3.3 The relation between water use and crop production

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3.3.1 The concept of the transpiration coefficient

To allow entrance of CO_2 into the plant, necessary for the assimilatory process, plants must have an open connection to the atmosphere. This connection is provided by small openings in the epidermis of the leaves, the stomata. In Figure 31, a schematic representation of a vertical section of a leaf is given, illustrating the position of the stomata. In this case stomata are only present on the lower side of the leaves, but in other species they may also be present on the upper side. Through these stomata, exchange of CO_2 takes places by diffusion.

The rate of diffusion can be described by a general Ohm's law equation:
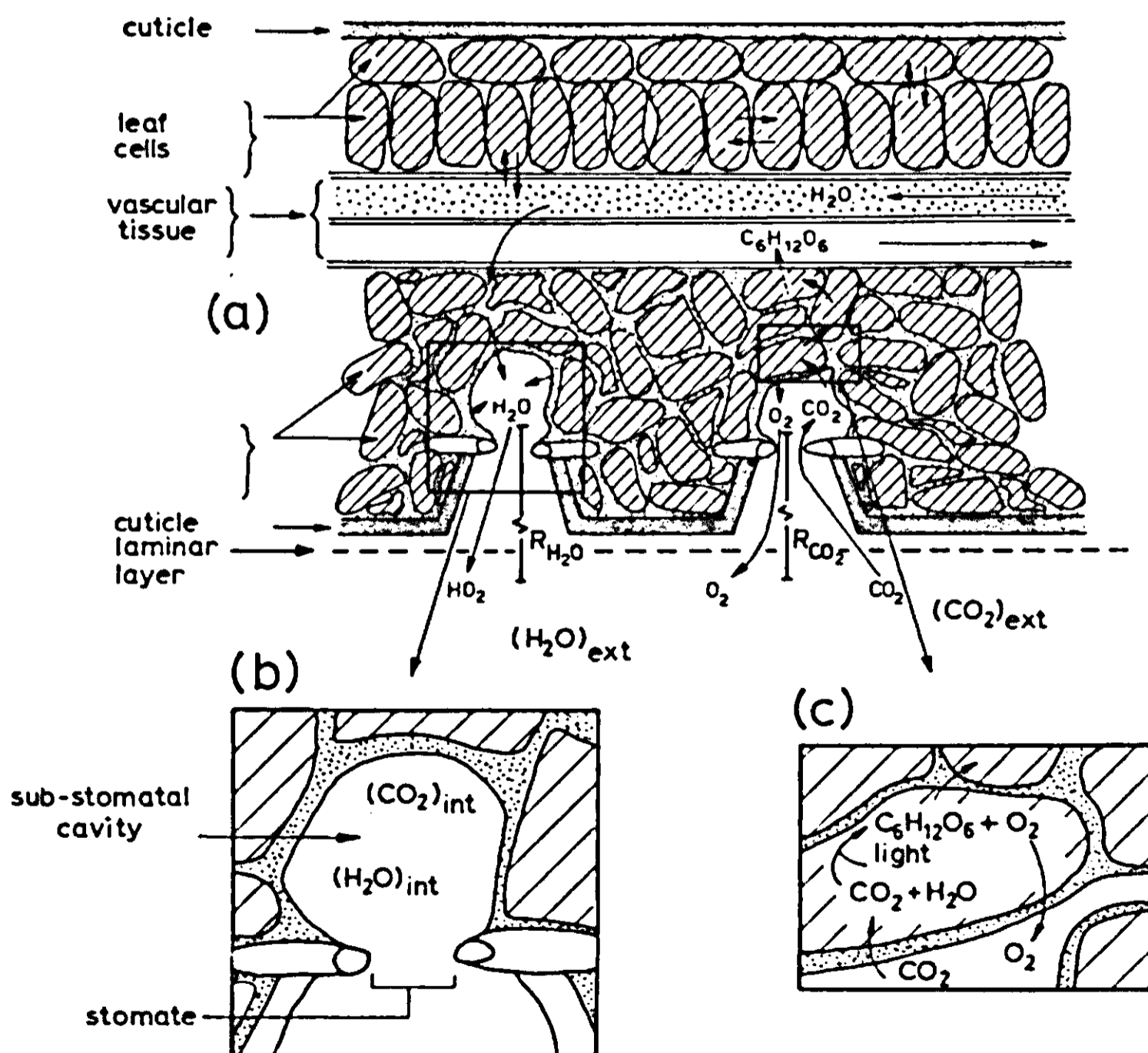

Figure 31. Schematic representation of a vertical section of a leaf (a). An enlargement showing a stomate (b) and an enlargement showing a photosynthetically active cell (c).

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$$V_{CO_2} = \frac{(CO_2)_{ext} - (CO_2)_{int}}{R_{CO_2}} \tag{65}$$

where

V_{CO_2}	is the rate of CO_2 diffusion into the plant ($kg\ m^{-2}s^{-1}$)
$(CO_2)_{ext}$	is the concentration of CO_2 in the external air ($kg\ m^{-3}$)
$(CO_2)_{int}$	is the concentration of CO_2 in the substomatal cavity ($kg\ m^{-3}$)
R_{CO_2}	is the resistance to CO_2 diffusion ($s\ m^{-1}$)

The total resistance to CO_2 diffusion is composed of two resistances in series: the resistance offered by a layer of still air, the boundary layer, just above the surface of the leaf; and the resistance offered by the stomata. In the total assimilation process a third resistance is of importance, that between the substomatal cavity and the chloroplasts, where the actual reduction of CO_2 takes place (Figure 31c). This resistance is referred to as the carboxylation resistance or the mesophyll resistance. In general, the latter resistance is small compared to the sum of the other two. The walls of the substomatal cavity (Figure 31b) are wet, hence the air inside the cavity is water-vapour saturated. When the stomata are open, this air is exposed to the atmosphere, which is normally not saturated with water vapour. The result is that water vapour diffuses from the substomatal cavity into the atmosphere. The rate of diffusion can be described analogous to Equation 65:

$$V_{H_2O} = \frac{(H_2O)_{int} - (H_2O)_{ext}}{R_{H_2O}} \tag{66}$$

V_{H_2O}	is the rate of diffusion of water vapour into the atmosphere ($kg\ m^{-2}s^{-1}$)
$(H_2O)_{int}$	is the concentration of water vapour inside the substomatal cavity, equal to the saturated vapour pressure at leaf temperature ($kg\ m^{-3}$)
$(H_2O)_{ext}$	is the concentration of water vapour in the atmosphere ($kg\ m^{-3}$
R_{H_2O}	is the resistance to water vapour diffusion ($s\ m^{-1}$)

Figure 31a illustrates that the resistance to diffusion of CO_2 from the substomatal cavity to the atmosphere, R_{CO_2}, is equal to that to diffusion of water vapour along the same pathway. Numerically the values differ, because CO_2 molecules are larger than H_2O molecules and the diffusion resistance is dependent on molecule size. Under the same conditions, R_{CO_2} is 1.66 times greater than R_{H_2O}. Taking this into account, it follows from Equations 65 and 66 that a relation exists between transpiration (water use) by a canopy and CO_2 assimilation. As explained in Section 2.1, the production of structural plant dry matter is directly proportional to CO_2 assimilation, adjusted for the respira-

tory losses. Because the latter depend also on the amount of dry matter present, it is not a fixed proportion of the gross CO_2 assimilation. Therefore, two different definitions are introduced to characterize the relation between water use and production: (i) the ratio of transpiration to assimilation (TAR), expressed in kg water transpired per kg of CO_2 fixed, (ii) the transpiration coefficient (TRC), expressed in kg water transpired per unit dry matter produced. The transpiration coefficient is not only dependent on the relation between assimilation and transpiration, but also on the quantity and composition of plant material present.

The relation between water use and dry-matter production was recognized already by early investigators in agricultural science and many experiments have been carried out to determine the exact dependencies between the two variables. Much of the earliest work was summarized by Briggs & Shantz (1913; 1914), who expressed the relation between water use and dry-matter production in the term 'water requirement', defined as the amount of water necessary to produce one unit of dry-matter weight (i.e. the equivalent of the transpiration coefficient). They established that differences exist between species, but also that for the same species different values were obtained in different years or in different environments. One of the main reasons for the latter variation may be deduced from a comparison of Equations 65 and 66. At a given value of R, that is at a fixed stomatal opening and a fixed thickness of the boundary layer, the rate of water loss will be higher when the difference in concentration of water vapour between the atmosphere and the substomatal cavity is larger. Thus, when the relative humidity in the atmosphere is lower, and the leaf temperature higher, more water will be lost. The gradient in CO_2 is hardly variable, because the CO_2 concentration in the atmosphere is fairly constant.

In a subsequent analysis, de Wit (1958) accounted for the influences of·

Table 35. Transpiration coefficients for maize, variety North Western Dent measured in pots, in Akron Colorado in different years.

Year	Production (g)	Transpiration (kg)	Transpiration coefficient (kg kg^{-1})
1911	160.7	58.8	365.9
1912	432.0	117.9	272.7
1913	356.3	141.1	396.0
1914	304.3	111.5	366.4
1915	112.0	28.4	253.6
1916	180.5	90.0	498.6
1917	336.8	120.5	357.8

(Source: Briggs & Shantz, 1913; 1914; Shantz & Piemeisel, 1927)

environmental conditions by relating production not directly to water use, but correcting the latter for the average evaporative demand (potential evapotranspiration, Section 3.1) during the growing period. This procedure is illustrated by the data in Table 35, giving values of the transpiration coefficient for maize grown in containers during various years. These values vary by a factor of almost two. In Figure 32 the production data are plotted against the ratio of total water loss and average evaporative demand during each growing period. The results illustrate that most of the variability in transpiration coefficient was indeed due to the varying evaporative demand during the various growing periods. This indicates that although dry-matter production and water use are closely associated, the actual quantitative relationships may be strongly modified by environmental conditions.

As mentioned before, also considerable differences were established between species growing under the same conditions. These differences mainly reflect different photosynthetic pathways, as explained in Section 2.1. The higher affinity to CO_2 of the carboxylating enzyme in C_4 species causes at a
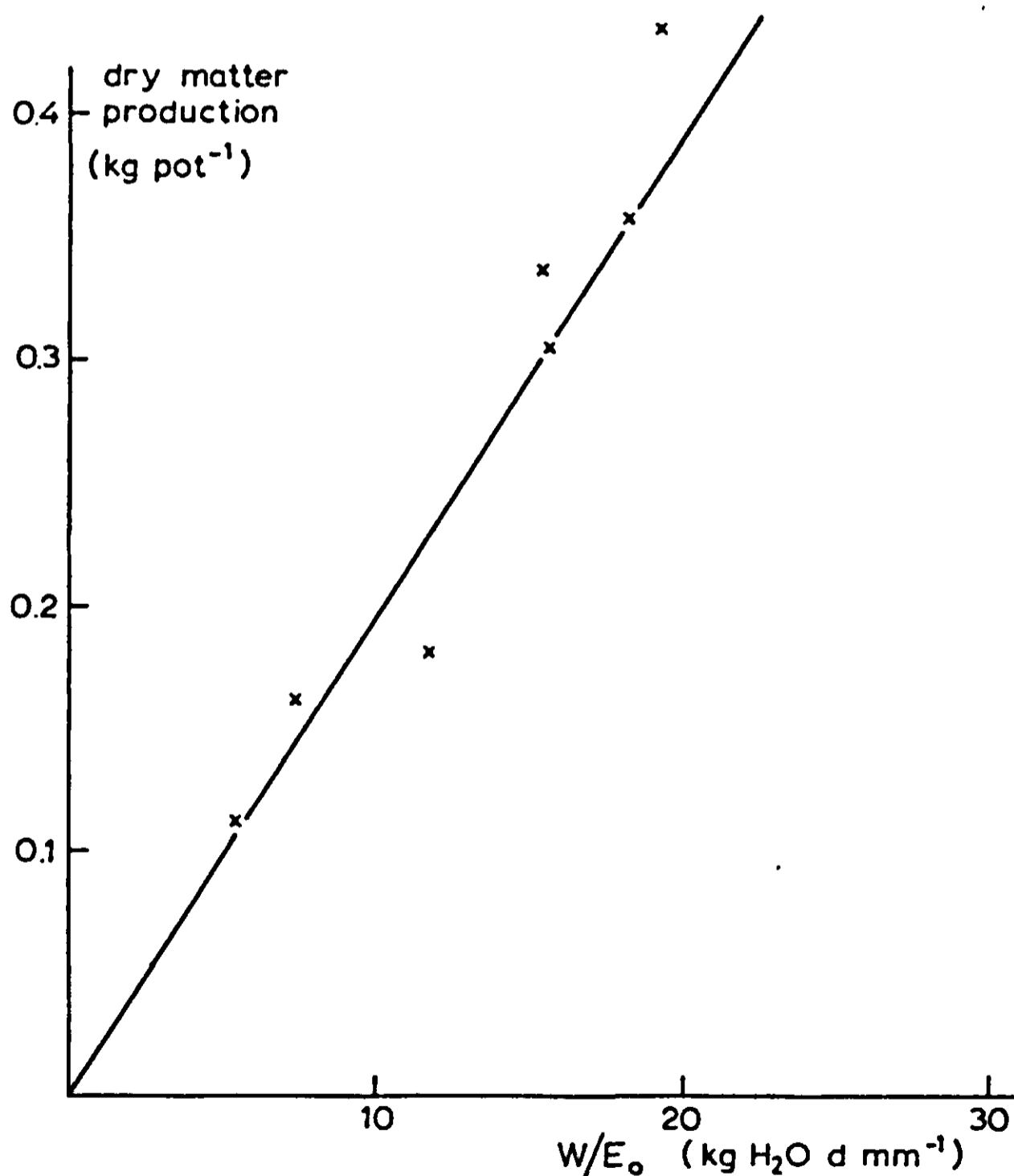

Figure 32. Relation between dry matter production and the ratio of transpiration to free water evaporation for maize cv. Northwestern Dent grown in pots. (Source: Briggs & Shantz, 1914)

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given stomatal aperture, and hence a fixed transpiration rate, a higher rate of CO_2 assimilation in plants of the C_4 type than in plants of the C_3 type. The transpiration/assimilation ratio is therefore higher in species having the latter photosynthetic pathway.

Another source of variability in the transpiration coefficient is the type of stomatal control of the canopy. Under certain conditions, the assimilation process is controlled in such a way that the CO_2 concentration in the substomatal cavity $((CO_2)_{int})$ is maintained at a constant level over a wide range of assimilation rates through adaptation of the stomatal opening (Goudriaan & van Laar 1978b). In terms of Equation 65 it means that a change in the gradient $(CO_2)_{ext} - (CO_2)_{int}$ is accompanied by a proportional change in the value of R_{CO_2}, so that V_{CO_2} remains constant. This is illustrated in Figure 33 where the relation between between V_{CO_2} and $1/R_{CO_2}$ is given for maize plants grown under controlled conditions. The result of this mechanism is that, for instance, under conditions of low light intensities, where CO_2 assimilation is determined by energy availability, plants having the regulatory mechanism
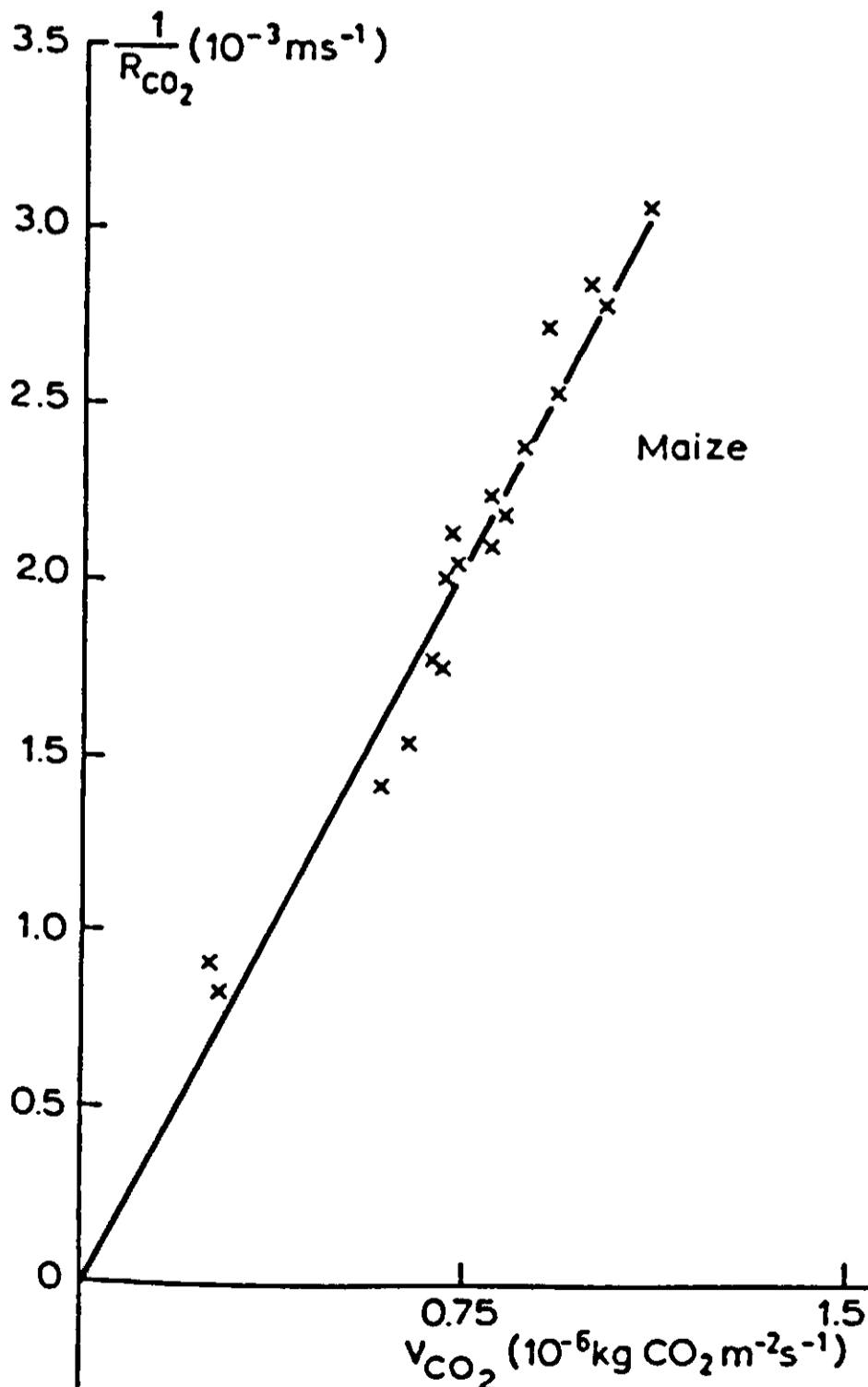

Figure 33. Relation between net CO_2 assimilation rate (v_{CO_2}) and total conductance for CO_2 for maize leaves.

will partially close their stomata, thus effectively reducing transpiration. Therefore plants having this regulatory mechanism exhibit a lower transpiration/assimilation ratio and hence a lower transpiration coefficient than plants in which the mechanism is absent. At high light intensities, the rate of CO_2 diffusion is determining assimilation. That rate is governed by the CO_2 gradient and, as the internal CO_2 concentration is higher in C_3 species than in C_4 species, again a difference in transpiration coefficient shows up at high light intensities.

Thus, in a schematized set-up, values of the transpiration/assimilation ratio in kg H_2O transpired per kg CO_2 fixed (or per kg CH_2O produced) can be determined for various conditions, i.e. for C_3 and C_4 species separately, for both groups further subdivided in regulating and non-regulating crops, and finally at different levels of vapour pressure deficit. An example of such data, calculated with a detailed simulation model of canopy assimilation and transpiration (de Wit et al., 1978), is given in Table 36.

3.3.2 Application of the transpiration coefficient

On the basis of crop characteristics and climatic conditions, potential daily gross CO_2 assimilation (F_{gc}) in kg ha^{-1} d^{-1} may be obtained for any arbitrary combination of time and place from Tables 1 and 2. By considering the average vapour pressure deficit during the period of interest, a value of the transpiration/assimilation ratio (TAR) may then be selected from Table 36. By multiplying the two values, the potential rate of transpiration is obtained in kg ha^{-1} d^{-1}.

Table 36. Transpiration/assimilation ratio (kg water per kg carbon dioxide) for various conditions.

C_3 species			
relative humidity (%)	25	50	75
R	84	70	56
NR	150	116	90
C_4 species			
R	57	45	35
NR	120	95	72

R denotes regulating stomata, NR non-regulating

Exercise 41

What is the conversion factor for the conversion of transpiration in kg ha^{-1} d^{-1} to the more common unit of mm d^{-1}.

In Section 3.1 potential evapotranspiration was calculated by Penman's combination method. In the case of a fully closed crop canopy, where soil evaporation is negligible, that value equals potential transpiration. In the preceding subsection it is argued that the value of the transpiration-assimilation ratio depends on plant type and stomatal behaviour. The considerable success of the Penman equation for the estimation of potential transpiration must be attributed to the fact that its value is very close to the value calculated for conditions of regulating stomata, which seems to be the most common field behaviour. The difference in transpiration-assimilation ratio between C$_3$ and C$_4$ species is mainly the result of differences in assimilation rate, transpiration being virtually identical, especially under high light conditions. In the situation where a crop has non-regulating stomata, the Penman equation underestimates potential crop transpiration. Correction factors for such conditions have been calculated, by comparing Penman values to transpiration values, calculated with a detailed physiologically based model of crop growth. The results are tabulated in Table 37 with a subdivision in C$_3$ and C$_4$ species and for overcast and clear conditions.

Under conditions of temporary water shortage in the soil, leading to partial stomatal closure, assimilation and transpiration are affected approximately to the same extent, hence the value of the transpiration coefficient remains constant. This characteristic permits an evaluation of the influence of moisture shortage on production. After determining potential transpiration, the amount of moisture available for plant uptake is determined from the soil-water balance, presented in Section 3.2. If that amount is lower than potential transpiration, actual transpiration falls short of the potential. Actual CO$_2$

Table 37. Correction factors for multiplying the Penman evapotranspiration to obtain potential crop transpiration in the absence of stomatal regulation.

Species	Sky condition	
	clear	overcast
C$_3$	1.47	2.1
C$_4$	1.6	3.0

assimilation (P_{gc}) is then directly determined from the amount of water transpired, by dividing the latter value by the earlier determined transpiration/assimilation ratio, hence $P_{gc} = T/TAR$, or

$P_{gc} = F_{gc} \times T/T_m$ (Section 3.2).

Exercise 42
Estimate the total dry-matter production for a hypothetical C_4 crop, exhibiting stomatal regulation, when 200 mm of moisture is available for transpiration during the growing period. Average relative humidity during that period is 75%. What would be the result if it was a C_3 crop lacking stomatal regulation?

3.3.3 The influence of nutritional status

A basic problem related to water-use efficiency is the influence of nutrient shortage on the relation between production and water use. The constancy of the transpiration coefficient, discussed in the preceding subsection, was restricted by de Wit (1958) in his analysis to situations where the 'nutrient status is not too low', and Viets (1962) concluded that 'all evidence indicates, that water use efficiency can be greatly increased, if fertilizers increase yield'.

The latter conclusion seems to be confirmed by experimental results obtained in natural herbaceous vegetation in the northern Negev desert of Israel (Figure 34), where the rate of water loss from the soil was practically identical under the nitrogen fertilized vegetation and the non-nitrogen fertilized one, although the former was growing at a substantially higher rate. Opposite results were, however, obtained in the Sahelian zone, where increased growth rates of natural pasture, resulting from fertilizer application, were accompanied by higher rates of transpiration (Stroosnijder & Koné, 1982).

For a more fundamental approach to the problem, the basic processes of CO_2 assimilation and transpiration must be considered. This is most conveniently done by measuring both exchange processes simultaneously under controlled conditions. The results of such an experiment are presented in Figure 35 for individual attached leaves of maize plants grown in the greenhouse, under both optimum and sub-optimum supply of nitrogen. The measured rate of net CO_2 assimilation is plotted versus the total conductance for water vapour exchange, that is the inverse of the sum of stomatal resistance and boundary layer resistance (R_{H_2O} in Equation 66), which is thus a direct measure of transpiration. The plants optimally supplied with nitrogen exhibit a markedly higher rate of net CO_2 assimilation than the plants under sub-optimum N supply, but they show a proportional increase in conductance for
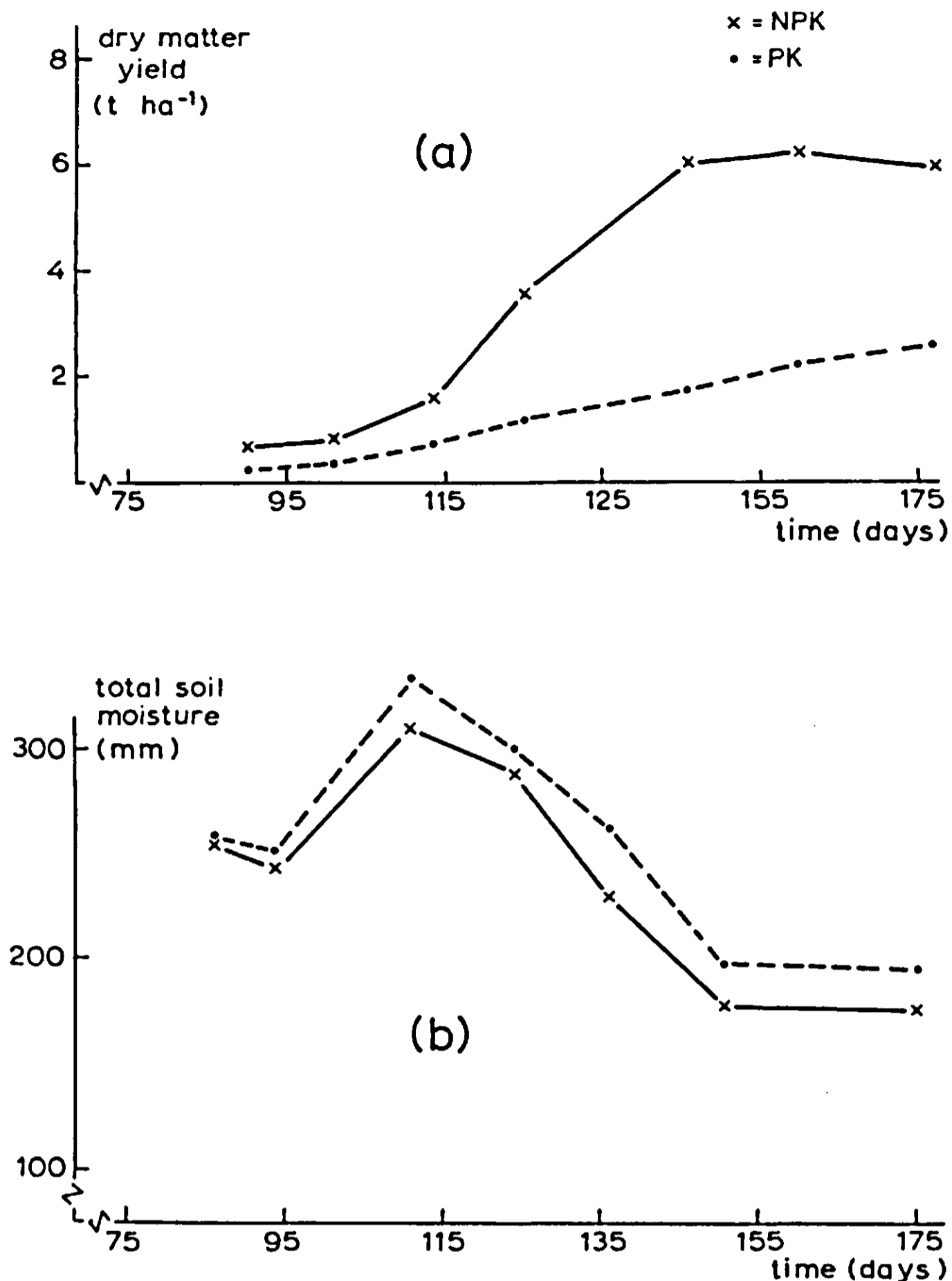
Figure 34. Cumulative dry matter accumulation of natural herbaceous vegetation with and without N fertilizer application (a) and time course of total soil moisture in the root zone (0−180 cm) of this vegetation (b). Data from Migda, Israel 1972/1973.

water vapour, hence a virtually constant assimilation/transpiration ratio. This behaviour is thus in accordance with that of the plants growing under the Sahelian conditions, and suggests, again, the existence of stomatal control by the internal CO_2 concentration, i.e. impaired assimilation due to nitrogen shortage is reflected in partial stomatal closure.

The slope of the line in Figure 35 represents the CO_2 gradient over the relevant resistance, i.e. the drop in CO_2 concentration from the atmosphere to the substomatal cavity. When the value of P_n at any point is divided by the relevant value of $1/R_{H_2O}$ (the latter multiplied by 1.66 to account for the
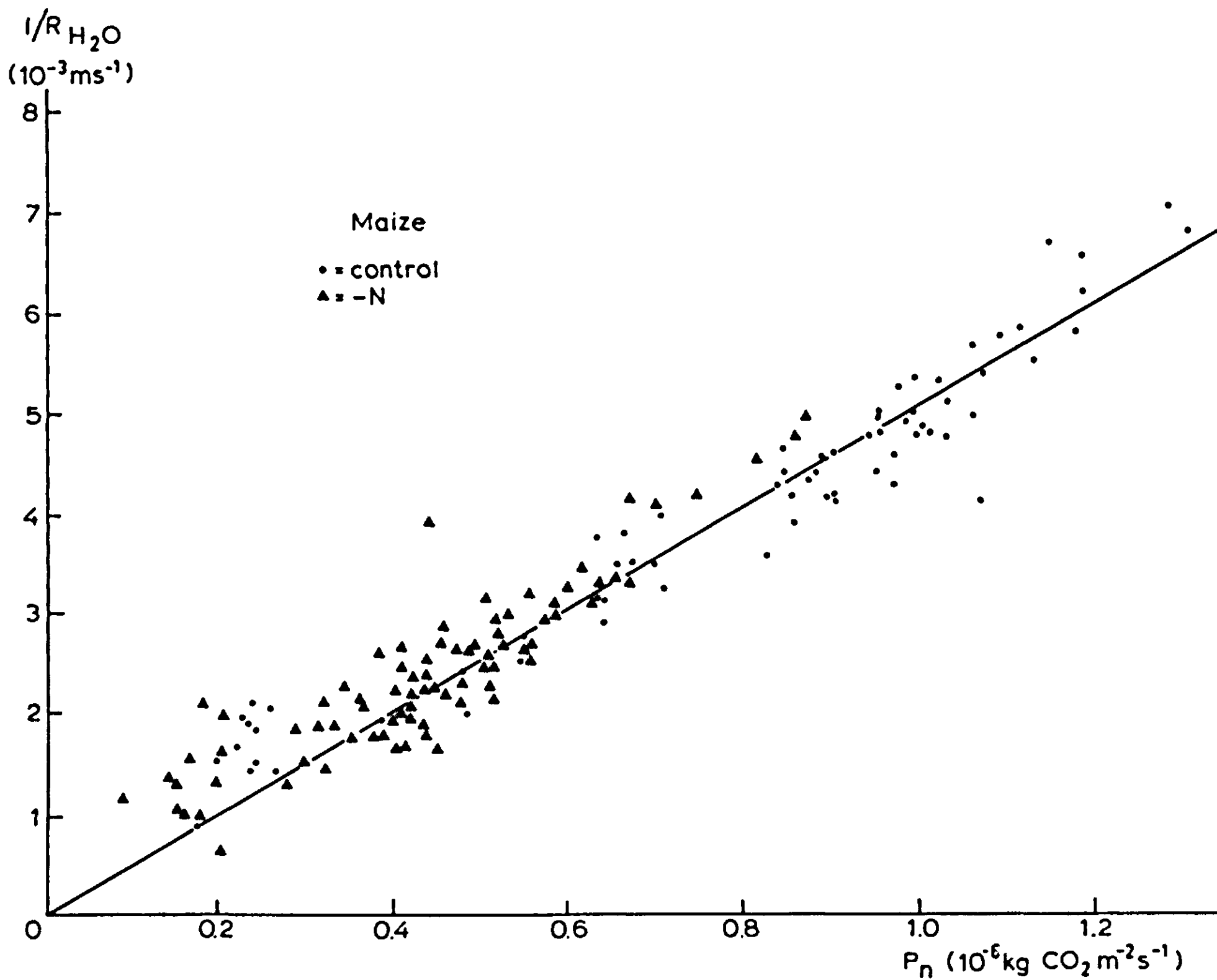
Figure 35. Relation between net assimilation rate, P_n, and total conductance for water vapour ($1/R_{H_2O}$) for leaves, grown under optimal and suboptimal nitrogen supply.

difference in molecule size between H_2O and CO_2) the drop in concentration is found.

Exercise 43

What is the concentration gradient for the maize leaves of Figure 33?
If the CO_2 concentration in the atmosphere is 330 vppm, what is the concentration in the substomatal cavity? Note that 1 mol of a gas at 20 °C has a volume of 24 dm³.

In Figure 36, data similar to those for maize in Figure 35 are shown for Phalaris minor, a C_3 type grass species from the natural vegetation in the northern Negev. Here a tendency exists for a more favourable assimilation-
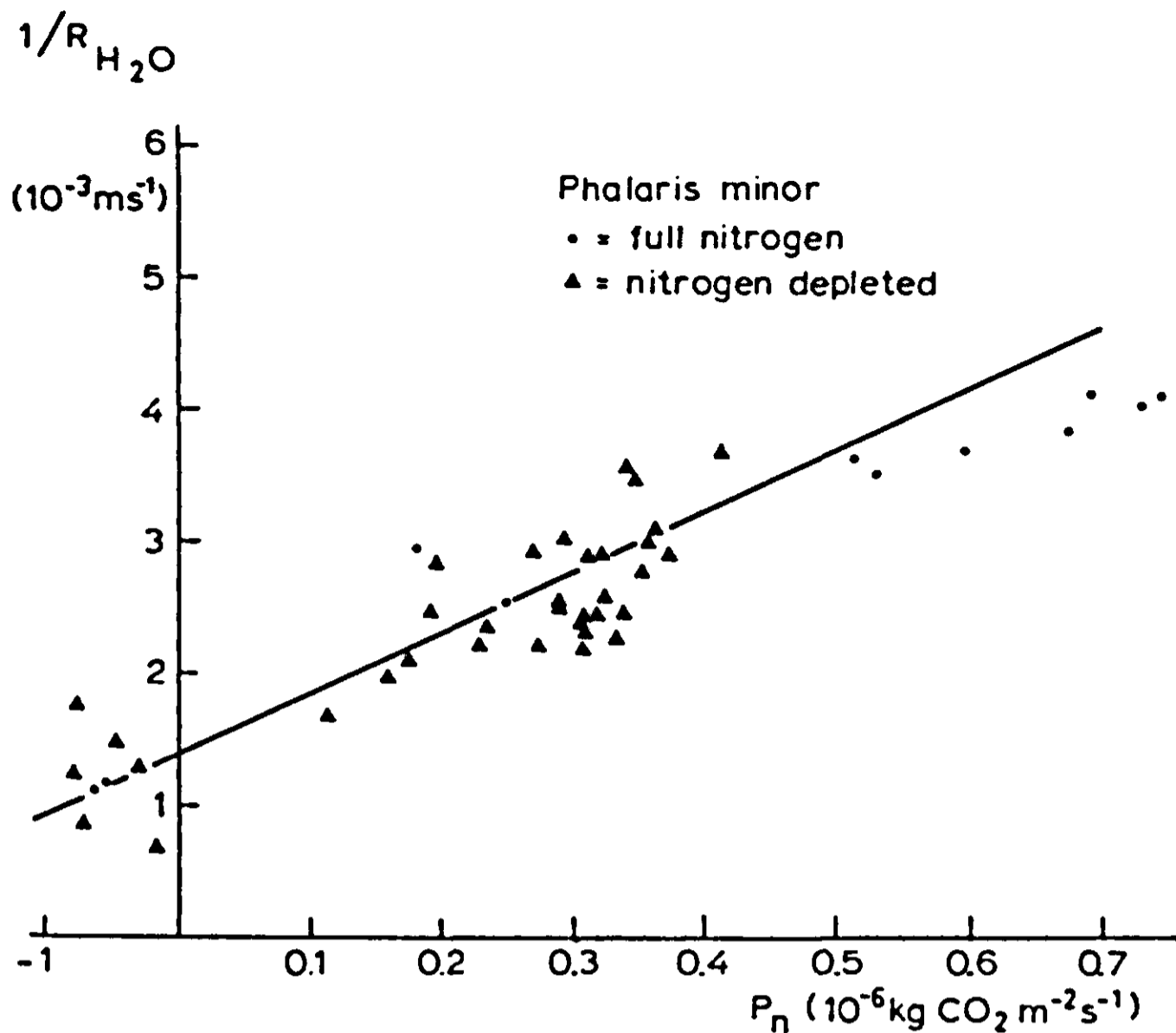
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Figure 36. Relation between net assimilation rate P_n and total conductance for water vapour* $(1/R_{H_2O})$ for leaves of *Phalaris minor*, grown with optimal and suboptimal nitrogen supply.

transpiration ratio in plants optimally supplied with nitrogen, although the evidence is not overwhelming. It could be, however, that at light intensities higher than those used in the measuring equipment, which are prevalent under field conditions, a more pronounced difference in assimilation-transpiration ratio would show up. In general, however, there are no strong indications for large differences in transpiration-assimilation ratio under different nutritional conditions. Therefore, in the present approach these differences are not taken into account.

3.3.4 Transpiration coefficient and water-use efficiency

Although the relation between transpiration and assimilation may not vary under different nutritional conditions, overall water-use efficiency, expressed as dry-matter production per unit of moisture applied, either because of rain or by irrigation, may well be affected. The vegetation growing at suboptimum nitrogen supply accumulates dry matter at a much slower rate (Figure 34) than the fertilized vegetation, which may lead to prolonged periods with incomplete soil cover. During those periods appreciable losses of moisture may occur by direct evaporation from the soil surface, especially when the surface remains wet by intermittent rain (Section 3.2). Such water losses do not contri-
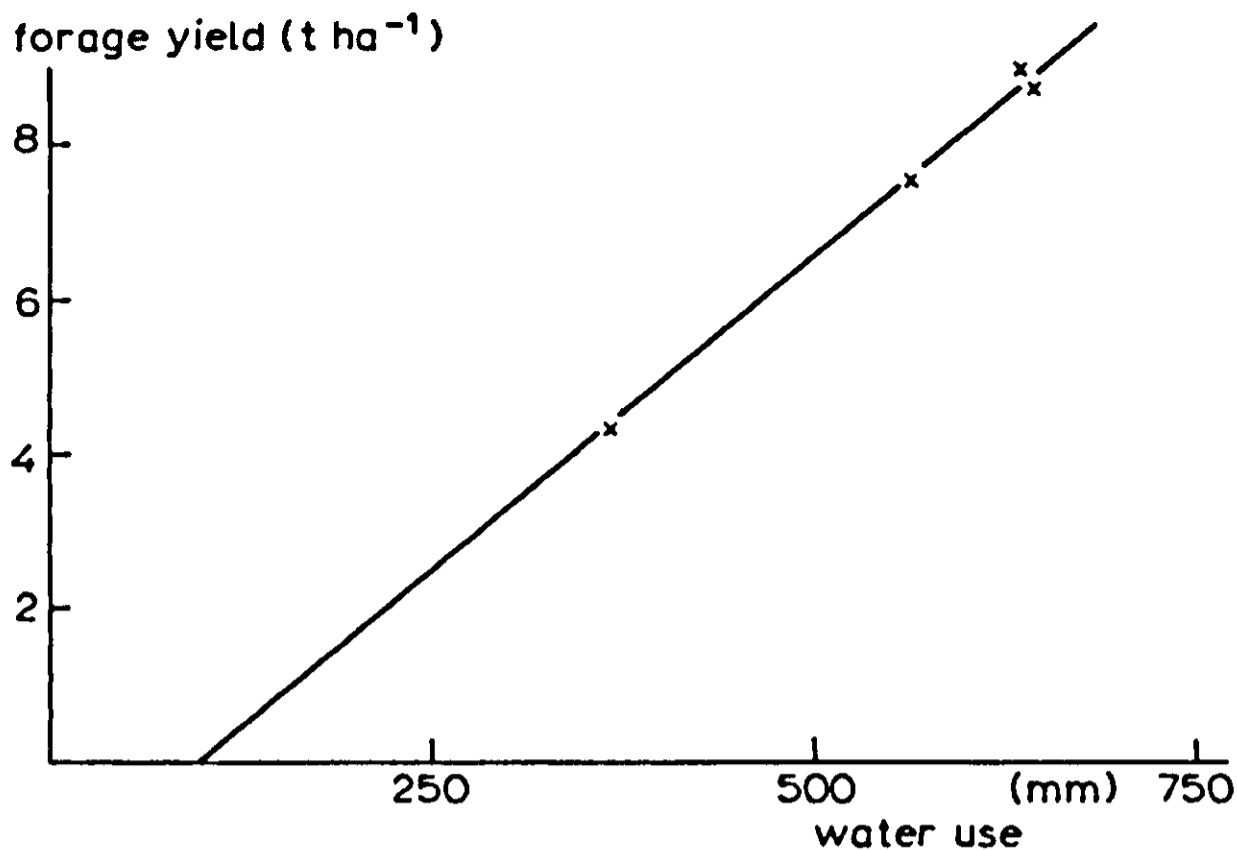
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Figure 37. Relation between total forage yield and water use for alfalfa. (Source: Bauder & Bauer, 1978)

bute to production and must therefore be substracted before calculating the transpiration coefficient. This is illustrated in Table 38 and Figure 37, which refer to an irrigation experiment with alfalfa (Bauder & Bauer, 1978).

The tabulated data would suggest a decreasing transpiration coefficient with increasing application of irrigation. Figure 37 shows, however, that all points fit the same straight line, indicating a constant transpiration coefficient. The intercept with the x axis represents the amount of non-productive water loss, i.e. direct evaporation from the soil surface in this case, but it may also comprise deep drainage under other conditions. Such a graphical analysis is therefore a better basis for explanation.

Table 38. Forage yield, water use and transpiration coefficient (kg water per kg dry matter) for alfalfa.

Treatment	Forage yield (kg ha^{-1})	Water use (mm)	Water use efficiency (kg kg^{-1})
W1	4324	363	839
W2	7536	561	744
W3	8994	635	706
W4	8747	643	735

(Source: Bauder & Bauer, 1978).

Exercise 44
What is the transpiration coefficient for the alfalfa of Figure 37?

Especially under arid and semi-arid conditions where rainfall is low, the rainfall pattern is generally erratic, which means that the same amount of precipitation in different years may result from widely varying numbers of rainfall events. This erratic pattern has a direct influence on the proportion of precipitation lost by soil surface evaporation. A large number of relatively small showers will result in long periods in which the soil surface is wet, leading to prolonged high evaporation rates. If the same amount of precipitation results from a small number of relatively large showers, the soil surface will dry out some time after the shower, leading to the so-called self-mulching effect, i.e. the formation of a dry layer acting as an effective barrier to water transport. In that way the water in the deeper layers is protected from evaporation and is stored for transpiration by the plants. The magnitude of soil-evaporation losses is illustrated in Table 39, for one measured and two hypothetical rainfall distribution patterns (van Keulen, 1975). It shows that evaporation losses may be as high as 60% of the total moisture input, whereas under Sahelian conditions even higher values have been established (Stroosnijder & Koné, 1982).

It is important therefore, to distinguish between field water-use efficiency, which may include all sorts of losses and the true transpiration coefficient, which expresses the amount of water actually transpired per unit of dry matter produced. In the water-balance calculations both processes are treated therefore separately (Section 3.2).

Table 39. Partitioning of rainfall in evaporation and transpiration under different rainfall regimes.

Total rainfall (mm)	Number of showers	Evaporation (mm)	Transpiration (mm)
270	19	79	191
250	10	91	159
250	20	140	110