BIOLOGIA PLANTARUM (PRAHA)

25 (6) : 462–467, 1983

Relationship between Soil Moisture and Leaf Water Potential of Three Forest Tree Species

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Abstract. A mathematic model of leaf water potential daily dynamics was employed to study the relationship between this characteristic and soil moisture for the species *Quercus cerris*, *Acer campestre* and *Carpinus betulus*. It was found that when evaluating the availability of soil water for a plant it is necessary to consider the vapour pressure deficit which remarkably affects the relationship between the soil moisture and leaf water potential. A quantitative description of the dependence between the leaf water potential and soil moisture enabled a physiological interpretation of the limit values of soil moisture — permanent wilting and reduced availability of soil water for the plant — as well as evaluation of the drought resistance of plants.

In our previous study (HUZULÁK and MATEJKA 1982) we have published a simple mathematic model characterizing the leaf water potential daily dynamics of three forest tree species under anticyclonic weather types. Input data for this model are vapour pressure deficit and soil moisture content. The aim of this study is to investigate the relationship between the soil moisture content and leaf water potential under constant atmospheric evaporative demand using a mathematic model of the leaf water potential daily dynamics.

MATERIAL AND METHODS

The research was carried out in an oak-hornbeam forest in Báb (south-western Slovakia, 48°10′ — north lat., 17°53′ — east long., 210 m altitude) which grows in well aerated clay and clay-sandy soils. The only source of water in the locality studied are atmospheric precipitations (annual average being 600 mm of which 310 mm in the growing period), which affect the dynamics of the soil moisture only to a depth of 50 cm (TUŽINSKÝ 1976). The average annual temperature of air is 9.3 °C, in the growing period 16.2 °C.

Received February 28, 1983; accepted May 23, 1983

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Dedicated to Dr. Jozef Kolek, DrSc . on the occasion of his 60th birthday.

The experimental objects were *Quercus cerris, Acer campestre* and *Carpinus betulus*, 17—19 m high, approximately 70—75 years old. These three species represent almost 80% of the species structure of the locality studied.

The leaf water potential (to be exact, xylem pressure potential, Ψ_x) was determined using the pressure method by Scholander (SCHOLANDER *et al.* 1965). The soil moisture content was determined at each 10 cm using the gravimetric method. The data on soil moisture content represent an average from a depth of 10—50 cm and are expressed in weight per cents.

On the basis of field measurements a mathematical model of leaf water potential daily dynamics has been elaborated (HUZULÁK and MATEJKA 1982), the analytic expression of which is the following logistic function:

$$\Psi_x = \frac{A}{1 + B\,e^{-C[d+D(w)]}} \tag{1}$$

where D(w), expressed in pascals, is the function of soil moisture content which can be characterized by the exponential relationship

$$D(w) = ae^{-bw} \tag{2}$$

The letters A, B, C, a, b are constants characterizing the given woody species, d is the vapour pressure deficit.

RESULTS AND DISCUSSION

The study of the relationship between the leaf water potential and soil moisture content involves an analysis of the partial dependence $\Psi_x = f(w)$ at a constant vapour pressure deficit, because — as it results from Equation 1 — the values Ψ_x affect the vapour pressure deficit besides the soil moisture content.

Let us have an arbitrary but fixed value of the vapour pressure deficit d and calculate the leaf water potential according to Equation (1) for different soil moisture contents from 9 to 24 weight per cent. When substituting concrete values Equation (1) for *Q. cerris* will be as follows:

$$\Psi_x = \frac{5.02}{1 + 13.28\,\exp\,[-0.001319d - 1345.38\,\exp\,(-0.538w)]} \tag{3}$$

and for *Acer campestre* and *Carpinus betulus* it will be as follows:

$$\Psi_x = \frac{3.61}{1 + 12.88\,\exp\,\{-0.001274\,[1.54\,10^7\,\exp\,(-0.721w) + 248 + d]\}} \tag{4}$$

The course of the dependence of leaf water potential on soil moisture content for different values of the vapour pressure deficit is shown in Figs. 1 and 2. The results obtained can be interpreted as follows: at high values of soil moisture content the leaf water potential does not practically depend on the soil water content because of soil water availability satisfying the high atmospheric evaporative demand without the necessity of increasing the suction pressure significantly. If soil moisture content drops under a certain value, depending on the plant species and atmospheric evaporative

demand (approximately from 16 to 18 weight per cent), the leaf water potential begins to respond sensitively to the soil water content. This is probably due to the non-linear relationship between the leaf water potential and soil moisture content. If the soil moisture content drops below another significant value (in case of *Q. cerris* it is approximately 10—11 weight per cent) the woody species is not able to reduce the leaf water potential any longer, it does not react to the atmospheric evaporative demand. This is reflected in unchanged values of Ψ_x which approach the most negative value, in absolute terms the highest possible value, numerically equivalent to the constant A in Equation 1.

The lower curve in Fig. 1 and Fig. 2 represents the relationship of the base leaf water potential (Ψ_B) measured at dawn, and the soil moisture content. To verify the validity of this theoretically derived relationship Figs. 1 and 2 show measured values of Ψ_B. The measured values are in a good agreement with the theoretically derived curve in spite of the fact that the actual values d were different from the zero value used for the curve calculation.

Equations 3 and 4 presented in Figs. 1 and 2 offer a possibility for physiological interpretation of the limiting situations from the aspects of soil moisture content — permanent wilting and reduced soil water availability.

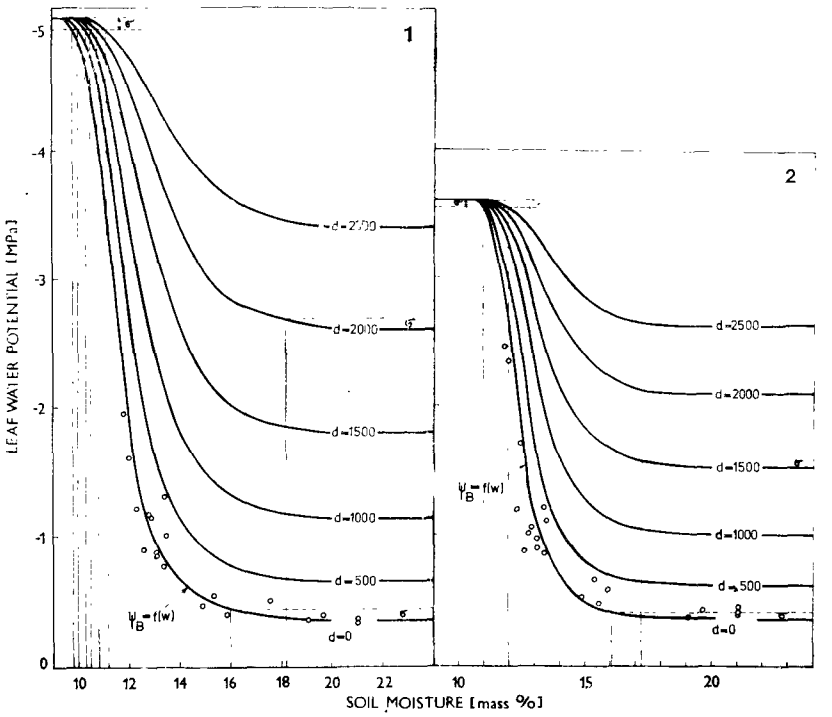

Fig. 1. Dependence of leaf water potential of *Quercus cerris* on soil moisture (w) at a constant value of vapour pressure deficit (d). The points indicate the measured values of the base leaf water potential (Ψ_B), σ indicates the standard deviation of the errors in leaf water potential measurements.

Fig. 2. Dependence of leaf water potential of *Acer campestre* and *Carpinus betulus* on soil moisture (w) at a constant value of vapour pressure deficit (d). For legend, see Fig. 1.

The described model enables the characterization of permanent wilting as a soil moisture content at which the Ψ_x value differs from the minimum possible value (the maximum one in absolute terms) by exactly the standard deviation of the measurement errors. The moisture content of permanent wilting also depends on the vapour pressure deficit, and as seen in Figs. 1 and 2, it can differ for each plant species. It does not represent one value but a certain interval of soil moisture contents as illustrated in both figures.

It results from this physiological interpretation of permanent wilting that the plant species with a lower value of permanent wilting also react to the atmospheric evaporative demand at a lower soil moisture content as compared to species with a higher value of permanent wilting. Using the permanent wilting one could characterize the degree of drought resistance by a single number providing that we consider the value corresponding to the zero vapour pressure deficit. This value depends only on the plant species and the soil type. For *Q. cerris* the soil moisture content is 10 weight per cent, and for the remaining two species it is 11 weight per cent. In this connection it should be remembered that the regime which corresponds to closed stomata was not considered in the construction of the model expressed by Equation 1. Therefore, in case of the considered drought resistance it is a matter of drought tolerance and not drought avoidance.

The data from Figs. 1 and 2 can provide information also on another limiting value — reduced availability of soil water. The procedure will be analogous to that of permanent wilting. At high soil moisture contents the Ψ_x value at a certain d value remains practically unchanged. We are interested in the determination of the soil moisture content to which the plant reacts by changing the leaf water potential. To the Ψ_x value at a soil moisture content of 24% we add the value of the standard deviation of the measurement errors Ψ_x. At this distance we draw a parallel with the horizontal axis. This parallel intersects the corresponding curve in the graph of the relationship $\Psi_x = f(w)$ in the point the horizontal axis of which represents the soil moisture content required. The above described procedure can be repeated for different vapour pressure deficits. Thus, we get an interval of soil moisture contents representing reduced soil water availability at different atmospheric evaporative demands. The soil moisture content for *Q. cerris* is 16—18.2%, for *A. campestre* and *C. betulus* it ranges from 16 to 17.2%.

At sufficient reserves of soil water in the root zone the rate of transpiration is influenced more by the energetic level on the transpiring surfaces than by the physiological requirements of the plant. Only when the water content starts to be limited the plants control the transpiration flow through the stomata (BENECKE 1976). The threshold value of the leaf water potential (called also the stress potential) at which the stomata are closed, is of great importance. According to FEDERER (1977) the stress potential for *Acer rubrum* is −1.8 MPa and for oaks −2.08 to −2.23 MPa. Published threshold values for closing the stomata (HINCKLEY *et al.* 1981) are −2.25 to −3.70 MPa for oaks, and the lowest leaf water potential over the range of −3.3 to −3.94 MPa. Unfortunately, the species we were interested in were not given, and neither were meteorological data at which the above mentioned values were obtained. The species we have studied have shown lower Ψ_x values than compared species. ELIÁŠ (1979) who measured at the same time the

leaf resistance on the same species during a strong water deficit reports that *Q. cerris* Ψ_x values ranging from −2.33 to −4.12 MPa had the stomata resistance of 6.4—10.8 s cm^{-1}, that means that the stomata were not closed. On the same day the leaf resistance of *A. campestre* were 16.3—37.9 s cm^{-1}, and those of *C. betulus* were 21.1—44.2 s cm^{-1} at minimum values of Ψ_x being −3.46 and −3.30 MPa, respectively.

The limiting values of soil moisture content for plants characterized statistically (field capacity, permanent wilting point) are according to the present ideas on the water transport in the soil-plant-atmosphere continuum not satisfactory and should be redefined. The quantity of water taken by the plant and the rate of its input depend on the plant properties (especially of the root system as well as on physiological ability of the plants to reduce Ψ_x), soil properties and micrometeorological conditions which determine the transpiration rate. Thus, the soil moisture content itself is not a sufficient criterion for the evaluation of water availability for the plant. As it follows from our analysis, it is necessary also to know the vapour pressure deficit — characteristics of the atmospheric evaporative demands. This approach is in agreement with the dynamic characteristics of the relationships in the soil-plant-atmosphere continuum.

The interval of soil moisture contents characterizing the permanent wilting point is close to a value of 10.2 mass per cent determined for the given locality (TUŽINSKÝ 1976) as a double of the maximum hygroscopicity. However, we have to remember a criticism concerning the wilting point as the soil "constant" (SLATYER 1967). Wilting begins when the dynamic equilibrium between the water potential of soil, water potential of leaves and osmotic potential of cell liquid in the leaves is established. Therefore, the soil water potential at which wilting starts depends on osmotic properties of the cell liquid of plants, which show daily and seasonal fluctuations.

At present it is generally accepted that availability of soil water for plants decreases with decreasing soil moisture content, and it is also known that many physiological processes are already influenced at low water deficits. Therefore, the method of determination of the beginning of reduced soil water availability for plants is not only of theoretical but also of practical importance, *e.g.* for the determination of fruit trees and grape-vine irrigation needs, for which a mathematical model of leaf water potential daily course should be established.

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BOOK REVIEWS

STRATHERN, J. N., JONES, E. W., BROACH, J. R. (ed.): THE MOLECULAR BIOLOGY OF THE YEAST SACCHAROMYCES. MONOGRAPH 11B. METABOLISM AND GENE EXPRESSION. — Cold Spring Harbor Laboratory 1982. 680 pp. Cloth US $ 60.— (outside USA 72.—).

The budding yeast is an eukaryote which is amenable to genetic as well as biochemical and physiological analyses. The first book of this two-volume monograph on molecular biology of the yeast dealing with its life cycle and inheritance was published in 1981. The second book presents a comprehensive examination of the metabolism and gene expression of yeast. In the initial chapters, emphasis is primarily on the carbohydrate, nitrogen, galactose and phosphate metabolism while the subsequent chapters deal with membrane lipids of yeasts and with the regulation of amino acid and nucleotide biosynthesis. One of the major impacts of yeasts in molecular biology is its use for investigating processes that are different in prokaryotes and eukaryotes. Data presented in a chapter on translation reveal that the nucleotide sequence that effects the initiation of translation in yeasts may be fundamentally different from the features in *Escherichia coli*. In addition to chapters on transport, the secretory process, cell wall and cell surface, the book covers the organization and expression of tRNA, ribosome structure, function and synthesis and the nuclear RNA polymerases. The final chapter discusses the principles and practice of recombinant DNA research with yeasts. Useful appendixes provide a genetic map of yeasts and a list of biochemical markers of yeast organelles.

Serving both as a review of fundamental theory and a summary of recent research, these two volumes on the molecular biology of the yeast will be a valuable reference for workers in the field of yeast research.

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ORGANIZATION OF THE CYTOPLASM. COLD SPRING HARBOR SYMPOSIA ON QUANTITATIVE BIOLOGY Vol. XLVI. — Cold Spring Harbor Laboratory, Cold Spring Harbor 1982. 1047 pp. in two parts. Cloth US $ 130.00 (USA), 156.00 (elsewhere).

In the last years, the Symposia on Quantitative Biology, organized by the Cold Spring Harbor Laboratory, have been predominantly devoted to the problems of molecular genetics. The subject of the Symposium in 1981, however, was cytoplasm, which has attracted attention of molecular biologists especially in the last decade, when tremendous scientific efforts have been aimed at the molecular genetics of eukaryotic cells. In spite of the fact that the molecular mechanisms of cytoplasmic organization and functioning are not known as well as in the case of nucleus, considerable progress is unmistakable. It is possible to note that the most interesting information in this respect is obtained with approaches and methods of molecular genetics, starting with cloning and sequencing of genes for important cytoplasmic components, and following with studies on their organization and expression. Moreover, many conventional biochemical techniques have been improved and have helped largely to characterize molecular organization of cytoplasm. Traditional view on cytoplasm has been overcome and the new one shows the cytoplasm as structurally and functionally highly organized cell region. The reviewed book, the lectures given at the CSH Symposium are collected in, represents the survey of contemporary knowledge of molecular biology of cytoplasm. This theme is divided into four main blocks, as follows: Principles of Organization, Elements of Organization, Cell Surface, and Mechanisms of Organization. In the last chapter (Nucleus and Cytoplasm) and in the Summary as well as in many other contributions the dynamic view on the cell is emphasized, arising from close relations between nucleus and cytoplasm on one hand and cytoplasm and cell surface on the other.

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