1.2 Systems analysis and models of crop growth

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1.2.1 Systems of plant production

A way to consider the real world is to divide it into systems. A functional description of a system is 'a part of reality with strongly interacting elements, but little influence on its environment'. Ideally, boundaries are chosen such that the environment influences processes within the system, but that the system itself does not modify its environment (see also Section 1.1). What part of the real • world is singled out as a system depends first of all upon objectives. A system. may be defined with a plant, a crop or a farm in its focus, and with current weather conditions, insect pests or farm product prices as the environment for growth and production. A definition of a system can sometimes be given in a straightforward manner. But there may also be complications: some elements of a system, not directly related to the goals of the analysis, may still deserve special attention in the delimitation of a system because they interact strongly with the main elements. This is reflected by the term 'whole system approach'. Upon defining a system, one should thus account for objectives and for such natural contours, and consider all essential parts that co-determine the content of a system. An example may illustrate this point. Plant production in fields with fertile and irrigated soils may be visualized as a system in which processes like CO_2 assimilation, growth, maintenance and development interact intensively. The rates of these physiological processes depend strongly on weather conditions, but weather is not modified noticeably by plant growth. One can thus delimit this plant production system by drawing a line between physiological and meteorological processes. But in a greenhouse, air humidity, temperature and ambient CO_2 concentration are modified by crop growth, and the 'weather' has become part of the system. The boundaries of a system can thus move with changes that seem unrelated to the objective of the study. For concepts on models and modelling of systems see Section 1.1.

An elegant and practical delimitation of systems of growing vegetations and

- of crops was proposed by de Wit (de Wit & Penning de Vries, 1982). His approach to growth and production emphasizes dry matter production, and not so much morphogenetic development. He distinguishes four levels of plant production. The systems of plant growth and crop production at each of these levels can be considered as belonging to one broad class. Those levels in an order of descending productivity are:
- Production level 1

Growth occurs in conditions with ample plant nutrients and soil water all the time. The growth rate of the vegetation is determined by weather conditions and

in terms of dry matter amounts to 150-350 kg ha⁻¹ d⁻¹ when the canopy covers the soil fully. The absorbed radiation is often the factor limiting the growth rate during the growing season, but low temperatures may restrict growth earlier on. In fact, this is quite a common situation in cool climates. Major elements in this class of systems are the dry weights of leaves, stems, reproductive of storage organs and of roots, and the surfaces of photosynthesizing tissues; major processes are CO_2 assimilation, maintenance and growth, assimilate distribution and leaf area development. A situation with plant growth at this production level can be created in field and laboratory experiments, while it is approached in practice, for example, in glasshouses and in the very intensive production of sugar-beet, potato and wheat on some Dutch farms.

- Production level 2

Growth is limited by water shortage at least part of the time, but when sufficient water is available the growth rate increases up to the maximum rate set by the weather. Such situations can be created experimentally by fertilization in temperate climates and in semi-arid zones; it is approached in practice, for example in non-irrigated, but intensively fertilized, fields, such as many Dutch pastures. The extra elements of this class of systems are the water balances of the plant and soil; crucial processes are transpiration and its coupling to CO_2 assimilation, and all other processes of loss or gain of water by the soil, such as evaporation, drainage and run-off. The heat balance of the canopy needs consideration in detailed analyses at this production level because of its relation to the water balance.

- Production level 3

Growth is limited by shortage of nitrogen (N) at least part of the time, and by water or weather conditions for the remainder of the growth period. This is quite a common situation in agricultural systems using little fertilizer, and is also normal in nature. Even with ample fertilization, N shortage commonly develops in crops at the end of the growing season. Important elements of this class of systems are the various forms of N in the soil and in the plant; important processes are the transformations of nitrogenous compounds in the soil in forms less or more available to plants, leaching, denitrification, N absorption by roots, the response of growth to N availability and redistribution of N within the plant from old organs to growing ones.

- Production level 4

Growth is limited by the low availability of phosphorus (P), or by that of other minerals, like potassium (K) at least part of the time, and by N, water or weather for the remainder of the growth period. Lack of P is particularly interesting because of its relation to the metabolism of N. Growth rates in terms of dry matter are typically only 10-50 kg ha⁻¹ d⁻¹ during a growing season of 100 days or less. This situation occurs often in heavily exploited areas where no fertilizer is used, such as in the poorest parts of the world. Important elements of this class of systems are the P or mineral contents of the soils and of the plants; important processes are their transformations into organic and inorganic forms

of different availabilities, absorption of minerals by roots and the response of plant growth to their absolute availabilities. For P, the availability relative to that of N is also important.

It is rare to find cases that fit exactly into one of those four production levels, but it is a very practical simplification of a study to reduce specific cases to one of them. It focusses the attention on the dynamics of the principal environmental factor and on the response of the plants to it. Other environmental factors can then be neglected, because they do not determine the growth rate. It is rather the other way round: it is the growth rate that sets the rate of absorption or efficiency of utilization of this non-limiting factor. If, for example, plant growth is limited by the availability of N, there is little use in studying CO_2 assimilation or transpiration to understand the current growth rate. All emphasis should then be on N availability, the N balance and the response of the plants to N.

This textbook is organized according to those four production levels: after a general introduction into systems and modelling of plant growth and crop production (Sections 1.1-1.4) and in modelling techniques essential in this field (Sections 2.1-2.3), the Sections 3.1 to 3.4 deal with growth and light and energy utilization at Production level 1, the Sections 4.1 to 4.3 deal with growth and water use at Production level 2, the Sections 5.1 to 5.3 deal with growth and N use at the Production level 3. Simulation of growth at the lowest level of production will not be treated in this book, primarily because this subject is not sufficiently advanced. The Section 6.1 deals with simulation of effects of diseases and pests on growth of crops at Production level 1.

1.2.2 Simple systems of crop growth

Let us take this analysis one step further. The remarks about the primary environmental factor can be used to formulate very simple systems and models of the four levels of plant production and describe their basic forms. In other parts of this textbook, these models will be expanded.

At Production level 1 the intensity of the irradiation, the degree of interception and utilization of light and the efficiency of use of energy in the plant are key factors for the understanding of the growth rate. Irradiation is a driving variable, and its intensity is obviously not modified by the crop. The efficiency of utilization of light by a crop is a characteristic of the plant species and the canopy density. The assimilated carbohydrates, stored only temporarily in an easily accessible form like starch ('reserves'), are utilized for maintenance or growth. In growth processes, reserves are converted into 'structural biomass' with a certain efficiency. Structural biomass, in contrast with reserves, consists of those components that are not mobilized again for growth or maintenance processes elsewhere in the plant. The essence of models at this production level is presented in Figure 2.

At Production level 2, the degree of exploitation of soil water and the effi-



Figure 2. A relational diagram of the essence of a system at Production level 1 when light is the limiting factor. The diagram is drawn according to Forrester (1961): rectangles represent quantities, valve symbols represent flows, circles auxiliary variables and underlined variables external variables; drawn lines represent flows of material, broken lines flows of information (see also Figure 9).

ciency of its utilization by the crop are key factors. Water shortage leads to stomatal closure, and to simultaneous reduction of CO_2 assimilation and transpiration. The rates of both processes are therefore closely linked, and the calculation of canopy transpiration is a direct route to crop CO_2 assimilation. The amount of water stored in the soil is a buffer between rainfall and the processes by which water is lost. This buffering capacity of the soil and the simultaneous loss of water by transpiration and by non-productive processes cause the growth rate to depend only indirectly on the driving variable: rainfall. The relation of plant growth to the driving variable of this system is thus principally different from that at Production level 1. A relational diagram of this system is given in Figure 3.

At Production level 3, the nature of the availability of N to the plants from the soil is not much different from that of water: a pool of inorganic N exists in the soil, and most of it is available to the roots that are sufficiently close. Growth of the soil microflora may compete with the plants for N in this pool and other processes may interfere as well. Mineralization of organic N adds to the pool of inorganic N. But contrary to water in the plant at Production level 2, the N in plants must be distinguished in two fractions: a mobilizable and an immobilizable one. The amount of N that remains mobilizable from old tissues for the development of new organs is often considerable. This 'internal reserve of N' makes current increase in plant dry matter largely independent of the current absorption of N. The reason is that the concentration of N in the tissues can



Figure 3. A relational diagram of the essence of a system at Production level 2 where water shortage is the main limiting factor. For use of symbols see Figures 2 and 9.

often drop to half or a quarter of its original value (due to decomposition of proteins and export of amino acids) before the tissue stops functioning. Figure 4 illustrates this situation. New tissues can thus grow at the expense of old tissues. Only after exhaustion of the internal N reserve is growth directly related to the rate of absorption of N. The mobilizable fraction consists largely of enzymes, but all enzymes cannot be considered reserves because cells cannot function without them. (The 'internal N reserve' resembles money in a bank, and the plant resembles a *rentier* who lives from the interest: photosynthates, other metabolic products and cellular activities. In bad times, part of the capital is consumed and the *rentier* has to live with less interest.) The immobilizable frac-



Figure 4. A relational diagram of the essence of a system at Production level 3 where nitrogen shortage is the main limiting factor. For use of symbols see Figures 2 and 9.

tion of the N in tissues is tied up in stable proteins that are not decomposed and that are possibly a part of the cellular structures. When the growth rate is primarily determined by the availability of N from soil and internal reserve, the rate of CO_2 assimilation is a consequence of the growth rate and should no longer be considered as a driving variable of the system.

Production at level 4 (this discussion is limited to the element P) differs from that of Production level 3 in that a much higher root density is required for a good exploitation of the soil for P than for inorganic N, and that the quantity of the dissolved P in the soil is so small that its rate of replenishment controls the supply to the plant directly. Both organic and inorganic forms of P in the soil may provide and capture dissolved P. The concentration of P in old tissue may undergo a reduction as for N, so that one can also speak of an internal reserve of P in plants. Figure 5 presents a diagram of this situation.

This analysis of plant production systems thus allows a considerable narrowing of the subject of study and hence a more rapid progress in research. Diseases, insect pests and also competition with weeds may occur at each of these production levels, and give them, in a sense, an extra dimension. The fact that actual situations are often more complex does not contradict the general usefulness of this scheme of four production levels as a basis for distinction between causes and consequences of plant growth.

The definition of systems at different levels of production is rooted in the analysis of agricultural crops. But as this delimitation is based on the effect of external factors on physiological processes, it is not restricted to agronomic situations and applies to plant growth and production in general. Moreover, cultivation of crops has changed little or none in the basic physiology of species, and similarities in physiological and biochemical functioning of different species are often remarkably large. An example of this are the similarities between modern forms of wheat and their ancestors (Khan & Tsunoda, 1970). This analysis is



Figure 5. A relational diagram of the essence of a system at Production level 4 where phosphorus shortage is the main limiting factor. For use of symbols see Figures 2 and 9.

therefore applicable to all situations of plant growth in agricultural and in 'natural' environments. But the homogeneity of agricultural crops as compared to natural vegetations gives the modeller of agricultural systems an important advantage over his colleagues in plant ecology.

1.2.3 From one production level to the next

If shortage of water, or N or P is sufficiently severe, it is usually fairly easy to recognize the main growth limiting factor. In other cases, however, this is not quite clear because growth occurs in an intermediate situation where two environmental factors are almost equally important. This poses the question of how plant production between the production levels distinguished in the beginning can be approached. Figure 6 is a diagramatic representation of the way how the four levels of production can be related to each other, in particular for crop growth in arid and semi-arid zones. It is highly simplified, and has in fact too few dimensions for a fully appropriate connection of the four production levels. This diagram is based on the idea of successively diminishing levels of growth.

The main process determined at the Production level 1 (Figure 6, Quadrant a) is the growth rate: the slope of the line relates time of growth to production. In the example given, a typical growth rate in terms of dry matter of 200 kg ha⁻¹ d^{-1} has been used; it corresponds roughly with a rate of CO₂ assimilation of 500 kg ha⁻¹ d^{-1} . Irradiation is the single most important factor that determines this slope. The longer the growth period, the higher the final yield. The early exponential phase of growth has been included in the diagram to emphasize that the crop growth rate is only about 200 kg ha⁻¹ d^{-1} when it covers the soil fully. In early phases, growth is more or less exponential. The duration of this exponential phase depends on weather and seed density in particular, and is not further discussed here. In this example it is assumed that the biomass of the crop in terms of dry matter is 1000 kg ha⁻¹ at the end of a 15 day exponential growth phase.

Going to the situation that applies to Production level 2, it is the availability of water that determines in particular the duration of the growth period, as indicated in the same quadrant. This is particularly true for dry zones where the growing season is short (see Section 4.2). At a certain regime of precipitation, the period of growth at a constant rate may be 45 days, the example chosen in Figure 6, so that a biomass of 10 000 kg ha⁻¹ is attained at the end of the growing season. The more water available, the longer the growing season and the higher the production. Biomass, formed in presence of sufficient plant nutrients, has an N content of about 2% of the dry matter in mature tissue in C₄ type crops. This corresponds to a seasonal N uptake by the crop of 200 kg ha⁻¹. If less N has been available for the crop, as is the case at Production level 3, the final yield falls below the 10 000 kg ha⁻¹ level. The N concentration decreases initially faster than the biomass production (leaving it with a lower N concentration). At very



Figure 6. A diagram to show how crop production may be considered when moving from one production level to the next. Line ① refers to growth at Production level 1: the growth rate of an established crop is constant, assuming stable weather conditions. A restriction of the growing season to 60 d is a simple illustration of the effect of shortage of water (Production level 2, broken lines ②). The solid line ③ relates final yield to nitrogen absorbed (Production level 3): its maximum is that of Production level 2. The broken lines ③ illustrate the case that a nitrogen uptake of 120 kg ha⁻¹ corresponds with a biomass yield of 8 600 kg ha⁻¹. At Production level 4, the small absorption of phosphorus restrains absorption of nitrogen, and hence productivity. The broken lines ④ show that with 1.6 kg ha⁻¹ of phosphorus absorbed, no more than 40 kg ha⁻¹ of nitrogen can be contained in plants so that biomass production is limited to 4 800 kg ha⁻¹.

low levels of availability of N is the amount of biomass almost proportional with the amount of N that it contains. The slope of the curved line in the origin is 0.5% for C₄ type crops, as in the example of Figure 6. This subject is discussed further in Section 5.1. The Quadrant b shows this curvilinear relationship between biomass and N absorbed up to the level dictated by water availability. This curve could thus represent the final yields of a series of fertilization experiments in a particular growing season. In Quadrant b is shown with a broken arrow line how much biomass will be formed when only 120 kg ha⁻¹ of N can be absorbed. Compared with P, N is often more readily available to the plant early in the growing season. Since plants cannot contain an amount of N that exceeds 25 times its P content (Section 5.1), N uptake can be limited by the P uptake in young plants. Later on, the N content in such plants is diluted by growth to its

minimum value, whereas the P uptake continues. This is the reason that P shortage often ultimately expresses itself as N shortage (de Wit & Krul, 1982). In Figure 6, Quadrant c, this is shown for the situation where only 1.6 kg ha⁻¹ of P could be absorbed during the period that N was available, reducing the N absorption to 40 kg ha⁻¹, and hence the biomass produced to just below 5000 kg ha⁻¹ (in this particular example for a 60-day growing season).

Less common is straight P shortage with sufficient N all the time. In such cases the response curve of biomass formed to P absorbed is similar in form to the response curve of yield to N absorbed with sufficient P. The slope of the curve in the origin is about 0.05% P on a dry weight basis for C_4 type crops.

As far as the relation between N absorbed and N supplied is concerned: this is approximately proportionally to the gift above a minimal value supplied by the soil without any fertilization. A maximum of uptake, corresponding to the maximum biomass with the highest N concentration, is not exceeded. This is further discussed in Section 5.1.

1.2.4 Analysis of more complex situations

One environmental factor may affect another environmental factor, which then affects plant growth indirectly. In this way a basically non-limiting factor may influence the availability of a limiting factor. Soil water, for example, is not of direct importance to plant growth at Production level 3, but if it runs low it may reduce the availability of N and P. Such interactions may be intricate, but as they are not principally different from the limiting factor approach, they may be unravelled by straightforward analysis. However, our knowledge of interactions between factors is still limited, and its modelling is not yet far advanced.

In more detailed studies, the complex situation earns consideration in which different growth limitations occur successively, or even intertwine, during the growing season. The factor that limits growth in the beginning of the season may improve relative to other factors, and can consequently be replaced by another as the limiting factor. In a typical situation of plant growth in temperate regions the growth-weather relation is of major importance in the beginning of the growing season, and nutrient shortages may reduce crop growth at a later stage. But at any time, a brief dry spell may cause a water shortage and reduce growth. A nice illustration of quite a different situation is described for the Sahel (Penning de Vries & van Keulen, 1982), where it is not uncommon that the initial growth of grass seedlings is restricted by a scarcity of water. A very low P status of the soil reduces the growth in a next phase. But because of an expanding root system, continuous uptake of P, and a diminishing demand for it, P does not remain the limiting factor: the plants are finally limited in their growth by the very small quantity of N that they have been able to absorb from the soil. Many of the annual grasses in the Sahel flower under photoperiodic control and ripen a few weeks later; an internal mechanism that overrides all environmental



Figure 7. The effect of the relative availability of the four principle external factors - irradiation, water, N and P - on plant growth in the Sahel. The shaded area represents the zone of actual growth, the non-shaded area below the upper line represents the potential growth. Water poses a maximum to the growth rate after germination, the low availability of P for some time afterwards, while the availability of N limits growth at the end of the season. Annual grasses often mature photoperiodically before the soil dries out, as is shown here. The example is imaginary, but based on field observations.

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factors. Figure 7 presents this sequence schematically. Thus this approach basically follows Liebig's law of the minimum to describe the effect of limiting factors on growth.

If one is interested in day-to-day growth, one has to follow each environmental factor on a day-to-day basis and the plant response on a day-to-day basis. But if productivity at the end of the season is the principal point of the exercise, one could ask the question: is it not sufficient to study the availability of the factor that limits growth last? For absorption of light and for P absorption this is quite clearly not so: they are absorbed from a source that provides them at an almost constant rate (per ha and per cm of root, respectively), and loss of time for absorption cannot be compensated for. But also at the levels 2 and 3, with stocks of water and N in the soil, the answer is still negative, because other processes are competing with the plant for them, and these are more successful when plant growth is more restrained. For example, transpiration 'competes' with evaporation, and if transpiration is suppressed by N shortage, water will be lost from the soil anyway and does not remain for 'better times'; absorption of N by roots 'competes' with immobilization, leaching and denitrification, so that the N not absorbed rapidly by roots may be lost in other ways. As a result, in a more detailed study one should not only look to the factor that limits growth at the end of the growing season, but follow the dynamics of each of the factors water, N and P and determine which of them at any moment

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is the crucial one to limit growth. Plant production can then be seen as one large system in which the processes occurring at two or even three of the four plant production levels are combined, and in which their relative importance changes. The four production levels distinguished are only focal points of a large continuous system. For production and growth models, it is practical to consider the structure of a system to be invariable during the time-span of interest, and to consider the parts of the model that are temporarily unimportant as harmless ballast. However one might also argue that the structure of the system changes in such a case, and that one ought to change during the simulation run, e.g. from a model structured like the one of Figure 3 into one in Figure 4. That conception may become effective in stages of model development still to come.

Another problem in considering plant growth systems in detail is that the efficiency of use of one factor can be modified by a previous shortage of another factor. For example, in conditions of bright weather and optimal water and nutrient supply, a maize crop had a very high rate of CO_2 assimilation of about 850 kg ha⁻¹ d⁻¹ (Penning de Vries, 1982a). A very high transpiration rate, exceeding 10 or even 15 mm d^{-1} was coupled to this. When stomatal control of transpiration by photosynthesis is effective (see Section 3.2), probably induced by a brief water stress, the effectivity of water use is increased (the transpiration rate is reduced to about half of the previous values), but this is coupled to an increase in stomatal resistance. This higher resistance sets a lower maximum rate of CO₂ assimilation of about 650 kg ha⁻¹ d⁻¹, and this lower rate is maintained after relief of the stress. Although details of this switch are not yet known, this example makes it clear how strong the effect of previous stress can be. Another example of an after effect is the change in leaf morphology as an adaptation to drought that can modify CO_2 assimilation characteristics. If the induction period for such a change is short, it may well escape the modeller's notice if he uses a coarse simulation model. This is another reason for using a detailed, hour-tohour simulation, and to discourage the too quick and easy use of daily or even weekly averages of environmental factors to simulate plant growth.