

3.4 Grain formation and assimilate partitioning in wheat

3.4.1 Introduction

Rather than presenting a straightforward analysis of processes and of assimilate partitioning and their simulation, it will be demonstrated that the subject of regulation of distribution of assimilates and of redistribution of carbohydrate and protein reserves is not as thoroughly understood as processes discussed in earlier sections. This contribution consists particularly of a discussion and the development of hypotheses for these phenomena, and of a presentation of models on partitioning of substrates among plant organs. These models are still in a preliminary stage of development (cf. Subsection 1.3.2).

This section contains three parts, which are all focussed on growth of wheat. The first part (Subsections 3.4.2 – 3.4.6) describes the physiological basis of regulation of assimilate partitioning and arrives at a static, descriptive model of grain production. The second part (Section 3.4.7 – 3.4.9) presents a simulation model of CO₂ assimilation and N redistribution in plants during the reproductive phase. The third part (Subsection 3.4.10) demonstrates how assimilate distribution over competitive plant organs, like tillers and grains, can be viewed and simulated.

Part I. Ear development, assimilate supply and grain growth of wheat

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3.4.2 Sources and sinks

In cereals, grain yield is the ultimate goal and therefore the partitioning of dry matter between grains and vegetative parts is of great importance. The partitioning of dry matter depends on the relative sink strength of roots, leaves, stems and ears. After anthesis, the relocation of reserves from vegetative organs (e.g. stems) to the grains also plays an important role in assimilate distribution. Discussions on whether assimilate supply (= source) or storage capacity (= sink) limits yield refer mostly to the grain-filling stage, since most grain growth is supported by concurrent CO₂ assimilation rather than by stored reserves of carbohydrates. However, the sink or storage capacity for assimilates at the grain-filling stage is to a large degree determined by the extent of carbon (C) assimilation, nitrogen (N) assimilation and assimilate distribution before anthe-

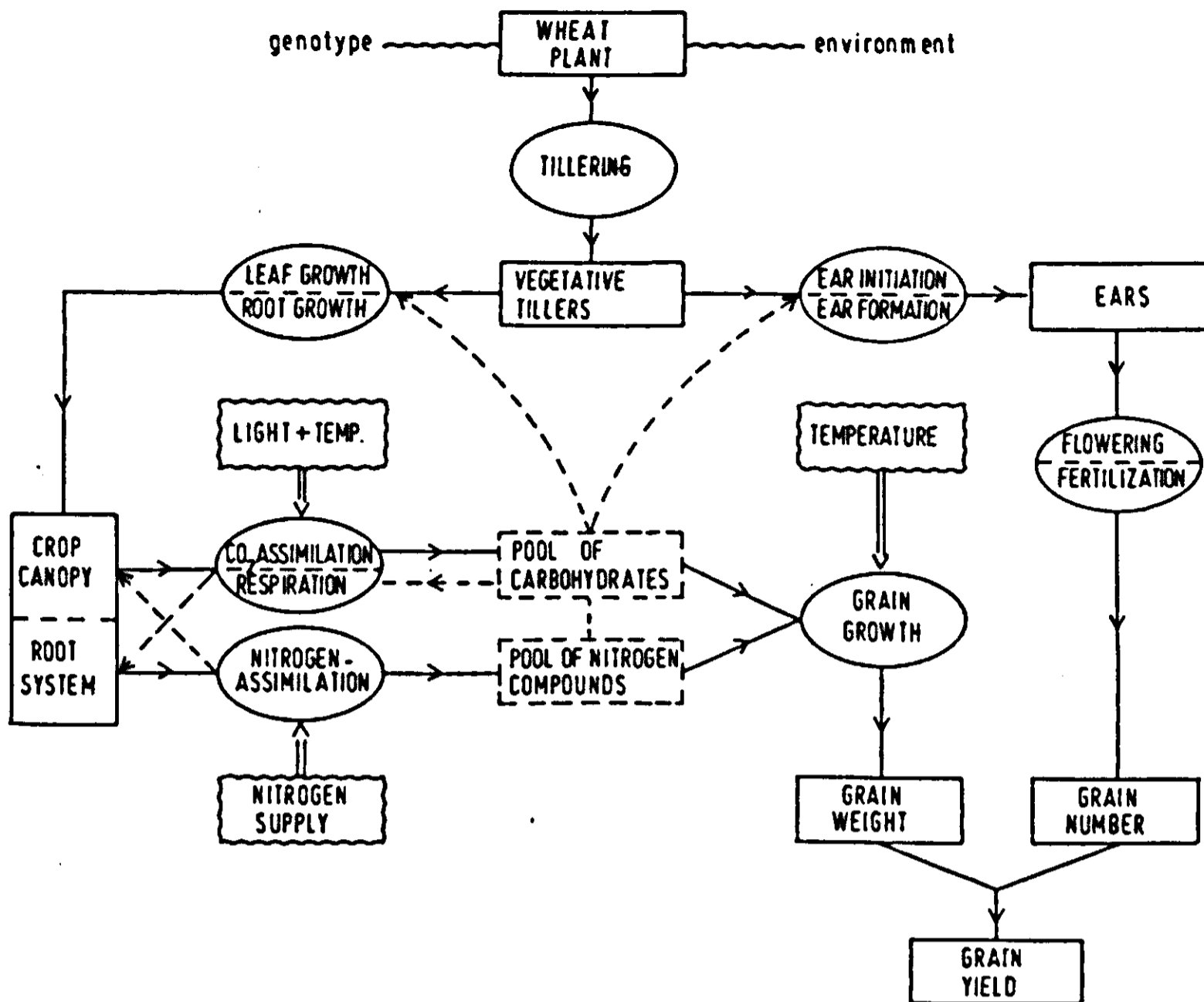


Figure 37. A scheme of factors and processes related to grain growth of wheat. Note that this scheme is not presented as a relational diagram (cf. Subsection 2.1.2).

sis, especially from ear initiation onwards. Thus, whether source or sink limits grain production depends on the balance between growth and development of the crop during the various stages of its life cycle.

A scheme of factors and processes related to grain growth of wheat is presented in Figure 37. Generally, crop physiology and simulation deal mostly with source-related processes (e.g. CO_2 exchange, light interception, transpiration); sink-related processes (e.g. formation and activity of structural or storage organs) are relatively neglected in experimental and simulation studies.

3.4.3 Crop development and ear formation

The development of a wheat crop is characterized by the succession of various phases with a specific pattern of crop growth. The three main phases are:

- germination and juvenile growth
- vegetative growth
- reproductive growth.

After emergence the seedling becomes dependent on its own C and N assimilation. The growth of the plant will initially be restricted by the size of the photosynthetically active organs and by the ability to absorb nutrients. Leaf growth is then essential for improving the light interception. Initially in most crops, leaf

area increases exponentially, because the expansion of the number of leaves and of leaf size occurs simultaneously.

A central problem in integration at the whole plant level is to establish what consequences the metabolic activities in one organ have on the balance of the system. For example, growth of roots into new volumes of soil may increase nutrient supply but it requires assimilates that might have been used in shoot growth. Brouwer (1963) developed the idea of a functional balance between the activities of shoots and roots in which each organ is dependent on certain unique functions of the other: leaves supply carbohydrates and lose water while roots supply the water and nutrients (cf. Subsection 3.3.6). The balance operates to restrict root or shoot growth depending upon whether root or shoot factors are limiting. There is evidence in literature that supports a role of N in such relationships. However, there is no obvious reason why comparable effects should not be caused by other nutrients; e.g. in the case of legumes by phosphate. Generally, N supply increases the shoot/root ratio of grasses (Ennik et al., 1980), with a clear tendency for the root mass to decrease with increasing N supply. During the early vegetative stage the roots and leaves are the dominant sinks, but from the onset of growth of storage organs these organs become the major sink.

In cereals and grasses the increase of leaf area is promoted supplementary by

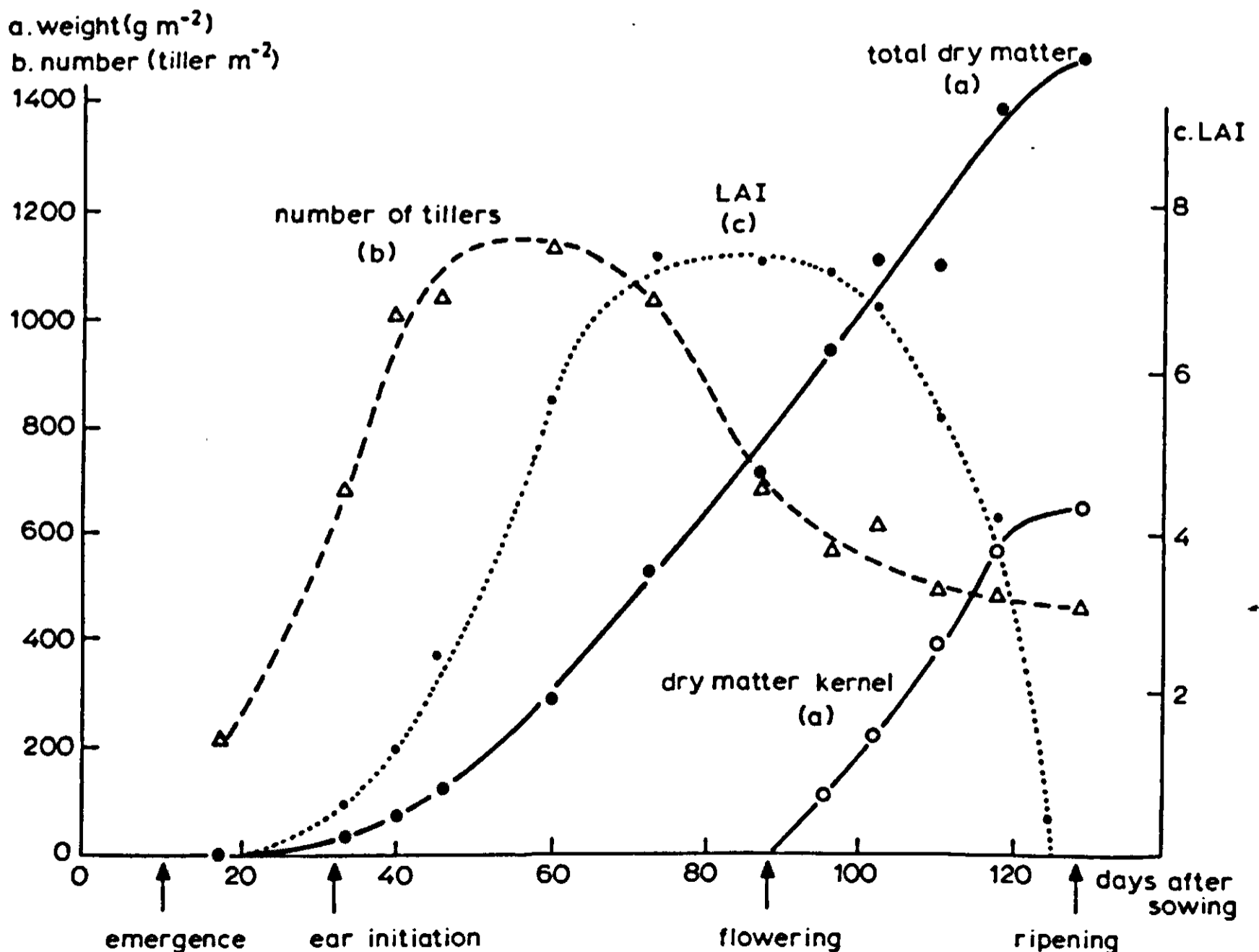


Figure 38. Course of shoot number, leaf area and dry matter production during the life cycle of spring wheat.

tillering (Figure 38; see also Subsection 3.4.10); in other crops a comparable effect is caused by branching of the main shoot. The maximum leaf area is attained at the moment that senescence of leaves offsets the increase in leaf area by formation of new leaves. Most crops can maintain a 'closed' canopy for two months or more. Reproductive crops with a determinate growing point, like cereals and maize, stop leaf growth before anthesis. After that stage, leaf area and photosynthetic activity are gradually declining due to ageing and subsequent senescence of the various leaf layers in an acropetal direction. The rate of leaf senescence depends on environmental conditions (temperature, water availability, nutrient supply, etc.) and on the occurrence of pests and diseases. An approach for modelling leaf growth is shown by Jones & Hesketh (1980).

The total sink strength and storage capacity is strongly associated in many crops with the number of storage cells in grains, seeds, tubers or roots. The morphogenesis of storage organs like grains is very important when considering the interdependence between growth and development and the relocation of assimilates to the various organs. The initiation of storage organs already takes place during the period of active vegetative growth. This very complex process is mainly under hormonal control but the development of storage organs is also strongly affected by environmental conditions that affect the availability of assimilates. The dynamic pattern of ear formation of cereals is shown in Figure 39. On average, ear initiation occurs in the four-leaf stage of a shoot, which coincides with tillering for the main shoot and the first tillers. Thus, even in the beginning a competition exists between the development of 'reproductive' shoots and the formation of new tillers. Late tillers suffer most from competi-

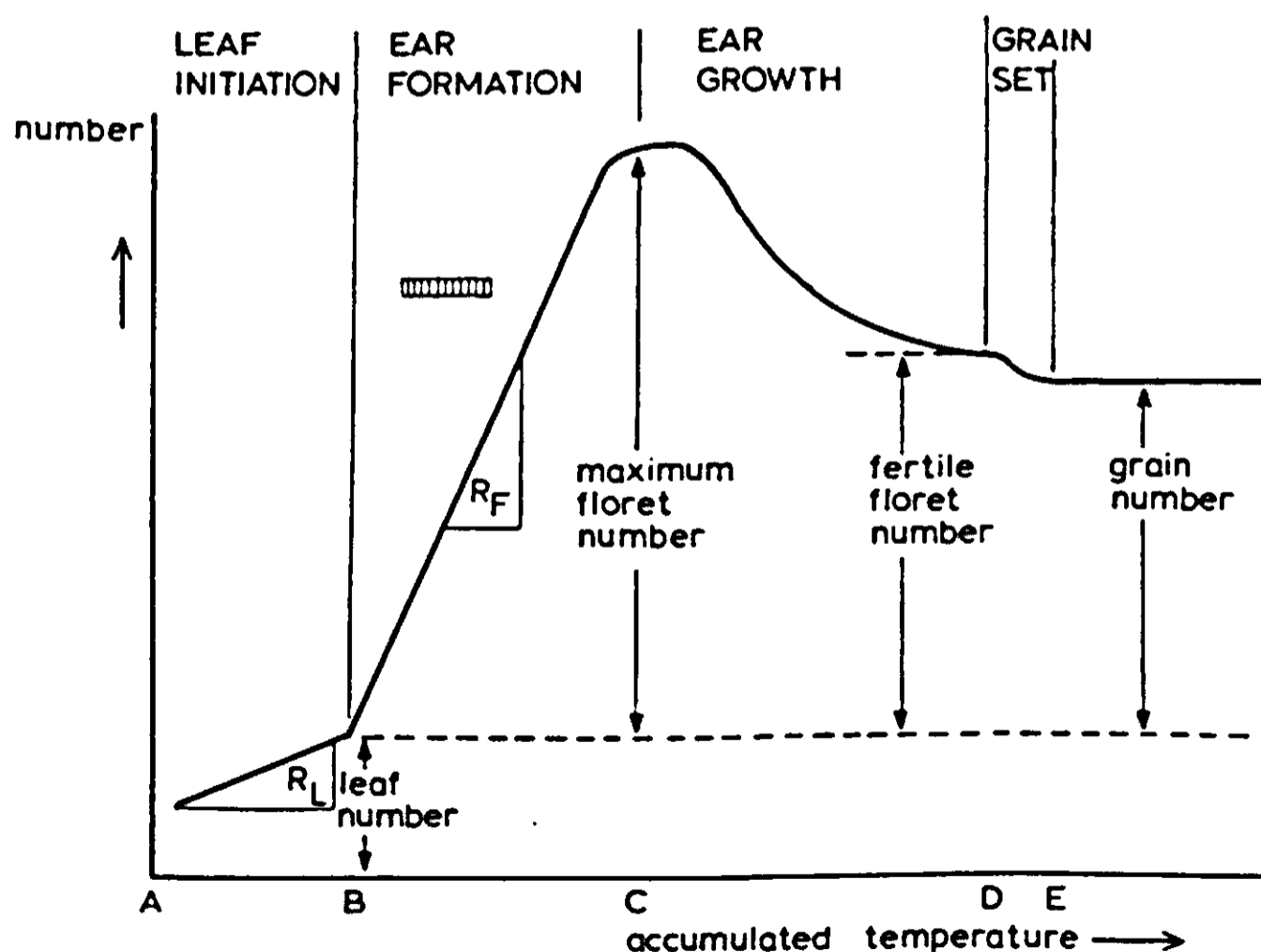



Figure 39. A general scheme for grain formation in cereals. R_L and R_F are the average rates of leaves and floret initiation, respectively;  represents the period during which double ridges first become visible (after Gallagher, 1979).

tion and do not become fertile in a dense stand. The formation of spikelets and florets in a fertile shoot shows a great plasticity. Out of nine floret primordia in a spikelet on a central position of the spike, only 2-4 florets develop a grain. This plasticity in sink formation acts as a mechanism for adaptation to constraints in the growth conditions, but also for compensating a low number of fertile tillers.

Most of the endosperm is formed during the cell division phase following anthesis and fertilization of the florets; cell division ceases approximately two weeks after anthesis. Differences in cell number in the wheat endosperm due to a variety of causes (irradiation levels, water supply, intergrain competition) have been shown to result from variation in the rate of production of cells with the duration of the cell division phase being unaltered (Brocklehurst, 1979). These results suggest that the rate of production of endosperm cells is associated with the level of carbohydrate available to the grain, but it is not clear whether this is a causal relationship.

The levels of one or more phytohormones may regulate, as intermediates, the rate of cell division; a possible group of regulatory compounds are the cytokinins (see Figure 40). During grain development in wheat, the maximum level of each phytohormone varies with the maturity stage. The sequence is cytokinin, gibberellin, auxin and abscisic acid. The validity of the conclusions drawn from determination of endogenous hormones is limited due to the complexity of the hormonal relationships.

3.4.4 Assimilate supply and grain number

The maximum weight of individual kernels is under genetic control, and is relatively stable under disease- and pest-free conditions. Under conditions when

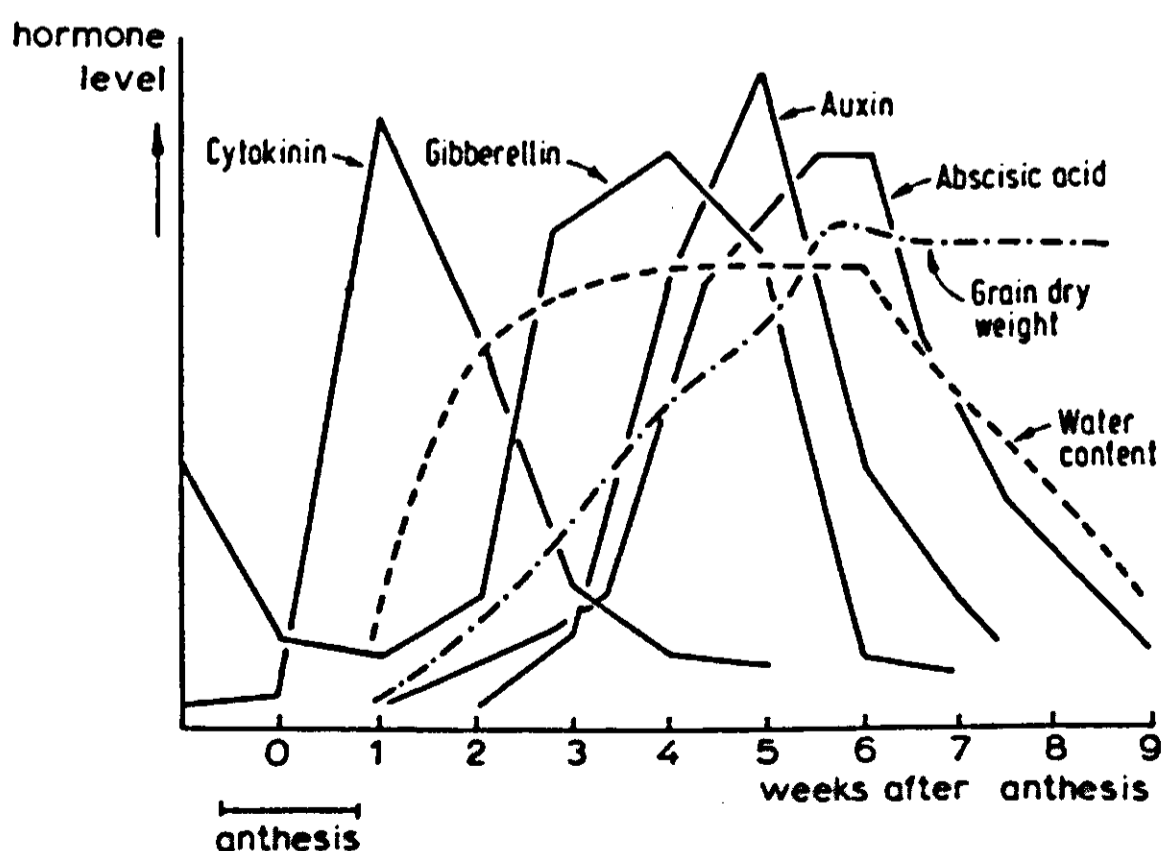


Figure 40. Endogenous levels of plant hormones in the developing wheat ear (after Gale, 1979).

this maximum weight is reached, the grain yield is directly related to the number of kernels. Hence, for temperate climate and optimal water and nutrient supply, the grain yield appears to depend more on the storage capacity than on assimilate supply. The number of grains, however, shows a strong response to environmental conditions. Therefore grain yield is quite often more strongly related to grain number than to grain size. Under temperate growing conditions at least 18-20 000 grains per square metre are required to achieve maximum grain yields. Clearly, actual grain yield might be below the potential level due to a low number of grains as well as to a low degree of grain filling. Grain weight often decreases with a rise in grain number due to mutual competition between grains for assimilates.

A close association between number of grains (N_g) per square metre and total above-ground dry matter yield at final harvest (DW_h) in g m^{-2} could be derived from data of a field experiment with winter wheat (Spiertz, 1980). This association can be represented by the following equation:

$$N_g = 12.4 DW_h + 270 \quad R^2 = 0.88 \quad (49)$$

Assuming that dry matter yield at anthesis is reflected by the straw yield at final harvest, the ratio between grain number and dry matter yield at anthesis amounts to about 20 kernels per gram dry weight. Rawson & Bagga (1979) found a good correlation between the number of grains per main ear and the ratio total visible radiation:accumulated degree-days between sowing and anthesis. Differences in the ratio between grain number and dry weight at anthesis might be explained by the rate of net CO_2 assimilation per unit degree-day. This parameter can be used to compare the relative availability of assimilates for growth in plants with a different rate of development. CO_2 assimilation is only slightly influenced by temperature in contrast to the rate of development, which is strongly affected. High temperatures shorten the period from ear initiation to anthesis, thus reducing supply of assimilates to the ear relative to the rate of development.

3.4.5 Assimilate supply and grain growth

Genetic differences between cultivars in dry matter distribution during ear formation may also play an important role. Generally, modern semi-dwarf cultivars produce more grains per unit dry weight than older long strawed cultivars, which is associated with a more favourable dry matter distribution to the ear before and after anthesis. The harvest index of modern cultivars, the weight of the grain relative to the total final shoot weight, ranges from 0.45-0.55. The major processes involved in grain filling are carbohydrate and protein conversion and accumulation. Carbohydrates may be derived from current CO_2 assimilation and from stem reserves (Figure 41). The carbohydrates are translocated as sucrose and in the grain endosperm converted into starch. Nitrogenous compounds for grain growth are mainly supplied by the vegetative parts and only to a smaller extent derived from post-anthesis uptake. Generally, the following

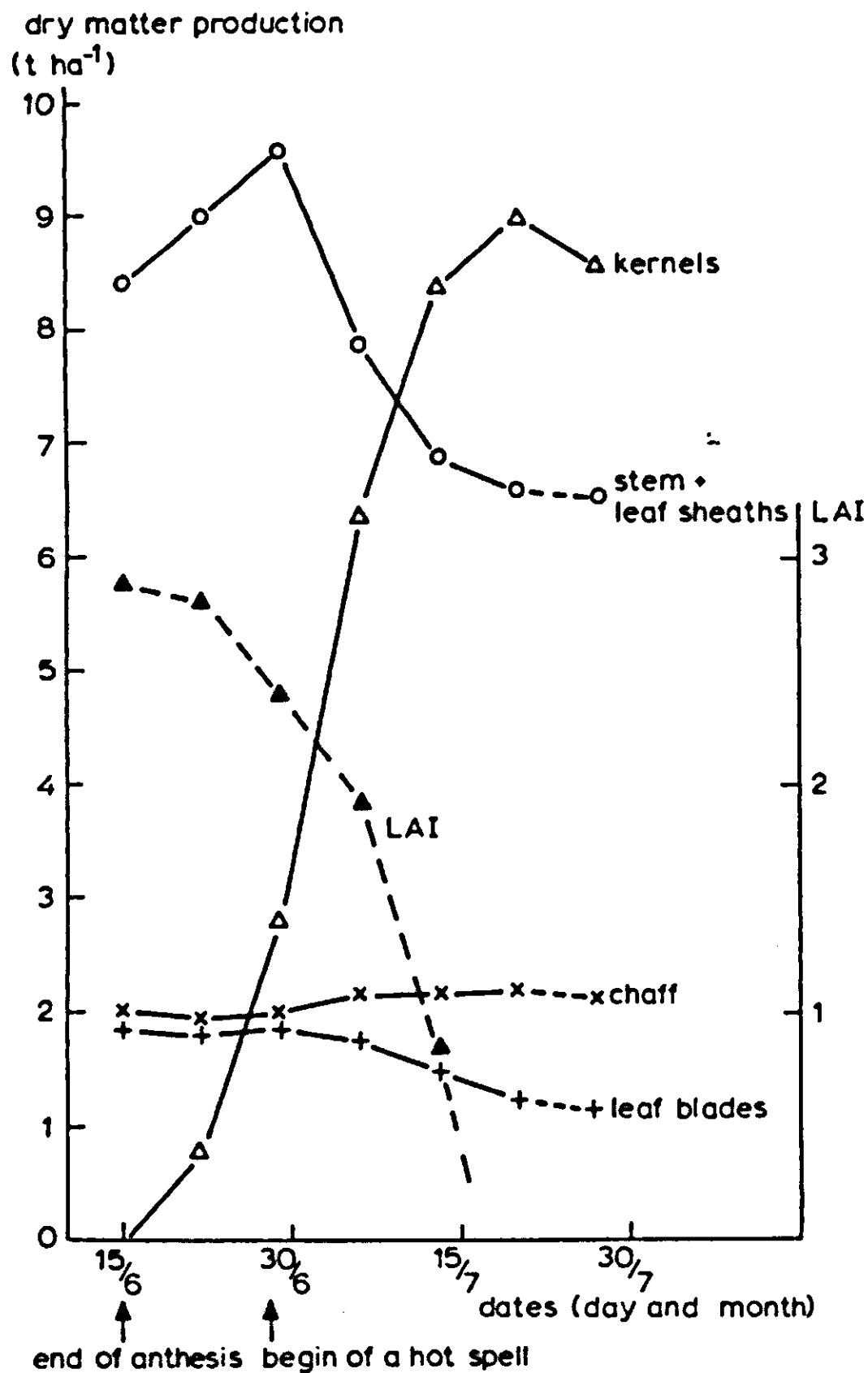


Figure 41. Dry matter distribution in wheat after anthesis (cv. Lely, fertilization with N at 200 kg ha⁻¹; 1976).

equation represents the post-floral balance of assimilates:

$$\text{STORAGE IN GRAINS} = \text{ASSIMILATION} + \text{MOBILIZATION OF RESERVES} \quad (50)$$

The rate of assimilate accumulation by grains is strongly governed by temperature; a rise in temperature enhances carbohydrate as well as N accumulation. N relocation and protein accumulation show a stronger response to temperature than carbohydrate accumulation. A high rate of grain growth can only be maintained with an ample assimilate supply. Because of the high rate of grain growth and a reduction of current net CO₂ assimilation, stem reserves may deplete very fast under warm growing conditions. It was found that the contribution to grain yield of assimilates stored prior to grain filling varies from 500 to 1500 kg ha⁻¹. However, the amount of mobile carbohydrates present at the end of anthesis ranges from 1500 to 3000 kg ha⁻¹. A large part of these reserves is apparently used in respiration processes or transported to the roots.

Adverse conditions during the grain filling period accelerate the depletion of N reserves in the vegetative parts of the wheat plant. This N depletion, especially of the leaves, might accelerate leaf senescence and thus reduce CO₂ assimilation towards the end of the growing season. It has been shown that late top dressings of N with control of pests and diseases increase the N content of the leaves and can delay their senescence. Under optimal conditions of water and nutrient supply the rate of crop CO₂ assimilation has been shown to remain at a constant level for about 3-4 weeks after flowering, after which there was a linear decline over the next 2-3 weeks.

The duration of maximum grain growth (D , in days) may be derived from the following equation:

$$D = R / (R_g - R_a) \quad (51)$$

in which R is the amount of crop reserves in kg ha⁻¹, R_g the rate of grain growth in kg ha⁻¹ d⁻¹ and R_a the rate of current assimilation or supply in kg ha⁻¹ d⁻¹. For instance, for optimal supply of carbohydrates, Equation 51 becomes:

$$\begin{aligned} D &= \frac{\text{Available carbohydrate reserves}}{\text{Rate of carbohydrate accumulation} - \text{Rate of net CO}_2 \text{ assimilation}} \\ &= \frac{1500 \text{ kg ha}^{-1}}{(200 - 150) \text{ kg ha}^{-1} \text{ d}^{-1}} = 30 \text{ d} \end{aligned}$$

and for optimal nitrogen supply:

$$\begin{aligned} D &= \frac{\text{Available N reserves}}{\text{Rate of N accumulation} - \text{Rate of post-floral N uptake}} \\ &= \frac{81 \text{ kg ha}^{-1}}{(4 - 1) \text{ kg ha}^{-1} \text{ d}^{-1}} = 27 \text{ d} \end{aligned}$$

This concept is included in a dynamic simulation model in Subsections 3.4.7 and 3.4.9.

3.4.6 Nitrogen use, growth and grain yield

The uptake of N by a wheat crop depends on the amount of available soil N and the recovery of fertilizer N. The amount of N uptake without N dressing is associated with the nitrate made available from soil organic matter and with rooting characteristics (root length and activity). The efficiency of utilization of N by the wheat crop, defined as the amount of grain produced per unit N absorbed, is determined on the one hand by the N harvest index and on the other hand by the N concentration in the grain. The N harvest index (NHI), the proportion of the total amount of N in the plants that is present in the grains at the harvest, usually ranges between 0.74 and 0.82. If, however, during the grain-filling stage a water shortage develops, translocation of N from the vegetative

tissue to the growing grains may be hampered, resulting in a lower N harvest index, thus decreasing the N use efficiency. This effect may become even stronger, when the moisture stress leads to accelerated senescence of the photosynthetic tissue. The developing grain cannot be properly filled so that at harvest kernels have a high protein content and a low dry weight, in extreme situations leading to shriveled grains.

With regular N supply to the plants, on average about 65% to 80% of the grain N was derived from the vegetative parts, the remainder originating from uptake by the roots after anthesis. Available N for relocation to the grains can be derived from N content of the crop at anthesis minus N residues in straw and chaff. The former amounts to about 150 kg ha⁻¹ and the latter to about 60 kg ha⁻¹ for an average wheat crop in the Netherlands. Mobile N for relocation to the grains is contributed by the leaves (40%), the stem and leaf sheaths (40%), and chaff (20%).

The rate of N accumulation in the grains is determined by dry matter growth rate and the N concentration of the grain. A growth rate of 200 kg ha⁻¹ d⁻¹ and a N concentration of 20 g kg⁻¹ results in a N accumulation rate of 4 kg ha⁻¹ d⁻¹. At low N levels the relation between grain yield and total N uptake in the grain is linear with a slope of about 60 kg kg⁻¹. At higher N supply levels the yield response curve deviates from the straight curve, reflecting an increase in the N content of the grains. The level of the plateau where increased N uptake does not result in higher grain yields is determined by other limiting factors (e.g. water shortage, diseases and pests) (cf. Subsection 1.2.3).

Increase in supply of N to grains cannot be obtained by further increasing the concentration of N in vegetative tissue, because this is strongly associated with the adverse effects of a too leafy wheat crop (risk of lodging and increased susceptibility to diseases). A substantial post-anthesis N uptake is therefore a prerequisite for achieving high grain yields.

Part II. Modelling of post-floral growth of wheat

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3.4.7 Description of the model

This section deals with aspects of modelling post-floral growth of wheat. A detailed treatment of such a model is described by Vos (1981). The model describes and interrelates gross CO₂ assimilation, respiration, accumulation of carbohydrates (starch) and proteins in the grains, redistribution and additional uptake of N and leaf senescence. Structural growth of all organs except grains is assumed to have ceased at anthesis. Grain dry matter is assumed to consist of carbohydrates and protein only. The model is designed to run with time steps of one day. Besides crop characteristics at anthesis, daily records of irradiation and