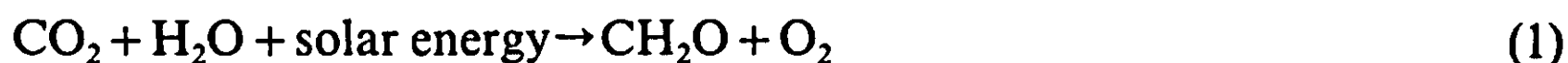


2.1 Physiological principles

H.D.J. van Heemst

In agriculture, solar energy is conserved for future use via its fixation in biomass by the process of photosynthesis. In this process CO_2 from the air is converted into carbohydrates $(\text{CH}_2\text{O})_n$ according to the overall reaction:



This process is also called CO_2 assimilation. Part of the carbohydrates produced is used as building material for structural plant dry matter, as cellulose, proteins, lignin and fats and part is used as a source of energy for plant processes. The release of energy from carbohydrates produced during the assimilation process is described by the equation:



This process is called respiration. About 40% of the weight of the carbohydrates formed during the assimilation process is lost by respiration. Subtraction of the rate of respiration from the assimilation rate gives the rate of increase in plant dry weight, i.e. the growth rate. In Figure 4, the time course of growth rate and total dry matter accumulation is in a schematic way presented for a summer wheat crop. The growth rates are obtained from the dry matter accumulation curve by determining at each point the slope of the curve.

With respect to the growth rate three phases may be distinguished: (i) during the first phase, the crop consists of individual plants that do not shade each other and the growth rate increases; (ii) in the second phase the crop covers the soil completely and the growth rate is constant; (iii) in the third phase the crop is maturing and the growth rate is decreasing..

In the first phase the major part of the assimilates is invested in leaf growth. This increase in leaf area is accompanied by a proportional increase in energy interception, because neighbouring plants are so small that mutual shading hardly plays a role. Individual plant weight increases by a constant proportion per day, thus leading to exponential growth. After a closed crop surface has been formed, more leaf growth does not lead to more light interception, hence the growth rate remains constant and total plant weight increases linearly. In the last phase leaf senescence leads to a decrease in the growth rate.

The major part of the total dry matter accumulation is achieved during the second phase. Total dry matter production of the crop is thus largely determined by the magnitude of the growth rate during the linear phase and the duration of that phase.

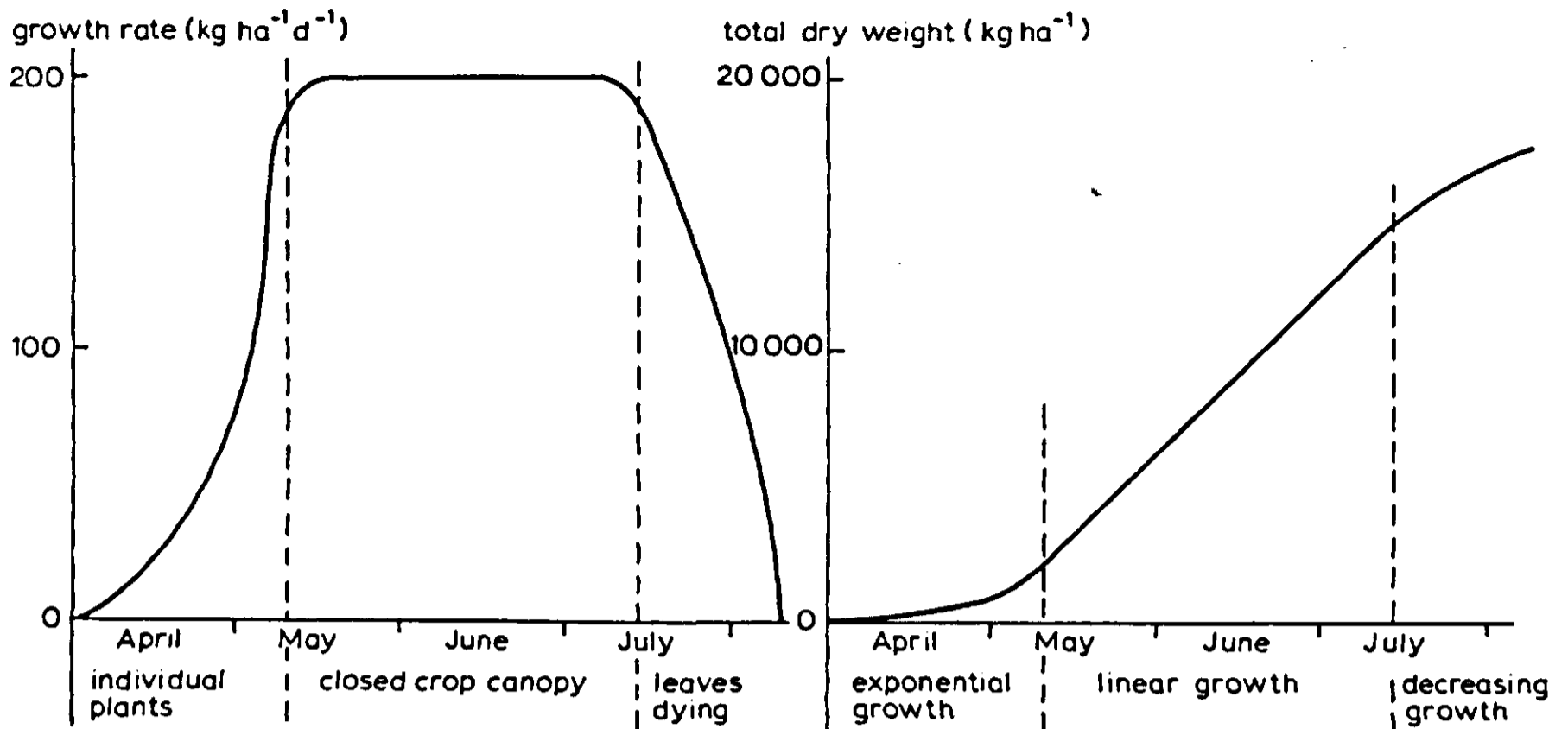


Figure 4. Schematized course of growth rate and total dry weight of summer wheat in time.

The duration of the period of linear growth is species and cultivar specific and, moreover, is influenced by environmental conditions (Section 2.2). The actual growth rate is predominantly influenced by environmental conditions, such as solar radiation and temperature, the supply of nutrients and water, and the occurrence of weeds, pests and diseases.

With an optimal supply of water and nutrients and in the absence of weeds, pests and diseases, the growth rate is determined by solar radiation and temperature and is referred to as the potential growth rate. Such conditions are supposed to prevail when discussing the basic processes of plant growth. A simple model for the calculation of potential dry matter production will be presented that may be applied to various crops at different locations.

2.1.1 *CO₂ assimilation of a single leaf*

In the leaves of a plant the photosynthetically active radiation is absorbed by green chlorophyll and other pigments and is used for the reduction of CO₂. Not all radiation of the sun is photosynthetically active, but only the visible radiation in the wavelength range from 400 to 700 nm, which represents about 50% of the total global radiation (Figure 5).

The rate of CO₂ assimilation of a leaf can be measured by enclosing a leaf in a so called leaf – chamber and analysing the CO₂ concentration of the incoming and the outgoing air, that passes the leaf at a known flow rate. When the assimilation rate is determined at various radiation intensities, a light response curve can be constructed as illustrated in Figure 6 for leaves of plant species referred to as C₃ and C₄ types. The main parameters characterizing these

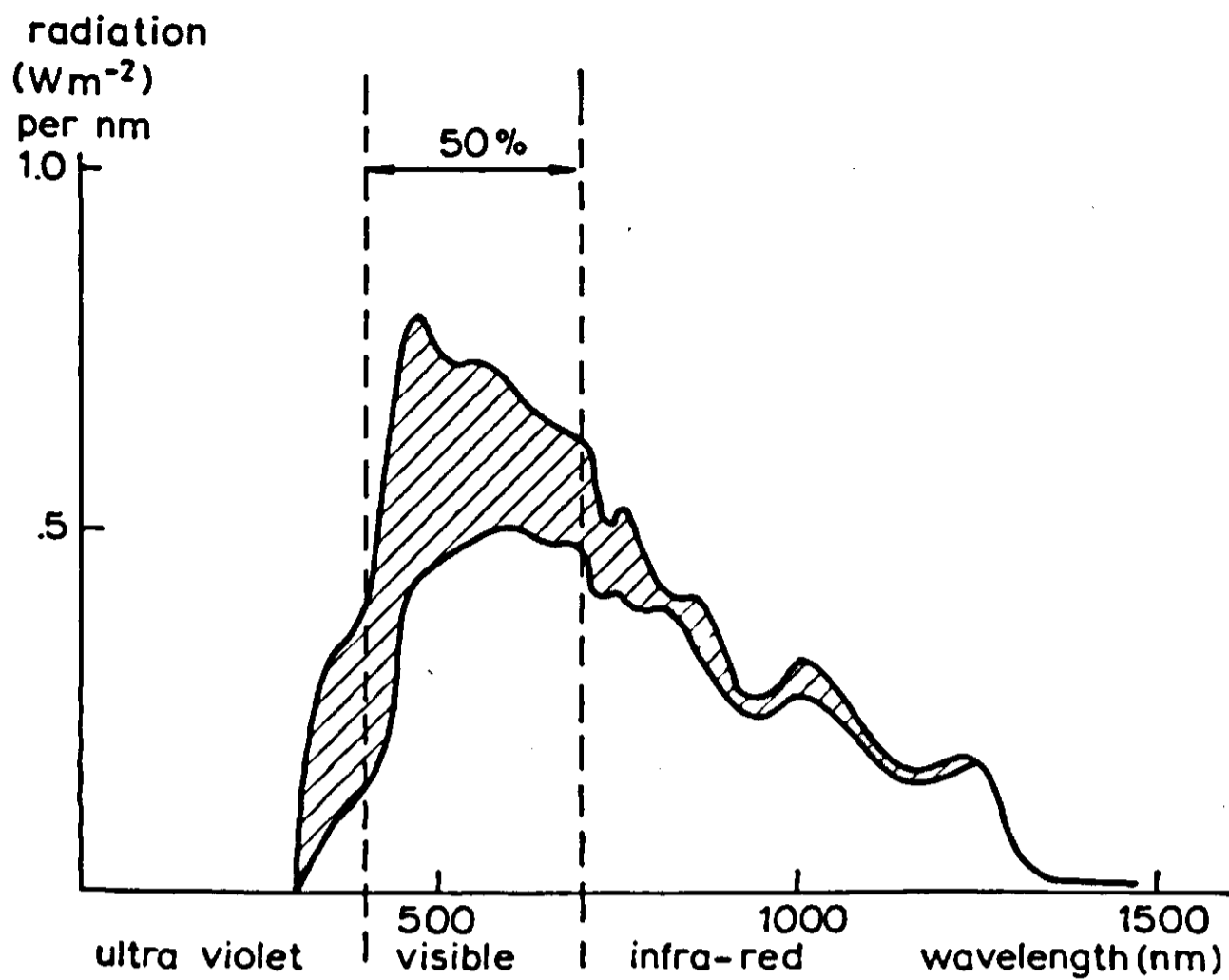


Figure 5. Spectral distribution of total solar radiation (upper curve) and direct solar radiation (lower curve). Solar elevation is 30° and precipitable water in the atmosphere is 21 mm. (Source: Monteith, 1973)

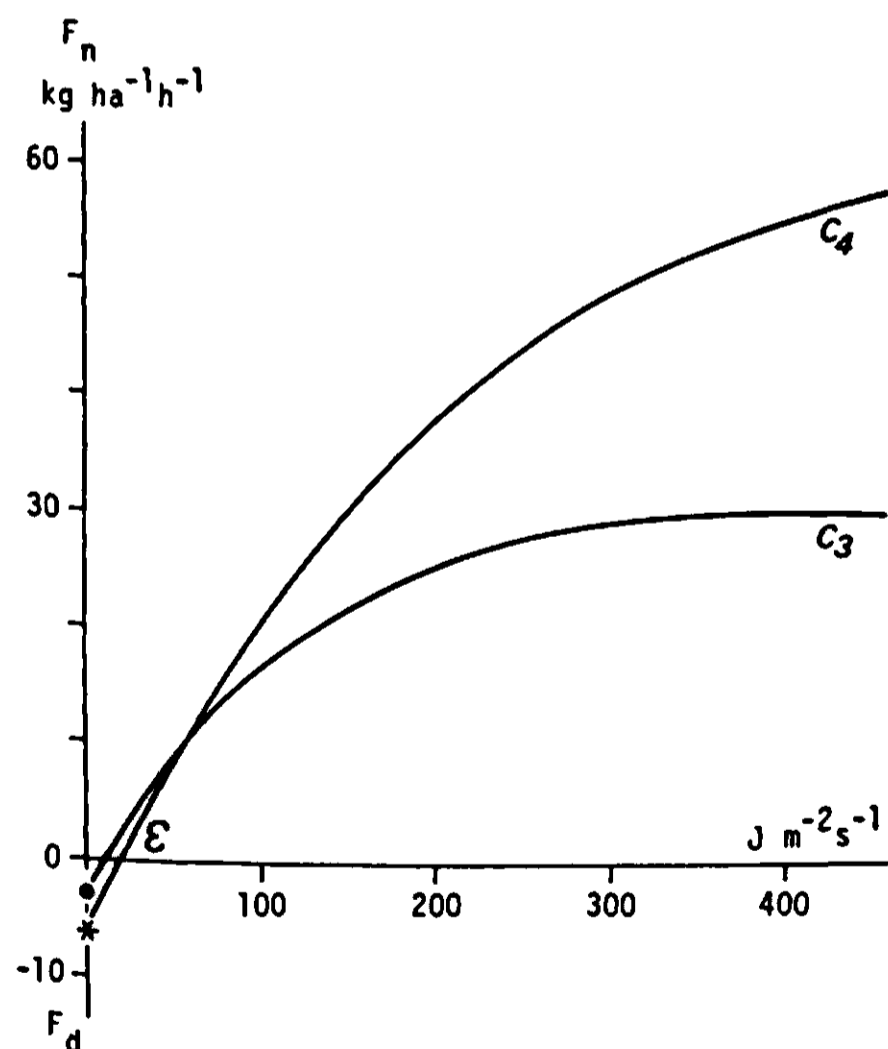


Figure 6. Characteristic net CO₂ assimilation functions for individual leaves of C₃ and C₄ plant species.

curves are the initial light use efficiency, ϵ , the respiration rate in the dark, R_d , and the maximum rate of net CO_2 assimilation at high light intensity, F_m . The latter ranges from $30-90 \text{ kg ha}^{-1} (\text{leaf}) \text{ h}^{-1}$ for C_4 type plants and from $15-50 \text{ kg ha}^{-1} (\text{leaf}) \text{ h}^{-1}$ for C_3 type plants, depending on environmental conditions. The gross rate of CO_2 assimilation, F_g , is the sum of the net rate and the concurrent dark respiration. The dark respiration is at normal temperatures roughly one-ninth of the maximum net assimilation rate.

The maximum net assimilation rate and the dark respiration rate are much more affected by temperature than the initial light use efficiency. The effect of temperature on the maximum assimilation rate is illustrated in Figure 7 for a C_3 and a C_4 type plant. However, these temperature responses were obtained with plants grown under controlled conditions at a temperature close to the optimum found in Figure 7. Under field conditions where plants are subjected to fluctuating temperature conditions, there appears to be adaptation of the photosynthetic apparatus. It was found that for such plants the maximum leaf assimilation rate was practically independent of temperature above about 13°C for C_4 species and above 8°C for C_3 species.

The difference in initial light use efficiency between the C_3 and C_4 types of photosynthesis is small, but the assimilation rate at light saturation is for the C_4 type plants generally higher. The names C_3 and C_4 refer to the length of the C skeleton of the first stable product in the photosynthetic process. Several characteristics of these two plant types are different (Gifford, 1974), such as: (i) the main carboxylating enzyme in the C_4 photosynthetic pathway has an affinity to CO_2 that is about twice as high as that in the C_3 photosynthetic pathway; (ii) in the C_3 type plants a respiratory process takes place in the light

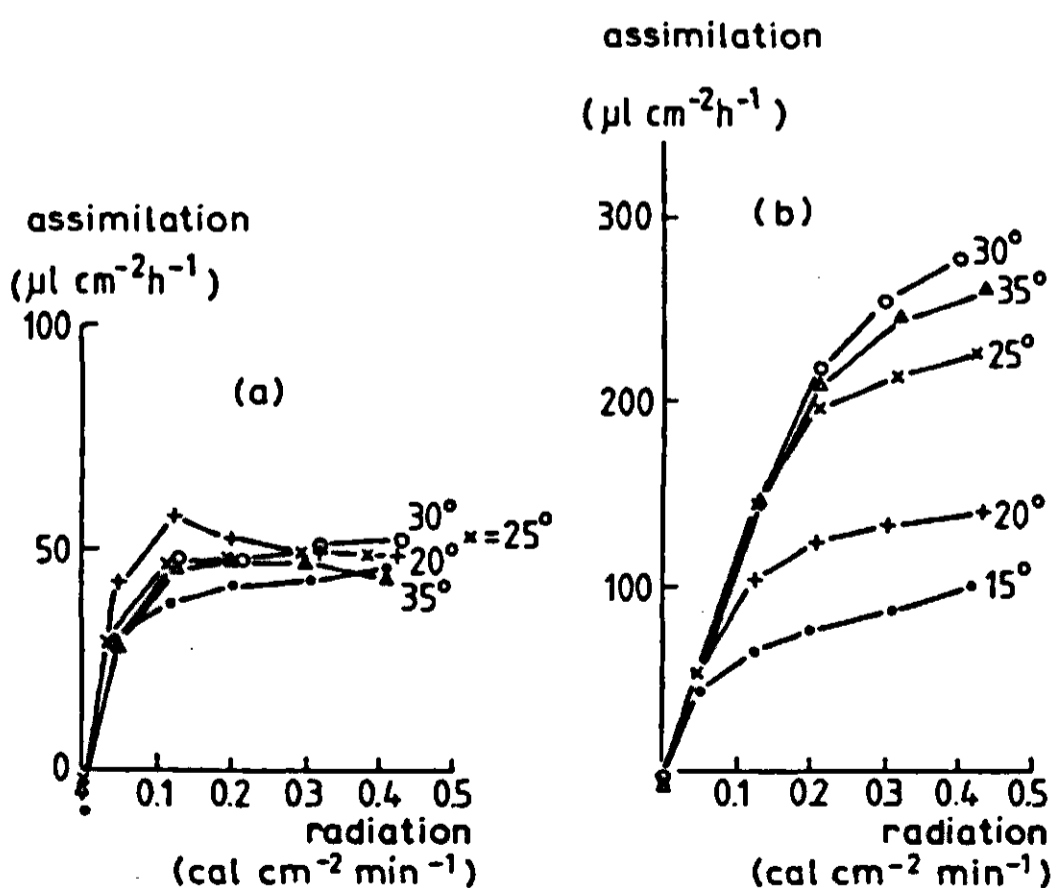


Figure 7. The relation between temperature and the maximum rate of CO_2 assimilation for a C_3 (a) and a C_4 (b) crop species.

which results in a dependence of assimilation rate on the oxygen concentration in the ambient air, whereas that process is absent in C_4 species; (iii) under conditions where the CO_2 concentration in the intercellular space is regulated over a wide range of external CO_2 concentrations and light intensities through adaptation of stomatal aperture, the level at which the internal concentration is maintained in C_4 types is about half of that in C_3 types (Raschke, 1975; Goudriaan & van Laar, 1978b). This last characteristic will be discussed in detail in Section 3.3.

Examples of species having the C_3 type of assimilation, which prevail in the temperate zones, are small grains, including rice. Species that are of the C_4 type, which are more abundant in subtropical and tropical regions, are maize, sorghum, millet, sugar cane and most tropical grasses. Extensive lists of C_4 species have been compiled by Downton (1975) and Raghavendra & Das (1978).

2.1.2 *Canopy CO_2 assimilation*

The rate of CO_2 assimilation of a crop depends on incoming visible radiation in the same way as that of an individual leaf. Suppose for simplicity a crop with a horizontal layer of large leaves, forming a closed surface. This layer acts as one big leaf, and knowing the light intensity, the rate of CO_2 assimilation can be read from Figure 6, taking into account that 10% of the incoming visible radiation is reflected, 10% is transmitted through the leaves, 10% is absorbed by pigments not contributing to photosynthesis, and that only the remaining 70% is absorbed by the chloroplasts. At an incoming visible radiation intensity of $300 \text{ J m}^{-2} \text{ s}^{-1}$ this crop, if it was a C_3 species, would have a CO_2 assimilation rate of about $25 \text{ kg ha}^{-1} \text{ h}^{-1}$. Such a crop has a leaf area index (LAI) of one, because there is 1 m^2 of leaf area per m^2 of soil surface area. When another layer of such big leaves is situated under the first one, the crop has a LAI of 2, because there is 2 m^2 of leaf area per m^2 of soil surface area. The incoming radiation intensity in the second layer is equal to the light transmitted through the first layer, thus 10% of 300, or $30 \text{ J m}^{-2} \text{ s}^{-1}$, resulting in an additional assimilation rate of about $3 \text{ kg ha}^{-1} \text{ h}^{-1}$. The result is a small increase in assimilation rate for the two layer crop. Adding more layers under the second one will not substantially increase the assimilation rate of such a crop with layers of large horizontal leaves.

In reality, a crop does not consist of horizontal layers of large closely fitting leaves, but the leaves of a crop are spread in every direction and the light is therefore more evenly distributed over the leaves. The light extinction in a canopy can be experimentally determined by measuring the light intensity at different levels in the crop, while at the same time measuring the cumulative leaf area at the same levels. The result of such an experiment is presented in Figure 8, which depicts the relation between the relative light intensity and the cumulative LAI, counting the leaf area from the top of the canopy down-

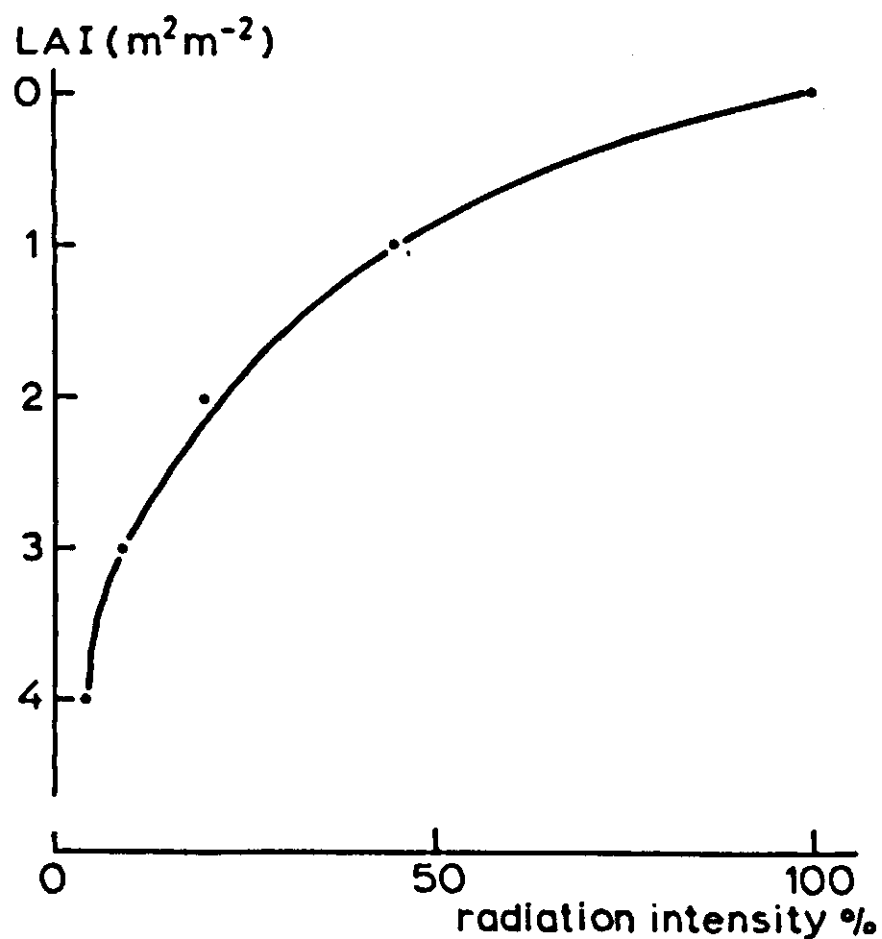


Figure 8. Extinction of radiation in a crop canopy.

wards. The extinction of the light is exponential for an increasing number of leaf layers. For any LAI the proportion of absorbed radiation can be read from Figure 8. In combination with Figure 6 this yields an estimate of the assimilation rate of the crop. For an LAI of four, the CO₂ assimilation rate is about 39 kg ha⁻¹ h⁻¹, or about one and a half times that of the crop with layers of large horizontal leaves. The reason for this is that in a real crop the light intensity distribution over the leaves is more even and therefore more leaves are exposed to light intensities in the linear part of the light response curve.

The procedure just outlined is a schematized way of calculating the rate of CO₂ assimilation of a crop. Reality is more complicated, as the influence of direct and diffuse light, total leaf area, leaf angle distribution, leaf optical properties and solar height on the light distribution within the canopy have to be taken into account. The problem has been tackled with computer models (de Wit 1965; Duncan et al., 1967; Goudriaan, 1977) which calculate the assimilation rate of a canopy at any moment of a day in response to the incoming photosynthetically active radiation, which is dependent on solar height and the degree of cloudiness of the sky.

In a schematized set up, two situations are considered: a completely clear sky and a completely cloudy sky. Integration of the instantaneous rates yields the daily total amount of CO₂ fixed. In Tables 1 and 2 these daily totals are presented as a function of geographical latitude for both completely clear and completely overcast days, under the assumption of zero respiration and an LAI of five, for two maximum rates of gross CO₂ assimilation of a single leaf at high light intensity, F_g : 40 kg ha⁻¹ (leaf) h⁻¹, typical for a C₃ type of plant,

Table 1. Calculated gross CO₂ assimilation rate (kg ha⁻¹ d⁻¹) of a closed canopy with a spherical leaf angle distribution, for clear (F_{cl}) and overcast (F_{ov}) days, and a maximum leaf CO₂ assimilation rate, F_g, of 40 kg ha⁻¹ d⁻¹.

Date	15	15	15	15	15	15	15	15	15	15	15	15
Northern Hemisph.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Southern Hemisph.	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June
Latitude												
0° F _{cl}	728	753	768	761	737	720	727	752	768	760	736	720
F _{ov}	306	320	328	324	311	302	306	319	328	324	311	302
10° F _{cl}	652	701	748	779	786	784	785	784	765	720	667	638
F _{ov}	270	295	319	334	336	333	335	336	327	305	277	262
20° F _{cl}	562	634	713	783	820	834	829	802	745	665	583	542
F _{ov}	226	261	300	334	351	356	355	343	316	276	236	216
30° F _{cl}	454	549	659	768	839	869	858	804	708	591	481	429
F _{ov}	175	219	271	324	357	371	366	341	295	239	187	163
40° F _{cl}	333	445	586	737	843	892	873	788	652	497	364	304
F _{ov}	120	169	233	304	354	377	368	329	264	193	133	107
50° F _{cl}	202	324	491	686	833	904	877	757	574	384	234	172
F _{ov}	63	114	187	275	343	375	363	307	224	140	77	52
60° F _{cl}	68	191	375	615	813	915	875	708	474	255	102	39
F _{ov}	15	57	132	236	323	368	351	277	175	83	25	8
70° F _{cl}	0	46	240	527	798	967	896	649	353	114	0	0
F _{ov}	0	10	73	189	302	369	341	240	118	27	0	0

(Source: Goudriaan & Van Laar, 1978a)

and 70 kg ha⁻¹ (leaf) h⁻¹, typical for a C₄ type of plant. On the basis of such tables, which for various maximum rates of CO₂ assimilation at high light intensity can be found in Goudriaan & Van Laar (1978a), potential crop assimilation can be calculated for any date, given the type of crop (C₃ or C₄), the latitude of the location and the fraction of the time the sky is clouded.

Crop type determines which table is used; given the latitude and the date, the assimilation rate of a closed canopy for a clear and an overcast day is obtained by interpolation. The assimilation rate for partially overcast days is obtained from the formula:

$$F_{gc} = f_o \cdot F_{ov} + (1 - f_o) \cdot F_{cl} \quad (3)$$

where

F_{gc} is the gross canopy CO₂ assimilation rate (kg ha⁻¹ d⁻¹)
 f_o is the fraction of the day the sky is overcast (f_o is 0 for completely clear days, f_o is 1 for completely overcast days)

Table 2. Calculated gross CO₂ assimilation rate (kg ha⁻¹ d⁻¹) of a closed canopy with a spherical leaf angle distribution, for clear (F_{cl}) and overcast (F_{ov}) days, and a maximum leaf CO₂ assimilation rate, F_g, of 70 kg ha⁻¹ d⁻¹.

Date	15	15	15	15	15	15	15	15	15	15	15	15
Northern Hemisph.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Southern Hemisph.	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June
Latitude												
0° F _{cl}	959	995	1017	1007	973	947	958	993	1018	1007	971	947
F _{ov}	326	341	350	346	331	321	325	340	351	346	331	321
10° F _{cl}	852	922	989	1032	1039	1035	1037	1038	1012	949	873	832
F _{ov}	285	313	340	357	358	356	357	359	349	324	294	277
20° F _{cl}	726	827	937	1035	1086	1103	1097	1062	983	870	755	698
F _{ov}	237	276	319	356	375	381	379	366	336	292	248	226
30° F _{cl}	577	707	860	1011	1109	1149	1134	1060	927	765	613	542
F _{ov}	182	229	287	345	381	396	391	363	313	251	195	170
40° F _{cl}	410	562	755	962	1108	1175	1150	1033	845	633	452	372
F _{ov}	123	176	245	322	377	402	392	349	278	201	138	110
50° F _{cl}	236	397	620	885	1086	1183	1145	982	733	477	278	198
F _{ov}	65	117	194	289	362	398	384	324	234	145	78	53
60° F _{cl}	71	220	460	779	1046	1182	1129	905	591	301	109	40
F _{ov}	15	58	136	246	340	388	369	290	181	85	25	8
70° F _{cl}	0	47	277	649	1006	1222	1132	810	421	121	0	0
F _{ov}	0	10	74	195	314	385	356	249	120	28	0	0

(Source: Goudriaan & Van Laar, 1978a)

F_{ov} is the gross CO₂ assimilation rate on completely overcast days (kg ha⁻¹ d⁻¹)

F_{cl} is the gross CO₂ assimilation rate on a perfectly clear day (kg ha⁻¹ d⁻¹)

The fraction of the day the sky is overcast is obtained from the measured actual daily global irradiation and the daily global irradiation on a perfectly clear day, which is tabulated in Table 3.

Daily global irradiation on a completely overcast day may be approximated by multiplying the value for a perfectly clear day with 0.2. Thus:

$$f_o = (H_g - H_a) / (H_g - 0.2 \cdot H_g) \quad (4)$$

where

H_g is total global irradiation on a perfectly clear day (J m⁻² d⁻¹)

H_a is measured total global irradiation (J m⁻² d⁻¹)

If the canopy does not form a closed cover, as at the beginning and the end of the growth cycle, not all incoming radiation is intercepted, and CO₂ assimilation is reduced relative to that of a closed canopy. The reduction is estimated from the fraction of the incoming radiation intercepted by the crop, as discussed earlier:

$$f_h = (1 - e^{-k_e \cdot LAI}) \quad (5)$$

where

- f_h is the fraction of light intercepted by the crop
 k_e is the extinction coefficient for visible light, the value being between 0.5 and 0.8, depending on crop geometry
-

Exercise 1

Calculate the daily gross CO₂ assimilation for the middle of each month of the year for a completely clear and for a completely overcast sky at your own location, assuming a closed canopy, for both a C₃ and a C₄ type of crop.

Exercise 2

Repeat Exercise 1 assuming LAI = 1.5

The rate of CO₂ assimilation has been expressed so far in amounts of CO₂. The absorbed CO₂ is reduced in the crop to carbohydrates or sugars (CH₂O)_n. To get an assimilation rate expressed in CH₂O, the rate in CO₂ is multiplied by 30/44 (the ratio of their molecular weights).

2.1.3 Respiration

The sugars produced in the assimilation process may be converted into structural dry matter, they may be accumulated and temporarily stored as reserves, or they may be used as a source of energy. The plant needs energy for two processes. On the one hand for maintenance of ionic gradients and resynthesis of degrading structural proteins; on the other hand for the conversion of primary photosynthetic products into structural plant material. In these processes CO₂ is produced, thus they are respiratory processes: the first one is

Table 3. Total global radiation, H_g , ($10^6 \text{ J m}^{-2} \text{ d}^{-1}$) for a standard clear day.

Date	15	15	15	15	15	15	15	15	15	15	15	15	15	15
Northern Hemisphere.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.
Southern Hemisphere.	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
Latitude														
0°	28.00	29.44	30.32	29.90	28.52	27.54	27.94	29.36	30.34	29.88	28.46	27.54	27.94	29.36
10°	24.34	26.88	29.34	30.86	30.96	30.68	30.82	31.02	30.18	27.90	25.10	23.60	30.82	31.02
20°	20.00	22.46	27.36	30.76	32.44	32.92	32.76	31.68	28.96	24.98	21.00	19.06	32.76	31.68
30°	15.18	19.30	24.42	29.62	32.90	34.24	33.74	31.28	26.74	21.34	16.34	14.10	33.74	31.28
40°	10.12	14.60	20.64	27.48	32.36	34.58	33.72	29.86	23.60	16.80	11.34	9.00	33.72	29.86
50°	5.22	9.60	16.14	24.40	30.88	34.02	32.82	27.50	19.60	11.92	6.38	4.22	32.82	27.50
60°	1.22	4.68	11.16	20.50	28.62	32.86	31.20	24.30	14.94	6.84	2.00	0.64	31.20	24.30
70°	0.00	0.76	5.96	15.98	26.12	32.18	29.70	20.56	9.78	2.20	0.00	0.00	29.70	20.56
80°	0.00	0.00	1.26	11.32	25.74	33.44	30.48	17.62	4.44	0.00	0.00	0.00	30.48	17.62
90°	0.00	0.00	0.00	9.72	26.04	33.98	30.94	17.46	0.38	0.00	0.00	0.00	30.94	17.46

(Source: Goudriaan & Van Laar, 1978a)

called maintenance respiration, the second growth respiration.

Maintenance respiration

The proteins in the plant, especially in the leaves, consist mainly of enzymes, which have only a limited life span. They deteriorate at a relative rate of about 0.1 per day at a temperature of 20 °C, and have to be resynthesized. The rate of protein turnover is temperature dependent with a Q_{10} of about 2 (Penning de Vries et al., 1979). This means that the rate of protein turnover doubles for temperature increases of 10 °C.

The concentration of ions in the vacuoles of plant cells is higher than in the surrounding tissue, which causes leakage of ions from the vacuoles. To maintain the desired internal concentration, the ions have to be taken up against a concentration gradient. That requires an active transport through cell membranes, which demands energy.

Although accurate data on maintenance requirements are scarce, reasonable estimates of the relative maintenance respiration rate can be made on the basis of the composition of the biomass present. Such estimates are given in Table 4 for four groups of crops, each group having approximately the same chemical composition.

Growth respiration

The conversion of primary photosynthates into structural plant material as cellulose, proteins, lignin and fats requires substrate for building materials and energy for synthesis of the end product, the transport of sugars and the uptake of nitrogen and minerals. Therefore, part of the sugars assimilated is respired to provide energy for the synthesis of new plant components. Another part is lost as refuse in the process of synthesis. The magnitude of growth respiration is determined by the composition of the end product formed. Thus the weight efficiency of conversion of primary photosynthates into structural plant material varies with the composition of that material. Fats and lignin are produced at high costs; structural carbohydrates and organic acids are relatively cheap. Proteins and nucleic acids form an intermediate group (Table 5).

Table 4. Relative maintenance respiration rate, R_m , at 20 °C ($\text{kg kg}^{-1}\text{d}^{-1}$), and conversion efficiency, E_g , (kg kg^{-1}).

Crop group	R_m	E_g
Root/tuber crops	0.010	0.75
cereals	0.015	0.70
protein-rich seed crops	0.025	0.65
oil-rich seed crops	0.030	0.50

Table 5. Efficiency of conversion, E_g , of substrate (sugars) into plant constituents (kg kg^{-1}).

Compound	E_g
Carbohydrates	0.826
Nitrogenous compounds (normal mix of amino-acids, proteins and nucleic acids) from NO_3^-	0.404
from NH_4^+	0.616
Organic acids	1.104
Lignin	0.465
Lipids	0.330

(Source: Penning de Vries, 1975)

For the same groups of crops distinguished above, the conversion efficiencies are tabulated in Table 4. At higher temperatures, the rate of conversion of primary photosynthates into structural plant material changes, but the conversion efficiency remains constant, because the biochemical pathway is not affected by temperature. Conversion of primary photosynthates into structural plant material occurs to a large extent at night. Low night temperatures may hamper this conversion to such an extent that not all the assimilates formed during the day can be converted into structural material. As a result, carbohydrates and starch accumulate in the plant and eventually this may affect the assimilation rate, either through a biochemical feedback or through physical damage to the chloroplasts. Under such conditions the assimilation rate is virtually determined by the capacity of the plant to convert the assimilation products.

2.1.4 Dry matter accumulation

On the basis of the processes presented in this section, the daily rate of increase in structural dry weight of a crop surface may be approximated by the formula

$$\Delta W = E_g \cdot (F_{gs} - R_m \cdot W) \quad (6)$$

where

ΔW is the rate of increase in structural dry weight ($\text{kg ha}^{-1} \text{d}^{-1}$)

E_g is the conversion efficiency of carbohydrate into dry matter (kg kg^{-1}); see Table 4

F_{gs} is the gross rate of crop assimilation expressed in carbohydrates ($\text{kg ha}^{-1} \text{d}^{-1}$)

R_m is the relative maintenance respiration rate ($\text{kg kg}^{-1} \text{d}^{-1}$); Table 4
 W is the total dry weight of the live parts of the crop (kg ha^{-1})

In a temperate, humid climate e.g. in the Netherlands, the potential growth rate, as calculated by Equation 6, appears to be about $200 \text{ kg ha}^{-1} \text{d}^{-1}$ during the growing season (Table 6). Experimental evidence confirming these estimates is given by Sibma (1968), who calculated growth curves for a number of field crops growing under near-optimal conditions, as shown in Figure 9. The main agricultural crops in the Netherlands all appear to have practically the same slope. That the C_4 type crop maize shows the same slope is because in the Netherlands it is grown at the limit of its temperature range.

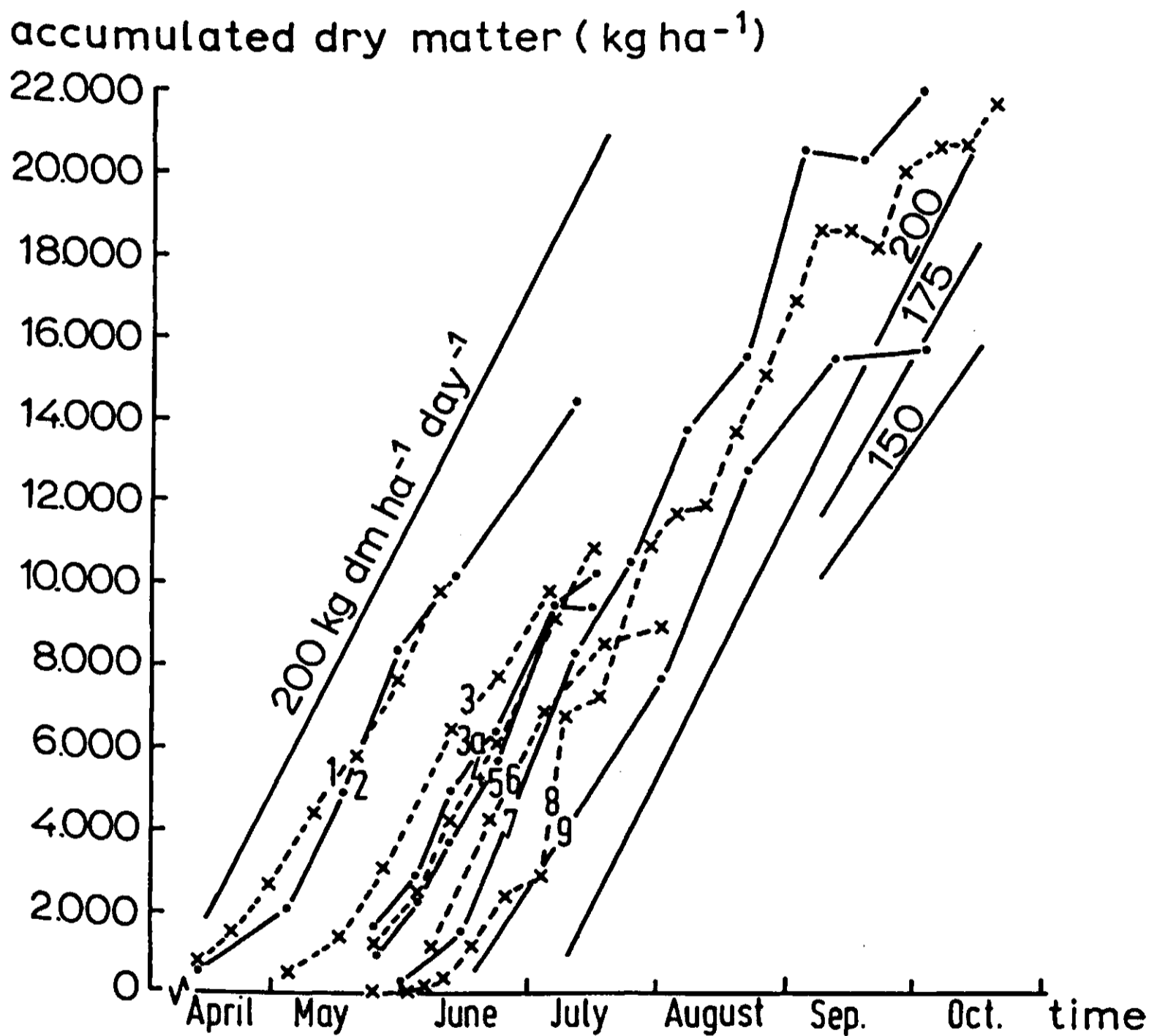


Figure 9. Growth rates of the main agricultural crops in the Netherlands under (near)-optimal growth conditions compared to growth rates of 200, 175 and 150 $\text{kg ha}^{-1} \text{d}^{-1}$, respectively. 1. grass 2. wheat 3. oats + barley 3a. oats + peas 4. oats 5. peas 6. barley 7. potatoes 8. sugar beets 9. maize. (Source: Sibma, 1968)

Exercise 3

Calculate the potential growth rate per month of a C₃ crop for your own location, following the scheme presented in Table 6.

Estimate the fraction overcast from your own experience, if no data on radiation are available (heavy clouds: $f_o = 1$; clear skies prevailing: $f_o = 0$).

Table 6. Example of calculation scheme for the potential growth rate at De Bilt, the Netherlands (52 °N) assuming the overall loss by respiration to be 40%.

Month	H _a	H _g	f _o	F _{cl}	F _{ov}	F _{gc}	F _{gs}	ΔW
May	16.92	30.43	0.55	829	339	560	382	229
June	18.60	33.78	0.56	906	374	608	414	249
July	16.45	32.50	0.62	877	361	557	380	228
August	14.57	26.86	0.57	747	301	493	336	202

H_a = long term average actual global radiation (10⁶ J m⁻² d⁻¹)

H_g = total global radiation on a clear day at 52° N.L. (10⁶ J m⁻² d⁻¹) (obtained by linear interpolation in Table 3)

f_o = fraction of the day the sky is overcast (Equation 4)

F_{cl} = gross CO₂ assimilation rate on completely clear days (kg ha⁻¹ d⁻¹) (interpolation in Table 1 or 2)

F_{ov} = gross CO₂ assimilation rate on completely overcast days (kg ha⁻¹ d⁻¹) (interpolation in Table 1 or 2)

F_{gc} = actual gross canopy CO₂ assimilation rate (kg ha⁻¹ d⁻¹) (Equation 3)

F_{gs} = gross canopy assimilation rate in carbohydrates (30/44 x F_{gc})

ΔW = the potential growth rate (kg ha⁻¹ d⁻¹) (0.60 x F_{gs})