameter resetting, variety Wilma under nitrogen treatment N1 in 1990 was selected. The original and the modified parameters are given in Fig. 5.3, results of the calculations in Fig. 5.16. At first sight the simulated clusters are more compact and more sharply distinguished in comparison with the original pattern (Fig. 5.15). Fig. 5.16 is also in better agreement with observations (Fig. 3.4.3).

Table 27: Calculation procedure for the growth of two grains within a spikelet.

---

1. Definition of parameter values
   - time parameters:
     - t0 - starting time for growth curves
     - Δt - time interval
     - t - starting time for simulation
     - tmax - end of calculation
     - t_stop - time at interruption of calculation
   - size of file n (number of spikelets considered in the model)
   - starting weights:
     - Wt1st - primary grains
     - Wt2nd - secondary grains
   - parameters of primary and secondary grain growth curves
   - growth rate modifications:
     - c1 for primary grain
     - c2 for secondary grain
   - probabilities for stage transitions p1, p2, and p3
   - degree of competition a
2. Calculation of probabilities for transition of stages (table 26)
3. Setting of spikelet stages at starting time t:
   - grain weight primary and secondary grains
   - grain stage primary and secondary grains
4. Generation of random numbers
5. Setting of the spikelet stages (E1-E9) with random numbers and their transition on the basis of the matrix of probabilities
6. Calculation of grain weight increases Δ W1 (for primary grain) and ΔW2 (for secondary grain)
7. Calculation of grain weigh with Ei, ΔW1, ΔW2, c1, and c2
8. Time increment with Δt and return to point 4
9. End of grain growth calculation after $(tmax-t)/\Delta t$ loops between points 4 and 8
10. Calculation of the characteristics of grain weight variability and linear regression between the primary and secondary grains
11. Presentation of results

Table 28: cross-reference table for presentation of experimental results and simulatin results.

Variant			Number of figure presenting		
Variety	Year	Nitrogen treatment	Experimental results	Simulation parameters	Results of simulation
Wilma	1990	N1	3.4.3	5.1	5.9
Wilma	1990	N3	3.4.5	5.1	5.11
Wilma	1991	N3	3.4.8	5.1	5.12
Cebeco 8852	1990	N1	3.4.9	5.2	5.13
Cebeco 8852	1990	N3	3.4.10	5.2	5.14
Cebeco 8852	1991	N3	3.4.14	5.2	5.15

```
                    SIMULATION PARAMETERS

TIMES [days]                                GROWTH CURVES
                              primary grain            secondary grain
tmax=50                       f1=.20                   f2=.26
dt=1                          m1=16                    m2=18
t=1                           l1=2.0                   l2=2.5
FILE SIZE                     g1=60                    g2=40
n=340
STARTING WEIGHTS
Wtist[mg]=11  -.1             PROBABILITIES
Wt2nd[proportion of Wt1st]=.3 -.6  p1=.15              t_stop=50
GROWTH RATE MODIFICATIONS          p2=.1
c1=.3   -.8                        p3=.02
c2=.1   -.3                        a= .15
```

b/ Nitrogen treatment N3 in 1990.

```
                    SIMULATION PARAMETERS

TIMES [days]                                GROWTH CURVES
                              primary grain            secondary grain
tmax=50                       f1=20                    f2=.26
dt=1                          m1=16                    m2=18
t=1                           l1=2.0                   l2=2.5
FILE SIZE                     g1=60                    g2=40
n=590
STARTING WEIGHTS
Wt1st[mg]=9      -.001        PROBABILITIES
Wt2nd[proportion of Wt1st]=.3 -.6  p1=.25              t_stop=50
GROWTH RATE MODIFICATIONS          p2=.1
c1=.3   -.8                        p3=.004
c2=.05  -.6                        a= .35
```

c/ Nitrogen treatment N3 in 1991

```
                    SIMULATION PARAMETERS

TIMES [days]                                GROWTH CURVES
                              primary grain            secondary grain
tmax=50                       f1=.20                   f2=.26
dt=1                          m1=16                    m2=18
t=1                           l1=2.0                   l2=2.5
FILE SIZE                     g1=60                    g2=40
n=720
STARTING WEIGHTS
Wt1st[mg]=9  -.001            PROBABILITIES
Wt2nd[proportion of Wt1st]=.3 -.6  p1=.2              t_stop=50
GROWTH RATE MODIFICATIONS          p2=.1
c1=.3   -.8                        p3=.004
c2=.1   -.6                        a= .35
```

Figure 5.1: Simulation parameters for variety Wilma; (a) Nitrogen treatment N1 in 1990; (b) Nitrogen treatment N3 in 1990; (c) Nitrogen treatment N3 in 1991.

a/ Nitrogen treatment N1 in 1990.

```
                    SIMULATION PARAMETERS

TIMES [days]                                GROWTH CURVES
                              primary grain          secondary grain
tmax=50                       f1=.20                 f2=.26
dt=1                          m1=16                  m2=18
t=1                           l1=2.0                 l2=2.5
FILE SIZE                     g1=60                  g2=40
n=340
STARTING WEIGHTS
Wt1st[mg]=11  -.1             PROBABILITIES
Wt2nd[proportion of Wt1st]=.3 -.6  p1=.5            t_stop=50
GROWTH RATE MODIFICATIONS          p2=.1
c1=.1   -.1.5                      p3=.015
c2=.6   -.6                        a= .1
```

b/ Nitrogen treatment N3 in 1990.

```
                    SIMULATION PARAMETERS

TIMES [days]                                GROWTH CURVES
                              primary grain          secondary grain
tmax=50                       f1=.20                 f2=.26
dt=1                          m1=16                  m2=18
t=1                           l1=2.0                 l2=2.5
FILE SIZE                     g1=60                  g2=40
n=550
STARTING WEIGHTS
Wt1st[mg]=9  -.001            PROBABILITIES
Wt2nd[proportion of Wt1st]=.3 -.6  p1=.5            t_stop=50
GROWTH RATE MODIFICATIONS          p2=.1
c1=.1   -1.4                       p3=.015
c2=.5   -.6                        a= .35
```

c/ Nitrogen treatment N3 in 1991.

```
                    SIMULATION PARAMETERS

TIMES [days]                                GROWTH CURVES
                              primary grain          secondary grain
tmax=50                       f1=.20                 f2=.26
dt=1                          m1=16                  m2=18
t=1                           l1=2.0                 l2=2.5
FILE SIZE                     g1=60                  g2=40
n=730
STARTING WEIGHTS
Wt1st[mg]=9  -.001             PROBABILITIES
Wt2nd[proportion of Wt1st]=.3 -.6  p1=.5            t_stop=50
GROWTH RATE MODIFICATIONS          p2=.1
c1=.4   -.8                        p3=.005
c2=.2   -.6                        a= .25
```

Figure 5.2: Simulation parameters for Cebeco 8852: (a) Nitrogen treatment N1 in 1990; (b) Nitrogen treatment N3 in 1990; (c) Nitrogen treatment N3 in 1991.

a/ Parameters used for the first part of simulation during the time interval t= 1-10.

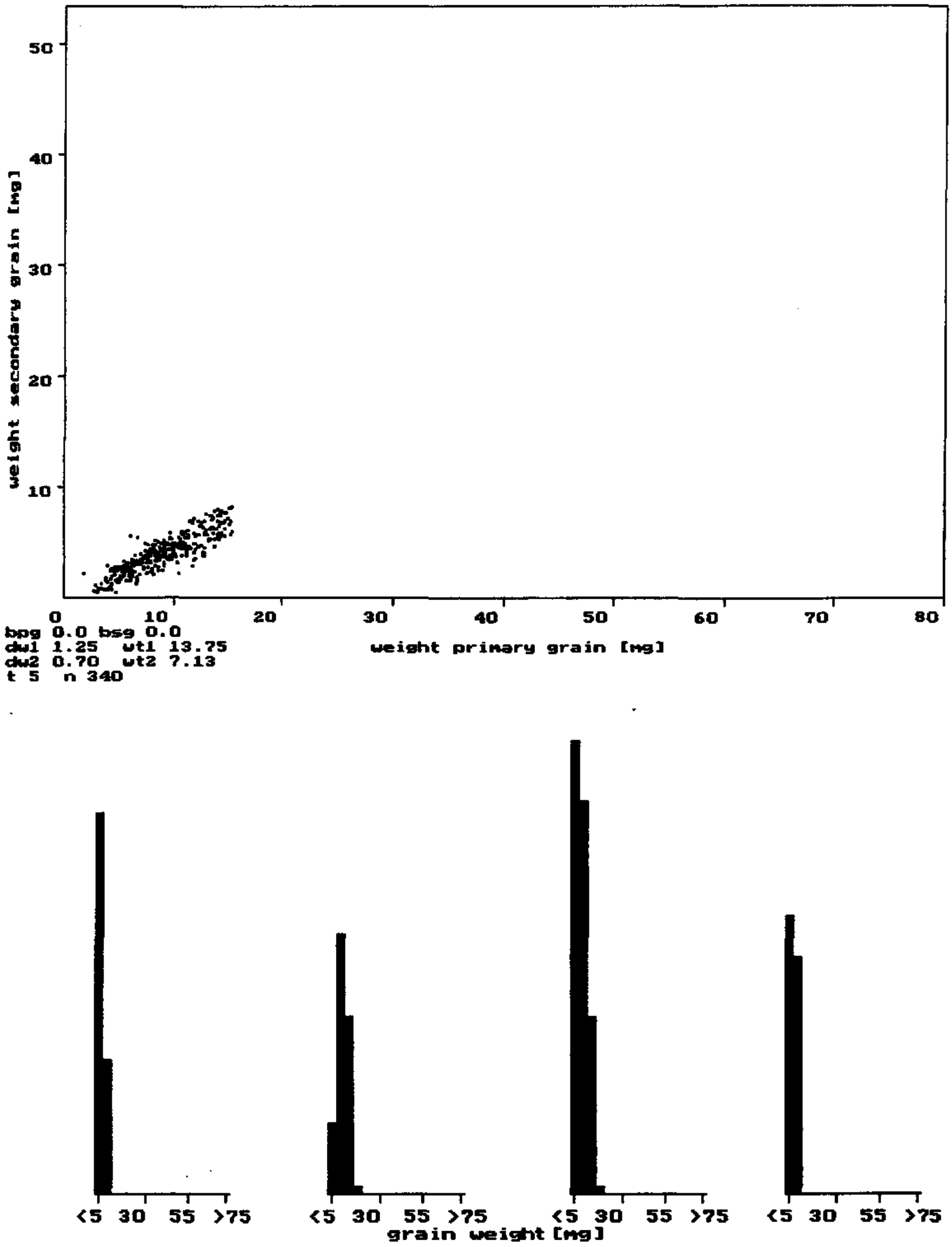
```
                    SIMULATION PARAMETERS

TIMES [days]                              GROWTH CURVES
                              primary grain          secondary grain
tmax=50                       f1=.20                 f2=.26
dt=1                          m1=16                  m2=18
t=1                           l1=2.0                 l2=2.5
FILE SIZE                     g1=60                  g2=40
n=340
STARTING WEIGHTS
Wt1st[mg]=11  -.1             PROBABILITIES
Wt2nd[proportion of Wt1st]=.3 -.6  p1=.15            t_stop=10
GROWTH RATE MODIFICATIONS          p2=.1
c1=.3   -.8                        p3=.02
c2=.1   -.3                        a= .15
```

b/ Resetting parameters at time t= 10 used for simulation during the time interval t= 11- 50.

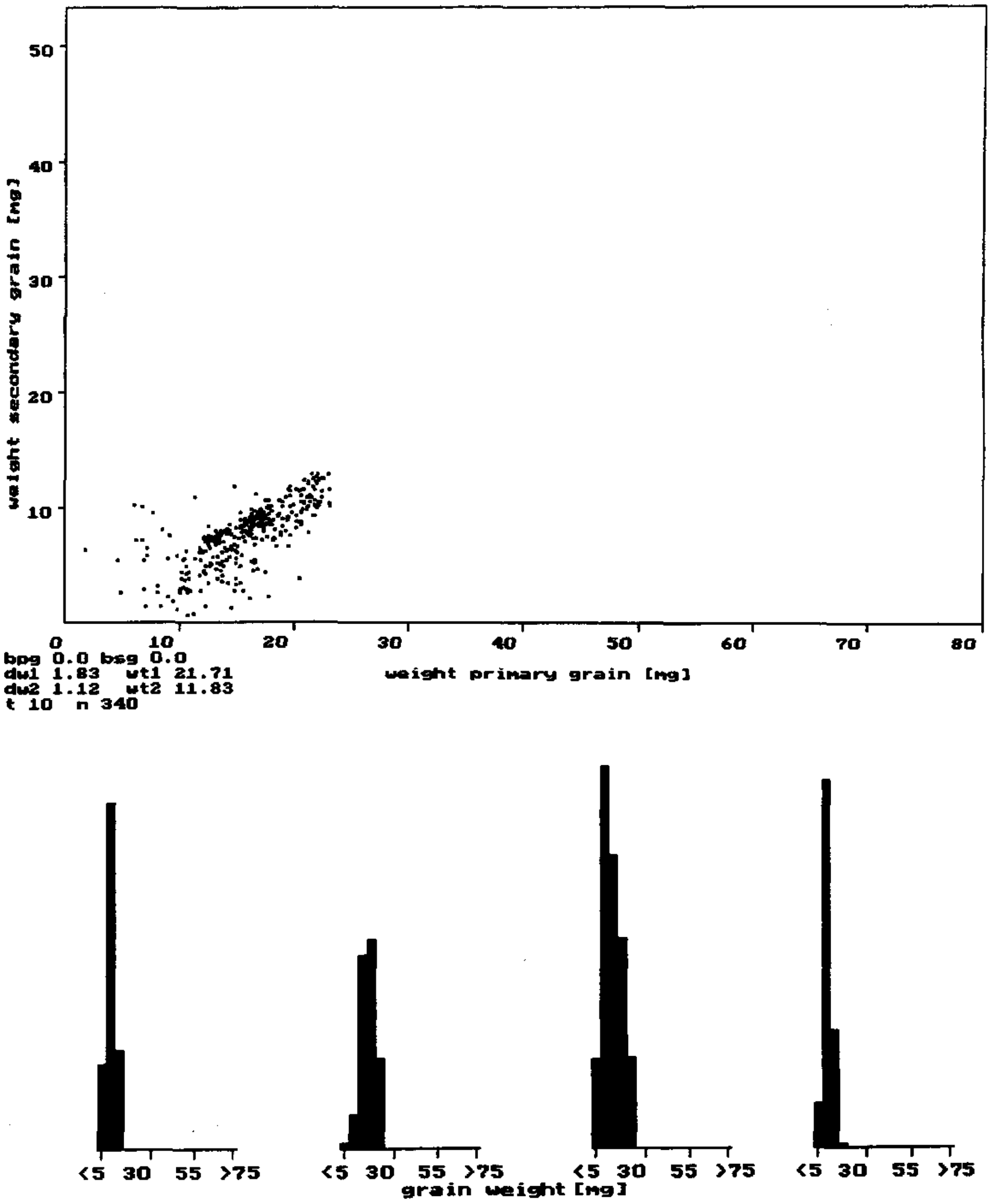
```
                               PROBABILITIES
                               p1=.25                t_stop=50
GROWTHRATE MODIFICATIONS       p2=.1
c1=.3   -.8                    p3=.005
c2=.1   -.3                    a= .1
```

Figure 5.3: Simulation parameters for variety Wilma under nitrogen treatment N1 in 1990; (a) Parameters used for the first part of simulation during the time interval t = 1 - 10; (b) Resetting parameters at time t = 10 used for simulation during the time interval t = 11 - 50.



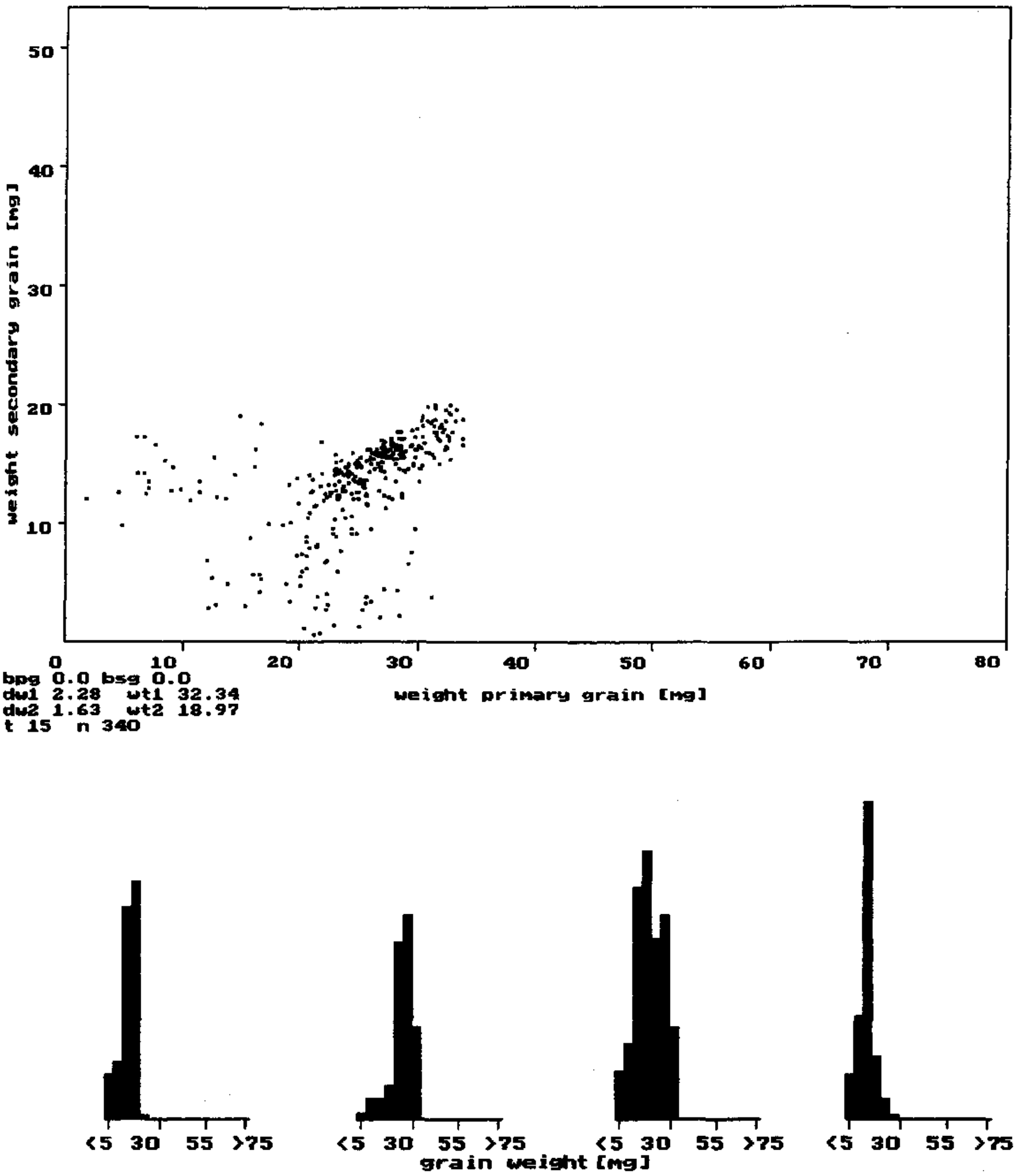
	secondary grains	primary grains	all together	differences
nobs	340	340	680	340
mean	4.05	8.89	6.47	4.85
min	0.49	1.76	0.49	-0.57
max	8.20	15.19	15.19	9.41
range	7.71	13.43	14.70	9.99
var	2.92	10.45	12.55	3.68
sdev	1.71	3.23	3.54	1.92
cv %	42.23	36.34	54.75	39.60
sum	1376.60	3024.08	2200.34	1647.48
skew	0.27	0.10	0.47	0.19
sesk	0.13	0.13	0.09	0.13

Figure 5.4: Results of simulation after 5 time steps (parameters are given in Fig. 5.1a).



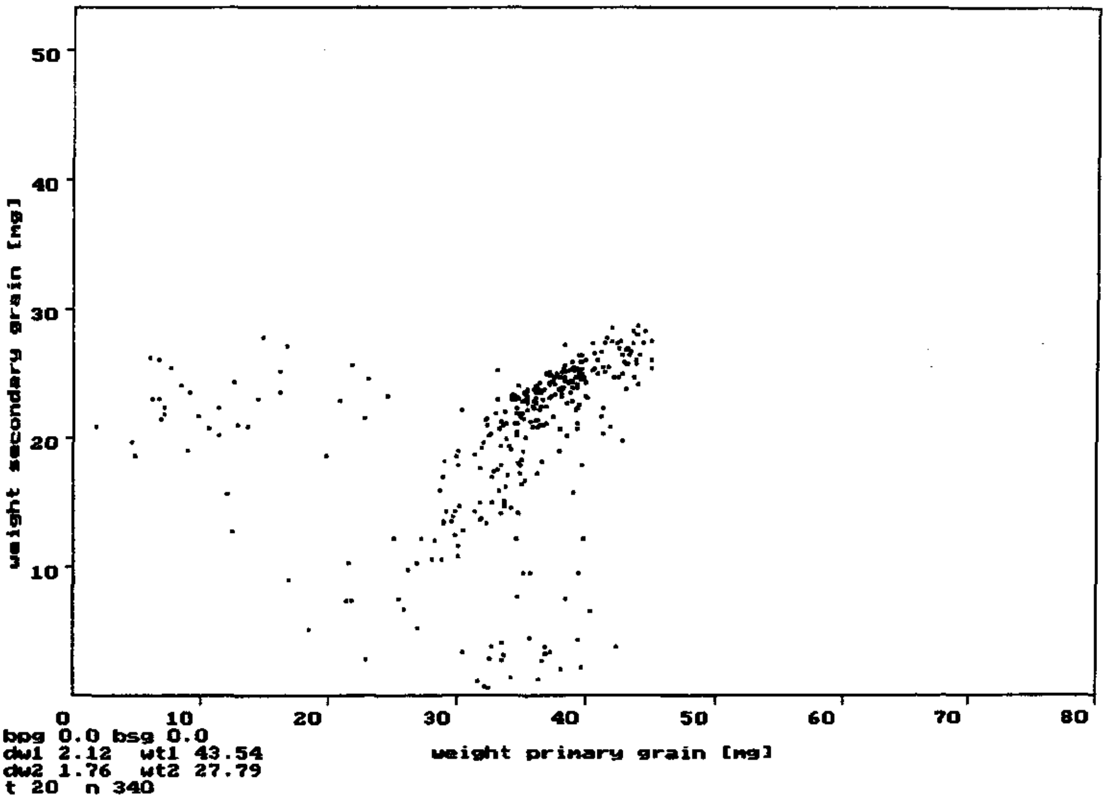
	secondary grains	primary grains	all together	differences
nobs	340	340	680	340
mean	7.71	15.64	11.67	7.93
min	0.60	1.76	0.60	-4.59
max	12.90	23.11	23.11	16.63
range	12.29	21.35	22.51	21.22
var	6.76	15.78	27.02	8.01
sdev	2.60	3.97	5.20	2.83
cv %	33.75	25.40	44.53	35.67
sum	2620.15	5317.61	3968.88	2697.46
skew	-0.41	-0.32	0.20	-0.96
sesk	0.13	0.13	0.09	0.13

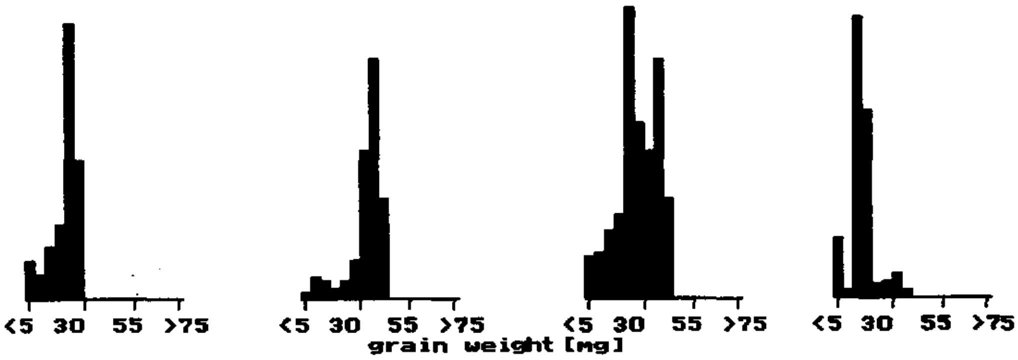
Figure 5.5: Results of simulation after 10 time steps (parameters are given in Fig. 5.1a).



	secondary grains	primary grains	all together	differences
nobs	340	340	680	340
mean	13.43	24.62	19.03	11.19
min	0.60	1.76	0.60	-11.34
max	20.04	33.74	33.74	27.25
range	19.43	31.98	33.14	38.59
var	18.34	36.10	58.53	32.72
sdev	4.28	6.01	7.65	5.72
cv %	31.88	24.40	40.21	51.11
sum	4567.34	8372.35	6469.85	3805.01
skew	-1.15	-1.30	-0.06	-1.37
sesk	0.13	0.13	0.09	0.13

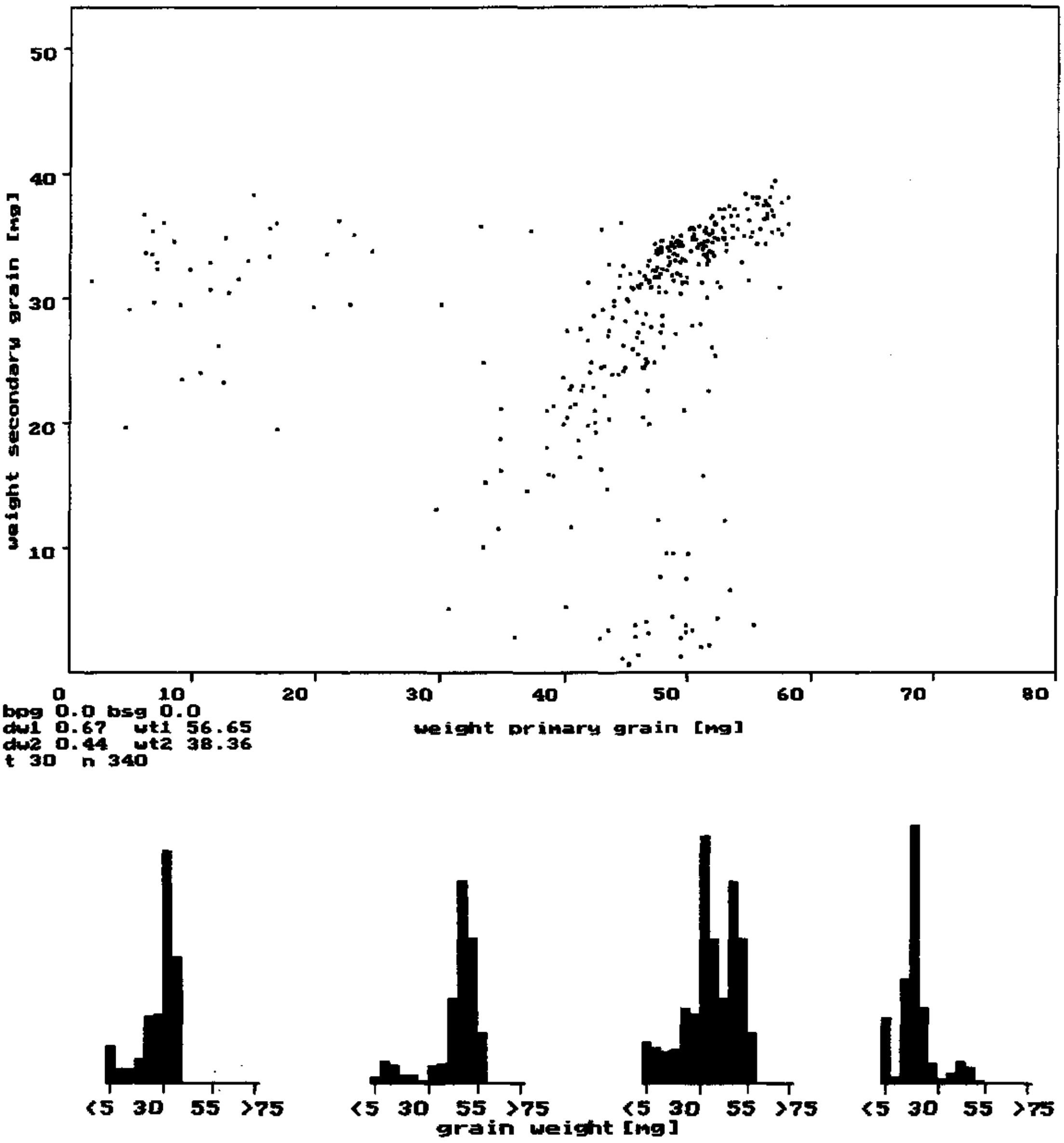
Figure 5.6: Results of simulation after 15 time steps (parameters are given in Fig. 5.1a).





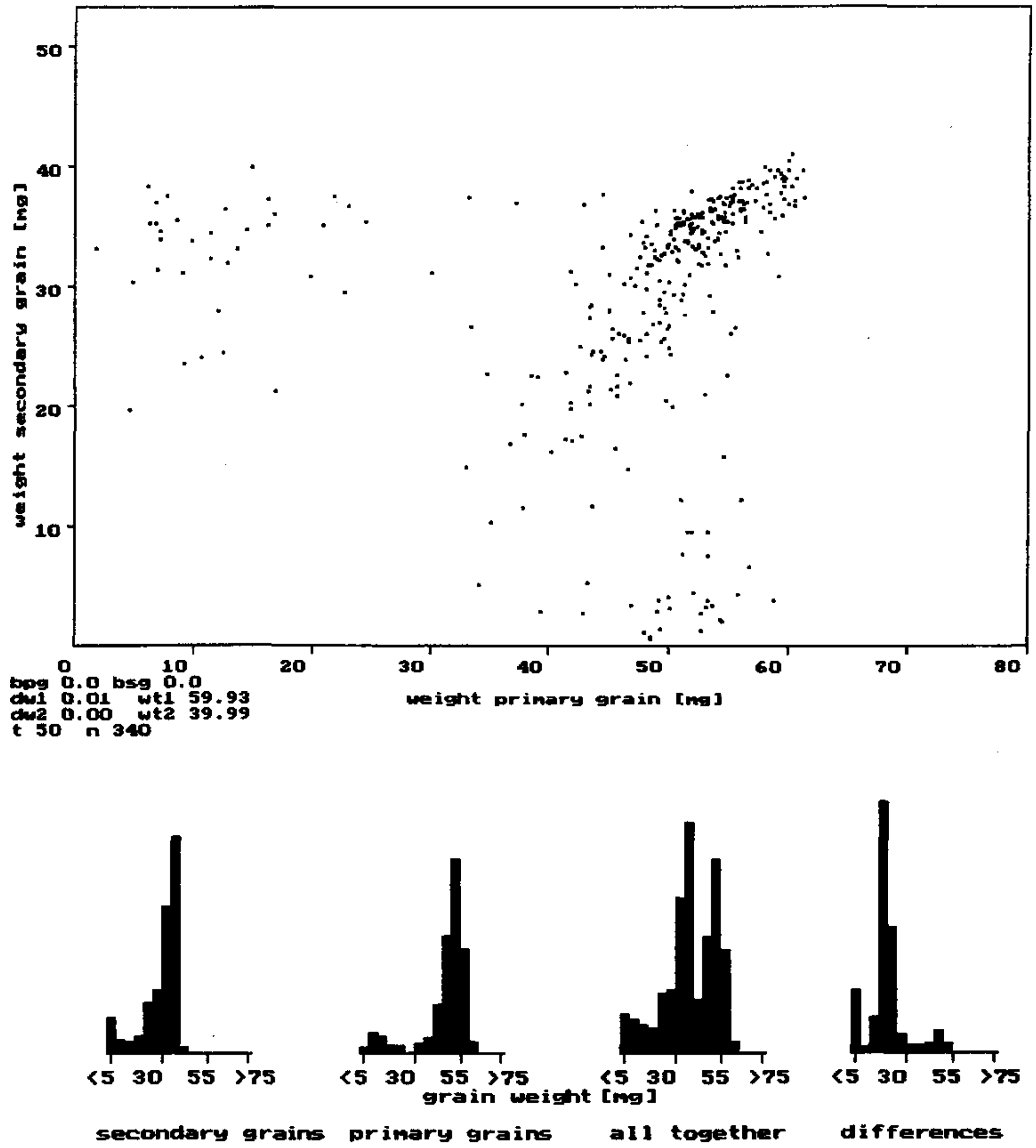
	secondary grains	primary grains	all together	differences
nobs	340	340	680	340
mean	20.33	33.83	27.08	13.50
min	0.60	1.76	0.60	-20.15
max	28.85	44.95	44.95	38.46
range	28.25	43.19	44.34	58.61
var	43.83	76.54	105.71	94.19
sdev	6.62	8.75	10.28	9.70
cv %	32.56	25.86	37.96	71.90
sum	6913.21	11502.38	9207.80	4589.17
skew	-1.37	-1.76	-0.29	-1.19
sesk	0.13	0.13	0.09	0.13

Figure 5.7: Results of simulation after 20 time steps (parameters are given in Fig. 5.1a).



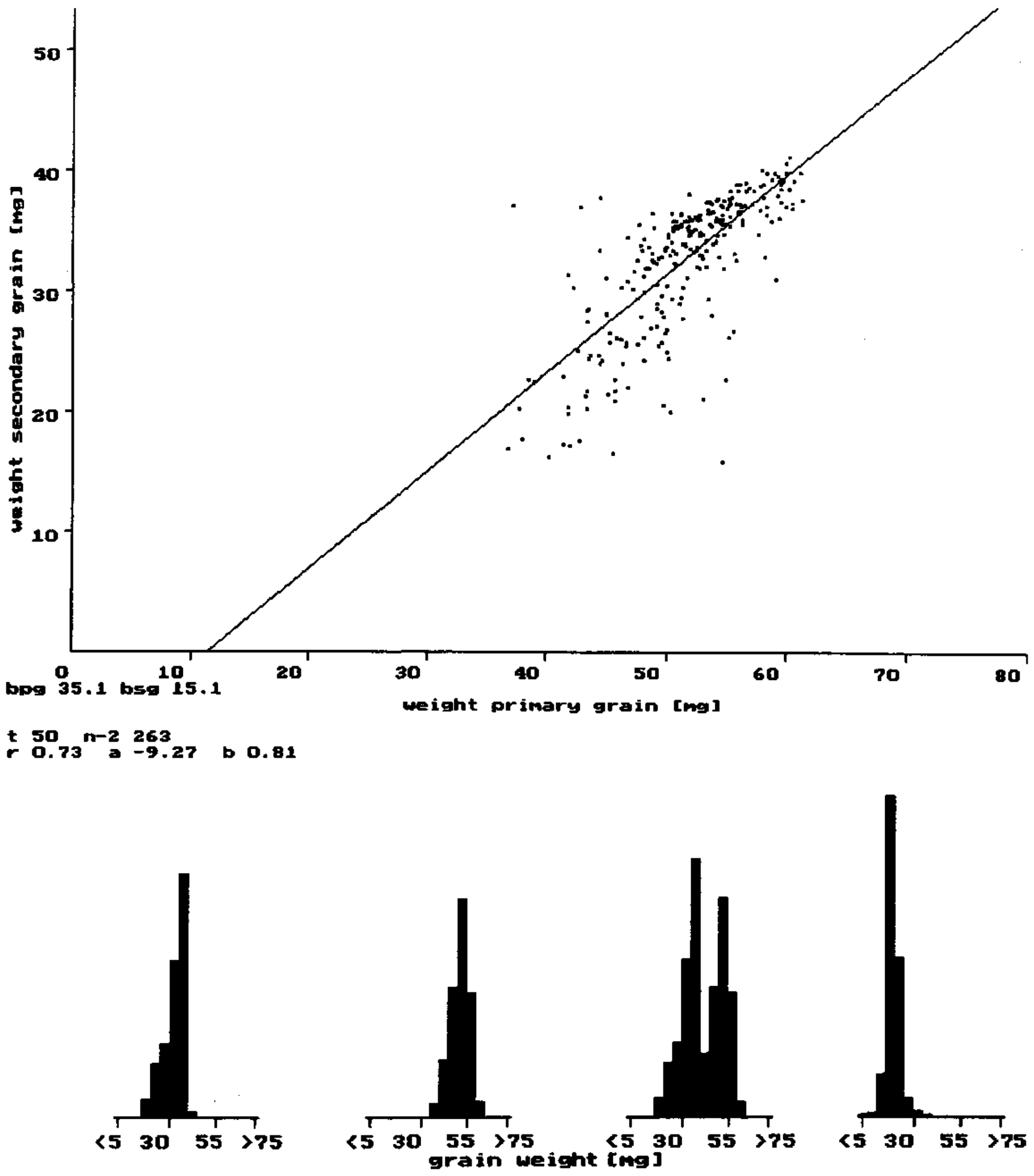
	secondary grains	primary grains	all together	differences
nobs	340	340	680	340
mean	28.42	44.34	36.38	15.93
min	0.60	1.76	0.60	-30.72
max	39.42	58.03	58.03	51.57
range	38.82	56.27	57.43	82.30
var	89.35	148.92	182.47	215.62
sdev	9.45	12.20	13.51	14.68
cv %	33.26	27.52	37.13	92.20
sum	9662.13	15077.25	12369.69	5415.12
skew	-1.51	-1.96	-0.49	-0.96
sesk	0.13	0.13	0.09	0.13

Figure 5.8: Results of simulation after 30 time steps (parameters are given in Fig. 5.1a).



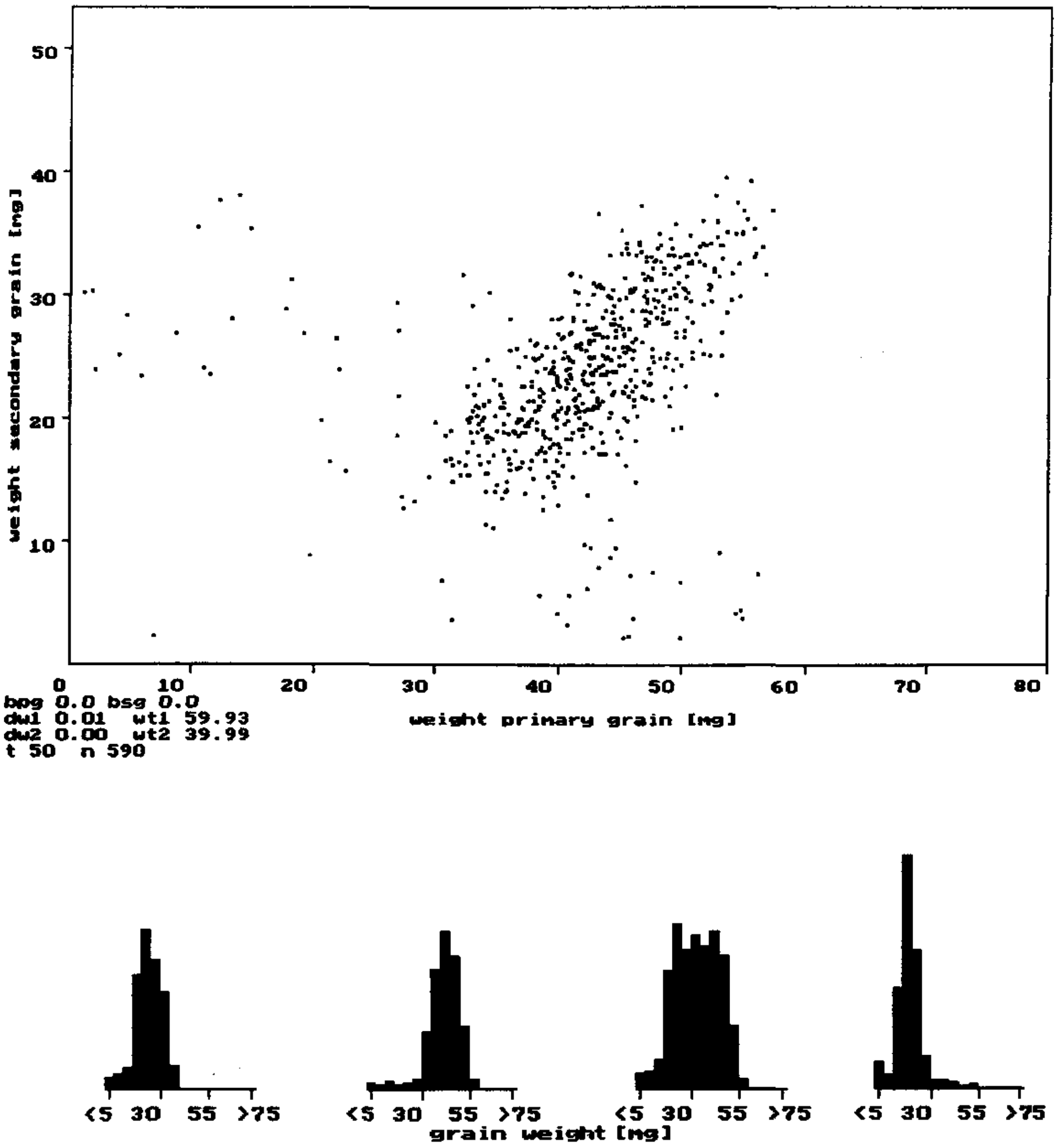
	secondary grains	primary grains	all together	differences
nobs	340	340	680	340
mean	29.64	46.87	38.26	17.23
min	0.60	1.76	0.60	-32.36
max	41.06	61.15	61.15	54.85
range	40.45	59.39	60.55	87.21
var	97.42	171.56	208.63	249.19
sdev	9.87	13.10	14.44	15.79
cv %	33.30	27.94	37.75	91.61
sum	10078.31	15936.97	13007.64	5858.66
skew	-1.53	-1.97	-0.46	-0.97
sesk	0.13	0.13	0.09	0.13

Figure 5.9: Results of simulation after 50 time steps (parameters are given in Fig.5.1a).



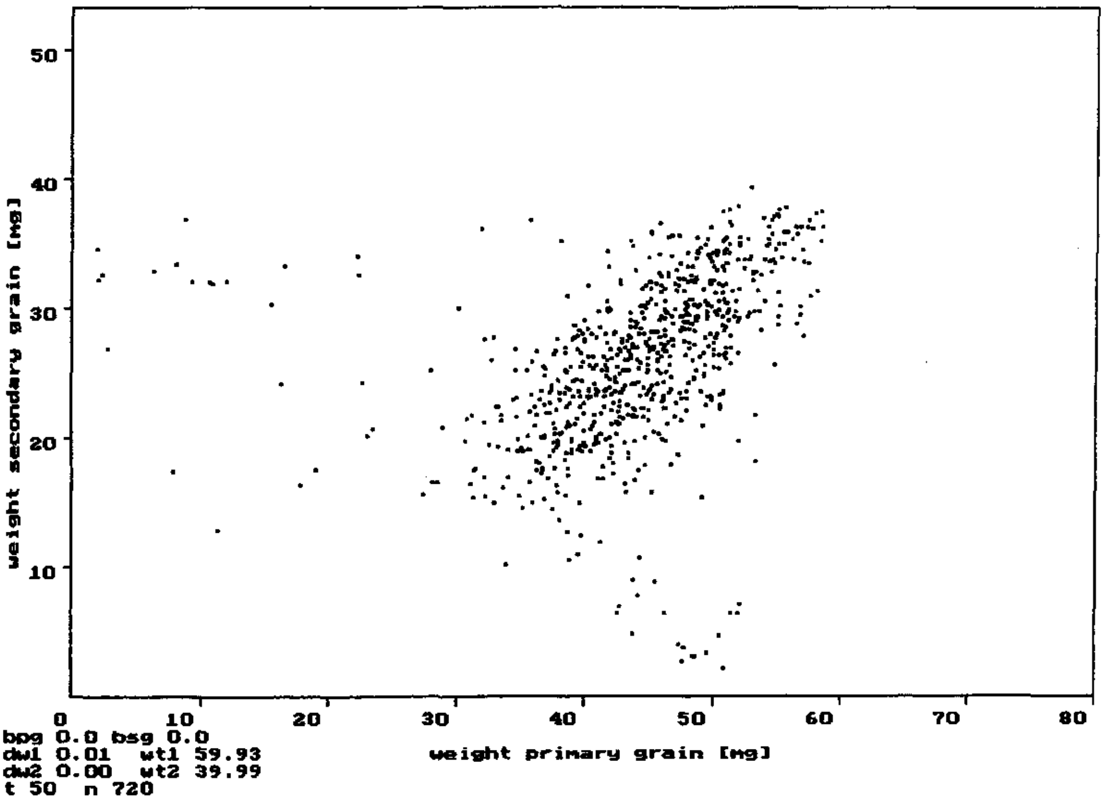
	secondary grains	primary grains	all together	differences
nobs	265	265	530	265
mean	32.47	51.40	41.94	18.93
min	15.81	36.70	15.81	-0.09
max	41.06	61.15	61.15	38.69
range	25.24	24.45	45.34	38.77
var	32.27	26.14	118.95	15.96
sdev	5.68	5.11	10.91	4.00
cv %	17.50	9.95	26.01	21.10
sum	8604.62	13622.28	11113.45	5017.66
skew	-1.06	-0.43	-0.12	0.39
sesk	0.15	0.15	0.11	0.15

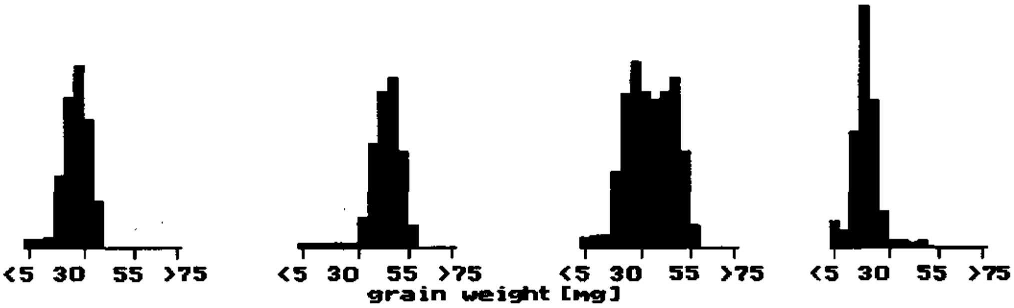
Figure 5.10: Selected central cluster from the results of simulation given in Fig. 5-10 (parameters are given in Fig. 3.4.7a).



	secondary grains	primary grains	all together	differences
nobs	590	590	1180	590
mean	23.82	41.57	32.70	17.75
min	2.29	1.08	1.08	-29.18
max	39.61	57.20	57.20	50.96
range	37.32	56.11	56.11	80.14
var	48.69	73.94	140.13	84.34
sdev	6.98	8.60	11.84	9.18
cv %	29.29	20.68	36.20	51.73
sum	14053.79	24528.26	19291.03	10474.47
skew	-0.45	-1.63	-0.11	-1.45
sesk	0.10	0.10	0.07	0.10

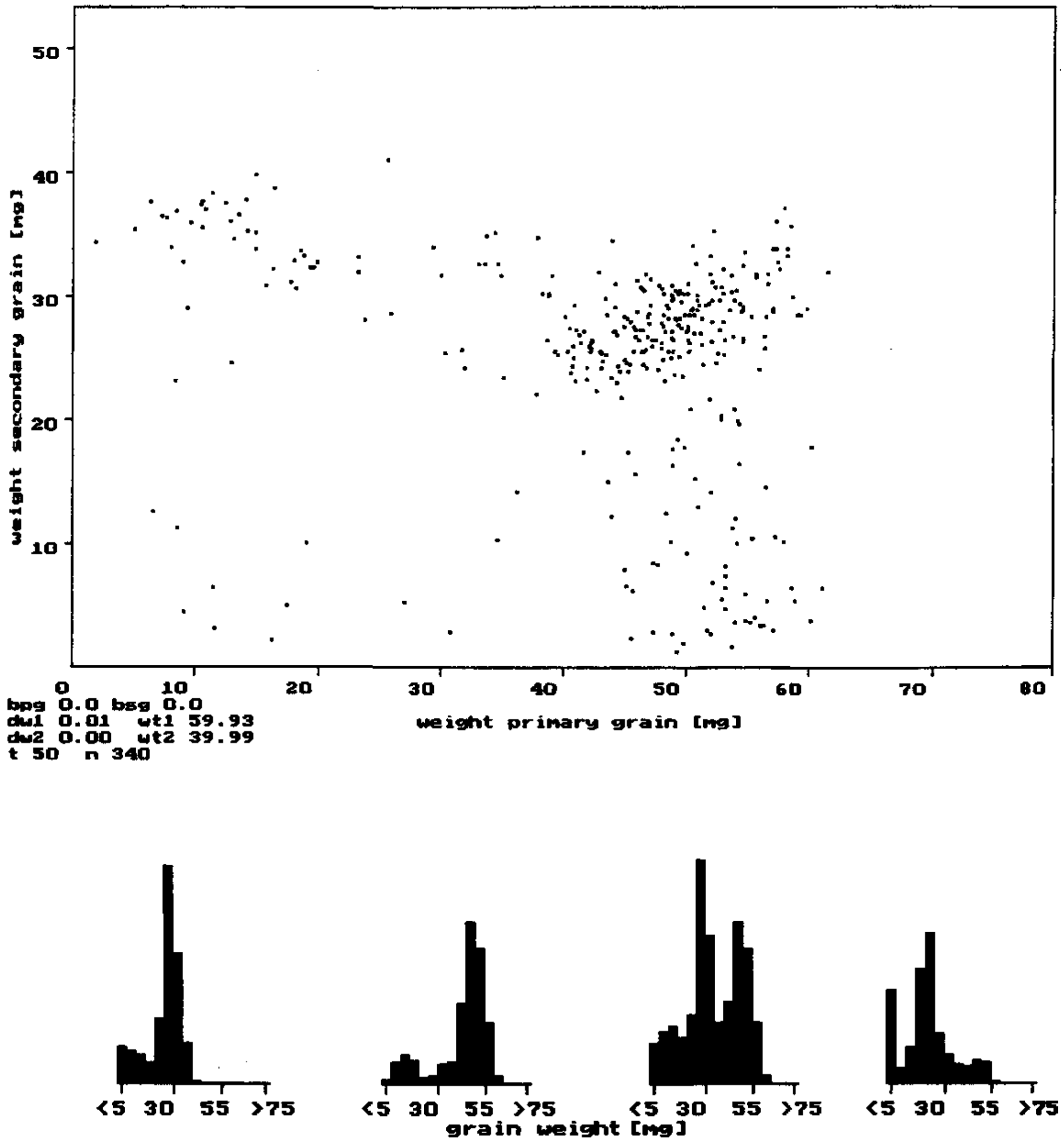
Figure 5.11: Results of simulation for variety Wilma under nitrogen treatment N3 in 1990 (parameters are given in Fig. 5.1b).





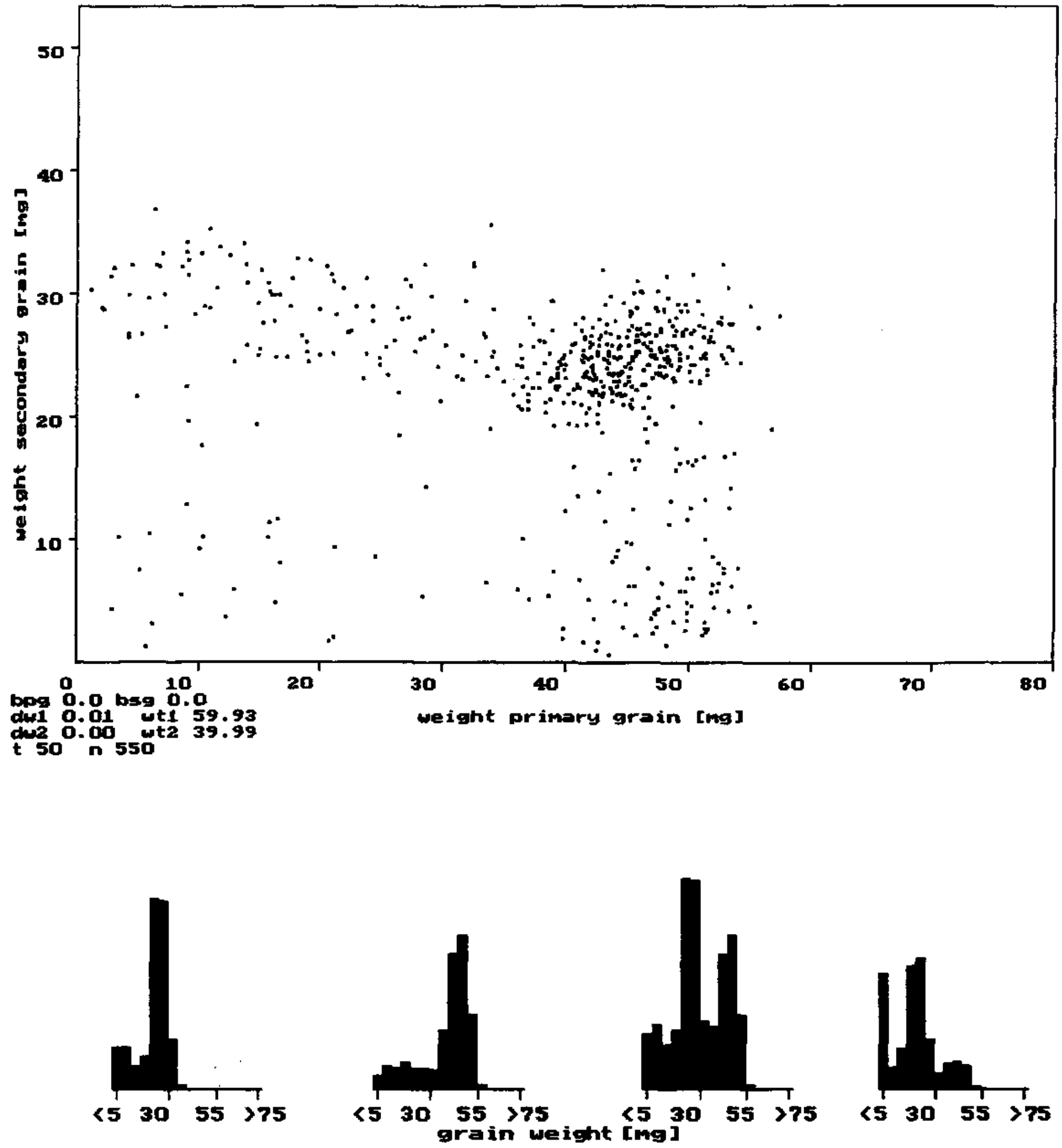
	secondary grains	primary grains	all together	differences
nobs	720	720	1440	720
mean	26.06	43.70	34.88	17.64
min	2.26	1.86	1.86	-32.78
max	39.42	58.45	58.45	48.55
range	37.16	56.59	56.59	81.34
var	43.19	69.07	133.93	76.48
sdev	6.57	8.31	11.57	8.75
cv %	25.22	19.02	33.18	49.58
sum	18763.18	31462.98	25113.08	12699.80
skew	-0.71	-1.80	-0.13	-1.72
sesk	0.09	0.09	0.06	0.09

Figure 5.12: Results of simulation for variety Wilma under nitrogen treatment N3 in 1991 (parameters are given in Fig. 5.1c).



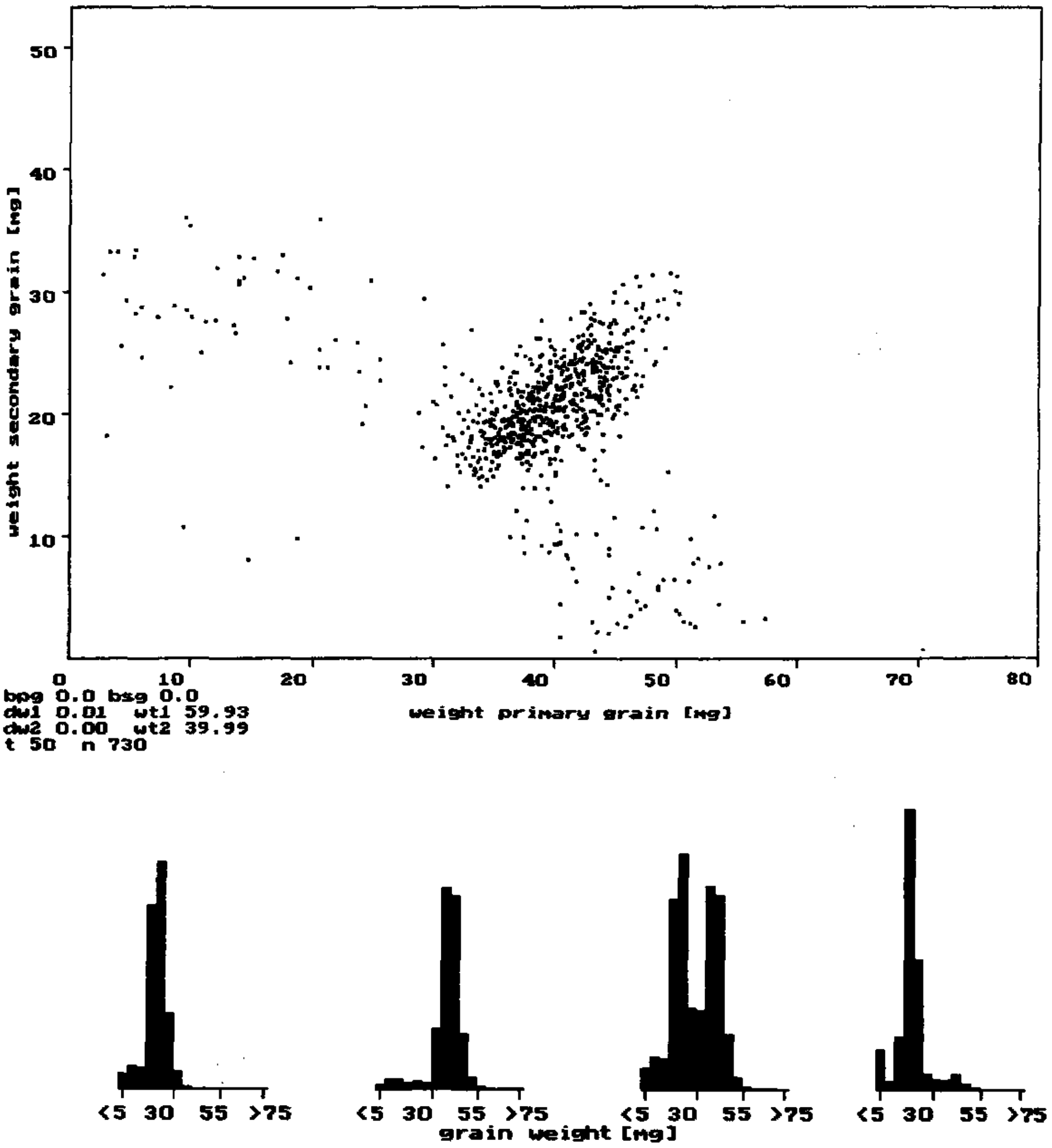
	secondary grains	primary grains	all together	differences
nobs	340	340	680	340
mean	24.84	43.30	34.07	18.46
min	1.32	1.79	1.32	-32.57
max	41.03	61.41	61.41	56.33
range	39.72	59.62	60.09	88.90
var	86.21	189.97	223.25	339.14
sdev	9.29	13.78	14.94	18.42
cv %	37.38	31.83	43.86	99.74
sum	8444.86	14722.73	11583.80	6277.87
skew	-1.11	-1.41	-0.18	-0.77
sesk	0.13	0.13	0.09	0.13

Figure 5.13: Results of simulation for Cebeco 8852 under nitrogen treatment N1 in 1990 (parameters are given in Fig. 5.2a).



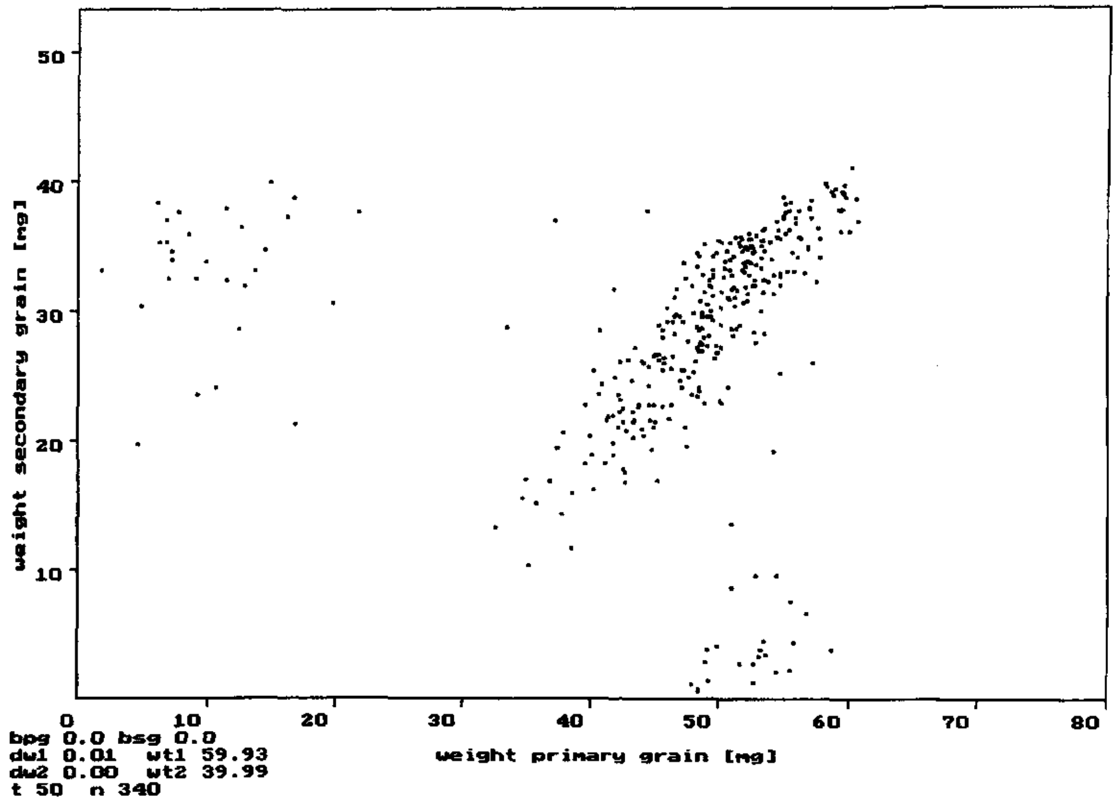
	secondary grains	primary grains	all together	differences
nobs	550	550	1100	550
mean	21.82	38.55	30.19	16.73
min	0.64	1.08	0.64	-30.72
max	36.96	57.31	57.31	51.94
range	36.32	56.23	56.67	82.66
var	67.81	180.62	194.15	291.39
sdev	8.23	13.44	13.93	17.07
cv %	37.73	34.86	46.15	102.03
sum	12003.51	21205.22	16604.36	9201.70
skew	-1.11	-1.23	-0.10	-0.66
sesk	0.10	0.10	0.07	0.10

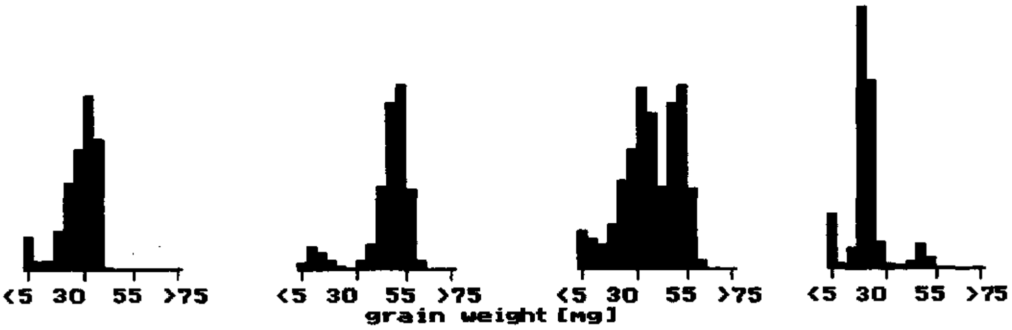
Figure 5.14: Results of simulation for Cebeco 8852 under nitrogen treatment N3 in 1990 (parameters are given in Fig. 5.2b).



	secondary grains	primary grains	all together	differences
nobs	730	730	1460	730
mean	20.45	38.28	29.36	17.83
min	0.71	2.60	0.71	-30.16
max	36.08	57.31	57.31	53.97
range	35.37	54.71	56.60	84.13
var	32.24	66.91	129.07	124.00
sdev	5.68	8.18	11.36	11.14
cv %	27.77	21.37	38.69	62.46
sum	14925.67	27941.14	21433.40	13015.47
skew	-0.78	-2.06	-0.08	-1.30
sesk	0.09	0.09	0.06	0.09

Figure 5.15: Results of simulation for Cebeco 8852 under nitrogen treatment N3 in 1991 (parameters are given in Fig. 5.2c).





	secondary grains	primary grains	all together	differences
nobs	340	340	680	340
mean	28.06	46.19	37.12	18.12
min	0.60	1.76	0.60	-32.36
max	41.06	60.68	60.68	54.85
range	40.45	58.92	60.07	87.21
var	80.16	149.38	196.85	222.59
sdev	8.95	12.22	14.03	14.92
cv %	31.91	26.46	37.79	82.32
sum	9540.86	15703.28	12622.07	6162.43
skew	-1.28	-2.10	-0.37	-1.26
sesk	0.13	0.13	0.09	0.13

Figure 5.16: Results of simulation for variety Wilma under nitrogen treatment N3 in 1990 by resetting the parameters after 10 time steps (parameters are given in Fig. 5.3).

6. DISCUSSION

Potential yields of cereals in the Netherlands are high. On the basis of physiological properties and environmental conditions, van Keulen et al. (1991) estimated production for oats at 20.5 t/ha of aboveground dry matter and between 9.7 and 10.3 t/ha of grain at 14% moisture content (Chapter 1). These calculations are based on a "source-limited" approach.

Considering yield formation from the point of view of crop morphology and yield components, the potentials and their degree of realization can be approximated by the following values:

Yield component	Potential	Observed	Degree of realisation (%)
Shoot density (no/m^2)	1 500	400	27
Number of grains per shoot	200	50	25
Grain density (no/m^2)	300 000	20 000	7

These potential values of various organs, which eventually determine sink size, form the boundary conditions for the degree of plasticity in morphogenesis and for regulation according to source supply. Whingwiri and Stern (1982) reported that for wheat 72 % of the florets initiated did not produce grains. The proportion of florets aborted can be modified by manipulating environmental conditions. Stockman et al. (1983) reported a significant effect of increased light or shade (+ 37 %, - 43 %, respectively) on the number of competent florets at anthesis. Similar effects have been observed on the number of grains per spike at maturity (Puckridge, 1968; Willey and Holliday, 1971; Fisher and Wilson, 1975; Satpathy and Mohapatra, 1985).

This self-regulation and the degree of reduction in density of the various organs is governed by the internal competion among sinks which is regulated by differences in position and in time of initiation. Allometry and time sequence in initiation thus create a hierarchy in plant structures which is the primary source of plant module variability. In the course of crop development also many other factors contribute to variations in plant growth and thus different levels and types of variability contribute to the final variation in morphological structures (Gustavsson et al., 1982).

In specific situations of variety x environment interaction, different factors may have a decisive influence, which complicates identification and quantification of variability sources. For potato tuber size distribution, these factors have been discussed by Struik et al. (1990; 1991). To explain the relationships among the various factors influencing the variability in grain weight distribution in small grain cereal stands, the modular approach to plant growth, described in Chapter 1, can be used, based on the following observations:

1. Assuming that the yield of organs of agricultural plants is only the consequence of assimilate availability is an oversimplification. It is more realistic to also consider the processes regulating plant morphogenesis. Only then can we explain how plant organs come to have their particular, detailed shape and size (Hardwick, 1984).
2. Under unfavourable conditions plants generally react by formation of a lower number of organs initiated at that moment, or by abortion of the youngest and weakest individuals of the precursor organs (Kirby, 1974).
3. Internal regulation is not only expressed in a reduction in number, but also in size of the sink-modules (Vlach and Kren, 1984).
4. Variation in sink size within a crop stand reflects changes in growth correlations or in degree of apical dominance (Phillips, 1969).
5. By identification and quantification of this source of variation, genotype x environment interactions can be evaluated (Kren, 1987).
6. Limited assimilate supply causes a reduction in initiation of new sinks and accelerates differentiation and reduction in the growing sinks, i.e. increases the dominance of older and larger sinks.
7. Abundant source supply results in higher initiation rates of new sinks, and in a more synchronous development, i.e. suppression of apical dominance.
8. Grain filling is influenced by two sets of processes which, in combination characterize source/sink interaction (Section 3.4):
   - interactions between environmental conditions and vegetative plants parts;
   - interactions between vegetative parts and grains.
9. The first set of processes determines the number and size of the morphological structures at the lower hierarchical levels (1 - 4 in Fig. 1.3) through both inter- and intra-plant competition, which finally results in a given number of grains per plant or per unit area (Kren, 1987).

The second set of processes, operating at the highest hierarchical level (5 in Fig. 1.3) affects mainly grain size through intra-plant competition (Wardlaw, 1968; Stoy, 1969).

These observations formed the basis for the development of the model for grain filling and grain size distribution (Chapter 4). As the current insights in the underlying processes are insufficient for a fully deterministic description of the growth of all individual subunits and their relationships in metapopulations, a combination of a deterministic and a stochastic approach was used.

The deterministic part consists of growth curves for individual primary and secondary grains, number of spikelets considered and grain weight ranges at the start of the calculations (Chapter 5). The growth curves represent hypothetical situations of potential grain growth in conditions without source limitation. Parametrization of the growth curves may be based on experimental data from the grains growing in the top spikelet of the main stem panicle, which are the eldest, and therefore presumably optimally supplied with assimilates (in accordance with the hierarchical structure of the plant). Both, the number of spikelets considered and the grain weight ranges at the onset of grain fill depend on the branching processes, i.e. their values are influenced primarily by source supply at the first level of the crop x environment interaction (observation no. 8). They may be quantified on the basis of knowledge about dry matter accumulation and partitioning, stand structure (Chapter 5) and the relation between assimilate supply and viable organ formation (van Keulen and Seligman, 1987).

The stochastic part consists of the parameters for modification of the growth trajectories of the individual grains in the spikelet metapopulation (c1, c2, p1, p2, p3 and a). For their specification the general rules described in Chapter 5 may be used for both interpolation and extrapolation. The results of calculations after iterative adjustment of the stochastic parameters, show in general good agreement with experimental patterns. Better agreement may be achieved by interactively adjusting parameter values in the course of the calculation procedure. In that way, insight may be increased in the processes influencing individual grain growth in various positions within the spikelet metapopulation.

The results of the model suggest that it presents almost unlimited possibilities for modification of grain growth trajectories, as a function of current assimilate supply. However, insufficient insight exists in the relations among assimilate supply, plant morphogenesis, plant hierarchical structure, inter- and intra-plant competition and the values of the stochastic parameters in the grain growth model, to formulate causal relationships. Description and quantification of such functional relationships need more detailed investigation of:

- temporal pattern of branching in relation to phenological crop development and assimilate supply for quantification of the probabilities of grain stage transition (p1, p2 and p3)
- relationships between current assimilate supply and the growth rate of primary and secondary grains in different positions within the panicle for quantification of growth rate modifications (c1 and c2) and degree of competition (a).

Variations in grain weight within the panicle can be the result of differences in growth rate during the linear dry matter accumulation phase (Pinthus and Millet, 1978), rates of cell division and expansion (Brocklehurst, 1977), size of the vascular transport system (Simmons and Moss, 1978) or phytochrome balances (Walpole and Morgan, 1973). Grafius (1978) found that insertion of pebbles, polysterene cubes and aluminium and styrofoam pellets into the flowers of wheat, oats and barley resulted in reduced grain weights, and concluded that maximum grain size was controlled by hull size (wich depends mainly on spikelet and grain position), while actual weight was limited by the supply of assimilates per grain (which depends on grain position and relative sink strength of the grains).

Investigations on grain formation in oat panicles as a function of the size of the stem vascular system, or following spikelet removal, have been carried out by Frey, 1962; Criswell and Shibles, 1972; Klick and Sim, 1976; Husley and Peterson, 1982; Peterson et al., 1982 and Peterson, 1983. All these studies, however, referred to the average situation, without consideration of grain filling in different positions within the panicle. To illustrate the heterogeneity in grain metapopulations, the variability in time of flowering in four main stem panicles of variety Wilma is presented in table 29.

The differences in time of flowering between the oldest spikelet (no. 8) and the youngest (no. 1) range between 11 and 20 days. This presents a substantial time lapse in grain initialisation, which logically results in a large variability in final grain weight. There is ample evidence in literature that final grain weight depends on the moment of anthesis and on ovary and floral organ size (Simmons and Moss, 1978; Simmons and Crookston, 1979; Ledent and Stoy, 1985; Millet, 1986). Later-formed grains exhibit lower growth rates, but the duration of the linear growth phase is practically identical. Cessation of dry matter accumulation (and the associated sharp decline in grain water content) appear to occur at approximately the same moment for all grains within spring wheat spikelets (Simmons and Crookston, 1979).

Oats exhibit a markedly lower tillering capacity than the other small grain cereals, but because of their plasticity in panicle size, oats are generally considered superior in compensating lower plant densities (Jones and Hayes, 1967). However, this extended panicle branching has unfavourable effects on grain uniformity and thousand grain weight.

Greater uniformity and higher average grain weights can be attained by synchronisation of the branching process. The importance of synchrony in cereal development has been reported by Tandon and Sing (1970), Paroda (1971; 1972) and Dahiya and Singh (1977). Stoskopf and Farey (1975) considered synchronisation in tiller formation as a potential yield-increasing trait in short winter wheat genotypes. Also Remeslo et al. (1979) emphasized the importance of vertical and horizontal synchronization in the development of ears for wheat breeding. The small difference in productivity among the first three plant culms is one of the important characteristics of the winter wheat variety Mironowskaya 808, extensively grown in the USSR, Eastern Europe and America in the seventies. Kren and Vlach (1988) concluded, after extensive research on tiller uniformity, that this property significantly correlated with yield in conditions for which the variety was adapted and only ecostable varieties maintain the same degree of uniformity in organs of the same order under a wide range of agro-ecological conditions.

The uniformity of stems in cereal stands may be improved by management practices affecting stand structure, i.e. by promoting synchronous tillering and stimulating competition during stem elongation, to select the biggest and most uniform stems (Muravyev, 1973).

As evident, the majority of investigations on synchronisation refers to the process of tillering. According to Cisar and Shands (1978) panicle development in the second tiller proceeded parallel to that in the first tiller with a delay of 2 to 4 days. To our knowledge, no information exists in the literature on synchronization of oat panicle branching. However, it may be assumed that more uniform grain size at sowing will produce plants with more extended and synchronous tillering, with reduced but synchronous panicle branching and with one or at most two grains per spikelet.

Finally, observation 5 about genotype x environment interaction assumes that under favourable conditions, where a variety can realize its biological potential, the growth of modules (i.e. various organs) is more synchronous and therefore their weight distribution is symmetric (the size of modules is influenced mainly by a large number of random factors). On the other hand, under unfavourable conditions, i.e. with limited source supply or under stress, apical dominance increases concurrently with the variability within modules, which is expressed in modifications of the skewness of their size distribution. The model of grain growth can describe these processes, as witnessed by the graphs depicting the relation between the weights of the primary and secondary grains, the degree of cluster separation and the linear regression characteristics for the central cluster. It may, therefore, be a tool in investigations on genotype x environment interaction and adaptation.

Table 29: Time of flowering of florets in different positions in four main stem panicles of oats in days after flowering of the first floret (source: van Hartingsveldt, pers. comm.).

Panicle	Spikelet	Floret	Spikelet position (no in Fig. 1-6)									
number	number	order	1	2	3	4	5	6	7	8	9	10
1	65	1	11	6.5	11	2.5	6.5	1.5	2.5	1	8.5	1.5
		2	15	8.5	15	4	8.5	4	4	2	11	4
2	78	1	13	6	8.5	3	6	2	3	1	6	3.5
		2	16	7.5	13	3.5	6	3	4.5	1.5	7.5	3.5
3	61	1	13	4.5	10.5	1.5	3.5	1	3	1	6	1.5
		2	16	6	14.5	3.5	6	3.5	4.5	3	8.5	3.5
4	77	1	16	6	13	3	8.5	1	3.5	1	10.5	4
		2	20	6	16	3.5	13	3	6	1	13	6

7. CONCLUSIONS

Conclusions have been formulated with respect to four areas.

A. For research methodology

1. A number of approaches exist with respect to the quantitative description of crop growth and yield formation in field crops, which refer to different hierarchical levels of crop organisation:
   - carrying capacity/plant population structure
   - source/sink
   - modular approach to plant growth.

   To simplify the terminology and establish unequivocal connections between these approaches, we suggest to use:
   - sink equivalent to module or plant subunit
   - sink variability and sink differentiation equivalent to module or plant subunit variability and differentiation, respectively.
2. Grain filling is influenced by two sets of processes, which in combination can be characterized as source x sink interaction:
   - between environmental conditions (carrying capacity) and vegetative plant parts (vegetative sinks);
   - between vegetative parts (source) and grains (sink).
3. The reaction of plants to environmental conditions is expressed in modifications of the intra-plant relationships which are reflected in changes in variability of sinks. In the course of crop development continuous interaction exists with environmental conditions (sources), which successively modifies the number and size of sinks at different levels of plant organisation in accordance with plant hierarchical structure.
4. To study sink variability originating from genotype x environment interactions the range of values, variance, skewness of distribution and graphs depicting the relationships between the same order sinks at different positions in the plant structure are the most suitable characteristics.
5. Greater uniformity and higher average grain weight may be attained by synchronization of the development of sinks of the same order, but it should be realized that plant hierarchical structure and the biology of plant development only allow synchronization of the same order plant parts to a limited extent.

B. For breeding

1. Selection of varieties adapted to specific agro-ecological conditions, so that plant development matches environmental conditions. Growth under unfavourable conditions results in increased differentiation and asynchronous development of the same order sinks.

2. Modifying plant morphology in such a way that branching processes, which under certain climatic conditions occur in an unfavourable period, are suppressed and those occurring in a favourable period are stimulated.

3. In the Netherlands, where conditions prevail with moderate temperatures and abundant moisture supply, that would imply increased and synchronized tillering and a reduction in panicle branching, as well as in the number of grains within the spikelet. That also broadens the scope for improved synchronization of productive tillers through crop management techniques.

C. For crop management

1. Management measures aiming at a high degree of homogeneity in all technological treatments.

2. Early sowing or higher sowing rates at later sowing. The latter, however, may cause problems due to interplant competition.

3. Nitrogen fertilizer application regimes aiming at synchronization in tillering and during stem elongation, to promote competition for selection of the biggest and uniform stems. Therefore, higher doses of nitrogen should be applied at tillering and in the final dressing at the beginning of stem elongation.

D. For modelling

1. The model for grain growth that has been developed, combines descriptive and explanatory characteristics and provides wide options for calculation of grain growth trajectories. It results in calculated patterns of grain weight distribution very similar to experimental

results.

2. Specification of the stochastic parameters on the basis of general rules on plant morphogenesis, plant hierarchical structure and inter- and intra-plant competition:
   a. Crops with spikelet cohorts formed over a longer period of time exhibit more extended ranges of grain growth trajectories, i.e. more trajectories are close to the x-axis.
   b. Lack of assimilates reduces grain growth rate, whereby the growth rate of the secondary grains is affected more strongly than that of the primary grains.
   c. Premature grain growth cessation occurs more often in crops with limited assimilate supply, where higher numbers of aborted grains and lower grain numbers per unit area are usually observed.
   d. Under conditions with competition for assimilate supply the dominance of the largest grain within the spikelet is intensified.

The agreement between calculated and experimental results may be improved by changing parameters (interactively) in the course of the calculation procedure. Such a change represents in fact modification of external conditions.

3. More accurate specification of parameters needs more detailed investigation of:
   a. branching as related to crop development pattern
   b. the relation between current assimilate supply and the values of the parameters in the grain growth model, that characterize the growth rates of the primary and secondary grains at different positions in the panicle.

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APPENDIX

Listing of program elaborated by B. A. W. Spitters to calculate the model for grain filling and grain variability description (written in Turbo Pascal).

APPENDIX

Listing of program elaborated by B. A. W. Spitters to calculate the model for grain filling and grain variability description (writen in Turbo Pascal).

```
 uses graph,crt;
 type stagetype=(ff,fs,ft,sf,ss,st,tf,ts,tt);
      weightset=(w1,w2,d);
      weighttype=array[w1..d] of real;
      resulttype=array[1..4] of real;
 var stwh,stwl,t0,dt,tmax,t,t_stop,p1,p2,p3,a,c1,c1h,c1l,c2,c2h,c2l,
     percenth,percentl:real;
     m,l,k,h,w0:array[1..2] of real;
     matrix:array[stagetype,stagetype] of real;
     s1,s2:stagetype;
     n:word;
     grain:array[1..1000] of record
                                  stage:stagetype;
                                  weight:weighttype
                                end;
     i1,i2,i3:integer;
     dw1;dw2,
     wt1,wt2,
     rand :real;
     stng1,stng2:string;
     gd,gm:integer;
     av,min,max,range,sum,v,s,cv,ske,ersk:resulttype;
     r,a_xy,b_xy:real;
     borx,bory:real;
     ch:char;

procedure read_starting_values;
begin
outtextxy(200,10,'SIMULATION PARAMETERS');
outtextxy(0,21,'TIMES [days]');
if ch='M' then begin outtextxy(0,37,'t0=')gotoxy(4,3);readln(t0);end;
outtextxy(0,53,'tmax=');gotoxy(6,4);readln(tmax);
outtextxy(0,69,'dt=');gotoxy(4,5);readln(dt);
outtextxy(0,85,'t=');gotoxy(3,6);readln(t);
outtextxy(0,101,'FILE SIZE');
outtextxy(0,117,'n=');gotoxy(3,8);readln(n);
outtextxy(0,133,'STARTING WEIGHTS');
outtextxy(0,149,'Wt1st[mg]=');gotoxy(11,10);readln(stwh);
outtextxy(115,149,'-');gotoxy(16,10);readln(stwl);
outtextxy(0,165,'Wt2nd[proportion of Wt1st]=');gotoxy(28,11);
readln(percenth);
outtextxy(250,165,'-');gotoxy(34,11);readln(percentl);
outtextxy(395,21,'GROWTH CURVES');
outtextxy(295,37,'primary grain');
if ch='G' then begin
 outtextxy(295,53,'f1=');gotoxy(41,4);readln(k[1]);
 outtextxy(295,69,'m1=');gotoxy(41,5);readln(m[1]);
 outtextxy(295,85,'l1=');gotoxy(41,6);readln(l[1]);
 outtextxy(295,101,'g1=');gotoxy(41,7);readln(h[1]);
end
else
begin
 outtextxy(295,53,'k1=');gotoxy(41,4);readln(k[1]);
 outtextxy(295,69,'h1=');gotoxy(41,5);readln(h[1]);
 outtextxy(295,85,'W1st0[mg]=');gotoxy(48,6);readln(w0[1]);
end;
outtextxy(495,37,'secondary grain');
if ch='G' then begin
 outtextxy(495,53,'f2=');gotoxy(66,4);readln(k[2]);
 outtextxy(495,69,'m2=');gotoxy(66,5);readln(m[2]);
```

```
 outtextxy(495,85,'l2=');gotoxy(66,6);readln(l[2]);
 outtextxy(495,101,'g2=');gotoxy(66,7);readln(h[2]);
end
else
begin
 outtextxy(495,53,'k2=');gotoxy(66,4);readln(k[2]);
 outtextxy(495,69,'h2=');gotoxy(66,5);readln(h[2]);
 outtextxy(495,85,'W2nd0[mg]=');gotoxy(73,6);readln(w0[2]);
end;
end;

procedure read_probabilities;
begin
outtextxy(0,181,'GROWTH RATE MODIFICATIONS');
outtextxy(0,197,'c1=');gotoxy(4,13);readln(c1h);
outtextxy(70,197,'-');gotoxy(11,13);readln(c1l);
outtextxy(0,213,'c2=');gotoxy(4,14);readln(c2h);
outtextxy(70,213,'-');gotoxy(11,14);readln(c2l);
outtextxy(295,149,'PROBABILITIES');
outtextxy(295,165,'p1=');gotoxy(41,11);readln(p1);
outtextxy(295,181,'p2=');gotoxy(41,12);readln(p2);
outtextxy(295,197,'p3=');gotoxy(41,13);readln(p3);
outtextxy(295,213,'a=');gotoxy(40,14);readln(a);
outtextxy(495,165,'t_stop=');gotoxy(70,11);readln(t_stop);
end;

procedure calculate_matrix;
begin
for s1:=ff to tt do for s2:=ff to tt do matrix[s1,s2]:=0;
{alles op 0}
matrix[ff,fs]:=(1-p1-p1*p3)*p1*a;                        {ff}
matrix[ff,ft]:=(1-p1-p1*p3)*p1*p3;
matrix[ff,sf]:=(1-p1-p1*p3)*p1*a;
matrix[ff,ss]:=p1*p1;
matrix[ff,st]:=p1*p1*p3;
matrix[ff,tf]:=(1-p1-p1*p3)*p1*p3;
matrix[ff,ts]:=p1*p1*p3;
matrix[ff,tt]:=p1*p1*p3*p3;
for s2:=fs to tt do matrix[ff,ff]:=matrix[ff,ff]-matrix[ff,s2];
matrix[ff,ff]:=matrix[ff,ff]+1;
matrix[fs,ff]:=(1-p1-p1*p3)*p2/a;                        {fs}
matrix[fs,ft]:=(1-p1-p1*p3)*p3;
matrix[fs,sf]:=p1*p2;
matrix[fs,ss]:=p1*(1-p2-p3);
matrix[fs,st]:=p1*p3;
matrix[fs,tf]:=p1*p3*p2;
matrix[fs,ts]:=p1*(1-p2-p3)*p3;
matrix[fs,tt]:=p1*p3*p3;
for s2:=ff to tt do if s2<>fs then matrix[fs,fs]:
=matrix[fs,fs]-matrix[fs,s2];
matrix[fs,fs]:=matrix[fs,fs]+1;
matrix[ft,st]:=p1*a;                                     {ft}
matrix[ft,tt]:=p1*p3;
matrix[ft,ft]:=1-matrix[ft,st]-matrix[ft,tt];
matrix[sf,ff]:=(1-p1-p1*p3)*p2/a;                            {sf}
matrix[sf,fs]:=p1*p2;
matrix[sf,ft]:=p1*p3*p2;
matrix[sf,ss]:=p1*(1-p2-p3);
matrix[sf,st]:=p1*(1-p2-p3)*p3;
matrix[sf,tf]:=(1-p1-p1*p3)*p3;
```

```
matrix[sf,ts]:=p1*p3;
matrix[sf,tt]:=p1*p3*p3;
for s2:=ff to tt do if s2<>sf then matrix[sf,sf]:
=matrix[sf,sf]-matrix[sf,s2];
matrix[sf,sf]:=matrix[sf,sf]+1;
matrix[ss,ff]:=p2*p2;                                          {ss}
matrix[ss,fs]:=(1-p2-p3)*p2;
matrix[ss,ft]:=p2*p3;
matrix[ss,sf]:=(1-p2-p3)*p2;
matrix[ss,st]:=(1-p2-p3)*p3;
matrix[ss,tf]:=p2*p3;
matrix[ss,ts]:=(1-p2-p3)*p3;
matrix[ss,tt]:=p3*p3;
for s2:=ff to tt do if s2<>ss then matrix[ss,ss]:
=matrix[ss,ss]-matrix[ss,s2];
matrix[ss,ss]:=matrix[ss,ss]+1;
matrix[st,ft]:=p2/a;                                           {st}
matrix[st,tt]:=p3;
matrix[st,st]:=1-matrix[st,ft]-matrix[st,tt];
matrix[tf,ts]:=p1*a;                                           {tf}
matrix[tf,tt]:=p1*p3;
matrix[tf,tf]:=1-matrix[tf,ts]-matrix[tf,tt];
matrix[ts,tf]:=p2/a;                                           {ts}
matrix[ts,tt]:=p3;
matrix[ts,ts]:=1-matrix[ts,tf]-matrix[ts,tt];
matrix[tt,tt]:=1;                                              {tt}
end;

procedure text_screen1;
begin
str(dw1:0:2,stng1);stng1:='dw1 '+stng1;
str(wt1:0:2,stng2);stng1:=stng1+'  wt1 '+stng2;
outtextxy(0,430,stng1);
str(dw2:0:2,stng1);stng1:='dw2 '+stng1;
str(wt2:0:2,stng2);stng1:=stng1+'  wt2 '+stng2;
outtextxy(0,440,stng1);
str(t:0:0,stng1);stng1:='t '+stng1;
str(n-2:0,stng2);stng1:=stng1+'  n-2 '+stng2;
outtextxy(0,450,stng1);
end;

procedure text_screen4;
begin
str(t:0:0,stng1);stng1:='t '+stng1;
str(n-2:0,stng2);stng1:=stng1+'  n-2 '+stng2;
outtextxy(0,450,stng1);
str(r:0:2,stng1);stng1:='r '+stng1;
str(a_xy:0:2,stng2);stng1:=stng1+'  a '+stng2;
str(b_xy:0:2,stng2);stng1:=stng1+'  b '+stng2;
outtextxy(0,460,stng1);
end;

procedure text_histogram;

procedure results_histogram(strng:string;result:resulttype;i:integer);
begin
outtextxy(0,360+i*10,strng);
for i1:=1 to 4 do begin
 str(result[i1]:10:2,stng1);
 outtextxy(60+(i1-1)*150,360+i*10,stng1);
```

```
end;
end;

begin
outtextxy(0,360,'nobs');str(n:10,stngl);
outtextxy(60,360,stngl);outtextxy(210,360,stngl);
outtextxy(510,360,stngl);
str(n*2:10,stngl);outtextxy(360,360,stngl);
results_histogram('mean',av,1);
results_histogram('min',min,2);
results_histogram('max',max,3);
results_histogram('range',range,4);
results_histogram('var',v,5);
results_histogram('sdev',s,6);
results_histogram('cv %',cv,7);
results_histogram('sum',sum,8);
results_histogram('skew',ske,9);
results_histogram('sesk',ersk,10);
end;

procedure histogram;
var histo1,histo2,histo:array[1..16] of integer;
begin
cleardevice;
for i1:=1 to 16 do histo2[i1]:=0;
for i1:=1 to n do
begin
 if grain[i1].weight[w2]<5 then histo2[1]:=histo2[1]+1
 else
  for i2:=2 to 15 do
   if (grain[i1].weight[w2]>5*(i2-1)) and (grain[i1].weight[w2]<5*i2)
        then histo2[i2]:=histo2[i2]+1
 else if grain[i1].weight[w2]>=75 then histo2[16]:=histo2[16]+1;
end;
for i1:=1 to 16 do
bar(60+5*i1,300,64+5*i1,300-round((histo2[i1]/n)*300));
for i1:=0 to 1 do line(67+i1*75,300,67+i1*75,305);
outtextxy(55,310,'<5');outtextxy(135,310,'>75');
for i1:=0 to 1 do line(95+i1*25,300,95+i1*25,305);
outtextxy(80,310,'30');outtextxy(110,310,'55');

for i1:=1 to 16 do histo1[i1]:=0;
for i1:=1 to n do
begin
 if grain[i1].weight[w1]<5 then histo1[1]:=histo1[1]+1
 else
  for i2:=2 to 15 do
   if (grain[i1].weight[w1]>5*(i2-1)) and (grain[i1].weight[w1]<5*i2)
        then histo1[i2]:=histo1[i2]+1
 else if grain[i1].weight[w1]>=75 then histo1[16]:=histo1[16]+1;
end;
for i1:=1 to 16 do
bar(210+5*i1,300,214+5*i1,300-round((histo1[i1]/n)*300));
for i1:=0 to 1 do line(217+i1*75,300,217+i1*75,305);
outtextxy(205,310,'<5');outtextxy(285,310,'>75');
for i1:=0 to 1 do line(245+i1*25,300,245+i1*25,305);
outtextxy(230,310,'30');outtextxy(260,310,'55');

for i1:=1 to 16 do histo[i1]:=histo1[i1]+histo2[i1];
for i1:=1 to 16 do bar(360+5*i1,300,364+5*i1,
```

```
300-round((histo[i1]/n)*300));
for i1:=0 to 1 do line(367+i1*75,300,367+i1*75,305);
outtextxy(355,310,'<5');outtextxy(435,310,'>75');
for i1:=0 to 1 do line(395+i1*25,300,395+i1*25,305);
outtextxy(380,310,'30');outtextxy(410,310,'55');

for i1:=1 to 16 do histo1[i1]:=0;
for i1:=1 to n do
begin
 if grain[i1].weight[d]<5 then histo1[1]:=histo1[1]+1
 else
  for i2:=2 to 15 do
   if (grain[i1].weight[d]>5*(i2-1)) and (grain[i1].weight[d]<5*i2)
        then histo1[i2]:=histo1[i2]+1
 else if grain[i1].weight[d]>=75 then histo1[16]:=histo1[16]+1;
end;
for i1:=1 to 16 do
bar(510+5*i1,300,514+5*i1,300-round((histo1[i1]/n)*300));
for i1:=0 to 1 do line(517+i1*75,300,517+i1*75,305);
outtextxy(505,310,'<5');outtextxy(585,310,'>75');
for i1:=0 to 1 do line(545+i1*25,300,545+i1*25,305);
outtextxy(530,310,'30');outtextxy(560,310,'55');

outtextxy(250,320,'grain weight [mg]');
outtextxy(60,340,'secondary grains');
outtextxy(210,340,'primary grains');
outtextxy(360,340,'all together');
outtextxy(510,340,'differences');
text_histogram;
end;

procedure draw_grains;
begin
outtextxy(30,410,'0');
settextstyle(defaultfont,vertdir,1);
outtextxy(9,110,'weight secondary grain [mg]');
settextstyle(defaultfont,horizdir,1);
outtextxy(250,430,'weight primary grain [mg]');
for i1:=0 to 4 do line(35,25+i1*75,39,25+i1*75);
for i1:=0 to 4 do
 begin str((5-i1)*10,stng1);outtextxy(15,25+i1*75,stng1); end;
for i1:=0 to 7 do line(639-i1*75,405,639-i1*75,400);
for i1:=0 to 7 do
 begin str((8-i1)*10,stng1);outtextxy(620-i1*75,410,stng1); end;
line(39,0,39,400);
line(39,400,639,400);
for i1:=1 to n do with grain[i1] do
begin
 for i2:=0 to 1 do for i3:=0 to 1 do
 putpixel(39+round(weight[w1]*7.5)+i2,400-round(weight[w2]*7.5)+i3,15);
end;
end;

procedure calculate_results;
var m2,m3:real;

procedure average_min_max(i:integer;ws:weightset);
begin
for i1:=1 to n do
begin
```

```
 av[i]:=av[i]+grain[i1].weight[ws];
 if grain[i1].weight[ws]>max[i] then max[i]:=grain[i1].weight[ws];
 if grain[i1].weight[ws]<min[i] then min[i]:=grain[i1].weight[ws];
end;
av[i]:=av[i]/n;
end;

function v_help(i:integer;ws:weightset):real;
var tmp:real;
begin
tmp:=0;
for i1:=1 to n do tmp:=tmp+sqr(grain[i1].weight[ws]-av[i]);
v_help:=tmp;
end;

function v_help_3(i:integer;ws:weightset):real;
var tmp:real;
begin
tmp:=0;
for i1:=1 to n do
 tmp:=tmp+sqr(grain[i1].weight[ws]-av[i])*(grain[i1].weight[ws]-av[i]);
v_help_3:=tmp;
end;

begin
for i1:=1 to n do
    grain[i1].weight[d]:=grain[i1].weight[w1]-grain[i1].weight[w2];
for i1:=1 to 4 do
    begin min[i1]:=maxint;max[i1]:=0;av[i1]:=0; end;
average_min_max(2,w1);
average_min_max(1,w2);
average_min_max(4,d);
av[3]:=(av[2]+av[1])/2;
if min[1]<min[2] then min[3]:=min[1] else min[3]:=min[2];
if max[1]>max[2] then max[3]:=max[1] else max[3]:=max[2];
for i1:=1 to 4 do begin range[i1]:=max[i1]-min[i1];sum[i1]:=n*av[i1];
end;
r:=0;
for i1:=1 to n do r:=r+(grain[i1].weight[w1]-av[2])*
(grain[i1].weight[w2]-av[1]);
r:=r/sqrt(v_help(2,w1)*v_help(1,w2));
v[4]:=v_help(4,d)/(n-1);
v[3]:=(v_help(3,w1)+v_help(3,w2))/(2*n-1);
v[2]:=v_help(2,w1)/(n-1);
v[1]:=v_help(1,w2)/(n-1);
for i1:=1 to 4 do begin s[i1]:=sqrt(v[i1]);
cv[i1]:=(s[i1]/av[i1])*100; end;
b_xy:=r*(s[1]/s[2]);
a_xy:=av[1]-(b_xy*av[2]);
ersk[4]:=sqrt(6/(n+3));
ersk[3]:=sqrt(6/(2*n+3));
ersk[2]:=sqrt(6/(n+3));
ersk[1]:=sqrt(6/(n+3));
m3:=(v_help_3(3,w1)+v_help_3(3,w2))/n;
m2:=(v_help(3,w1)+v_help(3,w2))/n;
ske[3]:=m3/(m2*sqrt(m2));
m3:=(v_help_3(2,w1))/n;
m2:=(v_help(2,w1))/n;
ske[2]:=m3/(m2*sqrt(m2));
m3:=(v_help_3(1,w2))/n;
```

```
m2:=(v_help(1,w2))/n;
ske[1]:=m3/(m2*sqrt(m2));
m3:=(v_help_3(4,d))/n;
m2:=(v_help(4,d))/n;
ske[4]:=m3/(m2*sqrt(m2));
end;

procedure initialize_grains;
begin
for i1:=1 to n do begin
 grain[i1].weight[w1]:=random*(stwh-stwl)+stwl;
 grain[i1].weight[w2]:=grain[i1].weight[w1]*
(random*(percenth-percentl)+percentl);
 i2:=random(4)+1;
 case i2 of
  1:grain[i1].stage:=ff;
  2:grain[i1].stage:=fs;
  3:grain[i1].stage:=sf;
  4:grain[i1].stage:=ss;
 end;
end;
end;

procedure write_border;
begin
 setcolor(15);
 str(borx:0:1,stng1);str(bory:6:1,stng2);
 outtextxy(0,420,stng1+stng2);
end;

procedure select;
var ch:char;
    n1:integer;
begin
borx:=0;bory:=0;
write_border;
repeat
setcolor(15);rectangle(39+round(borx*7.5),0,getmaxx,
400-round(bory*7.5));
ch:=readkey;if ch=#0 then
begin
 ch:=readkey;
 setcolor(0);
 outtextxy(0,420,stng1+stng2);
 rectangle(39+round(borx*7.5),0,getmaxx,400-round(bory*7.5));
 write_border;
end;
case ch of
 #72:bory:=bory+(1/7.5);
 #80:bory:=bory-(1/7.5);
 #75:borx:=borx-(1/7.5);
 #77:borx:=borx+(1/7.5);
end;
until ch=#13;
setcolor(15);
n1:=0;
for i1:=1 to n do
 if (grain[i1].weight[w1]>=borx) and (grain[i1].weight[w2]>=bory) then
  begin
   n1:=n1+1;grain[n1]:=grain[i1];
```

```
  end;
n:=n1;
end;

procedure draw_line;
begin
if a_xy>=0 then
 line(39,400-round(a_xy*7.5),39+round(120*7.5),
 400-round((a_xy+b_xy*120)*7.5))
else
 line(39+round((-a_xy/b_xy)*7.5),400,
              39+round(120*7.5),400-round((a_xy+b_xy*120)*7.5));
end;

function Miyagawa(time:real;order:byte):real;
begin
 miyagawa:=(k[order]/h[order])/(1+((k[order]/h[order])*
 (1/w0[order])-1)*exp(-k[order]*(time-t0)));
end;

function Gen_Loc(time:real;order:byte):real;
begin
 Gen_Loc:=h[order]/(exp(ln(1+l[order]*exp(-k[order]*
 (time-m[order])))*(1/l[order])));
end;

begin
clrscr;
write('simulation number ');readln(randseed);
repeat
  writeln('Miyagawa / Gen Log (M/G)');readln(ch)
until (upcase(ch)='M') or (upcase(ch)='G');
ch:=upcase(ch);
gd:=vga;gm:=vgahi;
initgraph(gd,gm,'');
read_starting_values;
read_probabilities;
calculate_matrix;
initialize_grains;
repeat
repeat
t:=t+dt;
if ch='M' then begin
 wt1:=miyagawa(t,1);
 dw1:=miyagawa(t,1)-miyagawa(t-dt,1);
 wt2:=miyagawa(t,2);
 dw2:=miyagawa(t,2)-miyagawa(t-dt,2);
end;
if ch='G' then begin
 wt1:=Gen_loc(t,1);
 dw1:=Gen_loc(t,1)-Gen_loc(t-dt,1);
 wt2:=Gen_loc(t,2);
 dw2:=Gen_loc(t,2)-Gen_loc(t-dt,2);
end;
for i1:=1 to n do
 with grain[i1] do begin
  c1:=random*(c1h-c1l)+c1l;
  c2:=random*(c2h-c2l)+c2l;
  if stage in [ff,fs,ft] then weight[w1]:=weight[w1]+dw1;
  if stage in [sf,ss,st] then weight[w1]:=weight[w1]+c1*dw1;
```

```
  if stage in [ff,sf,tf] then weight[w2]:=weight[w2]+dw2;
  if stage in [fs,ss,ts] then weight[w2]:=weight[w2]+c2*dw2;
  rand:=random;
  s1:=ff;repeat rand:=rand-matrix[stage,s1];s1:=succ(s1) until rand<=0;
  stage:=pred(s1);
 end;
until t>=t_stop;
calculate_results;
cleardevice;text_screen1;draw_grains;readln;               (*screen 1*)
histogram;readln;                                          (*screen 2*)
cleardevice;text_screen1;draw_grains;select;               (*screen 3*)
calculate_results;
cleardevice;text_screen4;draw_grains;write_border;draw_line;
readln;                                                    (*screen 4*)
histogram;readln;                                          (*screen 5*)
if t_stop<tmax then begin cleardevice;read_probabilities;end;
if t_stop>tmax then t_stop:=tmax;
calculate_matrix;
until t=tmax;
closegraph;
end.
```