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PLANT GROWTH AND SOIL MOISTURE RELATIONSHIPS

By

J. F. Bierhuizen
Institute for Land and Water Management Research
Wageningen, The Netherlands

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Many investigations on soil moisture in relation to crop yield have been performed in the Netherlands, amongst others by Stolp (1955) on vegetables, by Butijn (1959) on trees. A survey of the effect of the height of the water table and soil type was made in various parts of our country, a report of which has been published recently by various authors (C.O.L.N.). De Wit (1958) made a comparison on transpiration and crop yield of different species in various parts of the world.

The crop may be considered as an intermedium through which water in the soil is absorbed by the roots, transported to the leaves and transpired into the atmosphere. The rate of flow is continuous since the small moisture reserves in the plant do not allow a difference in rate of water absorption and transpiration for a long period. The plant influences this rate of flow by its suction force and the stomatal aperture both of which finds its origin in the transpiring leaves. Photosynthesis, which is the main source of dry matter production takes also place in the leaves. At the same time one may observe rapid changes in the water content, the osmotic pressure of the cell solution, the turgescence, etc. These internal changes affect growth processes such as cell elongation, leaf expansion and fresh weight yield to a high extent. Some considerations on transpiration and photosynthesis of leaves and other growth processes in relation to climatic and soil moisture conditions, therefore, will be given in the next section of this paper. In the next following one experimental results on the effect of soil moisture will be described in order to verify some of the above mentioned considerations. Part of these results may lead to important consequences for irrigation advice. The plant growth - soil moisture relation is affected by other conditions as well, such as fertility, salinity, etc., of which some examples will be given in the last section of this paper.

Some considerations on transpiration, photosynthesis and other growth processes in relation to climatic and soil moisture conditions

a Transpiration and photosynthesis of leaves

Transpiration is an important factor because it prevents excessively high temperatures that should be caused by intensive radiation through which other processes would be influenced unfavourably.

In the leaves the major part of the transpiration takes place through the stomata and only a minor part via the cuticle. Fig. 1 shows a transverse-section of a leaf with a stoma. The cells surrounding the intercellular space evaporate, for which process energy is necessary of course. Owing to this evaporation a suction force is built up from these cells via the xylem vessels and the roots to the soil, causing moisture transport to the leaves. The water vapour diffuses into the atmosphere via the stomata and is proportional to the vapour pressure gradient $C-C_1$, where

C = the maximal vapour pressure of water at leaf temperature

C_1 = the actual vapour pressure of the surrounding air, depending on air temperature and relative humidity.

The transport of water vapour from the leaf to the surrounding air is inversely proportional to its total diffusion resistance. This resistance consists of a laminary layer of the surrounding air, which depends on wind speed and a variable stomatal resistance.

The mechanism changing the stomatal resistance is - under normal circumstances - activated by light and appears to be related with photosynthesis. At unfavourable conditions for the plant, however, an osmotic system is the main regulator of the stomatal aperture (Kuiper and Bierhuizen, 1958). The exact nature of the stomatal reaction is not yet known, but the influence of high tensions of the cell solution due to desiccation of the plant is of great importance for the moisture relations discussed here.

The main process involved in dry matter production is photosynthesis, through which carbon dioxide is transformed in carbohydrates. The energy used in this process originates from the light absorption by the chlorophyll. This enzymatic process is temperature dependent. However, the main controlling factors in practice seem to be light intensity and carbon dioxide (Gaastra, 1959). Carbon dioxide flows through the stomata in a direction which is the reverse of that of the water vapour.

Under favourable soil moisture conditions, it was observed that the rate of photosynthesis of sugar beet leaves increased with an increase in light intensity up to approximately 0.2 $cal.cm.^{-2}min.^{-1}$ (fig. 2). At still higher light intensities no further increase in photosynthesis occurred, because of a carbon dioxide or other limitation at this saturation level. The increase in photosynthesis at low light intensities is coupled with opening of the stomata, by which the stomatal resistance decreases. The decrease of the latter causes an increase in transpiration up to approximately 0.2 $cal.cm.^{-2}$ $min.^{-1}$ as may be shown in fig. 3. At higher light intensities, however, transpiration still increases in contrast to photosynthesis. The increase in transpiration is mainly caused by an increase in the leaf temperature, increasing the vapour pressure gradient $C-C_1$. In order to investigate the effect of light on the stomatal diffusion resistance, the transpiration data were corrected on an equal vapour pressure gradient (fig. 3, dotted line). It was evident that no decrease in the stomatal resistance (increase in transpiration) occurred anymore at approximately 0.2 $cal.cm.^{-2}min.^{-1}$. Above this value, the increase in transpiration and an unchanged rate of photosynthesis, causes an inefficient water use (T/P) - transpiration-photosynthesis ratio - as is shown in fig. 4. The high ratio occurring at extreme low light intensities is due to the fact that transpiration (cuticular) has some value, whereas photosynthesis has to compensate the respiration first. It is obvious that in the temperate zones the existing radiation intensities occur generally at the minimum of the curve represented in fig. 4, whereas under conditions of high radiation intensity, as in arid and semi-arid zones, this ratio becomes less favourable. Comparable conclusions were given by De Wit (1958).

At unfavourable soil moisture conditions the osmotic regulation by closing of the stomata decreases transpiration. The lower transpiration will need less energy, resulting in an increased leaf temperature. This increasing leaf temperature tends to enlarge the vapour pressure gradient, increasing the transpiration again. Transpiration and leaf temperature also depend strongly on wind speed in various ways. Wind increases the thermal conductivity, through which leaf temperature and thus the vapour pressure gradient and the transpiration decreases. However, the resistance of the laminary layer is decreased also giving an increased transpiration. At what level a balance is struck is unknown, but this level will be more favourable to the plant. It may be assumed that photosynthesis is less affected by the above mentioned factors.

A calculation of the transpiration-photosynthesis ration (T/P) at low moisture conditions is rather difficult. Moreover, in the field one has to deal with several layers of leaves for which divergent micro-climatological conditions exist. One may assume, however, that low light intensities favour a low T/P ratio compared with those at high intensities and favourable moisture conditions. Under limiting conditions of soil moisture this ratio may decrease due to a decrease in transpiration and a lesser decrease in photosynthesis.

b Other growth processes in relation to climatic and soil moisture conditions

It has been mentioned already that a high suction force in the leaves occur at high evaporation and at unfavourable soil moisture conditions. Internal translocations in the plant from older leaves with a lower suction force to younger leaves with a higher suction force and vice versa occur as well. The suction force changes during day and night also. Kramer (1937) observed that the water absorption lags behind the transpiration, as has been shown in fig. 5. The diurnal changes of these processes are reflected in water content, turgescence, etc. A high water content of the plant is favourable for cell elongation, increase in leaf area and fresh weight during the night. Growth takes also place at favourable soil conditions and low evaporation during the day. Dry matter production for which photosynthesis is the main process, takes place during the day only. One may assume that a high evaporation and unfavourable soil moisture conditions affect cell elongation, leaf expansion and fresh weight more than the dry weight yield. One may observe such a result by an increase in the dry weight percentage.

Experimental results on the effect of soil moisture on various growth aspects

It is generally accepted that constant tensions higher than that at field capacity are hardly possible. In our experiments, therefore, the moisture content of the soil varied between field capacity and fixed tension limits. As soon as the latter were reached the soil was brought back to field capacity by irrigation. The results usually are expressed as the average moisture tension during the experimental growth period.

Some vegetables, such as lettuce, spinach and radish, showed a large decrease in yield of the vegetative parts with an increase of the mean moisture tension. The leaf area was smaller and the quality was unfavourably influenced. The yield in fresh weight varied according to the crop used: those with the highest fresh weight production showed the largest decrease. It appeared that this decrease was nearly the same for the various crops (fig. 6), when represented as a percentage of the maximum yield. The yield decreases from 100% to 20-30% (A) with an increase in mean pF from 2.3 to 3.4 under high evaporation. Under low evaporation conditions this decrease was less pronounced and amounted to only 50 to 60% under comparable soil moisture conditions (B).

An increase in dry weight percentage was usually observed with an increase in the mean moisture tension. At a given tension this percentage was higher at high evaporation conditions (fig. 6, A) than under conditions of low evaporation (fig. 6, B). In fig. 7, the fresh and dry weight yield of lettuce is plotted against the mean moisture tension. The dry weight production was far less affected than the fresh weight yield. Under Dutch climatic conditions a close relationship between dry matter production and radiation was observed.

Other experiments were performed in rooms at a constant temperature and under artificial light (TL day-light tubes). Table 1 shows the response of the mean moisture tension at 26° C on various plant aspects of tomato.

Table 1. The effect of mean moisture tension at 26° C on leaf number, gain in fresh- and dry weight, total transpiration and transpiration coefficient (gms. of water transpired per gm. dry matter produced) of tomato. The results are expressed as a percentage of that of the control at pF 2.2 (after Abd El Rahman and Bierhuizen, 1959)

mean moisture tension in pF	number of leaves	gain in fresh weight	gain in dry weight	total transpiration	transpiration coefficient
2.2	100%	100%	100%	100%	100%
2.5	100	100	106	96	91
2.8	91	68	77	55	73
3.1	98	37	53	27	51

It is obvious from the table that in this case as in those mentioned before, fresh weight production was more influenced than dry weight yield, whereas the number of leaves was hardly effected at all by the increase in mean moisture tension. The total transpiration was reduced to a large extent, amongst others by a smaller total leaf area and far more than the dry matter production. At higher mean tensions, dry weight has been produced with a smaller amount of water, which is shown by the decrease in the transpiration coefficient.

There is some evidence that the relation between soil moisture and plant growth depends partly on pot size due to differences in root distribution. Moreover, the various experiments in the field, in large and in small containers, were not performed under equal climatic conditions. Calculations comparing the various yield data have not been finished yet.

Experiments with various harvest periods were performed in one of the other investigations. In fig. 8, the effect of moisture tension on fresh weight yield (log. scale) is shown at four successive harvest periods. With a longer growth period, the yield increases at low as well as at high tensions. The effect of moisture tension shows at all periods, however, the same trend. Comparable results were obtained by Butijn (1959) in studies on the shoot length of trees in various periods. These facts prove that under conditions, existing in the Netherlands, no critical period in the vegetative growth occurred. These results show further that the optimum yield may be expected at a moisture tension of about pF 2.0.

Most of the experiments were carried out with vegetables in which the vegetative development of the plant was the main point of interest. There is some evidence, however, that the transition from vegetative to reproductive development often seems to be particularly drought sensitive. During this stage the root development generally diminishes, so the water absorption then mainly depends on the existing root system. If drought decreases the number of flowers or fruit set, it reduces the marketable product definitely, so that irrigation later on cannot compensate this reduction anymore.

In the preceding section some assumptions were made on the sensitivity to drought of various growth aspects. Experiments performed at different soil moisture conditions seem to verify these assumptions. Closing of the stomata is an important physiological aspect in preventing high water losses. Dry matter production seems to be less affected to drought, which can lead to a lesser irrigation frequency.

Other factors affecting the plant growth - soil moisture relation

Some species are more drought tolerant than others, either by their morphological character or by their physiological resistance. It has been observed for instance that a specific soil moisture tension affects various processes more in species with a sparse root system than in species with a dense one (Slatyer, 1956). Growth of root tips is largely influenced by moisture tension. In practice, frequent irrigations often lead to a more shallow and horizontally spread root system, which is unfavourable when dry conditions will occur. The top/root ratio of a plant is also an important aspect to be considered.

On saline soils, the uptake by the plant is affected not only by moisture tension, but by osmotic pressure as well. It seems possible that plants subjected to saline conditions for a longer period can adapt themselves to a certain extent by an increase in the suction force. These facts have to be considered as well.

The highest efficiency of irrigation will be obtained if other growth factors are favourable. The nutritional status of the soil for example must be held in a well-balanced condition. If this fact is not realized, frequent irrigation may lead to even worse conditions as originally present, especially for those nutrients sensitive to leaching. In fig. 9, the effect of nitrogen on the leaf area of tomato at various moisture conditions is given. It is evident from the figure that the full advantage of a high soil moisture content is obtained only, if the supply of nitrogen is adequate. The results on fresh weight yield showed more or less the same trend.

In other experiments with tomato (Abd El Rahman and Bierhuizen, 1959) it was observed that a high soil moisture content had the largest effect under optimal conditions of temperature. It may be assumed that climatic factors such as temperature and radiation may limit growth in temperate zones, whereas in arid areas the moisture in the soil is the main limiting factor for growth. Apart from this, other factors, such as fertility and salinity, affect the plant growth - soil moisture relation as well. Efficient water use requires careful consideration of all growth factors.

Summary

Many soil and climatic factors affect the growth of the plant. Some of these aspects has been discussed in this paper. Generally a notable increase in yield will be obtained, when the main limiting factor can be neutralized through some agricultural management, e.g. irrigation will give the highest benifits if the nutritional status of the soil is favourable at the same time.

Differences in reaction to drought of various species and various plant processes can be expected as well. Dry weight production for instance is less sensitive to drought than fresh weight yield, whereas, moreover in the latter case quality may play an important role as well, especially when vegetables are concerned. Crops cultivated for their dry weight permit a higher soil moisture tension without an appreciable decrease in yield, leading to a less frequent irrigation and a more efficient water use.

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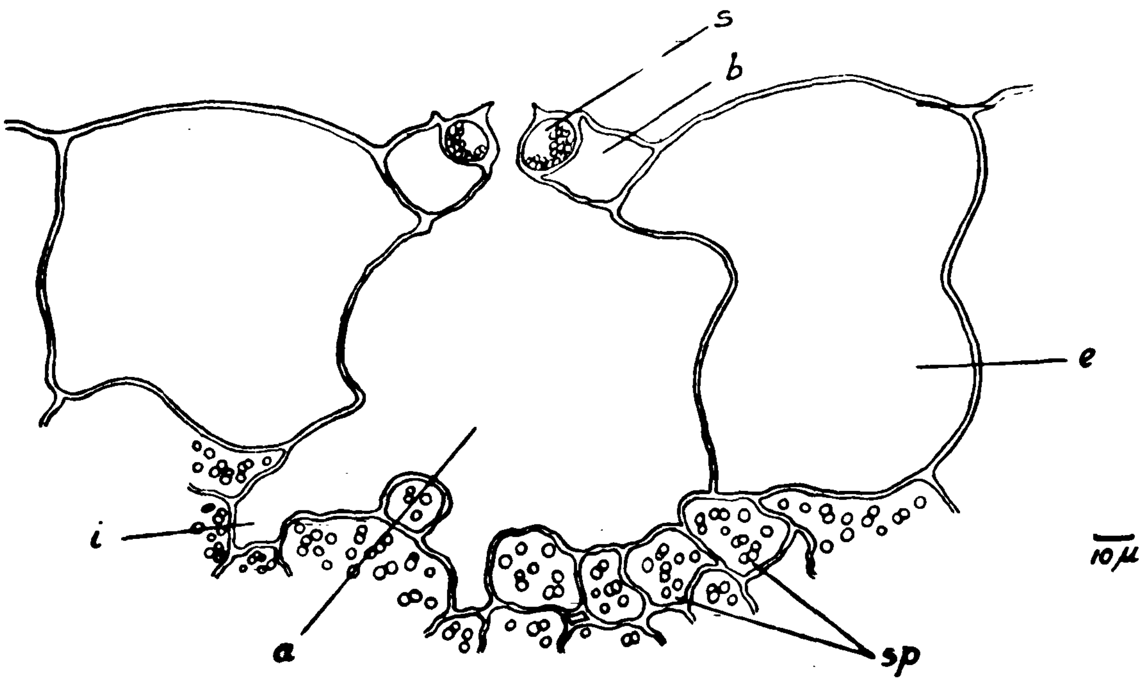

Fig. 1 Transverse section through a stoma of Zebrina pendula, after Bange (1953). s = guard cell, b = accessory cell, a = substomatal cavity, i = intercellular space, sp = spongeous parenchyma, e = epidermal cell

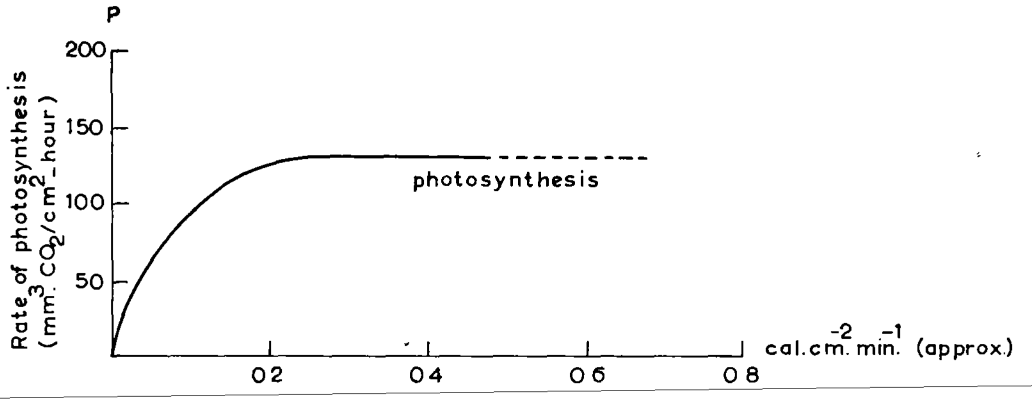

Fig. 2 The effect of radiation on the rate of photosynthesis (P) in a leaf, after Gaastra (1958)

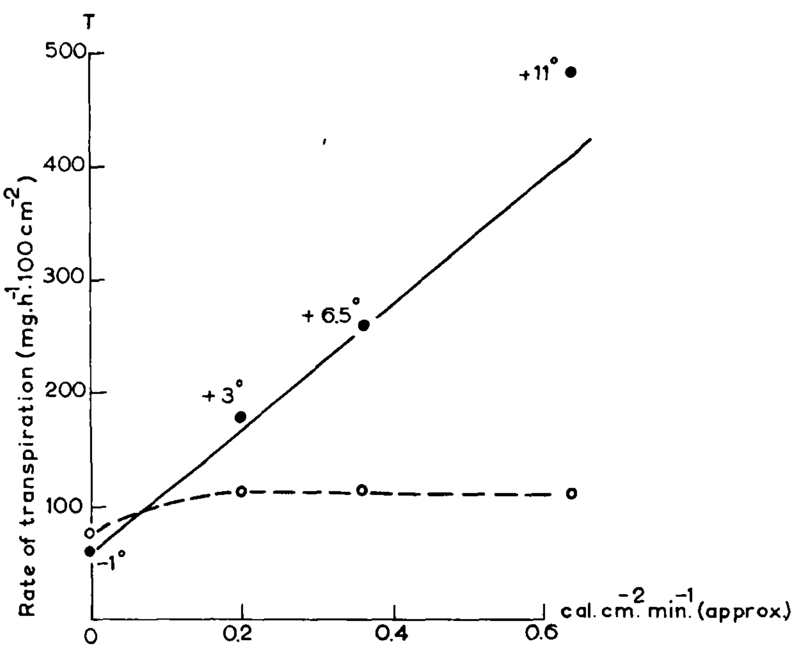

Fig. 3 The effect of radiation on the actual rate of transpiration (T) in a leaf. The dotted line gives the corrected transpiration at equal leaf temperature, after Kuiper and Bierhuizen (1958)

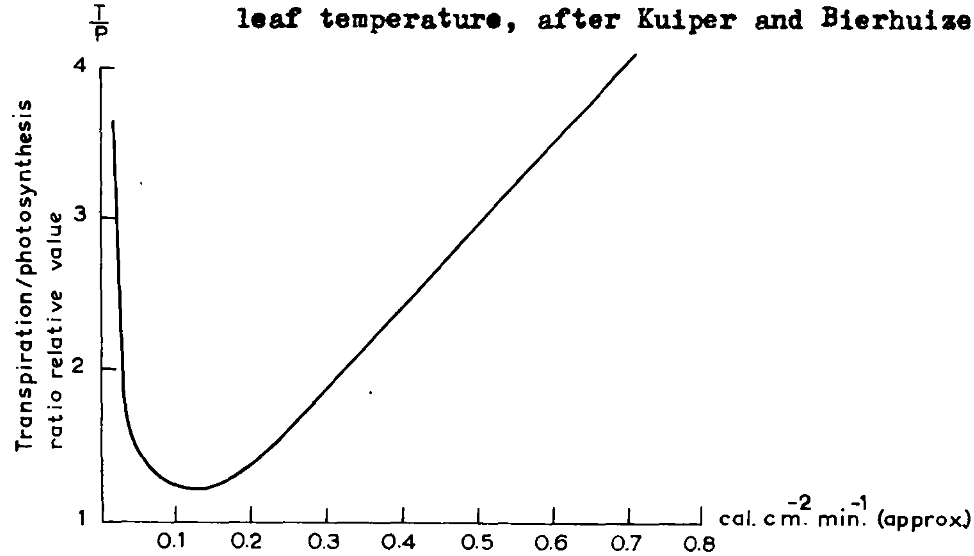

Fig. 4 The effect of radiation on the transpiration-photosynthesis ratio T/P as a relative value

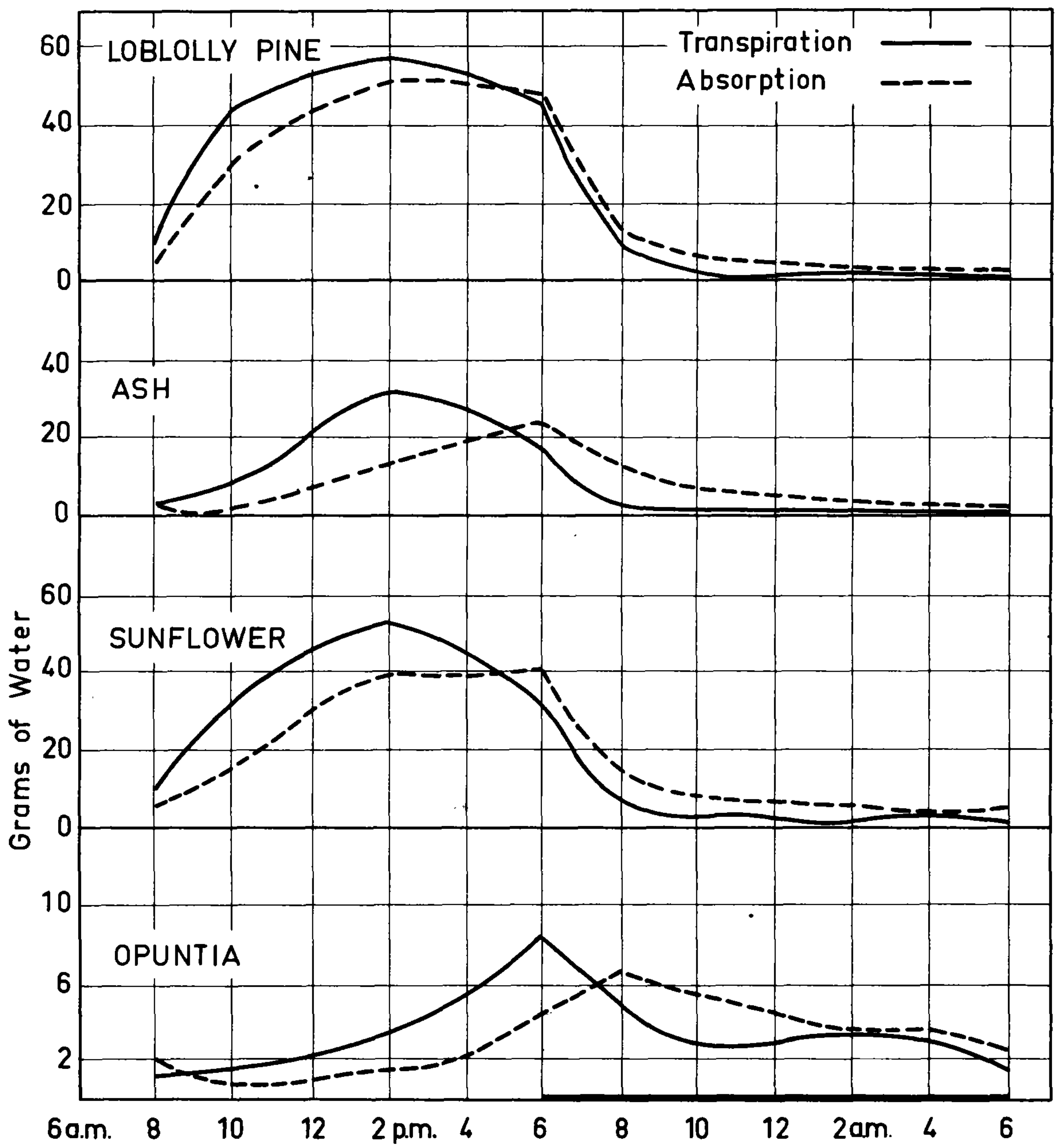

Fig. 5 Average rates of transpiration and absorption of four species of plants on a bright, hot summer day, after Kramer (1937)

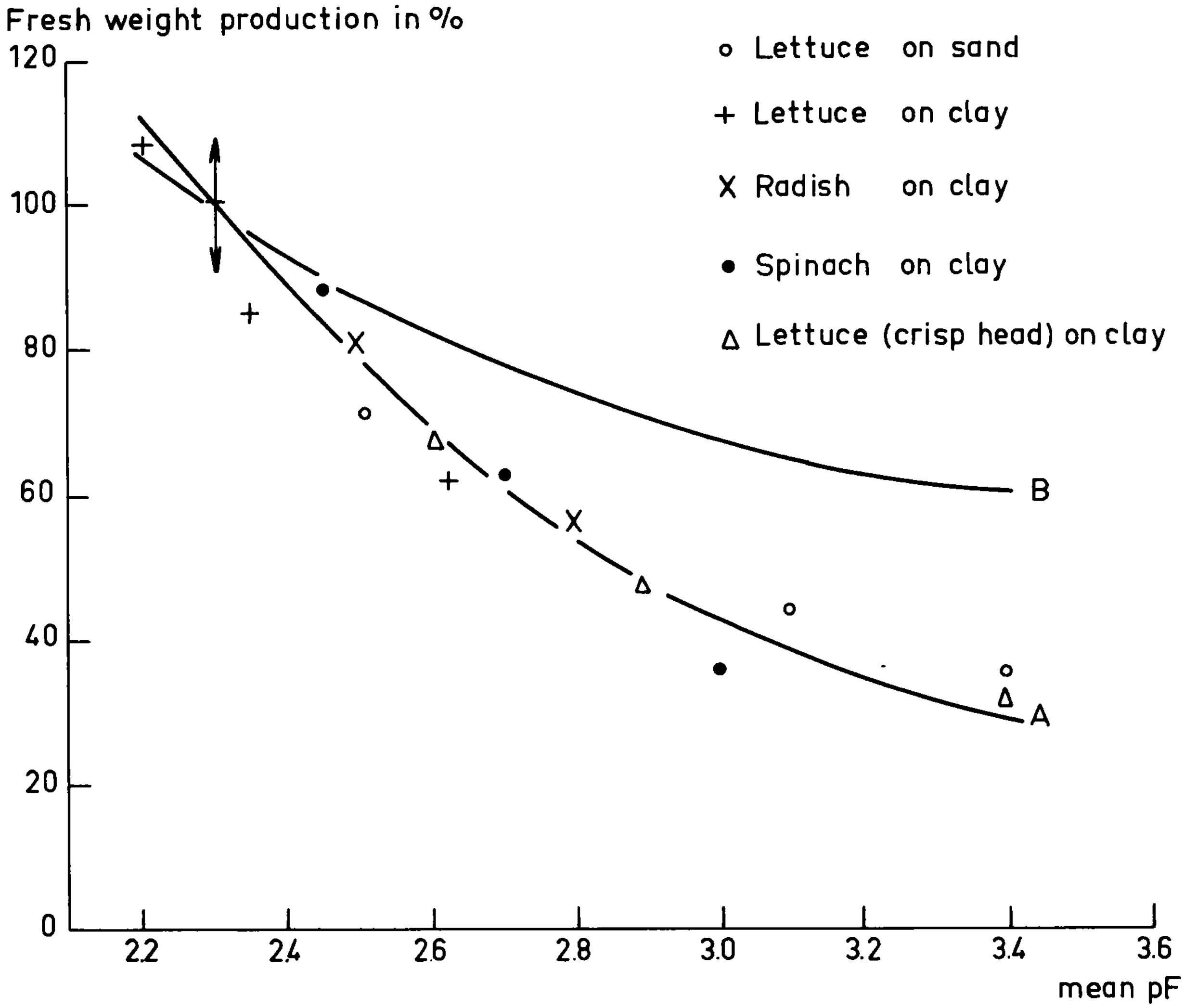

Fig. 6 The effect of mean moisture tension on fresh weight production (% of that at pF 2.3↕) of various crops in the spring (A) and in the autumn (B). The individual points of curve B were omitted, as the variation was nearly equal to that of A, after Bierhuizen and De Vos (1958)

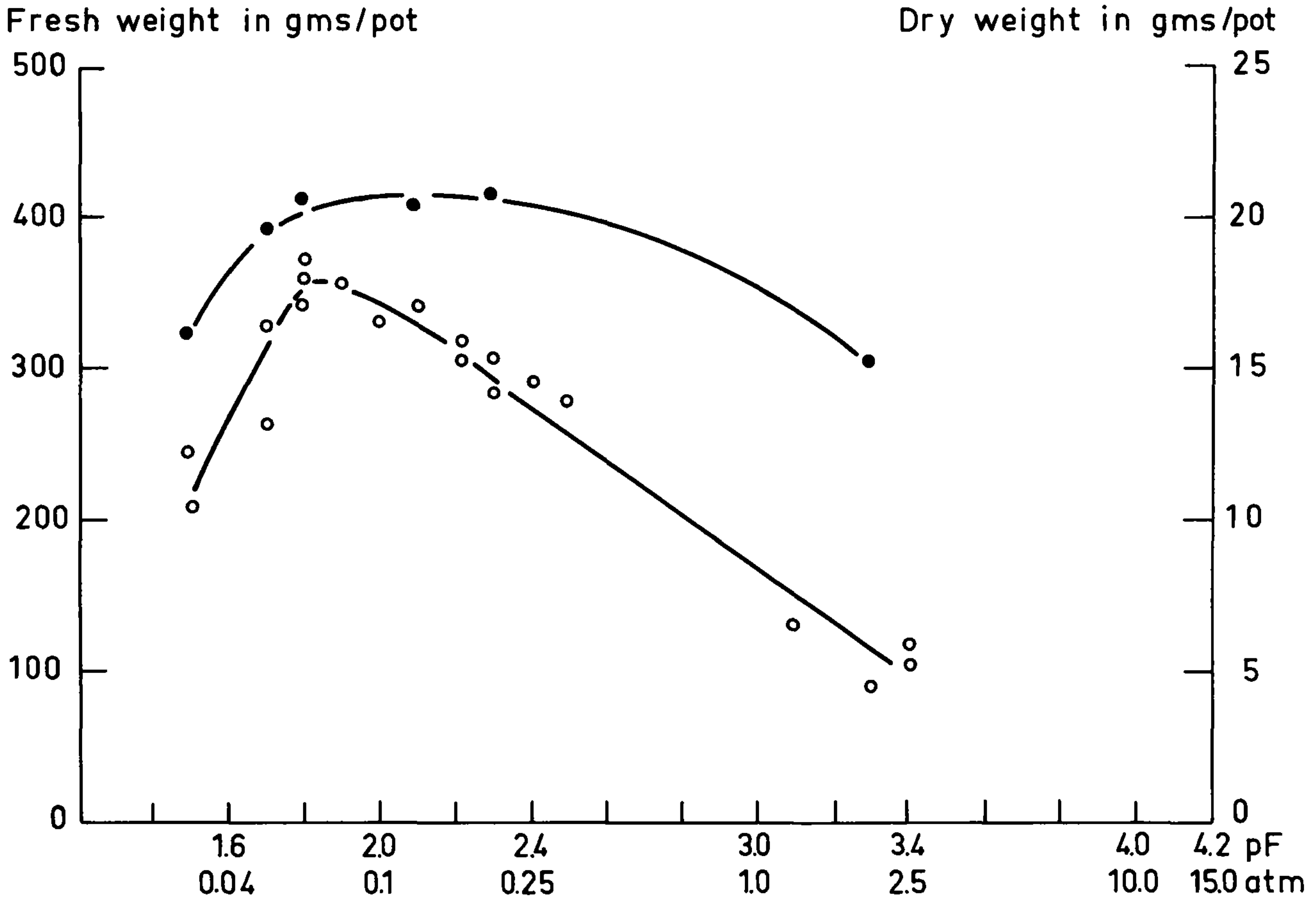

Fig. 7 **The effect of mean moisture tension on fresh weight (o—o) and dry matter production (•—•) of lettuce in spring 1957, after Bierhuizen and De Vos (1958)**

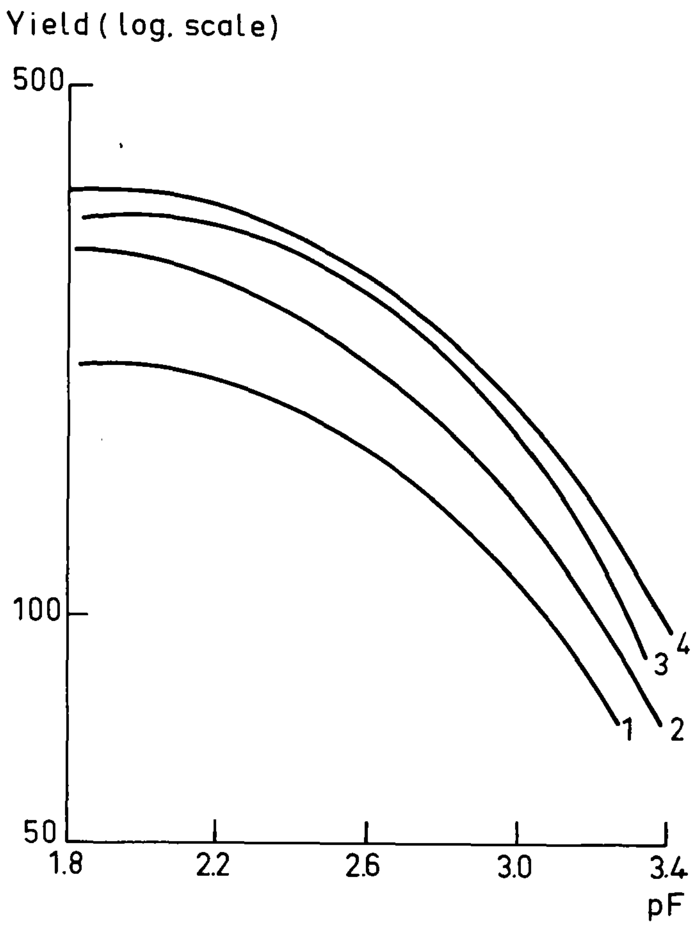

Fig. 8 The effect of mean moisture tension on fresh weight (log. scale). The numbers 1, 2, 3 and 4 represent various harvest data

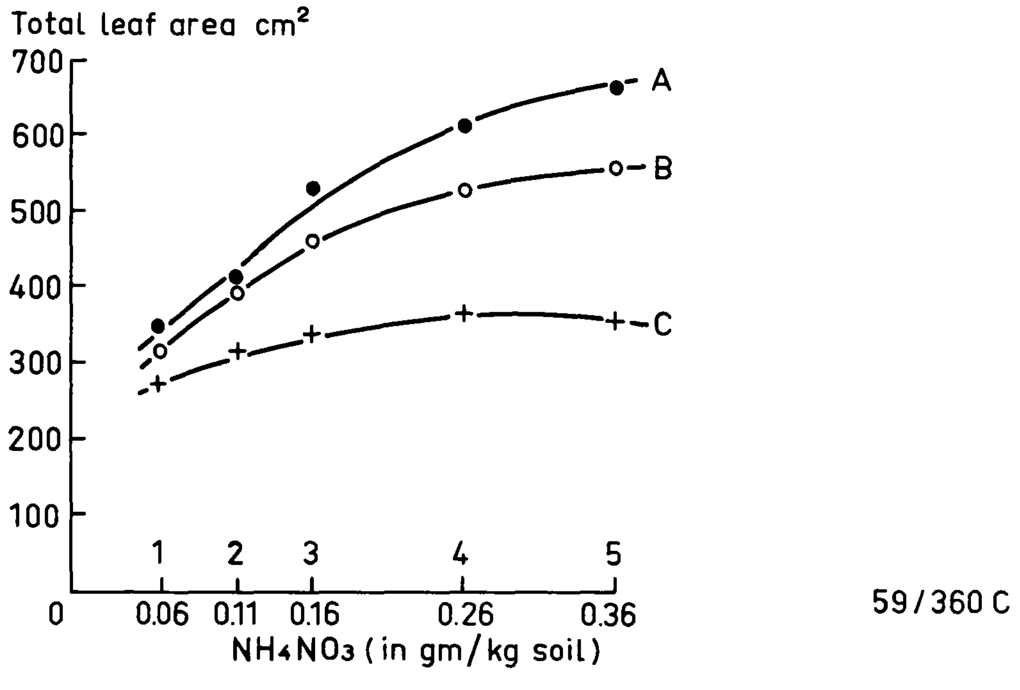

Fig. 9 The effect of nitrogen on leaf area at various levels of water supply (from A to C less frequent irrigations), after Bierhuizen, Abd El Rahman and Kuiper (1959)