PLANT-WATER RELATIONSHIPS

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Abstract

Some consequences are discussed on the subjects germination, shoot/root ratio, internal water relations of the plant and transpiration/photosynthesis relationships.

Germination depends to a large extent on temperature and moisture conditions prevailing in the soil. The effect of soil temperature on germination demonstrates a hyperbolic relation between minimum and optimum temperature from which heat units can be calculated. The heat unit can be used for the prediction of germination and gives an indication as regards its sensitivity towards adverse soil moisture conditions. The optimal soil moisture tension range for germination appears to be rather narrow and is affected by soil type.

The shoot/root ratio depends on the species and the prevailing climatic and soil conditions. A high ratio may be permitted with an intensive cultivation with automatic water and fertilizer supply. A low ratio and a great root depth is required with an extensive cultivation. The transition from vegetative to generative phase in plant development is important because root growth ceases during which the plant becomes rather sensitive towards drought conditions.

The pathway of water within the plant can be described on the basis of potential gradients and resistances in which the endodermis cells play an important role not only acting as a barrier for solutes but also because of their sensitivity as regards their resistance towards soil temperature and oxygen supply. Some consequences of physiological disorders related to Ca deficiency have been discussed.

The relation between transpiration and photosynthesis in the gaseous pathway has been described by means of gradients and resistances. Some consequences of the various photosynthetic pathways have been reviewed and also the effect of environmental factors on water use efficiency.

Introduction

In the preceeding decades many handbooks have been published regarding physiological aspects of water relations in plants, which emphasize the fact that this subject is extremely broad (Ruhland, 1956; Slatyer, 1967; Kozlowski, vol. 1-5, 1968-1978; Kramer, 1969; Lange et al., 1976). In this paper only a bird's-eye view can be given of some important items and some developments, which have lead to an improved understanding of plant growth. In subsequent paragraphs some consequences will be discussed on the subjects germination, shoot/root ratio, internal water relations of the plant and transpiration/photosynthesis relationships.

Germination

It is known that temperature and moisture content of the soil are the most important environmental parameters for seed germination and emergence. Seeds of certain species may require special treatments in advance because of dormancy problems. Surveys on seed germination were given e.g. by Mayer Poljakoff Mayber (1963), Heydecker (1973) and Khan (1977).

In general cardinal temperatures have been distinquished for seed germination viz. a minimum temperature (T_{min}) below which no germination is feasable, an optimum temperature (T_{opt}) at which the highest rate of germination occurs and maximal temperature (T_{max}) above which germination ceased due to excessive high temperatures. In the range between T_{min} and T_{opt} the effect of soil temperature (T) on the time in days (t) between sowing and emergence often shows a hyperbolic relation according to $S = (T - T_{min}) \times t$ in which S is a heat unit in degree days. Species having their origin in the tropics require a high T_{min} and those from temperate zones require a low T_{min} (Bierhuizen and Wagenvoort, 1974). The heat unit concept can be used to predict the germination period. Species with a high heat unit (long germination period) often are more susceptible towards drought or excessive rain.

Germination begins with the imbibition of seeds for which a high soil moisture content is necessary. Thereafter, various enzymatic and metabolic processes will be activated for which not only water but also sufficient oxygen supply is required. It is obvious that either too wet or too dry conditions limit the rate of germination thus increasing the heat unit and sometimes also reducing the ultimate germination percentage. Moreover, crops with a long germination period such as celery are extremely sensitive because the probability of adverse climatic conditions and the incidence of diseases is much higher. The soil moisture tension appeared to be rather narrow for optimal germination varying between pF 2.0 and 2.7 (Feddes, 1971; Bierhuizen and Feddes, 1973). However, the soil type may change this optimum. Spinach e.g. produces a gel under too wet conditions which further hampers the oxygen supply thus reducing the germination percentage. It was observed in peat and sandy loam that the germination percentage of spinach increases with an increase in pF from 1.0 to 2.0, whereas in a sandy soil an optimum exists at pF 1.4. In the latter case aeration is the limiting factor below this value and moisture above this one (unpublished results).

In order to ensure rapid germination, a high germination percentage and thus an equal stand of a crop, various applications in practice are feasable. Mulching e.g. prevents dessication of the soil surface, excessive high temperatures and muddiness of the soil. The depth of sowing depends on seed size (Wagenvoort and Bierhuizen, 1977) but is often more shallow in spring than in summer because in the former case temperature and in the latter water availability is the main limiting factor. Plastic cover has the advantage of preventing moisture loss and increasing soil temperature. It is still doubtful whether fluid drilling, in which seeds are pregerminated in a solution until a root length of 2-5 mm and subsequently sown in the field via a gel, will be applied in practice because of the high cost involved by this system.

Shoot/root ratio

Roots are important because of its anchorage of the plant, its water and ion uptake, and sometimes for its consumptive use purposes such as carrot. General aspects of root growth have been reviewed by Whittington (1970).

After germination and emergence, shoot and root growth will start, its ratio being dependent from the species and the environment (Bierhuizen, 1974). In general, a high nitrogen application, a low light intensity and a frequent irrigation increase the shoot/root ratio, causing a more susceptible crop towards high evaporation conditions later on.

It is difficult to ascertain an optimal shoot/root ratio or an optimal root depth. The required root depth can be extremely shallow and in the order of 10 to 20 cm e.g. in glasshouses with automatic trickle or sprinkler irrigation and fertilizer supply. Applications such as rockwool, nutrient film techniques also indicate that a high shoot/root ratio can be permitted with a regular supply of water, nutrients and oxygen to the roots. With an extensive cultivation in the field, however, it is necessary to endure drought periods so that a root depth of at least 80 to 100 cm is required. Root extension in depth can be in order of 2 to 4 cm per day depending on temperature, which means that the above mentioned required root depth is achieved in 1 or 2 months during which often irrigation is not necessary. In case artificial water supply is given too early the root depth will remain shallow.

An important aspect during plant growth is the transition from the vegetative to the generative phase. It is known that during this period root growth is often completely retarded, whereas the decay of roots still continues. As a result of this, the shoot/root ratio increases rapidly, whereas the crop becomes rather sensitive towards water shortage. Hence, the efficiency of irrigation (increase in yield per unit amount of water supply) during such a period is often very high.

Internal water relations of the plant

The amount of water within the plant is small in comparison with the amount of water transpired. As a consequence of this phenomenon, water absorption via the roots is necessary in order to meet the requirement which arises due to water loss. The water uptake from the soil (W) and the water transport through the plant depends on potential gradients and resistances according to

$W = \frac{\Psi s \quad \Psi l}{r_s + r_p}$ in which Ψ_s resp. Ψ_l is the soil resp. the leaf water potential and r_s and r_p are respectively the resistance in the soil, and in the plant. The latter resistance being more important than the former even when the soil dries (Behboudian, 1977). Methods to measure the various parameters in water relations has been described by Slavik (1974).

Within the plant the transport of water can be considered as a mass flow through small capillaries in the cell wall of the root cells, the xylem vessels, the veins in the leaves and the cell wall of the parenchymatous tissue cells towards the stomata through which most of the transpiration takes place. In the root endodermis, however, due to the Casparian bands the continuous system of capillaries is disconnected and water including the solutes has to pass through the endodermis cell and thus through its membrane. Weatherley (1963) demonstrated with an ingenious experiment that almost 75 % of the water transport takes place via the endodermis cells. The membrane resistance of the endodermis cell seems to depend on its active metabolism and thus on soil temperature and oxygen supply. It is known e.g. that flooding (lack of aeration) and too low temperatures induce wilting of the plants. In the sensitive range of soil temperatures the resistance may increase with 20 % with a decrease in temperature of 1 °C, whereas in the xylem vessels and the microcapillary system it is only in the order of 1 %. The latter decrease can be described to changes in viscosity. In the leaves more than 90 % of the water transport takes place in the cell walls (Weatherley, 1963). Rapid changes in transpiration cause rapid changes in water transport through the cell walls without affecting the water potential of the leaf cell to a great extent.

In the field a diurnal trend in transpiration exists. The absorption shows also a diurnal trend but lacks behind transpiration. This means that after sunset transpiration is almost zero because of lack of energy and closing of the stomates whereas absorption still may continue and decline gradually. With the gradual decrease in water absorption and water transport during the night, the concentration of solutes in the xylem sap increases. This fact may have important consequences for certain physiological disorders related to Ca-deficiency. It is known that e.g. Phosphate and potassium are rather mobile, whereas Ca is extremely immobile. Krug et al (1972) observed that crubs, cauliflowers became glassy when the water potential in the plant showed a small periodicity in water potential of the leaves. A large periodicity induced by high evaporation conditions leads to an alternating shrinking and swelling of the curds, a stronger calcium deposit via the xylem into the curd during the night and less glassiness. With tomatoes also evidence is obtained that during cloudy wheather conditions shringking and swelling during resp. day and night is less, thus resulting in calcium deficiency of the fruits.

Transpiration/photosynthesis relationships

In the past two decades enormous progress has been made regarding the knowledge of photosynthesis. At present 3 photosynthetic pathways can be distinguished viz. the Calvin-Benson (C3 photosynthesis), the Hatch Slack one (C4 photosynthesis) and the Crassulacean Acid Metabolism (the so-called CAM photosynthesis). A survey on its biochemistry, physiology and ecological implications has been given recently by Ehleringer (1979).

The C3 pathway seems to be the oldest and most primitive one, in which the RuBP carboxylase enzyme (ribulose biphosphate) plays an important role. This enzyme accepts also oxygen, giving rise to photorespiration, thus reducing the net uptake of CO_2 or net photosynthesis (NP). The ratio CO_2/O_2 in the air determines to a large extent the ratio between photorespiration and net photosynthesis. Under normal conditions 0.03% CO_2 and 20% oxygen photorespiration can be in the order of 30-40%. When the oxygen concentration is reduced till 1%, net photosynthesis increases largely and photorespiration becomes almost 0%. When the CO_2 concentration is increased to o.1% the photorespiration is also 0% and no significant differences were observed in net photosynthesis of tomatoes between 20 and 1% oxygen (Lakso and Bierhuizen, unpublished results). The internal CO_2 concentration $(CO_2)_{int}$ and the so-called mesophyllresistance r_m are usually higher in plants having only a C3 pathway as compared with a C4 cycle.

In the C4 pathway different biochemical and morphological characters exist as compared with the C3 pathway. The phosphoenol pyruvate (P.E.P.) enzyme carboxylase is extremely active in trapping CO_2 so that photorespiration in the so-called C4 plants as corn and sugarcane is almost absent. The efficiency of energy conversion (quantum yield) of this pathway however, is lower than that of the C3 one. It has been observed that in temperate zones at low ambient temperatures the habitat for C3 plants is more favourable due to the higher quantum yield and the relative low photorespiration as compared with C4 plants. At higher temperatures photorespiration of C3 plants, however, increased enormously and in such a habitat C4 plants grow better. The most extreme for drought survival is a CAM plant which opens the stomates during the night for CO_2 fixation via its crassulacean metabolism and closes the stomates during the day while reduction of CO_2 takes place. The role of photorespiration in the C3 pathway seems to be important in order to prevent the photosynthetic mechanism against adverse conditions (Lawlor, 1980).

Transpiration (T_r) and net photosynthesis (NP) can be described in the general form of diffusion equations depending on a gradient and a resistance according to

$$T_r = \frac{e_{max} - e_a}{r_a + r_s} \qquad \text{and } NP = \frac{(CO_2)_{ext} - (CO_2)_{int}}{r_a 1 + r_s 1 + r_m 1}$$

in which e_{max} is the maximum vapour pressure depending on the leaf temperature, e_a is the actual vapour pressure depending on ambient temperature and humidity, $(CO_2)_{ext}$ resp. $(CO_2)_{int}$ is the external resp. internal CO_2 concentration in the photosynthetic pathway, r_a, r_s and r_m are the laminary, the stomatal and the mesophyll resistance. The accents r_a and r_a1, r_s and r_s1 denote the difference in the diffusion coefficients for H_2O and CO_2 respectively. Constants have to be included in order to obtain the exact dimensions.

The ratio T_r/NP or transpiration coefficient (amount of water use per g dry matter produced) increases with an increase in Δe (e_{max} - e_a), which has been confirmed in simultaneous transpiration and phtosynthesis measurements of cotton and a comparison between growth and water use of various crops at different locations (Bierhuizen and Slatyer, 1965; Bierhuizen, 1976). Increasing the carbon dioxide gradient in glasshouses may increase the yield by 30% without an appreciable increase in water use. The transpiration coefficient in cotton calculated from photosynthesis and transpiration measurements declined from 400 to about 80 upon an increase in CO_2 external from o.o3% till 0.2% (Bierhuizen and Slatyer, 1965). Cotton is a C3 plant and the increase in NP with an increase in CO_2 external can be ascribed to a reduction in photorespiration. Carbon dioxide fertilization in C4 plants, because of the absence of photorespiration, however, will not reduce the ratio of T_r/NP. Moreover, there is some evidence that corn is already saturated at an external CO_2 concentration of 0.02%. Ehleringer (1979) gave avarage values of photosynthesis and transpiration ratio for the various pathways as follows:

pathway	maximum rate of photosynthesis $\mu mol\ m^{-2} s^{-1}$	transpiration ratio
C3	10 - 60	450 - 600
C4	30 - 60	250 - 350
CAM	3 - 10	25 - 150

Although CAM plants are extremely efficient, their rate of photosynthesis and growth is too small for practical purposes in agriculture. It has been observed that closing of stomates in C4 plants may have a similar reduction in transpiration and photosynthesis because of the low r_m value, whereas in C3 plants the percentual reduction in transpiration is greater (large r_m) upon closing of stomates (Bierhuizen, 1976). However, such a conclusion should be drawn with caution, because closing of stomates may induce a rise of leaf temperature, which in turn affects e_{max} but also photorespiration in C3 plants and not in C4 plants. It is important, therefore, to consider not only the diffusion equation but also the energy balance of a leaf or a crop canopy. The latter topic will be dealt with in a subsequent paper during this symposium.

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