5.4 Plant data

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In the foregoing chapters it was shown that a quantitative assessment of plant growth and crop productivity can be obtained in different production situations, on the basis of knowledge about basic properties of plants and soils. In this section some of the required plant data will be summarized, methods to obtain them outlined and indicative values provided for first estimates.

5.4.1 Photosynthetic capacity

As outlined in Section 2.1, gross CO_2 assimilation of a canopy, F_{gc}, may be calculated from the leaf area index and measured or estimated values for F_g, the diffusion – limited maximum gross assimilation rate of a single leaf at high light intensity. The latter characteristic may be experimentally determined by measuring the CO_2 absorption by a leaf of known surface area at high light intensities. This is most conveniently done by enclosing the leaf in a chamber through which air is passed at a known flow rate. The concentration of CO_2 is measured at the entrance to the chamber and at the outlet, so that the amount of CO_2 absorbed can be calculated. As assimilation and respiration proceed concurrently, the measured value represents the net assimilation rate, that is the difference between assimilation and respiration. Thus to obtain F_g, as used by Goudriaan & van Laar (1978a), the measured value must be augmented by the value of the dark respiration (Subsection 5.4.2) implicitly assuming that it proceeds at the same rate in the light. Such experiments are normally carried out under controlled conditions, with the disadvantage that it is often difficult to obtain sufficiently high light intensities from artificial light sources to reach light saturation, especially for plants of the C_4 type. Although the value of F_g varies with such characteristics as age of the leaf, its nitrogen content and its position in the canopy (especially its position with respect to the sun), characteristic values of maximum CO_2 assimilation range from $15-50$ kg ha^{-1} h^{-1} for plants of the C_3 type and $30-90$ kg ha^{-1} h^{-1} for C_4 species. If the value of F_g is unknown for a species, 40 kg ha^{-1} h^{-1} for a C_3 species and 70 kg ha^{-1} h^{-1} for a C_4 species is generally a reasonable guess.

Lists of C_4 species have been published by Downton (1975) and Raghavendra & Das (1978). Whether a species has the C_3 or the C_4 type photosynthetic pathway can be deduced from anatomical features. In C_4 type plants, mesophyll cells are arranged radially around chlorenchymatic bundle sheaths, whereas in C_3 type plants mesophyll cells are laminar. These differences are clearly

visible under a microscope.

An alternative method is based on the fact that the CO_2 compensation point, that is the value of the CO_2 concentration in the outside air, where net CO_2 assimilation becomes zero, is about 10 ppmv for C_4 species and 120 ppmv for C_3 species. When an unknown species is grown in an airtight environment in the presence of a C_4 species, it will cease functioning long before the C_4 species if it happens to belong to the C_3 group. It will hold out approximately equally long if it is a C_4 species. In the closed system, the photosynthetic process will lead to gradually declining concentrations of CO_2. When these have fallen below 120 ppmv, respiration of the C_3 species exceeds assimilation, whereas the C_4 species continue to assimilate at a positive rate untill about 10 ppmv.

5.4.2 Respiratory losses

Measurement of respiration is in principle identical to that of assimilation, i.e. the CO_2 exchange rate is determined in the absence of an energy source ('dark respiration'). When plants that have been in the light for some time are transferred to the dark and CO_2 exchange is measured, the general picture is that at first the rate of CO_2 evolution is high but gradually declines with time and finally reaches a more or less stable value. In analyzing such data it is often assumed that the stable value represents maintenance respiration, and that the additional component in the beginning results from the conversion of assimilates in structural plant material, i.e. growth respiration.

The magnitude of the respiration losses depends primarily on the chemical composition of the structural material of the plant (Section 2.1). Both maintenance respiration and growth respiration are higher, when the protein (nitrogen) concentration of the material is higher.

Values of the maintenance requirements may be estimated from the protein concentration and the ash concentration of the material, by assuming that at 20 °C the proteins require about 0.035 kg CH_2O per kg per day for maintenance and the minerals about 0.07. In a situation where each of these two components makes up about one tenth of the total weight of the standing crop, the maintenance requirement will thus be 0.0105 kg CH_20 per kg dry weight per day.

Exercise 75

Calculate the carbohydrate requirement for maintenance respiration in kg $ha^{-1}\,d^{-1}$, for a crop with a dry weight of 10 000 kg ha^{-1}, a nitrogen concentration of 0.025 kg kg^{-1} and an ash concentration of 0.01 kg kg^{-1} (N.B. the nitrogen concentration of proteins is 0.16 kg kg^{-1}).

In most cases, however, such detailed analyses cannot be performed, because insufficient data are available. Moreover, in the hierarchical approach presented here, the nitrogen concentration of the material is not known when the respiratory losses have to be calculated (Sections 2.3 and 3.4). In that situation approximate values may be applied, as illustrated in Table 3.

The effect of growth respiration may be expressed by the conversion efficiency, explained in Section 2.1. Thus, if the conversion efficiency is 0.7, growth respiration amounts to a fraction 0.3 of the weight of the primary photosynthates. Thus again, high proportions of proteins, but also fats, lead to high losses in growth respiration.

Exercise 76

Calculate the rate of increase in dry matter in kg ha^{-1} d^{-1} for a crop which, after maintenance, has a carbohydrate surplus of 400 kg ha^{-1} d^{-1}:

- if cassava tubers are filled (composition: proteins 0.075 kg kg^{-1}; starch 0.925 kg kg^{-1})
- if maize grains are filled (composition: proteins 0.125 kg kg^{-1}; starch 0.875 kg kg^{-1})
- if soybean seeds are filled (composition: proteins 0.4 kg kg^{-1}; starch 0.4 kg kg^{-1}, lipids 0.2 kg kg^{-1})

What are the carbohydrate losses due to growth respiration in these cases?

If no exact data are available for specific situations, the conversion efficiencies as tabulated in Table 3 may be applied for the various groups of crops. Chemical composition of storage organs of various crops are given by Sinclair & de Wit (1975) and Penning de Vries et al. (1983).

5.4.3 Phenology

One of the most important crop characteristics that has to be taken into account in establishing production potentials is phenological development (Section 2.2). It has been explained that various methods exist to describe phenological development as a function of temperature and day length. The most simple method, which, however, yields good results in many cases is referred to as the Thermal Unit approach. In that approach it is assumed that for each phenological period, the rate of development can be described as a linear function of temperature. The rate of development during such a period is then defined as the inverse of the duration of that period, thus:

$$R_v = 1/N_d = b_t(T_a - T_o) \qquad (94)$$

where

R_v is rate of development (d^{-1})
N_d is length of a phenological period (d)
b_t is a constant ($d^{-1}\,°C^{-1}$)
T_a is average daily air temperature (°C)
T_o is apparent threshold temperature or base temperature (°C), below which phenological development comes to a standstill

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Exercise 77
Calculate the rate of development for the wheat crop of the following example. N_{hm} denotes the number of days from heading to maturity.

Location	T_a	N_{hm}
Harrow	21.1	31
Ottawa	20.6	29
Normandin	15.0	54
Swift Current	19.1	41
Lacomoe	14.7	59
Beaverlodge	13.9	54
Fort Vermilion	15.3	48
Fort Simpson	16.4	38

Make a graph of the results, temperature on the horizontal axis and development rate on the vertical. Draw an eye–fitted straight line and estimate the values of T_o and b_t. How many days will it take this wheat variety from heading to maturity at an average air temperature of 12.5 °C?

Application of the Thermal Unit concept leads to the notion that a constant temperature sum, counted above the base temperature, has to be accumulated during a certain phenological period. That period can be between any two phenological events that are important from the point of view of production. For modelling purposes, in general two phases are distinguished, one before the moment that growth of the storage organs starts, one after that. In cereals that is the moment of anthesis, in root and tuber crops it is the moment of the start of bulking. For both periods a scale from 0 to 1 is then assigned. In most cases it is convenient to start the pre–storage organ phase from emergence, because the temperature relations for germination may be quite different.

In practice, the relation between temperature and development rate can be determined experimentally by observing the dates of emergence and that of the start of the storage organ growth and measuring the ambient temperatures

during that period. If only data for one year are available, base temperatures as given in Table 7 (Section 2.2) may be used to construct the linear relation. For a more accurate description, it will be necessary, as a rule, to perform at least two experiments under different temperature conditions to be able to derive the base temperature. Such experiments can easily be carried out under controlled conditions, i.e. in climate rooms or greenhouses. For the period after the start of storage organ growth, experimental determination may be more difficult, because the moment of maturity is often not clearly recognizable. For different crops, different criteria have been specified (for maize for instance formation of the black layer at the base of the kernel). On the basis of these criteria, the maturity point may then be estimated and an identical procedure applied. As a rule, the slope of the development rate – temperature relation is different for the period before the storage organ starts growing and the period thereafter.

Exercise 78

Calculate the rate of development for the period emergence to anthesis for two spring wheat cultivars. T_a is average air temperature in °C; N_{ac} is duration of the period in days.

cv. Timgalen		cv. Orca	
T_a	N_{ac}	T_a	N_{ac}
12.5	93	11.6	95
14.1	72	13.2	78
17.0	61	17.0	69

Do the same for the period of anthesis to maturity.

cv. Timgalen		cv. Orca	
T_a	N_{am}	T_a	N_{am}
19.5	49	17.6	43
20.5	48	17.6	40
22.1	41	16.9	39

Plot the calculated data as in Exercise 77 for the two different periods in two separate graphs. Draw eye – fitted curves. What do you notice about the slope of the two lines?

For modelling purposes the relation between temperature and development rate will thus have to be established for at least each group of cultivars (short duration vs. long duration) within a species.

5.4.4 Dry matter distribution

The distribution of the dry matter formed between the various plant organs is a major determinant for both total dry matter production and economic yield. If in the early stages of crop development a large proportion of the dry matter formed is invested in the root system, leaf area development is relatively slow, hence light interception will be incomplete for a long period of time and total production will remain low. In the same way, economic yield may be affected if during the period of storage–organ growth other organs of the plant still claim a substantial proportion of the available assimilates or if the green area rapidly declines because of translocation of essential elements to the developing storage organs, as may be the case under nitrogen shortage.

Since the basic processes governing dry matter partitioning are poorly understood, the subject is treated in an empirical way. The simplest method of analyzing distribution patterns would be to describe the increase in dry weight of the various plant organs in relation to the total increase in dry weight of the plant, i.e. to its age. However, as indicated in Section 2.2, the initiation and development of plant organs is governed by phenological development of the plant, which is a function of environmental conditions, such as temperature and day length, rather than of age. The partitioning pattern in plants is therefore related to the phenological stage of the crop. This starting point severely limits the availability of suitable experimental data for the determination of partitioning patterns, because the number of reports in which not only sufficiently detailed crop data are reported, but also environmental conditions, is very low.

If, however, all of these data are available, an analysis may be carried out, yielding information that can be used for extrapolation and prediction. This is illustrated with an experiment on bunded rice, reported by Erdman (1972). The basic data of the experiment are given in Table 57. These data are used to calculate the derived data as given in Table 58: for each harvest date the development stage of the vegetation is determined as the ratio between accumulated temperature sum and the temperature sum required from transplanting to anthesis (1950 d °C for this variety). As the distribution factors are calculated for periods between two consecutive harvests, the value of the development stage halfway between these two dates is entered in Table 58. For each period, the increase in dry weight of the various plant organs is calculated as the difference between the weight at two consecutive harvests. From these partial values, increase in total dry weight is obtained and from these numbers the fraction allocated to each of the organs in each period is calculated.

Table 57. Basic data on dry matter distribution from a field experiment with bunded rice.

Time (days after transplanting)	T_a (°C)	dry weight of plant organs (g plant $^{-1}$) roots	leaf blades	stems sheaths + ear structures	total
	26.0				
11		0.15	0.26	0.24	0.65
	26.3				
18		0.26	0.94	0.84	2.07
	26.3				
25		0.34	2.19	2.23	4.76
	26.3				
32		0.81	3.98	4.48	9.27
	26.3				
39		1.93	6.06	9.37	17.36
	26.2				
46		2.81	7.82	12.76	23.39
	26.2				
53		2.99	9.76	21.46	34.21
	26.2				
60		3.17	10.77	26.83	40.77
	26.2				
67		3.36	11.85	21.48	36.69
	26.3				
74		3.37	9.11	21.94	34.42
	26.3				
81					
	26.3				
88					

The accuracy of the individual observations is not high. Even with a reasonable number of replicates, the variance in dry matter yield is high, so the increase in dry matter of individual organs is even less accurate. In general, therefore, observations of several experiments have to be combined to obtain a useful relation. In Figure 54, the data of Table 58 are summarized by eye–fitted curves, illustrating the variability in the data. However, for the time being it is necessary to rely on this type of analyses.

After anthesis, only the grains increase in dry weight, the other organs either remaining constant or decreasing in weight, when translocation of substances, nitrogenous compounds as well as carbohydrates, to the developing grain takes place.

As explained in Section 3.4, this translocation process is taken into account in the calculations by assuming partitioning of part of the assimilates to the

Table 58. Derived data on dry matter distribution from a field experiment with bunded rice.

Period (days after transplanting)	R_d	Increase in dry weight					
		leaf blades		'stems'		roots	
		g plant^{-1}	fraction	g plant^{-1}	fraction	g plant^{-1}	fraction
0-11	0.075	0.26	0.40	0.24	0.37	0.15	0.23
11-18	0.195	0.68	0.48	0.60	0.42	0.14	0.10
18-25	0.29	1.25	0.46	1.39	0.52	0.05	0.02
25-32	0.385	1.79	0.40	2.25	0.50	0.47	0.10
32-39	0.475	2.08	0.26	4.89	0.60	1.12	0.14
39-46	0.57	1.76	0.29	3.39	0.56	0.88	0.15
46-53	0.665	1.94	0.18	8.70	0.80	0.18	0.02
53-60	0.76	0.99	0.15	5.37	0.82	0.18	0.03
60-67	0.855	1.08	n.a.**	negative	n.a.	0.18	
67-74*	0.955	negative	n.a.	negative	n.a.	0.01	

* Anthesis at Day 74
** Not applicable

grain before anthesis.

The grain weight calculated with the model is on a dry weight basis. For comparison with field data, the air dry moisture content of the grains has to be taken into account. Normally grain yields are reported at 12–14% mois-

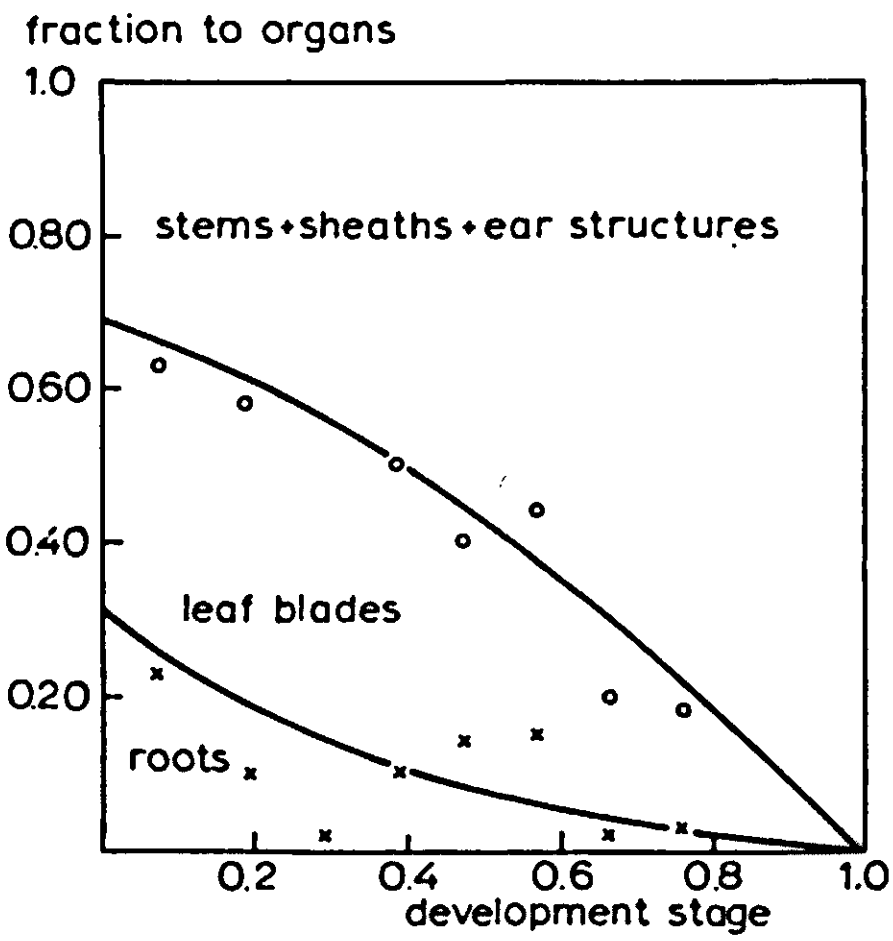

Figure 54. Partitioning pattern of total dry matter increase between various organs of bunded rice, as a function of development stage.

ture content, hence the calculated dry matter must be multiplied by a factor of 1.13. For crops other than grain crops special moisture contents may have to be taken into account. This emphasizes, however, that for experimental work too an accurate definition of the reported data is necessary.

For rice the situation is somewhat more complex: in most cases yield is expressed in rough rice (paddy) at a moisture content of 14%. Rough rice, however, consists of the true fruit (brown rice) and the hull, which consists of leaf–like structures. Brown rice is largely the endosperm and the embryo, but still contains several thin layers of botanically different tissues that are removed during milling, after which white rice, milled rice or polished rice is obtained. In the model, brown rice is the result of the calculations. To convert from white rice to brown rice a conversion factor of 1.25 is generally used, from brown rice to paddy a factor of 1.2.

If the growing conditions are suboptimal, i.e. when shortage of water or nutrients occurs, the plant will generally respond with a change in its distribution pattern. In both cases, the most common response is an increased investment in the root system, because that part of the plant is responsible for its supply with water and nutrients. This phenomenon is often referred to as the functional balance (Brouwer, 1963). A quantitative treatment of this phenomenon is difficult within the scope of the present approach, moreover the data base is narrow.

5.4.5 Stomatal behaviour

Stomatal aperture in plants can change in response to internal or external conditions, so that plants can react to the environment. One such reaction is that of closure of the stomata under conditions of water stress, which effectively reduces transpiration. However, even under optimum moisture supply, stomatal opening may vary. One mechanism governing stomatal aperture is the response to light, i.e. stomata open in the light and close in the dark, the transition zone being rather narrow. However, in certain plants, stomatal aperture is regulated in such a way, that the concentration of CO_2 inside the stomatal cavity is maintained within narrow limits. This may either be a constant value, which is around 120 ppmv for plants with the C_4 type of photosynthesis and around 210 ppmv for plants with the C_3 type. An alternative is that the internal concentration is adjusted in such a way that a constant ratio of about 0.7 for C_3 species and about 0.4 for C_4 species between external and internal CO_2 concentration is maintained (Goudriaan & van Laar, 1978b). Under present conditions there is hardly any difference between the two mechanisms in the field, because at an external value of 340 ppmv about the same internal values result for both situations.

The type of stomatal control is of prime influence on water use efficiency (Section 3.2). The ratio of the amount of CO_2 fixed to the amount of water lost is about twice as high for plants with CO_2 induced stomatal regulation as

for plants without that mechanism. It is therefore important to know what type of regulation operates in a given crop. Unfortunately, that is difficult to predict, because not only differences exist between different species, but apparently the same species may react in different ways, depending on external or internal conditions. The only way to determine experimentally the type of regulating mechanism is by measuring concurrently CO_2 assimilation and transpiration at a range of external CO_2 concentrations. Such data permit the construction of the type of graphs, schematically presented in Figure 55. Increased CO_2 concentrations in the external air lead to stomatal closure in regulating plants, hence decreased transpiration and a constant assimilation. In non-regulating plants assimilation increases, but transpiration is hardly

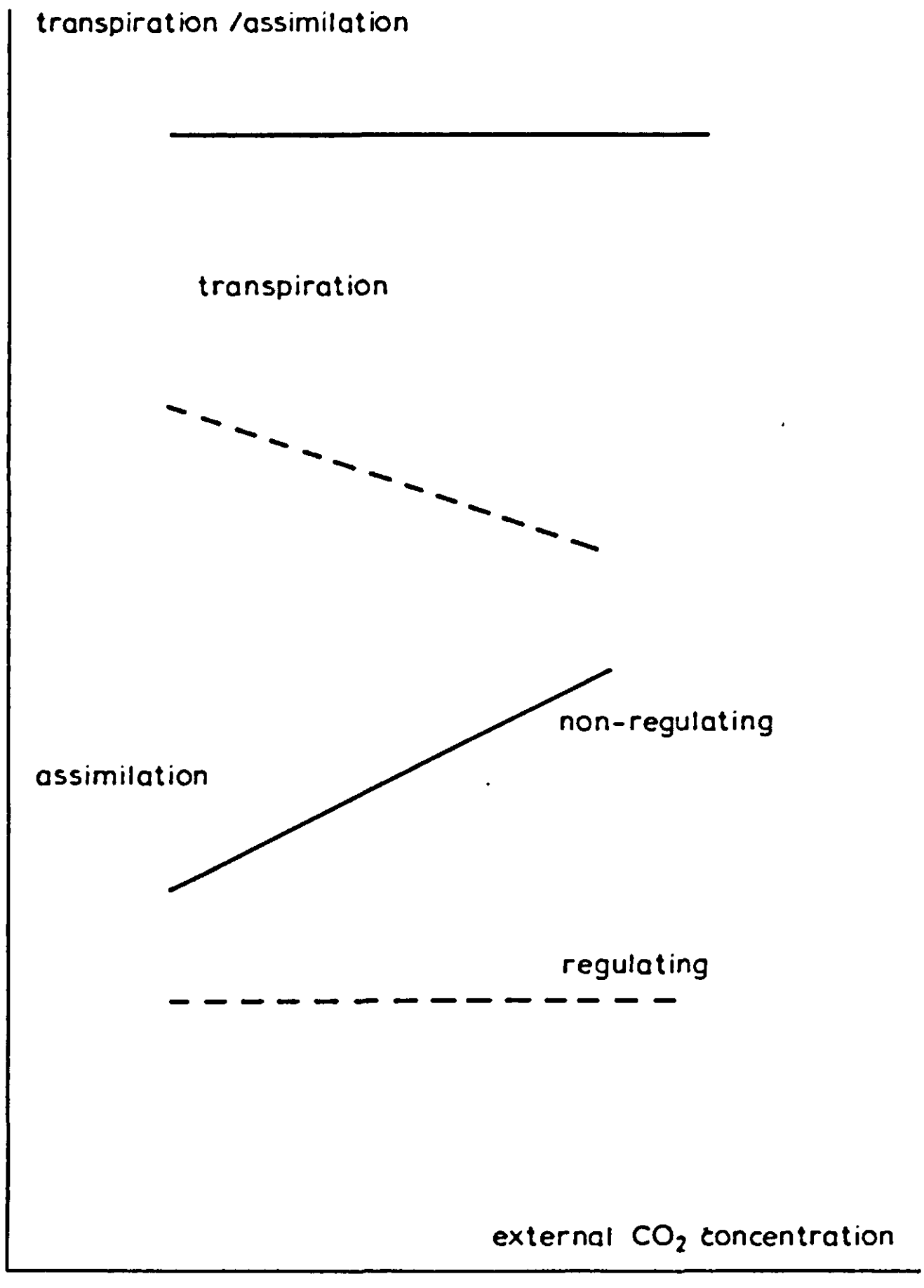

Figure 55. Schematic representation of transpiration and assimilation as a function of external CO_2 concentration for plants with and without CO_2 induced stomatal regulation.

affected as the stomata remain open. The most common type seems to be that in which a constant ratio between external and internal concentration is maintained. The absence of CO_2 induced regulation is most likely associated with maintenance of optimum moisture supply throughout the plant's life cycle. In situations where no information on stomatal behaviour is available, assumption of the constant ratio is most realistic.

5.4.6 Nutrient requirements

In Section 4.1 it was shown for maize and rice that under conditions where yield is determined by availability of a specific nutrient element, the concentration of that element at a given development stage of the crop reaches a species–characteristic minimum value. The determination of total nutrient requirements as proposed in this approach, require the minimum element concentrations at maturity. Such data can be determined for specific crops in pot experiments, because these values are independent of the growing conditions. As a first approximation, values have been collected from the literature pertaining to groups of crops. The determinant factor for each group is the chemical composition of the material formed. The data used in the model structure are summarized in Table 59.

5.4.7 Some additional data

For initialization of the calculations for Production Situation 1 or 2 (Sections 2.3 and 3.4), the values of above–ground dry weight and root dry weight are necessary. It is possible to determine these values experimentally for a specific trial. However a more general approach is to look at the conversion of the substrate contained in the seed into structural plant material. Experiments with a number of species have shown that about half of that energy is lost in respiration, whereas the remainder is equally divided between shoot and root (Penning de Vries et al., 1979). Thus both root and shoot dry weight at emergence may be estimated as about one fourth of the seed rate,

Table 59. Minimum concentrations (kg kg^{-1}) of the macro-elements in economic products and crop residues for a number of crop groups

Crop group	Economic product			Crop residues		
	N	P	K	N	P	K
grains	0.01	0.0011	0.003	0.004	0.0005	0.008
oil seeds	0.0155	0.0045	0.0055	0.0034	0.0007	0.008
root corps	0.008	0.0013	0.012	0.012	0.0011	0.0033
tuber crops	0.0045	0.0005	0.005	0.015	0.0019	0.005

Table 60. Indicative specific leaf area of major crops ($m^2\ kg^{-1}$).

	Crop Specific leaf area (S.L.A.)
Barley	25
Cassava	22
Chick pea	13
Chillie	27
Cotton	20
Cow pea	25
Grass pea	13
Groundnut	28
Jute, capsularis	31
Jute, olitorius	28
Kenaf	25
Lentil	33
Maize	18
Mungbean	30
Mustard (black)	23
Onion	25
Rapeseed	23
Rice	25
Sesame	23
Sorghum	20
Soybean	26
Sugarcane	10
Sweet potato	22
Tobacco	16
Wheat	20

provided that germination is almost complete.

The development of leaf area, important for interception of irradiance, depends on the one hand on the amount of dry matter invested in the leaf blades (Subsection 5.4.4), and on the other hand on the area that each unit of leaf blade dry matter produces. In Sections 2.3 and 3.4 this parameter was introduced as the specific leaf area. It follows directly from simultaneous measurement of dry weight and area of the leaf blades. Special leaf area meters are available that electronically scan the areas of the leaves. A widely used method that requires no sophisticated equipment is to measure leaf width and leaf length and establish a relation between the product of the two and actual leaf area, depending on leaf shape. For situations where experimental data on specific leaf area are not available, indicative values for different crops have been summarized in Table 60.

In general, it may be concluded that for the type of calculations at which the present approach is aiming, and their degree of accuracy, the available plant

data are of sufficient quality. It means that these estimations can be made without having to go into detailed plant physiological research.