3.2 Potential production processes

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3.2.1 Introduction

The potential production rate of a crop is defined as the growth rate of a closed, green crop surface, optimally supplied with water and nutrients, in a disease and weed-free environment under the prevailing weather conditions (see Subsection 1.2.2).

Growth will be used in the meaning of accumulation of dry matter, which mainly consists of carbohydrates. Since carbohydrate accumulation is a result of the combined effort of the leaves of a crop canopy it is logical to calculate crop production as the sum of the contributions of the individual leaves. Simulation of photosynthesis and photorespiration of leaves of C_3 and C_4 type plants is presented in the Subsection 3.2.2. With the information about the calculation of radiation levels and of penetration of light into a canopy (Subsection 3.2.3), this gives a basis for computation of canopy photosynthesis (Subsection 3.2.4). Many exercises are provided to facilitate the reader to become acquainted with simulation of photosynthetic processes. The energy balance of leaves and canopies is presented in Subsection 3.2.5. The simulation of the physiological link between the rates of CO_2 assimilation and transpiration is presented in Subsection 3.2.6.

3.2.2 Leaf photosynthesis

The major portion of the photosynthetic energy is used for the production of glucose from water and carbon dioxide. Therefore photosynthesis is loosely identified and measured as the rate of CO_2 uptake. In Figure 25 the dependence of leaf CO_2 assimilation on absorbed photosynthetically active radiation (PAR)

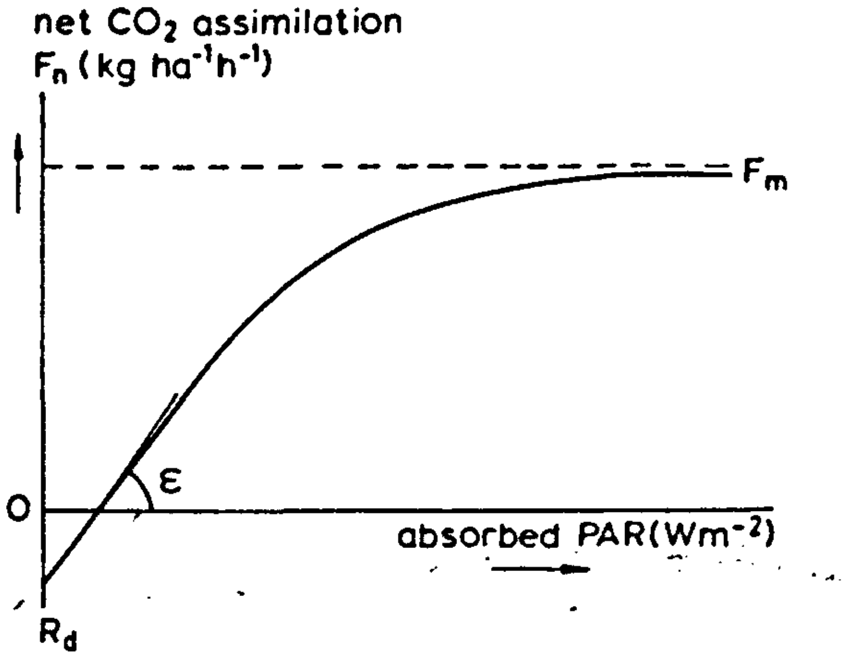

Figure 25. A typical light response curve of the assimilation of CO_2 for an individual leaf. R_d stands for the dark respiration, ε for the slope (or efficiency) at a low light level and F_m for the net assimilation rate at light saturation.

Table 11. Some C_3 and C_4 type species.

C_3	C_4
Small grains (wheat, barley, oats, rye, rice). Temperate grasses. Sugar-beet, potato, sunflower, cotton. All leguminous species with nitrogen fixation. Almost all trees (except Mangrove).	Tropical grasses as maize, sorghum, millet, *Cenchrus biflorus*, sugar-cane, Rhodes grass. Some halophytes as *Spartina townsendii. Salsola kali, Atriplex rosea,* Mangrove.

is given. At high light the assimilation rate is saturated with light and approaches a maximum value F_m. Other parameters that characterize the curve are the respiration rate in the dark R_d and the initial slope or light-use efficiency ε. The largest variation is in the maximum rate F_m; it ranges between 30-90 kg ha^{-1} h^{-1} for C_4 plants and between 15-50 kg ha^{-1} h^{-1} for C_3 plants. In Table 11 a concise list of some important C_3 and C_4 species is given. More extensive lists can be found in Downton (1975) and in Raghavendra & Das (1978). In C_4 species the main acceptor of CO_2 is phospho-enolpyruvate (PEP), yielding malate or oxalate with 4 C atoms. In C_3 plants Ribulose-Biphosphate (RuBP) acts as the acceptor yielding two 3 C atom components. The affinity of PEP for CO_2 is much higher than that of RuBP, which is part of the reason why C_4 plants have a higher maximum assimilation rate than C_3 plants. The temperature dependence of F_m is also different for C_3 and C_4 species: C_4 species have a higher optimal temperature.

The light-use efficiency for fixing CO_2 is about $14 \cdot 10^{-9}$ kg J^{-1} (absorbed PAR) in C_4 plants and about $11 \cdot 10^{-9}$ kg J^{-1} in C_3 plants. Its variation is much less than of F_m; it does however increase a little in C_3 plants with increasing CO_2 concentration. For the time being we will consider it as constant. The dark respiration rate R_d reflects the activity of the leaf and is therefore correlated with the maximum rate F_m. Usually it is less than 0.1 of F_m at 20 °C, but this fraction rises with increasing temperature. Experimental evidence indicates that a linear rise with temperature is more common than an exponential increase. There are two equations that are often used to describe the photosynthesis light-response curve:

$$F_n = (F_m + R_d)\,(1 - \exp(-H\varepsilon/(F_m + R_d))) - R_d \quad \text{(asymptotic exponential)} \quad (13)$$

and:

$$F_n = (F_m + R_d)\varepsilon H/(\varepsilon H + F_m + R_d) - R_d \qquad \text{(rectangular hyperbola)} \quad (14)$$

in which:

F_n is net CO_2 assimilation for leaves in kg ha^{-1} h^{-1}
F_m is the maximum rate of net CO_2 assimilation for leaves at high light intensities in kg ha^{-1} h^{-1}

R_d is dark respiration in kg ha^{-1} h^{-1}
H is the absorbed radiant flux in the 400-700 nm range in J m^{-2} (leaf) s^{-1} (= W m^{-2})
ε is the initial light use efficiency for fixing CO_2 in leaves in kg J^{-1} ($14 \cdot 10^{-9}$ kg J^{-1}, which equals 0.5 kg ha^{-1} h^{-1} J^{-1} m^2 s)

Exercise 27
Check the units in these equations. Analyse and compare their results, graphically and numerically. Assume that $F_m = 60$ and $R_d = 4$ kg ha^{-1} h^{-1}.

Although experimental evidence indicates that the asymptotic exponential gives a better fit for leaf photosynthesis (Peat, 1970; English, 1976), the hyperbolic equation has the appeal of its relatively simple structure. Essentially it is a Michaelis-Menten response to absorbed light, which enables the introduction of CO_2 concentration as a factor influencing assimilation. This is particularly important in C_3 plants, where the CO_2 dependent photorespiration reduces the net assimilation. Therefore a simple carboxylation model will be constructed to better understand the relation between net CO_2 assimilation, light intensity, CO_2 concentration and some leaf properties. First we shall assume that the gross assimilation F_g follows a hyperbolic response to the CO_2 concentration (C) at the carboxylation site and also to absorbed light H:

$$F_g = \frac{F_{mm}\varepsilon HC}{F_{mm}\varepsilon Hr_x + \varepsilon HC + CF_{mm}} \tag{15}$$

or:

$$F_g = \frac{F_{mm}\varepsilon H}{F_{mm}\varepsilon Hr_x/C + \varepsilon H + F_{mm}} \tag{16}$$

In this equation F_{mm} is the absolute maximum assimilation rate, which is approached when both light and the CO_2 concentration are very high. In that situation the processing of photosynthetic products and regeneration of RuBP becomes rate limiting, and not the external supply.

When the CO_2 concentration is low enough this equation can be simplified to:

$$F_g = C/r_x \tag{17}$$

where r_x has the dimension of a resistance. Since C is the CO_2 concentration at the site of carboxylation, r_x is called the carboxylation resistance.

Exercise 28
Construct a consistent dimensional set of units for all variables of Equation 16.

Exercise 29
Which equation arises from Equation 16 at both low light and low CO_2? What is then the Michaelis-Menten constant for CO_2?

The dark respiration R_d can be subtracted from the gross assimilation as given by Equation 16, which then results in the expression for the net assimilation in C_4 plants:

$$F_n = \frac{F_{mm} \varepsilon H}{F_{mm} + (F_{mm} r_x / C + 1) \varepsilon H} - R_d \tag{18}$$

Exercise 30
Reduce Equation 18 to Equation 14 and express F_m in F_{mm}, r_x, C and R_d.

When the net assimilation rate is zero, the compensation point is reached. From Equation 18 one can see that there is not just one compensation point, but a continuous range of H and C values, which may be called the compensation line. When the light intensity is high enough, the corresponding CO_2 concentration of the compensation line approaches a stable value, which is usually called the CO_2 compensation point.

Exercise 31
Derive the expression for the compensation line, and also for the light and CO_2 compensation points. What are the numerical values of the CO_2 and light compensation points when $R_d = 4$ kg ha^{-1} h^{-1}, $r_x = 80$ s m^{-1}, $F_{mm} = 200$ kg ha^{-1} h^{-1}.

In C_3 plants, photorespiration occurs besides the dark respiration, so that the net assimilation rate is lower than in C_4 plants. The photorespiration takes place during the CO_2 assimilation process only, and it does not use sugars from the reserve pool. Normally its magnitude is about 0.2-0.3 of the gross assimilation rate, and because it follows gross assimilation with a delay of less than a minute its effect is normally included when net CO_2 assimilation is measured. Therefore, F_g and F_n in the Equations 15, 16 and 18 contain the effect of photorespiration. Still, it must be considered separately, because photorespiration is reduced when the CO_2 concentration rises, and also when the O_2 concentration is lowered. Oxygen interferes because it competes with CO_2 in reacting with RuBP (oxygenation instead of carboxylation). Photorespiration occurs later in the reaction cycle to recover RuBP from its oxygenation. According to Laing et al. (1974) the ratio of photorespiration R_f and gross assimilation F_g is

$$\frac{R_f}{F_g} = \frac{t V_o O r_x}{K_o C} \tag{19}$$

where t is the fraction of glycolate carbon released (0.25), V_o the maximum rate of oxygenation, K_o the Michaelis-Menten constant for the O_2 concentration O. The gross rate F_g itself is also reduced by the competing effect of O_2, which is reflected in an extended Michaelis-Menten equation:

$$F_g = \frac{\varepsilon H C}{\varepsilon H r_x (1 + O/K_o) + C} \tag{20}$$

This expression shows that the carboxylation resistance r_x has been multiplied by a factor $1 + O/K_o$ (about 1.7).

At high light F_g approaches $C/(r_x(1 + O/K_o))$. The net assimilation rate F_n is given by $F_g - R_f - R_d$, or (Equation 19):

$$F_n = F_g \left(1 - \frac{t V_o O r_x}{K_o C}\right) - R_d \tag{21}$$

The CO_2 compensation point Γ at high light can be found as the CO_2 concentration at which Equation 21 gives $F_n = 0$:

$$\Gamma = t V_o O r_x / K_o + R_d r_x (1 + O/K_o) \tag{22}$$

At low light the expression for F_n approaches:

$$F_n = \varepsilon H \left(1 - \frac{t V_o O r_x}{K_o C}\right) - R_d \tag{23}$$

so that the apparent light-use efficiency is reduced. Because the second term in Equation 22 is relatively small in C_3 plants the multiplication factor for ε is practically equal to $1 - \Gamma/C$.

Experimental results with C_3 plants show that Γ is of the order of 50-70 cm^3 m^{-3} and C of 200-250 cm^3 m^{-3}, so that the light-use efficiency is lowered by about 25%. When the CO_2 concentration is increased, the light-use efficiency will also go up, and gradually approach the value of C_4 plants.

In a simulation model the light-use efficiency of C_3 and C_4 type plants can be found as the product of a common value (14.10^{-9} kg J^{-1}) multiplied by the factor $(1 - \Gamma/C)$. The compensation point Γ should then be given as an input parameter, or perhaps be made dependent on temperature and water stress (Lawlor & Pearlman, 1981; Bykov et al., 1981).

3.2.3 Radiation

Radiation drives both photosynthesis and transpiration, so that it must be included in models for plant growth and water use. All radiation, as a source of thermal energy, is important for transpiration, but only the photosynthetically active radiation (PAR) keeps photosynthesis going. For all practical purposes PAR can be identified with visible radiation (400-700 nm) and is about 50% of the global irradiation (as measured with a Kipp radiometer) under a clear sky and about 60% under an overcast sky. Irradiation under an overcast sky is extremely variable, but as a rule of thumb we adopt that it is one fifth of what would have been measured under a very clear sky (de Wit et al., 1978). The dependence of incoming PAR (in W m^{-2}) under a clear sky on solar height β can be expressed as follows:

$$S_v = 640 \cdot \sin\beta \cdot \exp(-K_{atm}/\sin\beta) \tag{24}$$

where K_{atm} ranges between 0.1 for a very clear atmosphere, and 0.18 for a rather humid and dusty one. More details can be found in Ross (1981).

The extinction of radiation in a canopy is approximately exponential with leaf area index (LAI) reckoned from the top. In a simple model situation one can visualize the leaves as arranged in layers below each other. If the leaves are horizontal and black, each layer will intercept a fraction equal to its own leaf area index. In this situation there is no mutual shading within such a layer. As a result the downward flux decreases in a geometric series, which can also be represented as:

$$S(\mathrm{LAI}') = S_0 \exp(-K \cdot \mathrm{LAI}') \tag{25}$$

where LAI′ is the leaf area index reckoned from the top, K is the extinction coefficient and S is the downward flux. Above the canopy S equals S_0.

Exercise 32

Calculate the effective K and the fraction of light absorbed in the described situation for LAI = 3 and for black model layers of leaf area index 0.5, 0.1 and 0.01, respectively.

If the leaves scatter light, the radiation will penetrate deeper than with black leaves, so that the extinction coefficient is smaller. If the leaf transmission coefficient and reflection coefficient are each equal to half the scattering coefficient σ, if the sublayers are infinitesimally small and if the leaves are horizontal, the extinction coefficient equals (Goudriaan, 1977):

$$K = (1 - \sigma)^{0.5} \tag{26}$$

The reflection coefficient ϱ_c of the canopy (if LAI is large enough) is then:

$$\varrho_c = (1 - K)/(1 + K) \tag{27}$$

Exercise 33

Why must the LAI be large enough? Make a graph of ϱ_c as a function of σ. How large is crop reflection as compared to individual leaf reflection for low σ?

Green leaves absorb less green light (550 nm) than red (680 nm) or blue (450 nm) light. A dramatic increase in scattering occurs at the transition from visible to near infrared light (700 nm). This phenomenon justifies the rough distinction between these two wavelength bands. Averaged over the wavelength bands the scattering coefficient of green leaves is about 0.2 for visible radiation and about 0.8 for near-infrared radiation. Reflection and transmission share their portion rather equally.

The leaf angle influences the extinction coefficient. Model computations indicate that for an isotropic or spherical leaf angle distribution the extinction coefficient is approximately equal to:

$$K = 0.5(1 - \sigma)^{0.5}/\sin\beta \qquad \text{for direct light} \tag{28}$$

and:

$$K = 0.8(1 - \sigma)^{0.5} \qquad \text{for diffuse light} \tag{29}$$

The radiation absorbed per leaf area can be calculated by using the exponential extinction. The difference of the net radiation flux between two levels is divided by the leaf area between them.

Exercise 34

Assume a solar height of 60 degrees, overcast sky, $K_{atm} = 0.15$, LAI = 5., horizontal leaves. Calculate absorbed visible radiation per leaf area in five subsequent layers of leaf area of unity. Choose the values 30 kg ha^{-1} h^{-1} for F_m, 3 for R_d and 0.4 kg ha^{-1} h^{-1} m^2 s J^{-1} for ε, and calculate the net CO_2 assimilation rates of the five layers using Equation 13.

When the sun shines, sunlit leaf area must be separately considered from shaded area within the same layer. Also the sunlit leaf area must be classified according to the angle of incidence of the direct light on the leaf. Most of the sunlit leaf area will be light-saturated. If the leaf area index is sufficiently high the sunlit leaf area can be simply calculated as the inverse of the extinction coefficient for direct irradiation and black leaves.

Exercise 35

Why the inverse of the extinction coefficient? What is the value of the sunlit leaf area index for a horizontal and for a spherical leaf angle distribution?

Solar height depends on latitude, day of the year and time of the day as follows:

$$\sin\beta = \sin\lambda \sin\delta + \cos\lambda \cos\delta \cos(2\pi(t_h + 12)/24) \qquad (30)$$

where λ is latitude, δ declination of the sun and t_h hour of the day (be sure to use local solar time). Declination varies with the day of the year as follows:

$$\delta = -23.4\cos(2\pi(t_d + 10)/365) \qquad (31)$$

where t_d is the number of day since 1 January, and δ is expressed in degrees.

Exercise 36

Make a CSMP program that calculates daily total irradiation on clear days (DRAD) and day length (DLENG) for different latitudes and seasons.

To calculate crop photosynthesis we need to know the fractions of diffuse and direct irradiation under a clear sky. When no measurements are available, the following equation can be used as an estimate of the fraction direct irradiation out of the total:

$$\frac{S_{dir}}{S_{tot}} = \exp(-0.15/\sin\beta) \qquad (32)$$

In fact this ratio is higher for near infrared (NIR) than for PAR. A differentiated partitioning can be obtained by using an extinction coefficient of 0.1 for NIR and 0.2 for PAR, to replace 0.15 in Equation 32.

We have seen in Exercise 34 how extinction and absorption of diffuse radiation is treated. Now attention will be focussed on direct radiation, and on the diffuse scattered radiation caused by it. The direct incoming component S_1 (Fig-

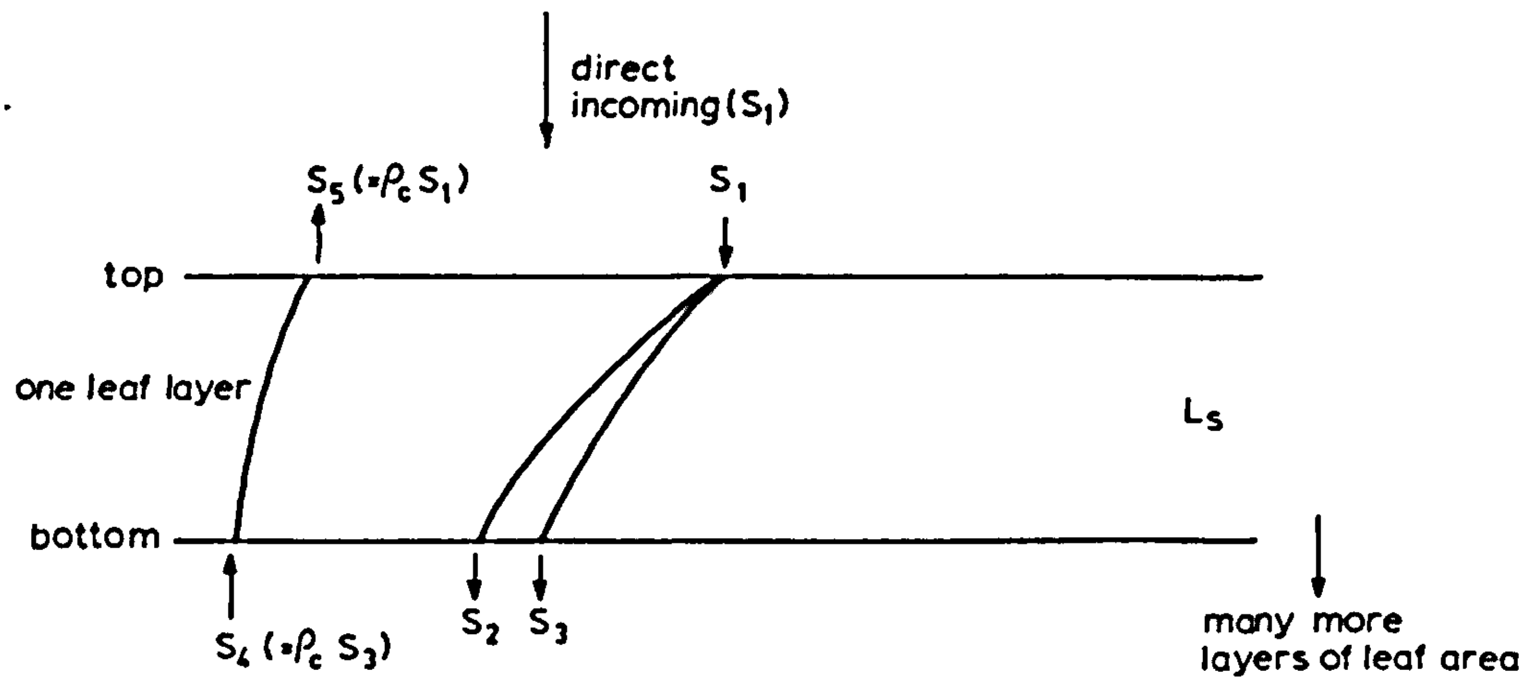

Figure 26. A scheme of the different fluxes of the direct incoming irradiation (S_1) in a leaf layer.

ure 26) causes a reflected flux $S_5 = \varrho_c S_1$. After passing the first layer with leaf area index L_s, the direct flux S_2 has been more reduced than the total downward flux S_3, because of the addition of scattered radiation.
The equations for S_2 and S_3 are:

$$S_2 = S_1 \cdot \exp(-K_{dir} \cdot L_s) \tag{33}$$

$$S_3 = S_1 \cdot \exp(-K_{dir} \cdot \sqrt{(1 - \sigma)} \cdot L_s) \tag{34}$$

Because there are many more layers of leaves underneath there is also a reflected flux entering the first layer from below:

$$S_4 = \varrho_c S_3 \tag{35}$$

By taking the balance of the incoming and outgoing fluxes we find that the flux absorbed in this layer is given by

$$S_1 + S_4 - S_3 - S_5 = (1 - \varrho_c) \cdot S_1 \cdot (1 - \exp(-K_{dir} \cdot \sqrt{(1 - \sigma)} \cdot L_s)) \tag{36}$$

The intercepted part of the direct flux is given by $S_1 - S_2$, but must be multiplied by $1 - \sigma$ to find the absorbed portion of it. In the model BACROS (Subsection 3.3.8) the absorbed direct and diffused fluxes together (Equation 36) are called VIST (for PAR) or NIRT (for NIR) and the absorbed direct fluxes only are called VISD and NIRD, respectively. The difference VIST – VISD gives the diffuse background absorption, which is common for sunlit and shaded leaves. These numbers are still expressed per ground area, and to find them on a leaf area basis they must be divided by the leaf area index of that layer, L_s.

3.2.4 Canopy photosynthesis

With Equation 13 on leaf photosynthesis and the radiation levels described above, a sufficient number of elements are presented to simulate canopy CO_2 assimilation on an instantaneous and on a daily basis.

Exercise 37

With this knowledge it is possible to construct a simulation model for net leaf photosynthesis of a crop canopy with horizontal leaves and a LAI of 5, under a clear sky. Try to formulate the most important equations yourself and study the listing.

A result of this simulation is presented in Figure 27. It is obvious that these results grossly overestimate the real respiration of the canopy. In this simple model all leaves, the heavily shaded ones too, respire at the same rate. As a result the lowest layers operate below compensation point, which would presumably lead to abscission of these leaves. Moreover, the horizontal leaf angle distribution causes a strong levelling of photosynthesis around noon.

To simulate canopy photosynthesis the sunlit leaf area in each canopy layer (see Exercise 35) must be calculated. In horizontal leaves there is only one angle of incidence of direct irradiation on individual leaves. In a spherical leaf angle distribution, the density distribution of leaf area with sine of incidence is uniform. Therefore the fraction of leaf area receiving direct irradiation between two sines of incidence is equal to their difference.

Now that we have developed the models for the instantaneous rates of radiation flux and assimilation it is only one step further to integrate the rates and

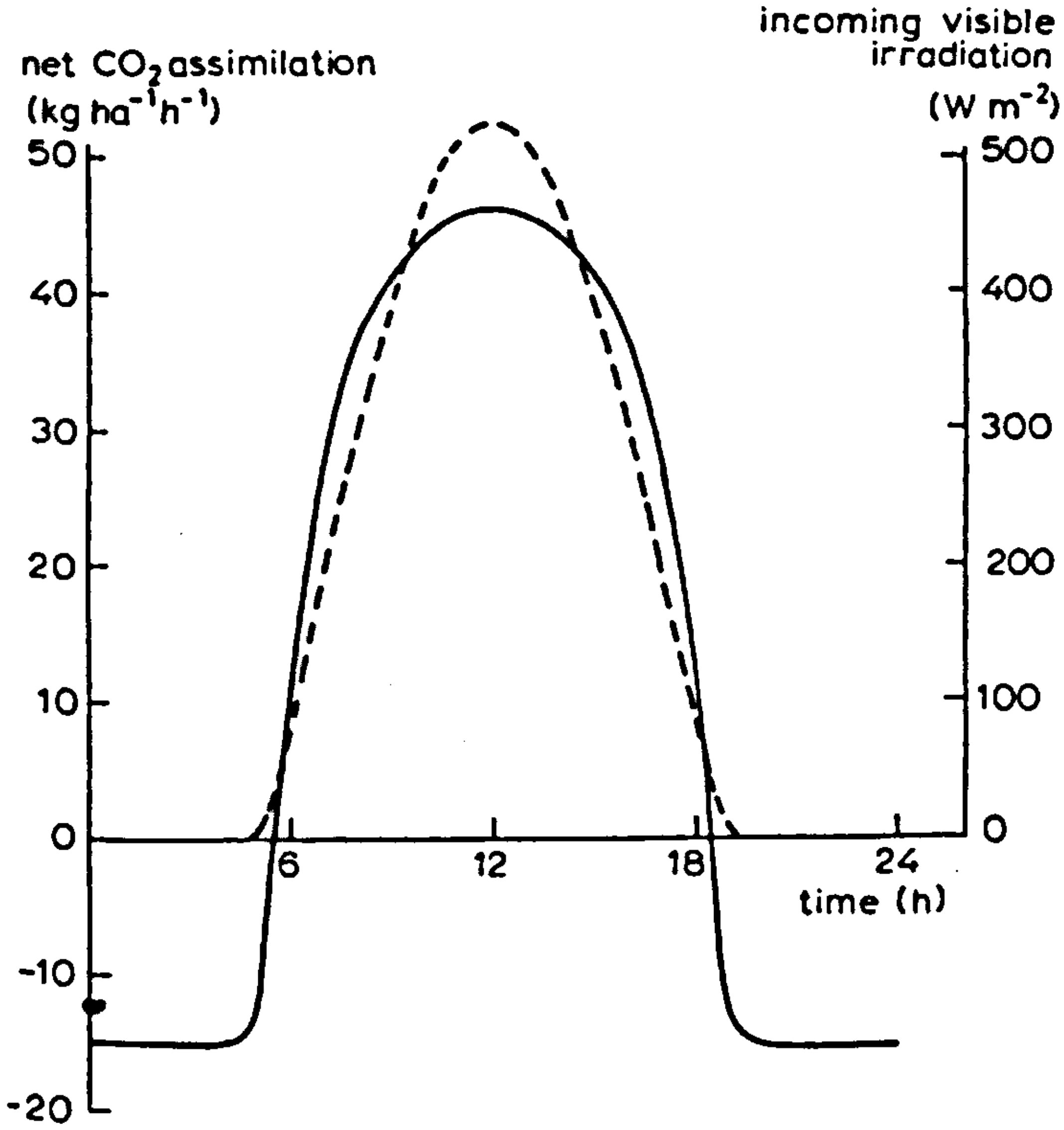

Figure 27. The simulated daily course of visible irradiation and of net CO_2 assimilation of a crop canopy with horizontal leaves and an LAI of 5, under a clear sky as simulated with a simplified example.

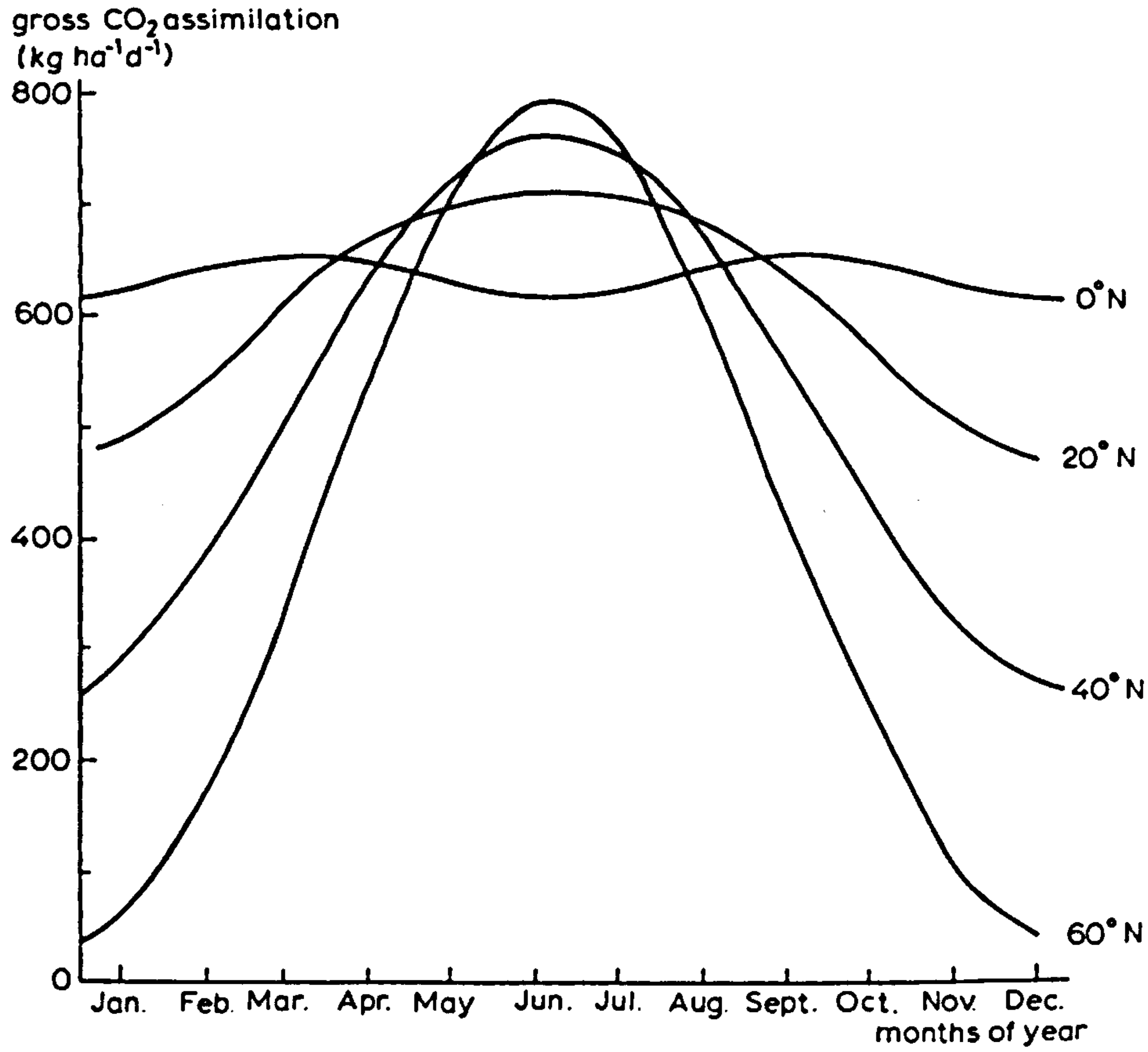

Figure 28. The simulated annual course of daily gross CO_2 assimilation on clear days for a closed green canopy at latitudes ranging from the equator to 60° N (F_m = 30 kg ha^{-1} h^{-1}; ε = 14.10^{-9} kg J^{-1}).

find the daily totals. In Figure 28 the simulated annual course of daily gross CO_2 assimilation on very clear days for a closed green canopy with F_m = 30 kg ha^{-1} h^{-1} and ε = 14.10^{-9} kg J^{-1} has been plotted for four different latitudes on earth. The major component of variation is related to daily total of irradiation as appears from Figure 29. In midsummer the same daily total of irradiation is used more efficiently, because of the longer day length. Also on overcast days the light-use efficiency is much higher at all latitudes (dashed line in Figure 29). These graphs may be used for a quick estimate of daily gross assimilation on basis of a measured daily total irradiation. In a computer model with time steps of one day it may be convenient to use a summary model in a tabular form, or in a CSMP procedure (Goudriaan & van Laar, 1978), or as a small group of sortable statements (Subsection 3.1.2).

3.2.5 Leaf energy balance and transpiration

The rate of transpiration *E* of a canopy can be simulated on basis of its energy balance. This can be done because of the strict coupling of the amounts of water and energy involved in the process: the heat of vapourization of water, λ, is 2390 J g^{-1}. The energy flux (or latent heat loss, in W m^{-2}), used for transpira-

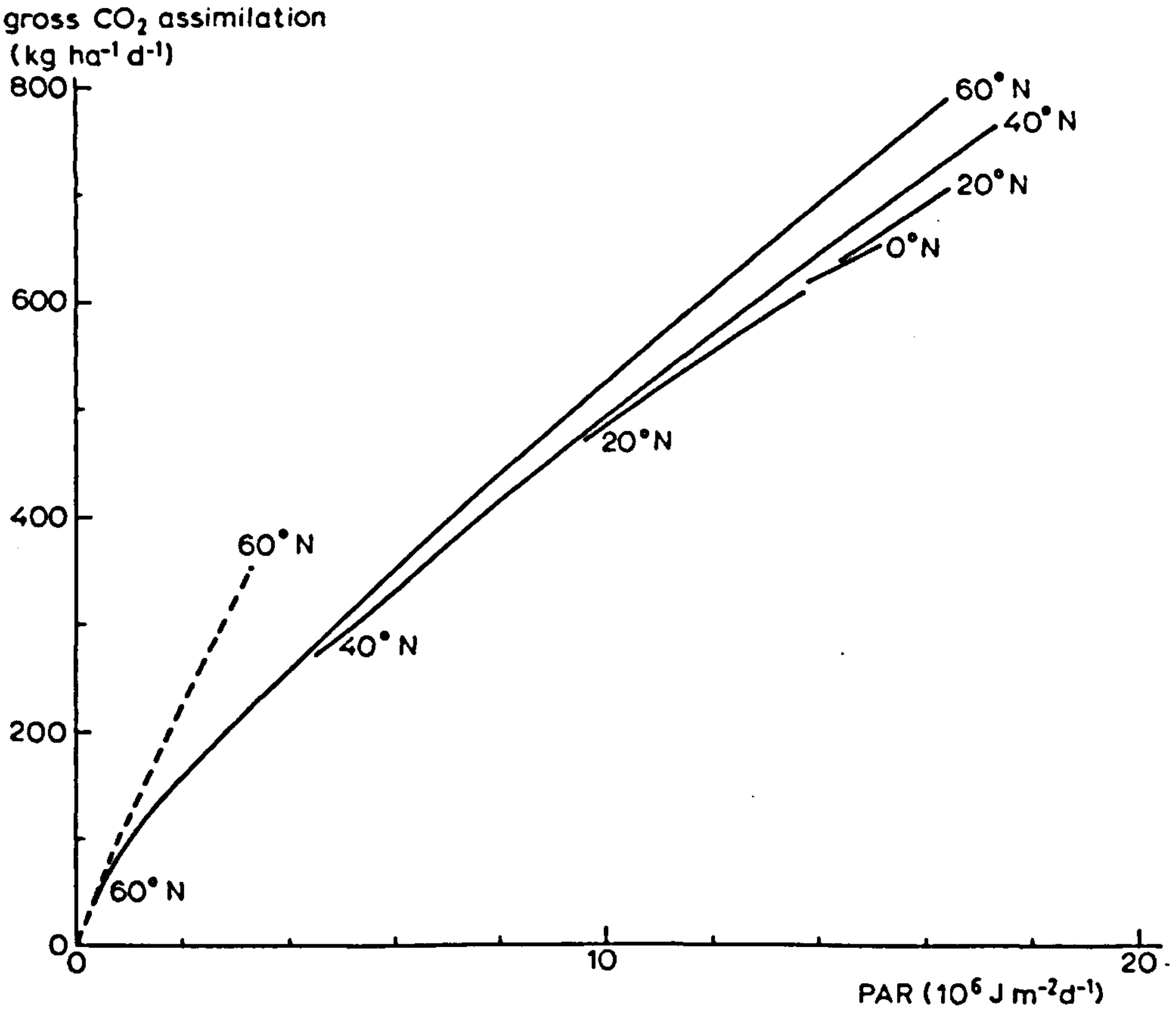

Figure 29. The relation of daily gross CO_2 assimilation on clear days with the daily total of irradiation at latitudes ranging from the equator to 60° N (solid lines) and on overcast days (broken line).

tion, is given by:

$$\lambda E = \frac{sR + \delta}{s + \gamma *} \tag{37}$$

In this equation s is the slope of the saturated vapour pressure curve at air temperature in mbar K^{-1}, R is the absorbed radiation per leaf area (all wavelengths), δ the drying power of the air (given below), and $\gamma *$ the apparent psychrometer constant. The drying power of the air is defined by:

$$\delta = \frac{(e_s - e_a)\varrho c_p}{r_b} \tag{38}$$

where e_s is the saturated vapour pressure at air temperature and e_a is the actual vapour pressure, ϱc_p is the volumetric heat capacity of the air (about 1200 J m^{-3} K^{-1}), r_b is the boundary layer resistance. The apparent psychrometer constant is defined by:

$$\gamma * = \gamma \cdot \frac{(r_b + r_l)}{r_b} \tag{39}$$

where γ is 0.63 mbar K^{-1} and r_l is the leaf resistance to water vapour. By the energy balance equation, the heat flux to the air or sensible heat loss W (in W m^{-2}), can be found:

$$W = R - \lambda E \tag{40}$$

Note that this equation neglects the small amount of energy incorporated in photosynthetic products. These equations describe the partitioning of the net absorbed radiant energy among transpiration and heat loss to the air. The equation for the temperature of the leaf (T_l) is simply:

$$T_l = T_a + W\left(\frac{r_b}{\varrho c_p}\right) \tag{41}$$

where T_a is the air temperature in °C.

The derivation of Equation 37 is based on combination of the following four equations. Since this was first done by Penman (1948), Equation 37 is often called the Penman equation.

$$R - W - \lambda E = 0 \qquad \text{(energy balance)} \tag{42}$$

$$W = \frac{(T_l - T_a)\,\varrho c_p}{r_b} \tag{43}$$

$$\lambda E = \frac{(e_s(T_l) - e_a)\,\varrho c_p}{\gamma(r_l + r_b)} \tag{44}$$

$$e_s(T_l) = e_s(T_a) + s(T_l - T_a) \tag{45}$$

The last equation is an approximation, but a good one if the leaf and air temperature are not too different. This can be checked in Table 12 where e_s and s are tabulated against temperature. In the simulation program e_s is approximated by

$$e_s = 6.11 \cdot \exp(17.4T/(T + 239)) \tag{46}$$

In Equation 42 there is no term for storage of heat in the leaf, so that equilibrium of leaf temperature is assumed.

Exercise 38

Write a simulation program to calculate leaf temperature, latent heat loss and sensible heat loss. Assume R = 200 W m^{-2}, r_b = 20 s m^{-1}, T_a = 20 °C, e_a = 15 mbar, areal heat capacity of the leaf = 10^3 J m^{-2} °C^{-1} and volumetric heat capacity ϱc_p of the air 1200 J m^{-3} °C^{-1}. Make reruns for r_l = 0, 10, 100, 1000 and 10^4 s m^{-1}, respectively. Compare a dynamic simulation where heat content of the leaf is a state variable, with a static solution according to the Penman approach.

Table 12. The saturated water vapour pressure e_s, as a function of temperature. The results of an analytical expression to approximate e_s are also given. The last column gives the derivate of e_s with respect to temperature.

T (°C)	e_s (mbar)	$6.11 \cdot \exp(17.47T/(T + 239))$	s (mbar K^{-1})
0	6.11	6.11	0.445
5	8.72	8.73	0.609
10	12.27	12.29	0.823
15	17.04	17.07	1.10
20	23.37	23.42	1.45
25	31.67	31.74	1.89
30	42.43	42.54	2.44
35	56.24	56.40	3.12
40	73.78	74.04	3.94

It is also possible to use an iterative technique to solve the simultaneous Equations 42-46. In Section 2.3 some iteration methods have been discussed that can be applied here.

Exercise 39

Try the IMPLicit loop of CSMP and the halving/doubling method for the situation as described in Exercise 38.

3.2.6 *Leaf conductance and CO_2 assimilation*

Because water vapour and CO_2 pass through the same stomatal pores, transpiration and assimilation are tied together. The direction of the causal relationship (of the information flow) depends on the circumstances. The situation is obvious for high light and low CO_2 conditions, when we may safely assume that diffusion of CO_2 is a limiting factor for the net assimilation rate. In a simple resistance scheme leaf resistance and mesophyll resistance (which consists of a small transport component and a dominating carboxylation component) are series-circuited between the external (C_e) and internal CO_2 concentration (C_i). Then a hyperbolic relation between net assimilation and leaf conductance should be expected. Experimentally such a result is hard to obtain, because almost every action to change leaf conductance will also independently change net assimilation, and vice versa. Only when stomatal oscillations occur in a constant environment can a hyperbolic relation be observed (Farquhar et al., 1980).

When assimilation and conductance are simultaneously affected by the environmental conditions often a linear relation exists between them (Goudriaan & van Laar, 1978; Wong et al., 1979; Louwerse, 1980). Since the drop in CO_2 concentration across the leaf resistance is proportional to the ratio of assimilation to conductance, the slope of the line indicates an asymptotic value of the drop. Typically this drop is about twice as high in C_4 plants as in C_3 plants. In maize and some other C_4 plants, the internal CO_2 concentration in full light is about 0.4 of the external value, whereas in C_3 plants it is at least 0.7 of the external concentration. Whenever this relation exists it offers an easy way of modelling stomatal behaviour. The method consists of first calculating the net assimilation rate of the leaf, and then deriving the leaf resistance required to obtain a preset value of the internal CO_2 concentration. This resistance is then used in the calculation of the leaf transpiration rate after division by a factor of 1.6 to allow for the faster diffusion of H_2O compared to CO_2. The role of the cuticle is not quite clear. Here the cuticular conductance of CO_2 is assumed to be the same as for water vapour divided by 1.6. Therefore its treatment is the same as stomatal conductance, and together they give rise to the leaf conductance. The factor to account for the difference in the rate of diffusion in the boundary layer resistance is 1.3 (Monteith, 1973). The resulting equation for r_l (water vapour) is:

$$r_l = ((C_e - \mathrm{C_i})/F_n - 1.3 \cdot r_b)/1.6 \tag{47}$$

Equation 47 links the rate of net CO_2 assimilation of individual leaves to their conductance, and hence to their rate of transpiration (Equations 37 and 39). However, as a result of the regulating mechanism that maintains a more or less constant concentration of CO_2 in the stomatal cavity under most light levels, the equations are also approximately valid when applied to a whole canopy. The leaf resistance r_l becomes then the canopy resistance r_c, and C_e the average concentration of CO_2 in the air within the canopy. When C_e is measured above the canopy, where it is more constant, an additional resistance for transport of water and CO_2 must accounted for: the so-called turbulence resistance (r_t). Its value is in the order of 50 s m^{-1}, and is equal for water vapour and CO_2. In this case, $r_t + 1.3 \cdot r_b$ replaces $1.3 \cdot r_b$ in Equation 47. A detailed discussion of the computation of r_t is presented elsewhere (van Laar et al., 1983; Goudriaan, 1977).

This regulation mechanism accounts for opening of stomata with increasing light, and also with a decreasing external CO_2 concentration. A complication occurs when the stomatal resistance required for photosynthesis is smaller than is permitted by the actual water status of the plant. Under water stress mesophyll resistance also increases, so that a further drop in internal CO_2 concentration is not likely to occur. The best modelling procedure is therefore to invert the used relationship and to recalculate net assimilation as:

$$F_n = (C_e - C_i)/(1.6 \cdot r_l + 1.3 \cdot r_b) \tag{48}$$

In this equation r_b and r_l are resistances to water vapour, and r_l is the lowest value permitted by the water status of the plant. In BACROS this value (called SRW) is a function of the relative water content of the crop (see Subsection

3.3.7).

Exercise 40

Make a graph of computed r_l versus absorbed PAR by using the Equations 13 and 47. Do it for a C_3 plant and also for a C_4 plant, assuming a value of C_i at 210 and 120 cm³ m⁻³, respectively.

Average values for the variables in the equations are:

	F_m	R_d	ε	C_i	C_e	r_b
C_3	30	4	0.4	210	330	10
C_4	60	4	0.5	120	330	10

The observed PAR may range from 0 to 300 W m^{-1}.

Exercise 41

Calculate the transpiration-assimilation ratio of a leaf, expressed in weight H_2O/weight CO_2 when $T_a = T_l = 20$ °C, $e_a = 15$ mbar, the external CO_2 concentration is 600 mg m^{-3} and the internal 400 mg m^{-3} (how much are these concentrations in cm^3 m^{-3}?). Convert the vapour pressure to weight per m^3 by using the density of air at 1 bar and 20 °C (1200 g m^{-3}) and the molecular weights of water (18) and air (average 29).