5.1 Crop production in relation to availability of nitrogen

F.W.T. Penning de Vries

5.1.1 Introduction

This section has a character that is different from the others in this book: the text is largely reflective in nature, and it describes the difficulties in developing simulation models on the level of production where nitrogen (N) limits productivity. It neither considers dynamic models, nor the modelling of processes. This is because there are still too many unanswered questions to permit the construction of dynamic simulation models of the depth and quality described in preceding sections. The underlying concepts at this level of production are often not clear, and the existing simulation models are still of a preliminary type (Subsection 1.3.2), i.e. very interesting for specialized scientists, but of little predictive value. Two attempts will be presented to show how far one can go currently with modelling in this field (Sections 5.2 and 5.3).

In the Subsections 5.1.2 and 5.1.3, some of our knowledge of the plant-soil system at this production level will be presented, but it is our approach that will be underlined. Some of the unresolved questions are posed in Subsection 5.1.4. Shortage of phosphorus can have a direct effect on the N uptake of plants, as discussed in Subsection 5.1.5.

5.1.2 Crop yield responses to nitrogen

In a situation in which shortage of N limits the productivity of the crop, there is a clear response within a set of experiments of crop yield to fertilization (e.g. Quadrant a of Figure 65). But if one compares results of fertilization experiments at different sites or in different years, the responses are often less clear. The observations are easier to interpret if data are plotted as in Figure 65, with N absorbed by the crop as an intermediate variable: yield versus N absorbed (Quadrant b), and N absorbed versus intensity of fertilization (Quadrant c). The response curve of yield to N absorbed goes through the origin, and has a horizontal asymptote. The recovery of fertilizer N is a constant fraction (r) of the dose applied, which is represented by a straight line with a positive intercept (Nu) with the horizontal axis, the N absorbed from the unfertilized soil. By introducing this type of analysis, van Keulen (1975) found that he could eliminate much of the variability of the dose-yield response curve of different experiments, and explain it in terms of varying values of the N absorbed from the unfertilized soil and of different values of the recovery fraction of fertilizer N. N absorbed refers to the N contained in the above-ground biomass at flowering or at maturity (the highest of both).

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The upper limit of the yield response for any particular case is, of course, equal to the potential production in that situation (Subsection 1.2.1), and can be simulated with models described in the preceding sections. It equals 8500 kg ha^{-1} in this example (Quadrants a and b), that was taken from experiments reported elsewhere (Penning de Vries & van Keulen, 1982). The slopes of two important lines in this figure are also known: those representing minimum and maximum N concentration in the dry biomass at maturity: 5 and 20 g kg^{-1}. Those lines indicate, respectively, the initial slope of the yield response curve and the amount of N absorbed at the potential production level. Together, these three lines describe the response curve of total production to N absorbed already fairly well. Of those lines, only the position of the maximum yield level depends on the actual growth conditions, in particular on the duration of the growing season. The degree of curvature of the response curve is not quite predictable. It may depend on conditions during the growing season, and it may also be that some species are more inclined to dilute their N to the minimum levels than other species are.

The value of the N absorbed from the unfertilized soil is highly variable from one place to another: from as low as 10 kg ha^{-1} yr^{-1} or less on very poor soils and in natural grasslands in semi-arid regions, to values above 300 kg ha^{-1} yr^{-1} on freshly reclaimed soils, rich in organic matter. Its basis is usually the mineralization in the soil. The recovery of fertilizer N is generally between 0.3 and 0.7 g of nitrogen absorbed in above-ground parts plus, eventually, the N in below-ground storage organs, per gram of N applied. Recovery values of about 0.1 have been established in very unfavourable conditions, but also values as high as 0.8 or more have been reported. These values depend on conditions in the soil,on its aeration in particular, on the timing and method of fertilization, and also on the crop or vegetation type.

It is remarkable, but confirmed for many cases, that the value of the recovery fraction at a certain site is usually a constant and does not depend on the level of fertilization. It strongly suggests that all physical, chemical, plant physiological and microbiological processes that remove or utilize N from the soil depend in the same way on the soil nitrogen concentration.

The analysis of response curves according to Figure 65 has been quite useful in temperate and in semi-arid grassland systems (van Keulen & van Heemst, 1982; Penning de Vries & van Keulen, 1982; van der Meer, personal communication), and its generality points towards a common underlying basis of physiological, soil physical and soil chemical processes.

About this basis, there are two groups of questions: those concerning the soil as the source of N, and those concerning the response of the crop to a certain availability of N. Questions about the soil are in particular those about the amount of N provided by the unfertilized soil, the degree of recovery of fertilizer N, and also about the dynamics of the N balance in the soil: rates of mineralization, of immobilization, of nitrification, of denitrification, of leaching, of absorption of N by plants, etc. Section 5.2 will discuss them (except absorption)
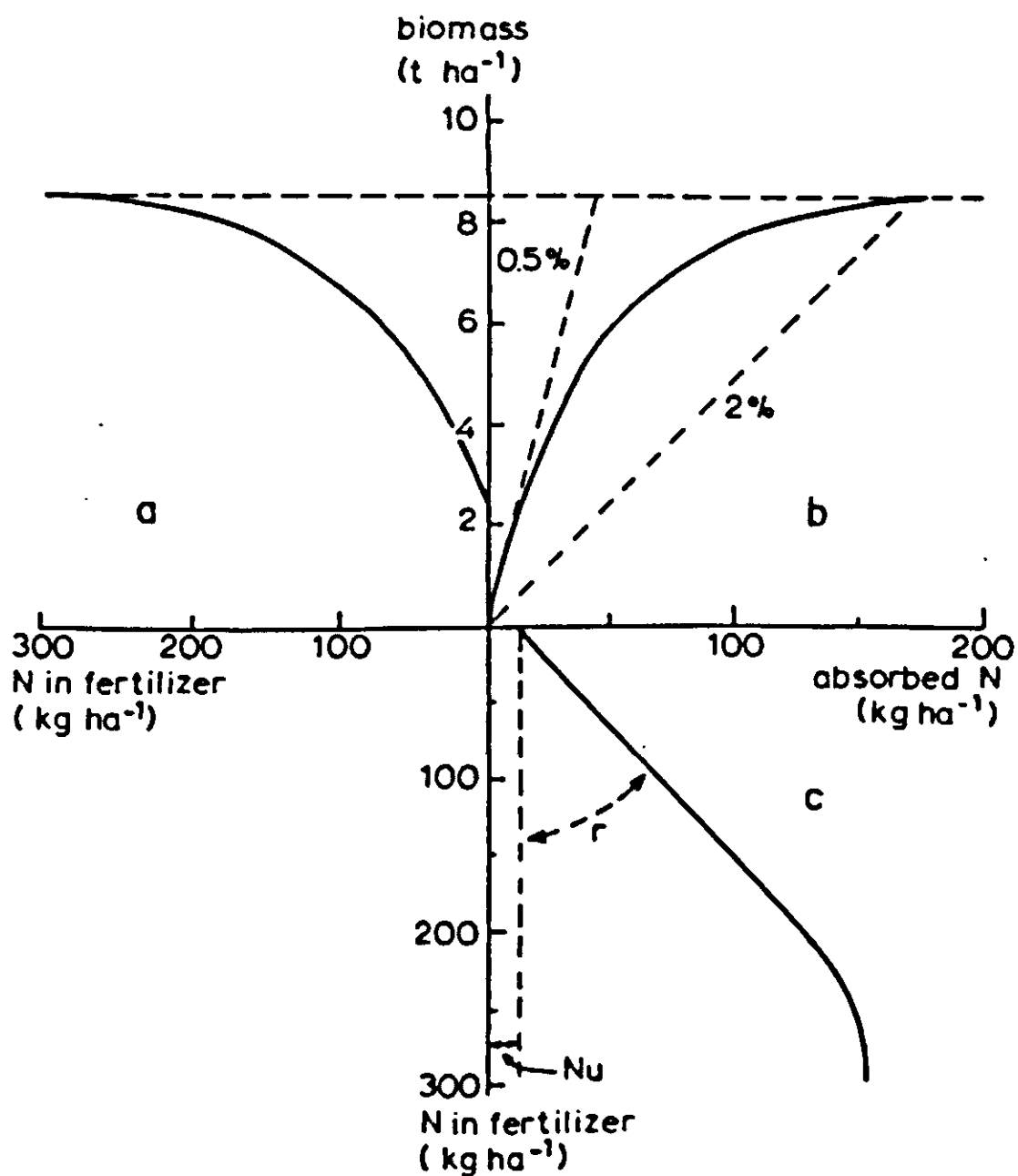
Figure 65. The relations of N absorbed, N applied and biomass yield in one set of experiments with a vegetation consisting of C_4 grasses (Penning de Vries & van Keulen, 1982). Nu is the N absorbed from the unfertilized soil and r is the recovery fraction of fertilizer N.

and show some of our difficulties in their modelling. The remainder of this section concentrates on the response of the crop to N shortage. Questions to be asked are: what is the quantitative response to N shortage, how does it vary between types of organs (in order to predict economic yields), and does it change during physiological development? Section 5.3 presents a preliminary dynamic simulation model that includes many elements of this section and of the next.

5.1.3 Maximum and minimum N concentrations

The supply of N to the plants is often relatively high in the beginning of the growing season, and lower later on. This means that growth of new tissue later in the season must take place with less N than earlier, and one finds that the concentration of N is lower in vegetative tissues that are formed later. This new biomass contains less proteins and more N-free or N-poor material, such as cellulose and lignin. But not only in new tissue does the concentration of N decrease, it commonly drops in old tissues too. A fine example is the work by van Egmond (1975), who studied in detail the concentrations of plant nutrients in
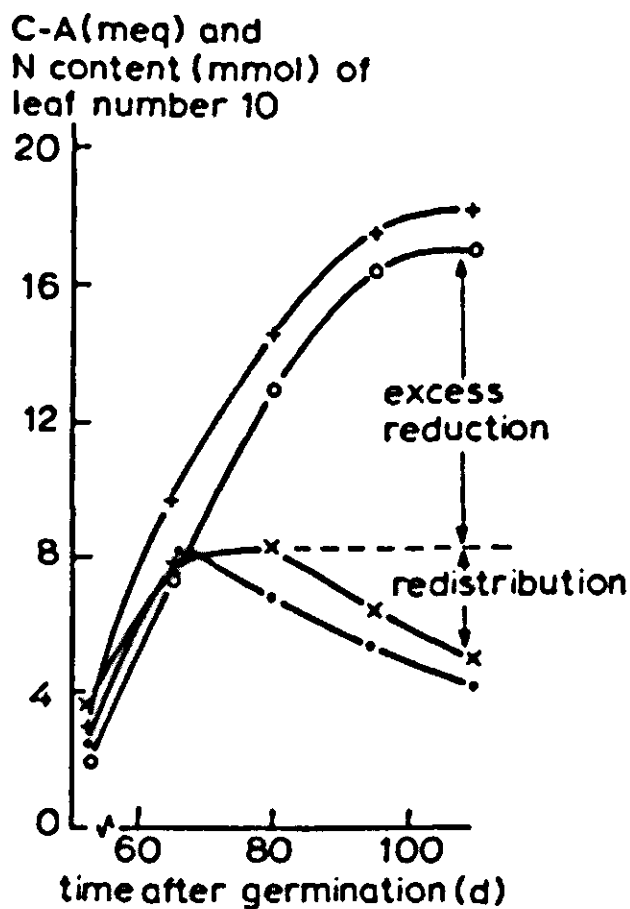
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C-A(meq) and
N content (mmol) of
leaf number 10

Figure 66. The course of N formed (C-A, upper lines) and N contained (N organic, lower lines) in some sugar-beet leaves (van Egmond, 1975). Of each set of lines, the upper ones correspond with a high intensity of fertilization, the lower ones with a low dose.

organs of developing sugar-beet plants (Figure 66). He concluded that 'leaves with numbers up to about 20 exported a great deal of the organic N they produced, e.g. leaf 10 about 70% at 109 days', and 'leaves with numbers over 25... have imported much of their organic N from the old leaves, e.g. leaf 40 about 30-50% at 109 days'. That import into young leaves concerns not only export of current products of old leaves, but includes also much of what was structural protein before, can be seen in Figure 66: the fraction 'C-A' in the figure represents all nitrate that has been reduced in this leaf and 'N organic' represents the N that is still in the leaf. The C-A fraction consists of organic acids, and is in a sense an immobile slag of nitrate reduced in this species (see van Egmond, 1975). The difference between C-A and N organic is the amount of organic N exported from this leaf. Much of it was N in nitrate form that was reduced in excess of the needs of the leaf, particularly in the young but fully extended leaf (see Figure 66).

Particularly because of synthesis of N-poor components, the concentration of N in the total above-ground biomass decreases in time, even in constant growth conditions. If the source of N becomes exhausted the decrease is even more important because of intensive redistribution. It is therefore of interest to know the range of N concentrations that can be encountered in plants. From a large number of analyses made of the above-ground parts of annual C_4 grasses, C_3 herbs and legumes, Figure 67 has been constructed (Penning de Vries & van Keulen, 1982). It depicts the highest and lowest concentrations of N in the total above-ground dry matter of plants of different development stages, observed in the field and in laboratory conditions. For reasons stated below, it is supposed that the three groups distinguished in this figure apply to the groups of annual C_4 plants (including C_4 dicotelydons), C_3 plants (including C_3 grasses) and legumes in general, rather than just to the smaller groups of species in which the observations are made. The individual species within the three groups distin-
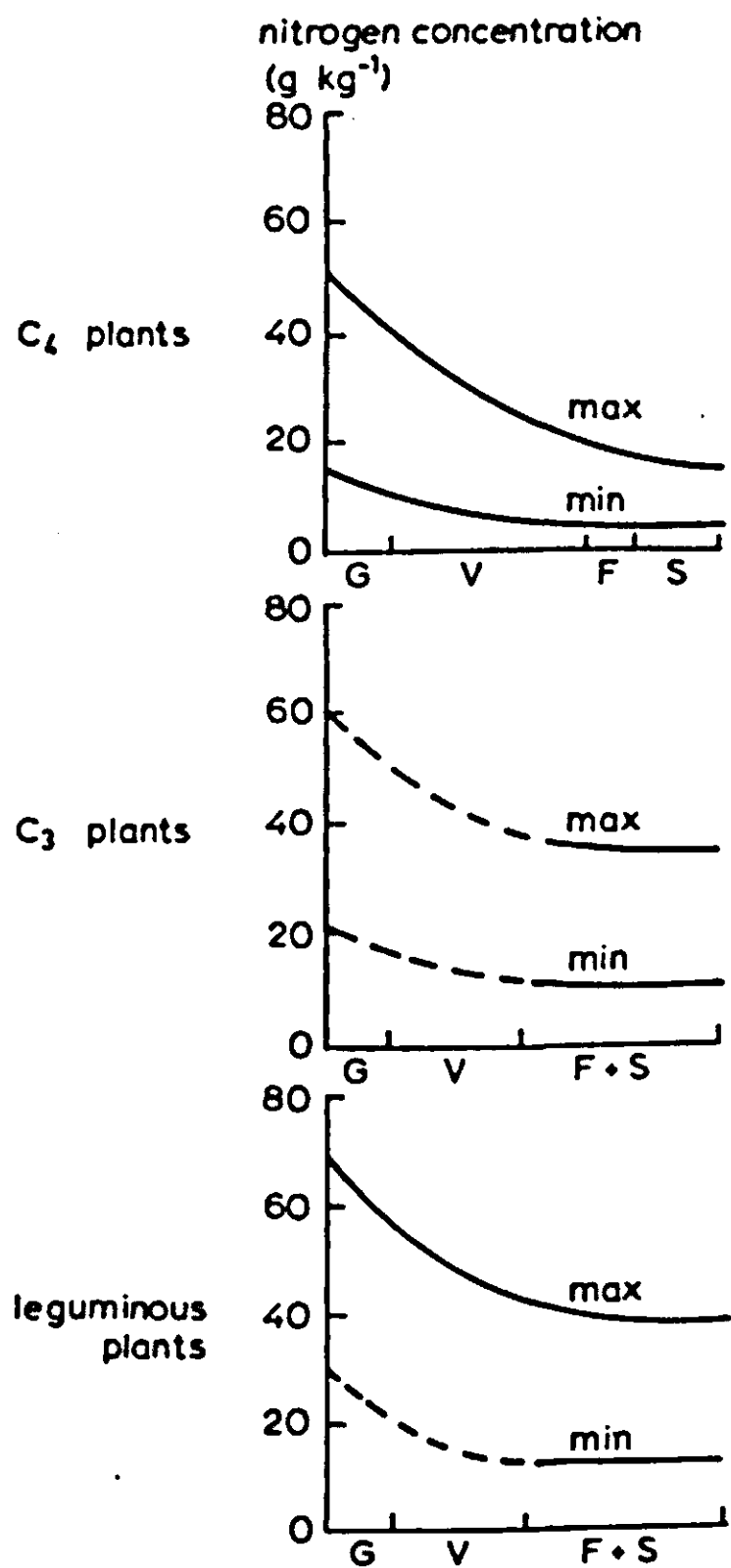
Figure 67. The course of the maximum and the minimum concentration of N in whole plants at different development stages: G stands for germination and early growth, V for vegetative phase, F for flowering and S for seed filling. Broken parts of the lines are based on a few observations only.

guished behaved similarly, but considerable differences occur between the groups.

Figure 67 is only a rough graph because it lumps all organs and many species. Yet one recognizes that there is a level of N in the dry matter below which the plant does not function, the minimum level. This level is about 20 g kg^{-1} in young C_3 plants and the minimum level drops to about 10 g kg^{-1} in mature C_3 plants. The maximum level seems to be about four times the minimum level at any moment in C_3 species. Leguminous species, all of the C_3 type, may form an exception and have still higher minimum values (but these are possibly not really minimum values, because those plants supply themselves with N). Both the maximum level and minimum level in C_4 plants appear often to be about half that of C_3 plants. The practical implication of this aspect of efficiency of N utilization is considerable: C_4 plants function well at much lower levels of N than C_3 plants do. Biomass production on poor soils can therefore be considerably higher with C_4 species than with C_3 species. (However, this may be a disadvantage, as biomass with a N concentration below 9 g kg^{-1} dry matter has lost much of its value as fodder for cattle.) In suitable conditions, it is recalled,

C_4 plants are also more efficient utilizers of solar energy and of water (Sections 3.2 and 4.1).

The major reason for the difference between the minimum concentration of N in C_3 and C_4 plants may be found at the biochemical level. A considerable fraction of N in crop plants is contained in enzymes. The C_4 plants contain small amounts of the enzyme Phospho-Enol-Pyruvate-Carboxylase (PEPC-ase), which increases the efficiency of Ribulose-Bi-Phosphate-Carboxylase (RuBPC-ase) to such an extent that photosynthesis can be intensive with much smaller amounts of the latter enzyme than in C_3 plants that lack PEPC-ase. This remark becomes more significant if one realizes that the enzyme RuBPC-ase alone makes up 25-60% of the total leaf proteins in C_3 plants, and 8-23% in leaves of C_4 plants (Ku et al., 1979, Pheloung & Brady, 1979). There is no reason to expect that C_4 plants need much more enzyme of another kind for other processes than C_3 plants do, so that the difference in photosynthesis system can express itself clearly in the minimum and maximum N concentration of photosynthesizing organs.

The decrease of the amount of organic N after it has attained a maximum in the leaf represents export of protein. This phenomenon of redistribution has been observed often in many crops. This is why in Figure 4 of Section 1.2 the total N in the plant has been divided into a part that remains in old leaves (N stable), while another part can be remobilized for growth (N mobilizable). Because of the redistribution phenomenon, plants can continue for some time to grow new tissue without uptake of N. This is clearly an advantage for plants growing on poor soils, but it provides a considerable handicap for research workers in the interpretation of growth curves in fertilization experiments.

Redistribution of N and other nutrients is closely linked with the process of senescence of organs. A decrease of the rate of photosynthesis in relation to a decrease in protein level in leaves has often be reported (e.g. Lugg & Sinclair, 1981). Section 3.4 discusses the relation of redistribution of N from vegetative parts towards the grains in wheat, and the causal relation of N export to plant senescence. Another good example on the relation between redistribution and senescence is provided by soybean plants, according to an analysis by Sinclair & de Wit (1976). They called the fast redistribution during pod filling 'self destruction' of the plant. If too few proteins remain in the cells, these cells will become unable to maintain themselves and deteriorate. A little before this level is reached, they will stop functioning properly.

From the observation that the amount of proteins in cells can drop, one must either conclude that this was storage protein, or that functional protein has been degraded and exported. The latter is most likely. The definition of reserves of carbohydrates (Section 3.3) as components different from structural material, is thus not applicable to protein. Proteins are like a capital that provides interest, but that also can be consumed if the need arises.

5.1.4 Principal questions that remain

To improve our capability of dynamic simulation of growth in N limiting conditions, there are some important questions to be answered by experimental and theoretical research:

- How variable are maximum and minimum concentration of N in tissues of different organs? To what extent is it a function of growth conditions? In what biochemical sense does remobilizable N distinguish itself from non-remobilizable N? The answer to this question is essential in the determination of how much N is remobilizable at each moment for growth elsewhere in the plant.

- The minimum level is defined as that concentration at which the plant stops growing. How far above this minimum level does the plant begin to function normally? How much 'luxury consumption' of N takes place?

- How low must the rate of N supply be before redistribution starts? Is there a minimum rate of supply related to the current growth rate? Or is there always a redistribution of N, even in well supplied tissues, but difficult to detect because protein resynthesis is continuously in equilibrium with degradation and export?

- What is, quantitatively, the relation between protein turnover processes as a result of maintenance processes in the cell (Subsection 3.3.5), redistribution and senescence?

- What does Figure 67 look like for individual organs? Or even better: what is the range of N concentrations for individual processes, like growth, photosynthesis (C_3 and C_4 type) and development. They are definitely different: stems function at very low N contents (and xylem vessels even lower), but growing cells need much N and P for proteins and nucleic acids. Van Keulen (Section 5.3) presents a suggestion for the reducing effect of low N levels on the intensity of processes.

- The uptake of N by the crop after flowering is often small. This is in many cases because the soil is exhausted, in particular at the production level where low N availability limits productivity. But also when there is plenty of nitrate in the soil, the crop does not take up much after flowering (cf. Subsection 3.4.7). It may be presumed that this results from a decreased root activity, possibly as a consequence of the strong demand of the reproductive organs for carbohydrates. A thorough analysis has still to be made.

- What about losses of N from the vegetation and from the soil? As for the vegetation, Wetselaar & Farquhar (1980) made a review and found inexplainable losses of N from growing plants. There are many questions as to when, where and by what process the N gets lost. But there is little doubt that losses of 10-30% of the plant N content can occur in a period of a few weeks at the end of the growing season. Volatilization of NH_3, leaching and insect damage are among the suggested explanations. NH_3 can also be absorbed from the air. The concentrations of NH_3 in the air is one aspect of absorption or loss, the concentrations of NH_3 and NH_4^+ in the plant is another. Of the first value few measurements exist, of the second hardly any. The NH_3 exchange processes with am-

bient air have not yet received much attention. Difficulties in measuring it are certainly an important cause of this. However, a better quantification and understanding of such loss and absorption processes is needed for the simulation on the crop N balance.

— What is the water use efficiency in case of N limitation? As large as when water limits growth (in other words: is the transpiration coefficient a constant?), or does it decrease because water is not limiting anyway. There is some experimental evidence to suggest that the water-use efficiency decreases to some extent in the field (Penning de Vries & van Keulen, 1982), though an indication from a laboratory study points to the constancy of this efficiency (Goudriaan & van Keulen, 1979). Further research is required.

5.1.5 Complications with phosphorus

Much of the considerations for N availability and growth could be repeated for phosphorus (P), only the absolute values are generally about 10-times lower than those for N (Figure 68). P is a constituent of nucleic acids and nucleotides, and it functions as such in energy transfer processes (ATP is a nucleotide). P is also mobile in the plants: van Egmond notes that 55% of the P in a mature sugar-beet has been redistributed. Much less research has been done on P and the effect of P shortage on growth than for N. But there seem to be many similarities between the approach to the effect of P shortage on growth, to that for N (see e.g. Figure 5, Section 1.2). The dynamics of P in the soil, however, are still more difficult than that of N and are not discussed here at all. Readers are referred to Beek (1979), Cole et al. (1977) and Krul et al. (1982).

There is, however, one important phenomenon that should not be overlooked: the concentrations of N and of P in plants are interdependent. From the Figures 67 and 68 it might be concluded that at any development stage, the ratio of P to N could vary about 20-fold: the concentration of N is always between its minimum and its maximum value, the latter being four to five times larger than the first at any moment; the same observation holds for the concentration of P. However, these values were measured in different plants. If a single plant is analyzed, one never finds a ratio of P to N lower than about 0.04 g g^{-1}, and rarely one higher than 0.15 g g^{-1}. This is a much narrower range, which indicates that the concentrations of N and of P are coupled to a certain extent. This reflects a biological feature: both elements play a role in active processes, so that their concentrations cannot be completely independent. From laboratory experiments, Dijkshoorn & Lampe (1980) conclude that the ratio of organic P to N in proteins and nucleic acids together equals 0.055 g g^{-1}. In addition, there is inorganic P in the plants, among others as a result of the splitting up of ATP into ADP and inorganic P during energy transfer. This inorganic P amounts to almost as much as the organic fraction. They conclude therefore that a plant must contain at least a ratio of P to N (total organic N) of 0.10 g g^{-1} for healthy growth.

phosphorus concentration (g kg⁻¹)

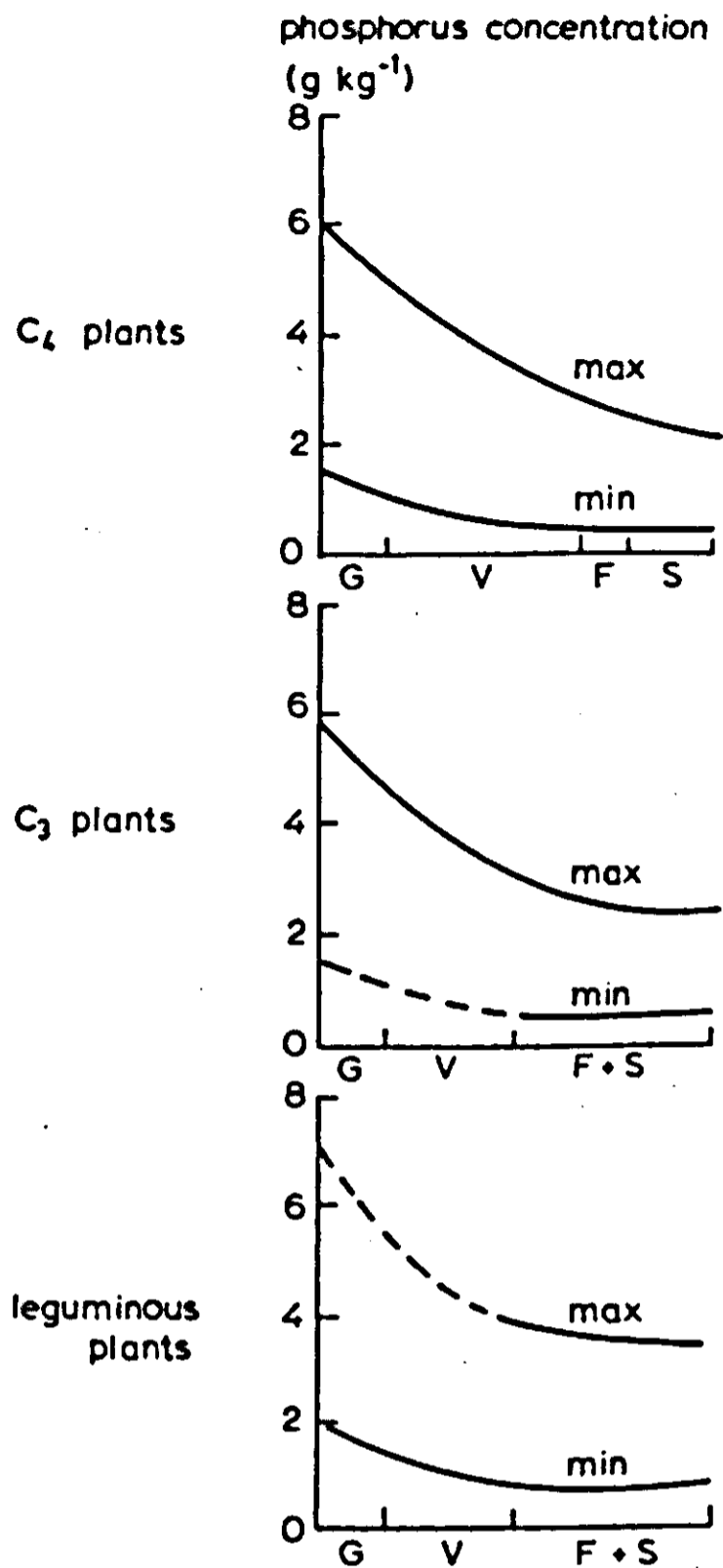C_4 plants

C_3 plants

leguminous plants

Figure 68. The course of the maximum and the minimum concentration of P in whole plants at different development stages: G stands for germination and early growth, V for vegetative phase, F for flowering and S for seed filling. Broken parts of the lines are based on a few observations only.

The implication of the coupling of N and P concentrations is that at a very low availability of N, P absorption is restricted, and that at a very low availability of P for growth N absorption, or N fixation in the case of legumes, may be restricted. In terms of a simulation model: availability of N and of P are not independent reduction factors between 0 and 1. Their ratio also needs to be considered. It is a question of how far the same ratio applies to all organs, and for the different functions. It is conceivable that N shortage has quite different effects on certain processes than P shortage has.