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THE WATER ECONOMICS OF *SPERGULA VERNALIS* WILLD.

ABSTRACT: The study is concerned with the most important aspects of the water economics of a pioneer dune species – *Spergula vernalis* Willd. Examination was made of transpiration, suction power of leaves and water content in leaves during the course of 24 hours and in the ontogenesis of the plant in relation to several habitat factors. In addition the maximal water content in leaves and wilting point in the early stage of development and also during the flowering period, were determined for this plant. Measurements were made during two growing seasons on a dune in the Toruń Basin.

Contents

1. INTRODUCTION

The study forms part of more detailed investigations on the ecology and morphological variability of *Spergula vernalis* Willd. (Symonides 1974a, 1974b, 1974c), and presents the more important aspects of water economics, as being of particularly great significance to dune plants. It is a well known fact that its water balance constitutes an individual character of each species and the range of adaptation and tolerance of plants to water deficit differ even in closely related species (W a l t e r 1951). It is on this account that despite the very large number of publications devoted to the problem of water economics of land plants, an increasingly large number of researchers emphasises the need for treating species separately in studies on circulation of water in whole ecosystems (S z y m k i e w i c z 1932, A b d E l R a h m a n and B a t a n o u n y 1965b), since it is difficult on the basis of a knowledge of the water balance of one species to draw conclusions in relation to another species, even when the two species form a component of one ecosystem and grow under identical biotope conditions.

Studies on the water economics of *Spergula vernalis* were made principally for two reasons: (a) in order to establish whether this species is a xerophyte, as might be gathered judging solely on the basis of analysis of biotopes, or whether it belongs to one of the different ecological groups distinguished by W a l t e r (1962), and (b) to estimate the tolerance of the species for periodical water deficit and its adaptation to specific dune conditions.

Studies were made from 1970 to 1971 in the Toruń Basin. From the phytosociological aspect the area chosen for the studies is represented by a poor patch of the *Spergulo-Corynephoretum* (Tx. 1928) Libb. 1933 association growing on an extensive wind-eroded sand bank.

2. PREMISES

Two basic elements from among the many aspects composing the general picture of the water balance of a plant were taken into consideration in the studies, i.e., transpiration and suction power. In the original study plan it was intended to examine the two processes in relation to the plant's ontogenesis and to describe the course they take over a 24-hour period, taking into account the habitat factors which affect their intensity. Unfortunately the short life cycle of *Spergula vernalis*, the greater part of which takes place during the early spring, when rainfall is generally heavy, made it impossible to carry out regular, frequent daylong studies, and it only proved possible to make 17 of such measurements during the two growing seasons.

If intake and conduction of water compensates for the losses caused by transpiration the state of water supply to the plant tissues does not vary. In order to evaluate these processes each measurement was supplemented by definition of water contents in the plant.

The degree and tolerance of water deficit (in relation to maximal hydration of tissues) and the moisture value of lasting wilting point form some evidence of the plant's requirements and adaptation to given conditions of soil and air humidity.

Among the habitat factors affecting intensity of transpiration and suction force the following were taken into consideration: soil humidity, soil temperature, air humidity deficiency, evaporation, air temperature, intensity of light and wind force.

The unusual abundance of individuals of *Spergula vernalis* occurring on the stand was the reason it was chosen for the studies, as it facilitated selection of the most similar plants. This is important, as this permits of eliminating any possible individual differences.

3. METHODS

Measurements of transpiration were made in accordance with the generally accepted method given by H u b e r (1927) and S t o c k e r (1956), with the use of the Roller--Smith torsion balance, as being the most accurate under field conditions. From 3 to 4 weighings were made during each hour of the measurement period in order to obtain average values.

The suction power of leaves was defined by Schardakow's method (S t e u b i n g 1965). Although R h e d e r and K r e e b (1961) emphasise that there are certain drawbacks in this method, consisting in disturbances of the suction powers due to contact between the cut surfaces of the leaf and the sugar solution, these same authors recommend this method for studies under natural conditions, as it does not involve the use of complicated apparatus nor a long period of study time, but permits of making a large number of readings easily and quickly, which is essential for estimating daily fluctuations in suction power. As all the results are burdened with the same error this is not of any particular importance when making comparisons. The suction power of leaves was measured parallel to measurements of transpiration.

Maximal water content in the plant and wilting point were defined in the laboratory. The plants, which had been dug up for this purpose together with the soil adhering to the roots, were at once placed in narrow beakers. The soil was saturated with water; 10 hours later water content in the plant was examined (in 6 tests), taking the average value obtained as the state of maximal hydration.

The wilting point was obtained by the Briggs Shantz method (S z y m k i e w i c z 1932). These measurements were made in the early stage of the plant's life (state of two leaf whorls) and during the flowering period.

Evaporation was measured by means of a Pishe evaporimeter; humidity deficiency was calculated by means of Sprung's equations, based on difference in temperatures in Assman psychrometer, and light intensity using a luxometer. Soil humidity was defined by taking a sample of soil from the stand and driving off water at 105°C. The percentage of water held by the soil on a dry basis is the moisture content. Soil moisture is expressed on a percentage by weight basis.

4. DISCUSSION OF RESULTS

The daily course of transpiration, suction power and water content in the leaves in relation to microclimatic and soil factors is presented in Figures 1–11, plotted by B a r n e r 's (1965) method. Results are given in the following units: suction power – in atmospheres, water content in leaves – in percentages of fresh mass, transpiration – in mg/g of water per minute, evaporation – in ml of water/hour, air humidity deficiency – in mm Hg, soil humidity – in percentages, air temperature – in °C, soil temperature – in °C, light intensity – in luxes, wind force – in m/100 sec.

Although soil temperature and humidity were measured at four depths (5, 15, 30 and 50 cm), in the same way as air temperature and humidity deficiency were measured at four heights (10, 20, 50 and 100 cm) these parameters are entered on the figures at a depth of 15 cm and height of 10 cm respectively, that is, at a depth reached by the roots and a height reached by the upper parts of plants.

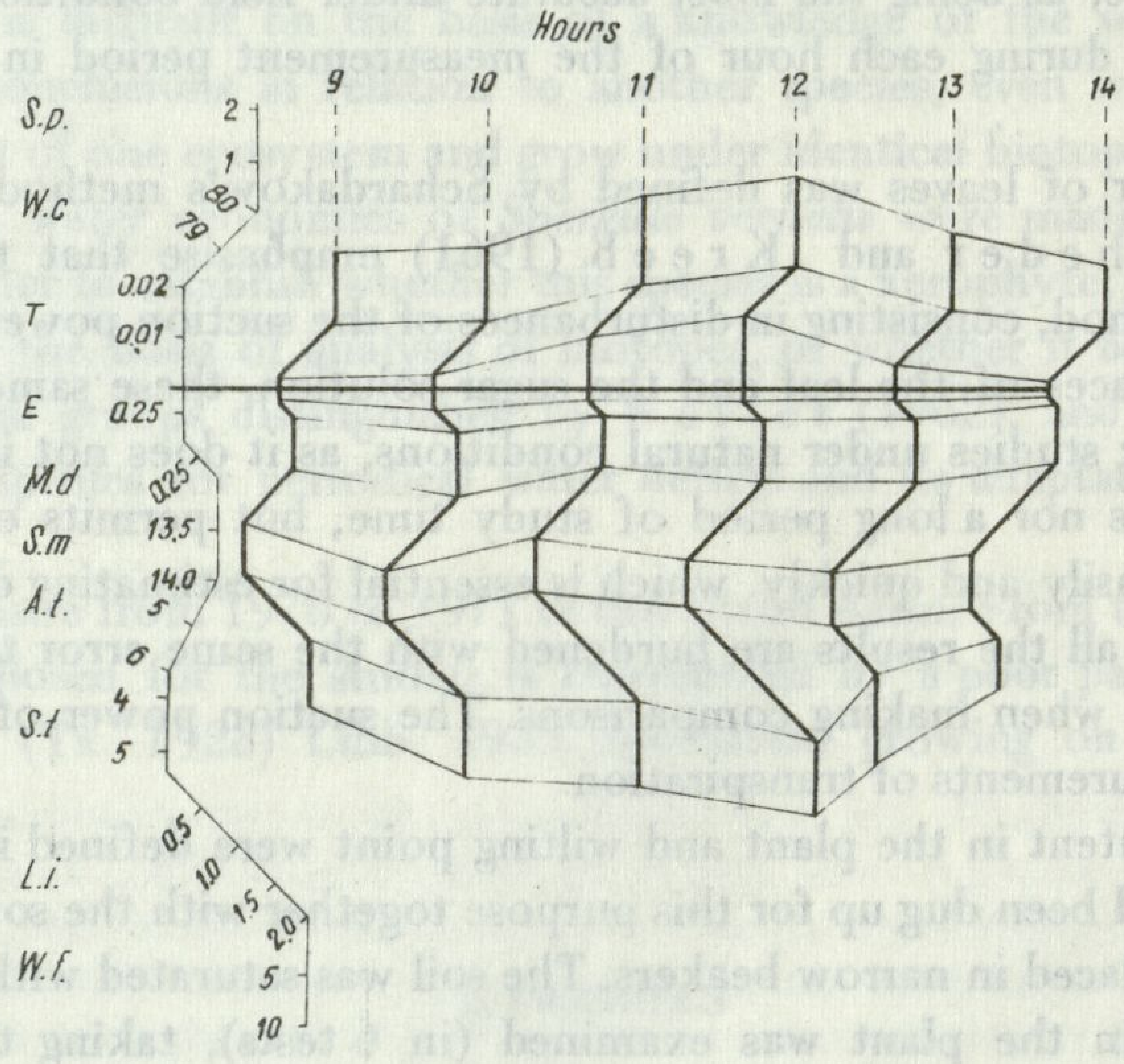

Fig. 1. Suction power, water content in leaves and transpiration in relation to habitat conditions (8 April 1970)

S.p. – suction power (in atmospheres). *W.c.* – water content in leaves (in per cent), *T* – transpiration (mg/g/minute), *E* – evaporation (ml H_2O/hour), *M.d.* – air moisture deficiency (mm Hg), *S.m.* – current soil moisture (in per cent), *A.t.* – air temperature (°C), *S.t.* – soil temperature (°C), *L.i.* – light intensity (in luxes), *W.f.* – wind force (m/100 sec.)

Analysis of results showed that:

1. Irrespective of the prevailing microclimatic conditions transpiration is most intensive in the forenoon hours. On cloudy and cool days the decrease in this process takes place between the hours of 13–14,00 (Fig. 1, 2, 6); with hot sunny weather the hour is earlier – about noon (Fig. 3, 5, 7, 9–11); sometimes, when soil humidity is low, as early as 11,00 (fig. 4, 8). Transpiration is always very weak in the afternoon hours.

A transpiration curve of this kind is characteristic of the majority of plants growing in dry biotopes (Walter 1951, Abd El Rahman and Batanouny 1965a). An abrupt decrease in transpiration in the hot afternoon hours was also frequently observed in a number of other plants growing on moister soil (cf. Pisek and Tranquillini 1951, Walter 1951). The abrupt decrease in transpiration is the plant's reaction to excessive water loss; it takes place as the result of loss of turgor and closing of the stomatal apparatus of the transpiring organs. Although tolerance to decrease in turgor and the defensive mechanism of the plants are not as yet fully known (Bannister 1964), it is thought that radiation and the high temperature of the leaves connected with it under direct light conditions play a fundamental part in this (Konis 1950, Janke 1970). Hence also the plants of dry biotopes usually have a smaller leaf surface, a small ratio of surface to volume of leaf and different anatomical structure from that of hygro-

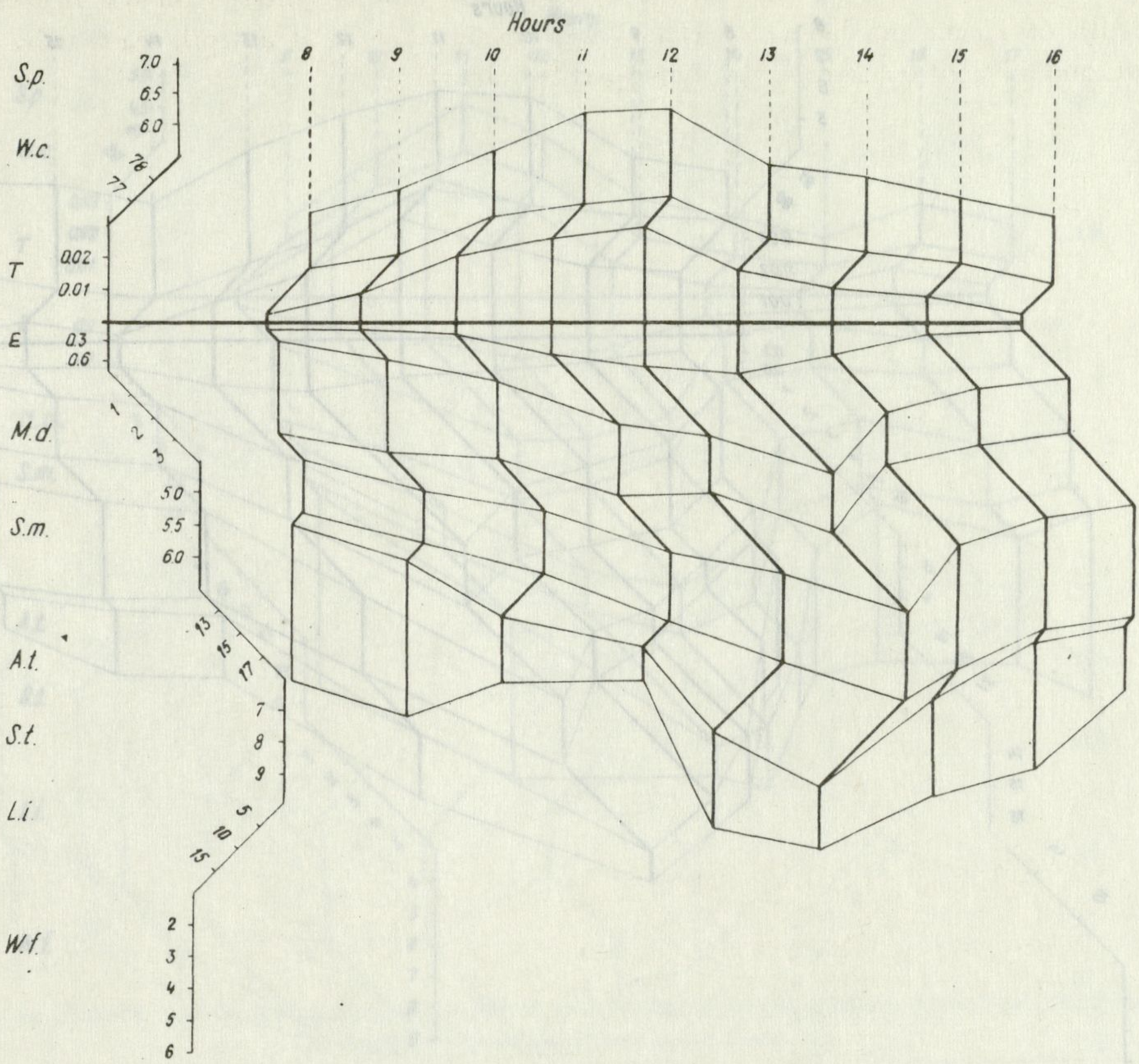

Fig. 2. Suction power, water content in leaves and transpiration in relation to habitat conditions (6 April 1971) (explanations as for Figure 1)

phytes and mesophytes (H y g e n 1951). A frequent adaptation is the capacity of the plant for abrupt changes in leaf surface with a decrease in turgor (H u g h e s, C o c k s h u l l and H e a t h 1970), and lateral positioning of leaves in relation to the rays of sun falling on them, which protects them from excessive heating.

2. In the forenoon hours intensity of transpiration increases with increase in light intensity, air temperature, air humidity deficiency and evaporation. This relation was observed during all the measurements. Although the factors mentioned act jointly, opinions expressed in literature are divided as to the fundamental importance of any one of them. For instance, according to K o n i s (1950) and K o c h (1956), intensity of transpiration depends primarily on light and wind, R i t c h i e (1969) emphasises the role of temperature, A b d E l R a h m a n and B a t a n o u n y (1965a, 1965b) the effect of evaporation and air humidity deficiency. The opinion held by the last of the above-mentioned authors, who found by experimenting that transpiration is intensive under conditions of dry, sunny weather, with simultaneous sufficient water supply to the plant, would appear the most correct. In their opinion the soil humidity factor plays the most

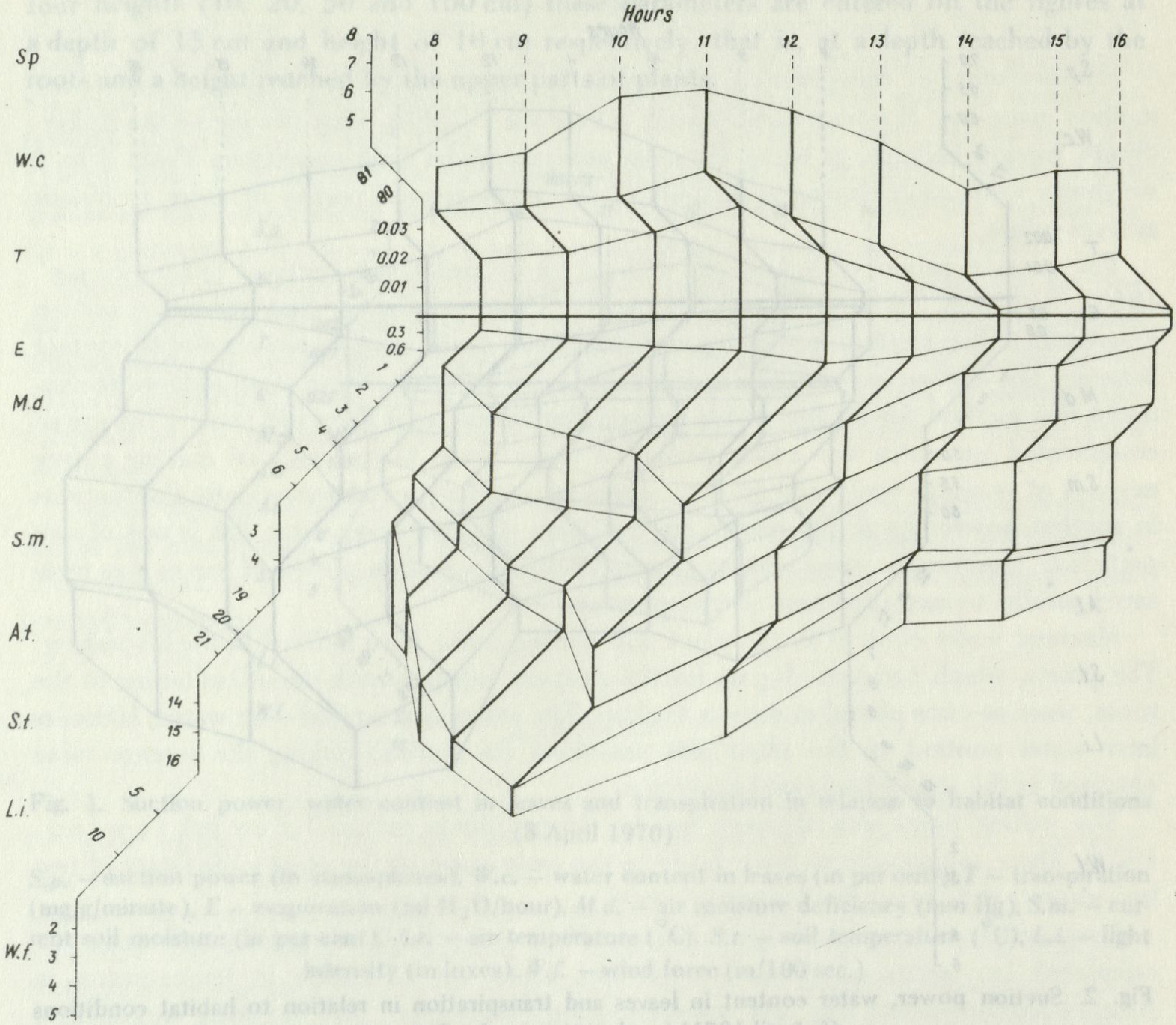

Fig. 3. Suction power, water content in leaves and transpiration in relation to habitat conditions (20 April 1971) (explanations as for Figure 1)

important part here. Soil temperature is of great importance in the process of water intake: the higher the temperature, the easier the assimilation of water by the plant. W i l l i s et al. (1959) emphasise the factor of soil temperature in dry biotopes; in their opinion, relatively warm light soils make vegetation possible even under poor humidity conditions.

The results obtained confirm the studies made by the authors referred to above. Maximal absolute values of transpiration were observed on April 26, 1970 (Fig. 5) due to relatively high soil humidity (10–12%) and high soil temperature, with simultaneously dry and warm air.

3. The transpiration values obtained for *Spergula vernalis* are similar to the transpiration of a large number of other plants growing in similar biotopes, but are far lower than for typical xerophytes (cf. M o t y k a 1962, S t o c k e r 1970).

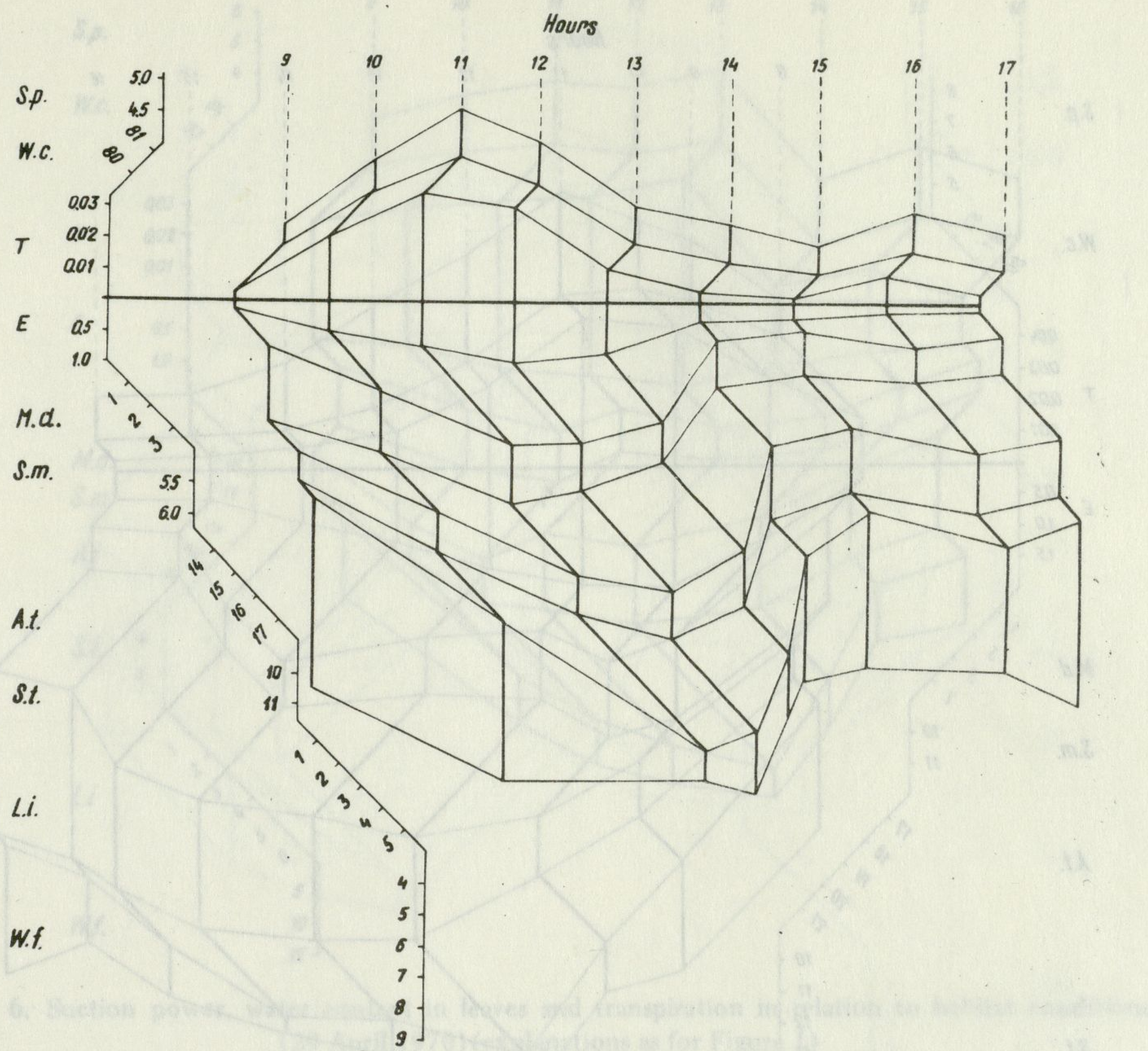

Fig. 4. Suction power, water content in leaves and transpiration in relation to habitat conditions (23 April 1971) (explanations as for Figure 1)

4. Increase in transpiration caused increase in the suction power of leaves, which is a common phenomenon in the plant kingdom. Similarly therefore, as in the case of transpiration, a systematic increase in suction power was observed in the early hours, followed by decrease. In the afternoon it is subject to very slight fluctuations, but its values were always lower than in periods of intensive transpiration.

In general, relatively low suction power is found for this plant, coming within the limits typical of mesophytes.

5. During a period of intensive transpiration there was usually a decrease in water content in the leaves, despite the simultaneous rise in suction power. This phenomenon points to disturbance of the water balance of the plant and therefore to insufficiently rapid flow of water into the leaves (S t r e b e y k o 1966). It is probably that this is a case of the plants limiting transpiration at noon as a precaution against excessive water loss. A repeated rise in water content in the leaves took place in the afternoon hours, although hydration of the leaves was still lower at 17,00 hours than in the morning hours.

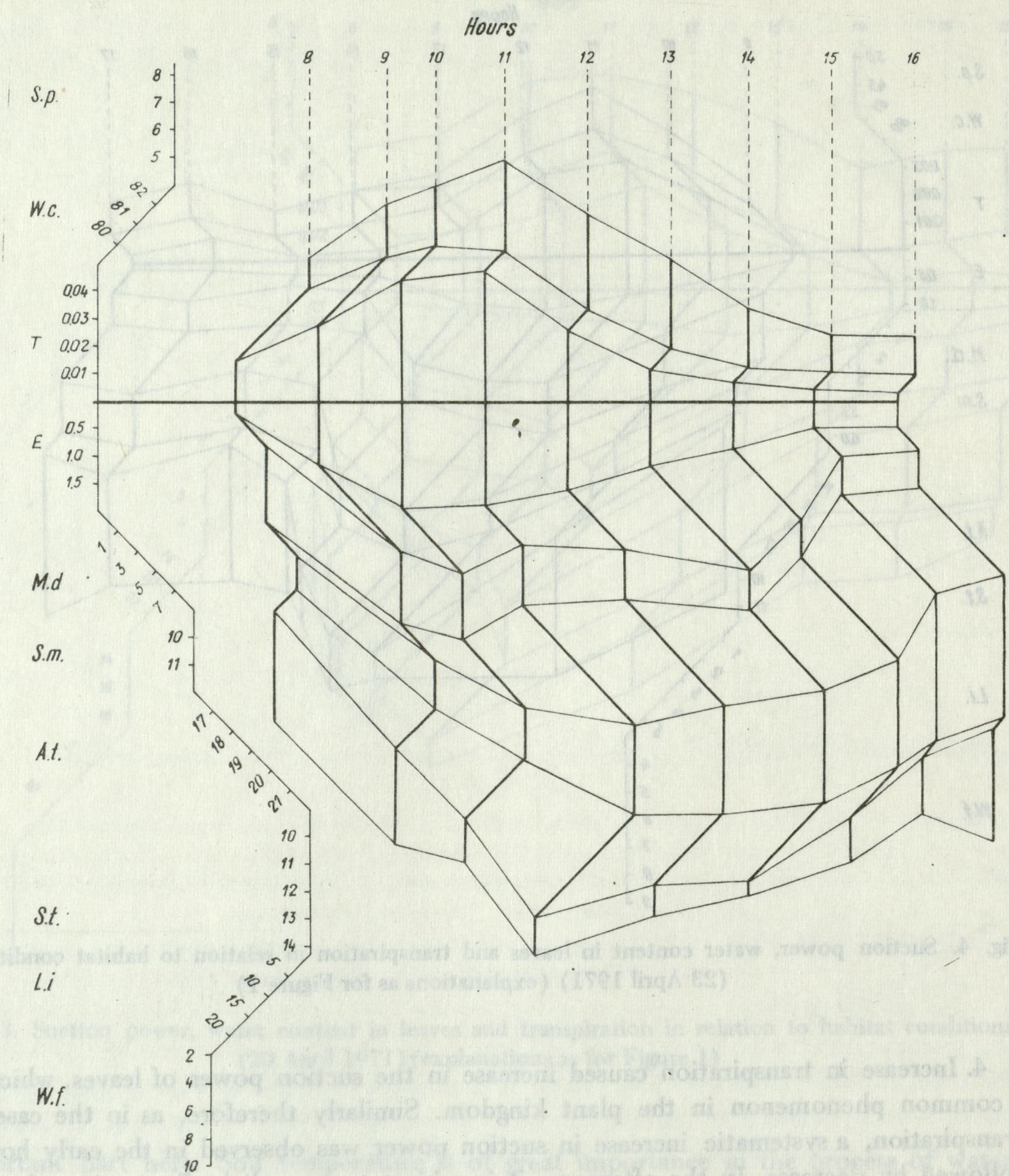

Fig. 5. Suction power, water content in leaves and transpiration in relation to habitat conditions (26 April 1970) (explanations as for Figure 1)

6. Maximal water content in leaves was 89–91% at the stage of two leaf whorls and 88–89% during the flowering period. In general, therefore, under natural conditions this plant lives in a state of slight water deficit of about 8–10%. The limit of hydration below which the plant dies is 68–69% in the juvenile stage and 61–62% during the mature period. The values given refer to the wilting point.

7. Soil humidity at which lasting wilting occurs is 1.0–1.2% in the early stages of development and 0.5–0.7% in the mature period. It is clear from the foregoing that the plant's humidity requirements decrease with age.

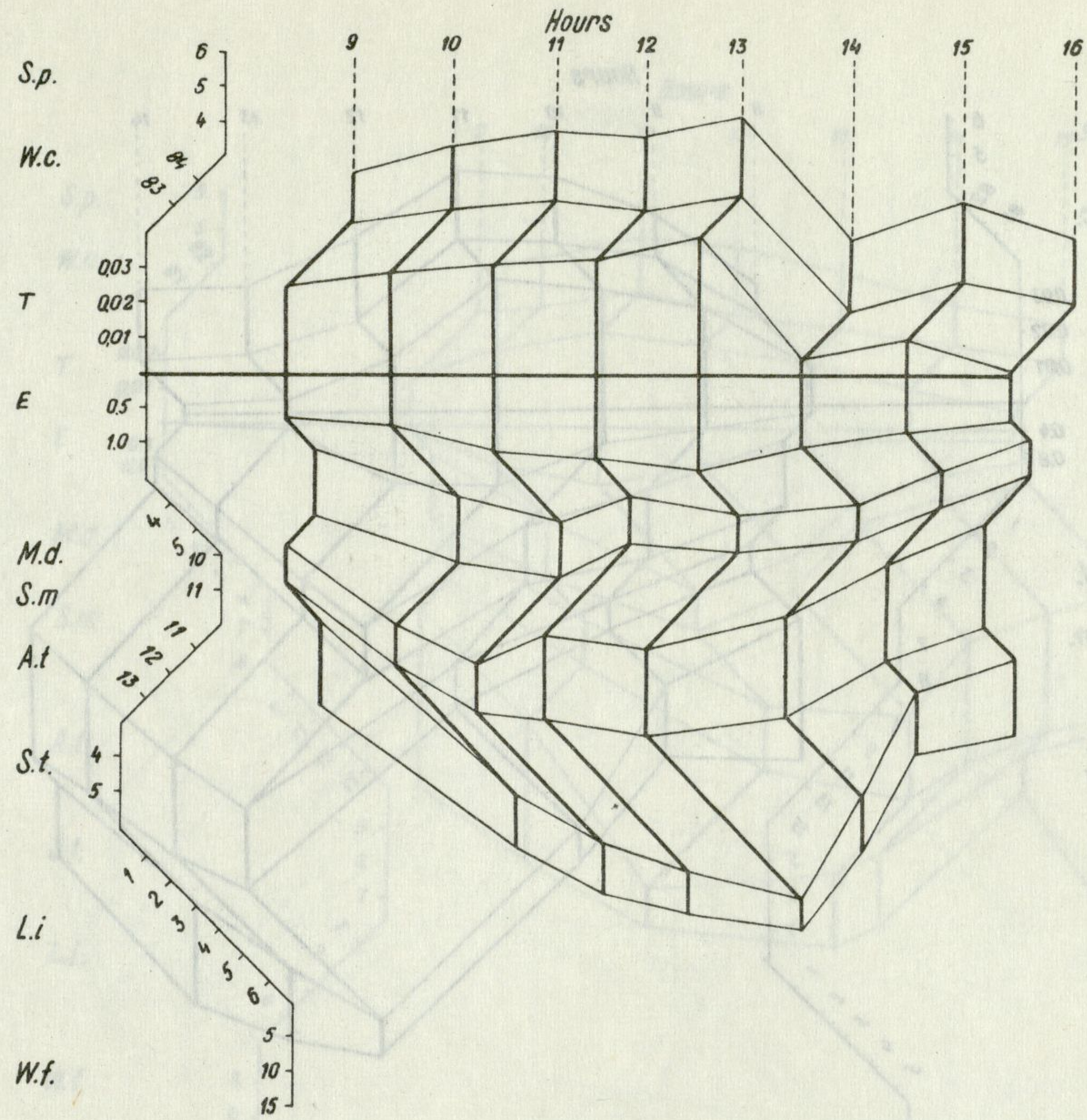

Fig. 6. Suction power, water content in leaves and transpiration in relation to habitat conditions (29 April 1970) (explanations as for Figure 1)

The results given are similar to those observed in the majority of cases of sandy soils.

8. To sum up it can be said that despite certain grounds for allocating *Spergula vernalis* to the group of xerophytes (small cylindrical leaves, low ratio of area to volume of the leaves, thick epithelium, capacity for limiting transpiration under water deficit conditions and finally the dry sunny biotope with which it is connected), its water economics decidedly differ from that typical of xerophytes, being more similar to that of mesophytes. This is shown both by the weak development of the root system, low transpiration value and suction power and also the ease with which it relapses into a state of water deficit. Usually the xeromorphy of therophytes of dry sites is only faintly evident (S z y m k i e w i c z 1932) and despite the biotope typical of them they are not resistant to drought. This phenomenon becomes understandable if we take into consideration the period of intensive development of therophytes occurring in early spring, that is, under conditions of relatively good water supply to the soil (cf. S y m o n i d e s 1974c).

Before the onset of summer heat therophytes scatter their seeds, which are resistant to drought and the effect of high temperatures. The rhythm of growth and development of *Spergula vernalis* (like that of many other therophytes such as *Teesdalea nudicaulis* (L.) R. Br., *Veronica Dillenii* Cr., *Arenaria serpyllifolia* L.) thus form fundamental adaptation to life under the conditions prevailing in poor dry dune biotopes.

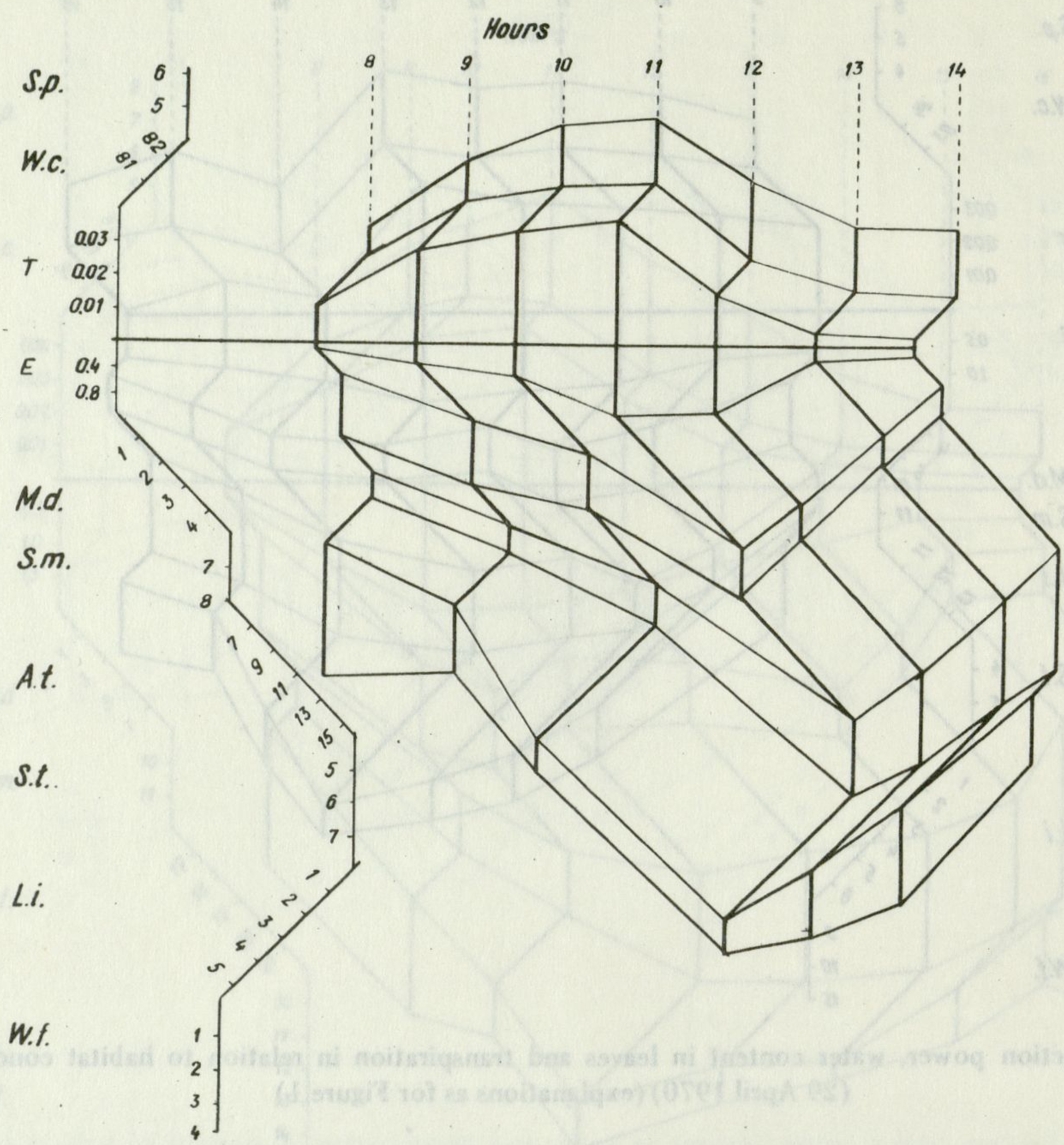

Fig. 7. Suction power, water content in leaves and transpiration in relation to habitat conditions (4 May 1970) (explanations as for Figure 1)

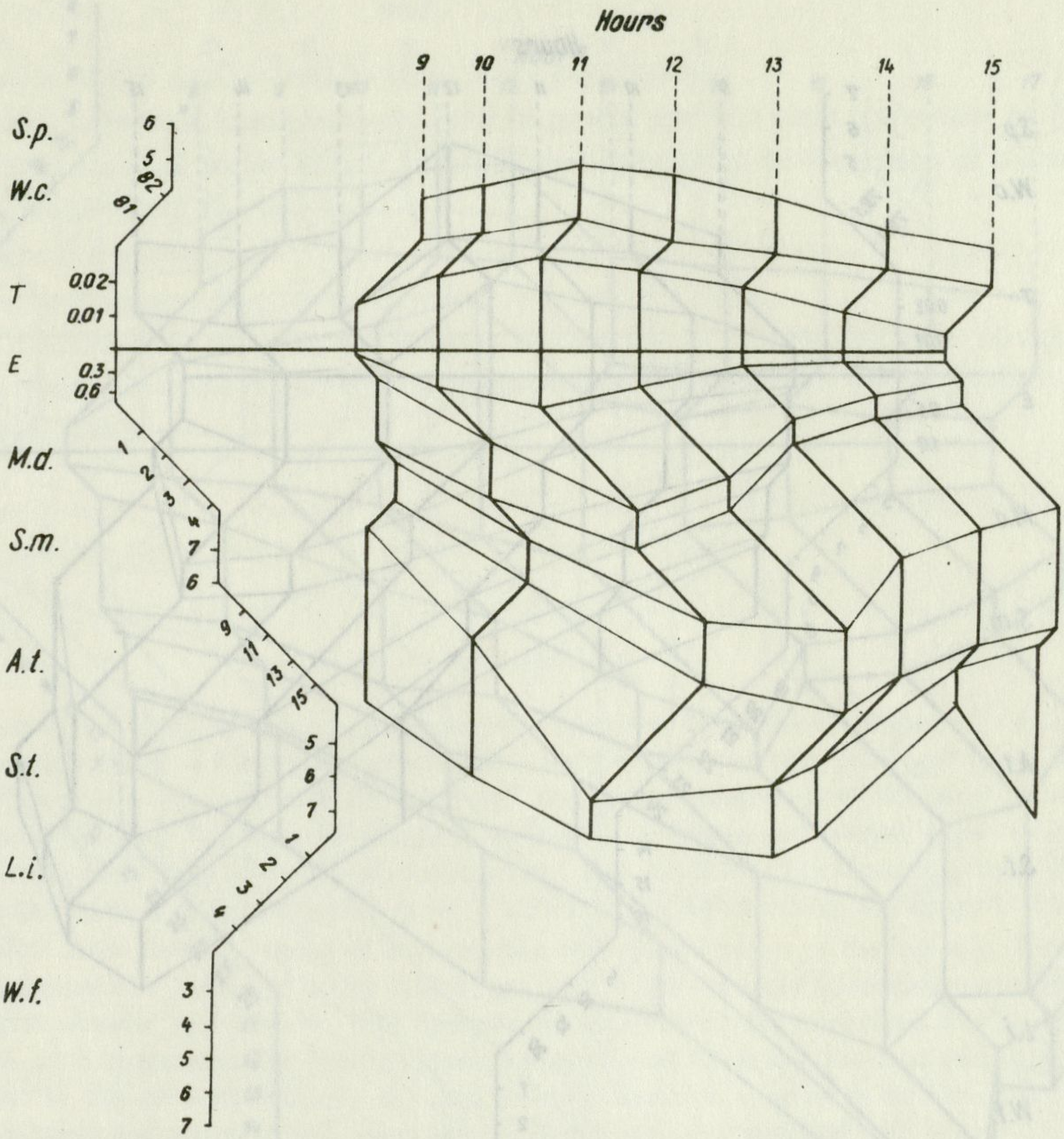

Fig. 8. Suction power, water content in leaves and transpiration in relation to habitat conditions (6 May 1971) (explanations as for Figure 1)

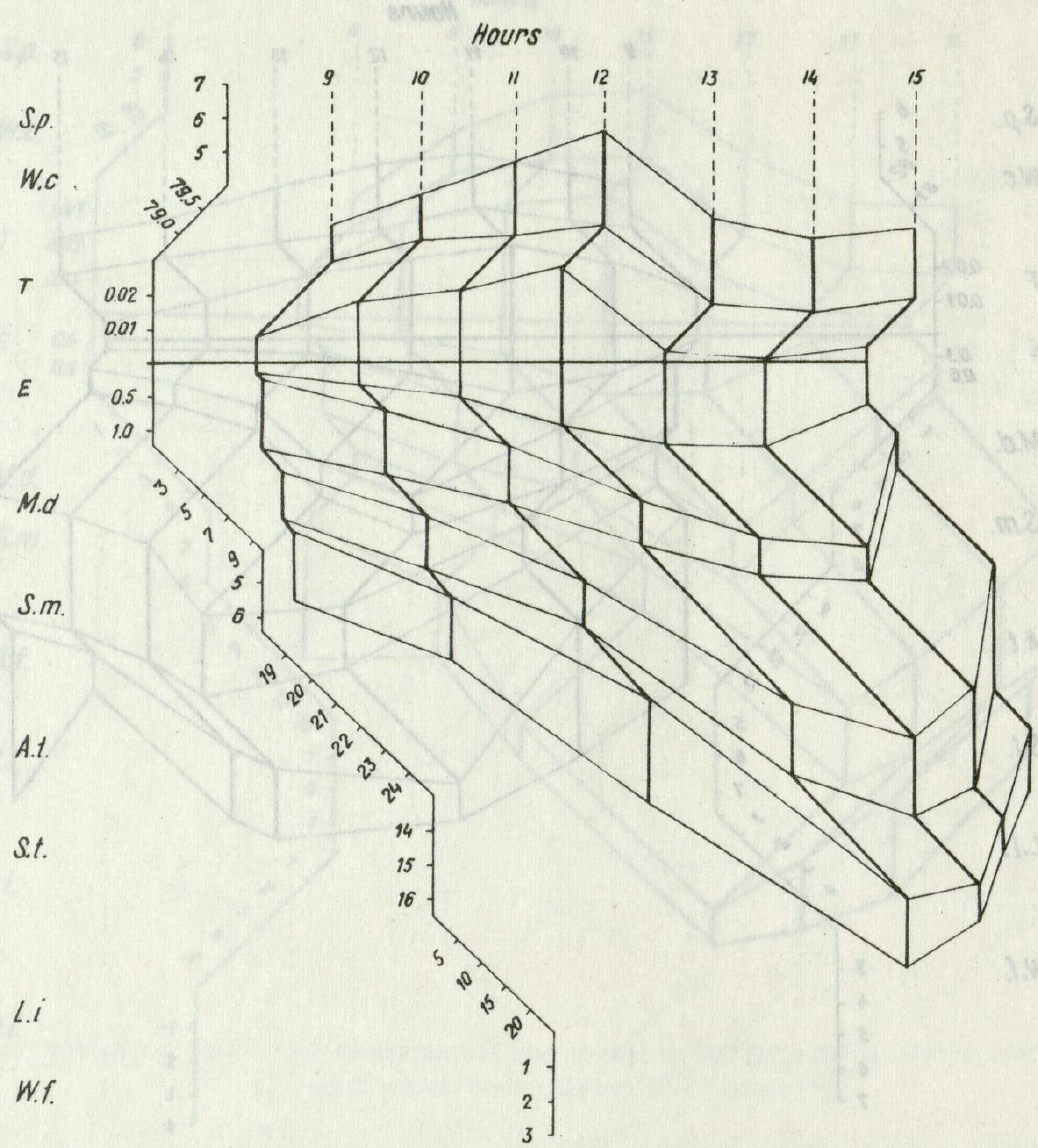

Fig. 9. Suction power, water content in leaves and transpiration in relation to habitat conditions (9 May 1970) (explanations as for Figure 1)

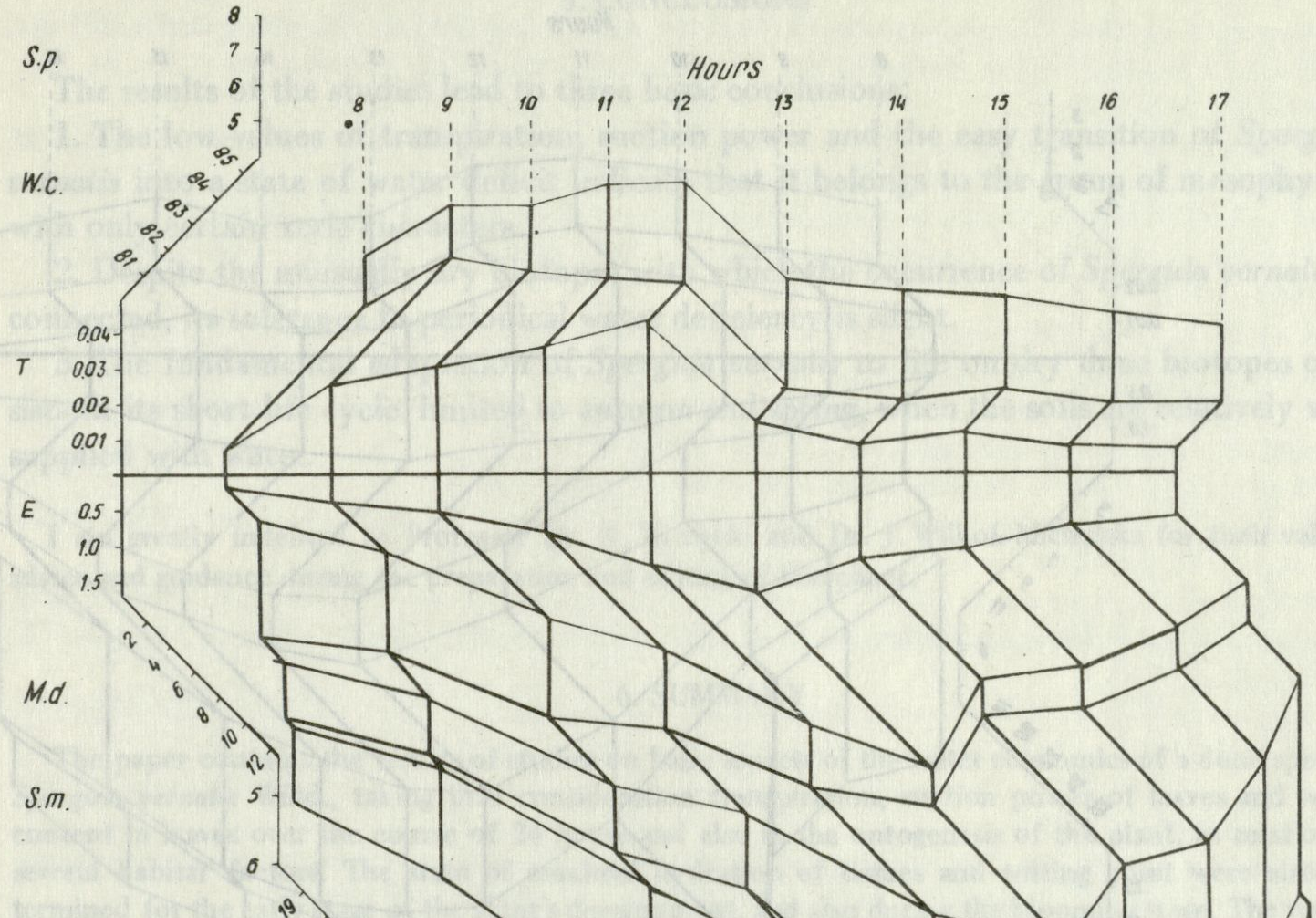

Fig. 10. Suction power, water content in leaves and transpiration in relation to habitat conditions (10 May 1971) (explanations as for Figure 1)

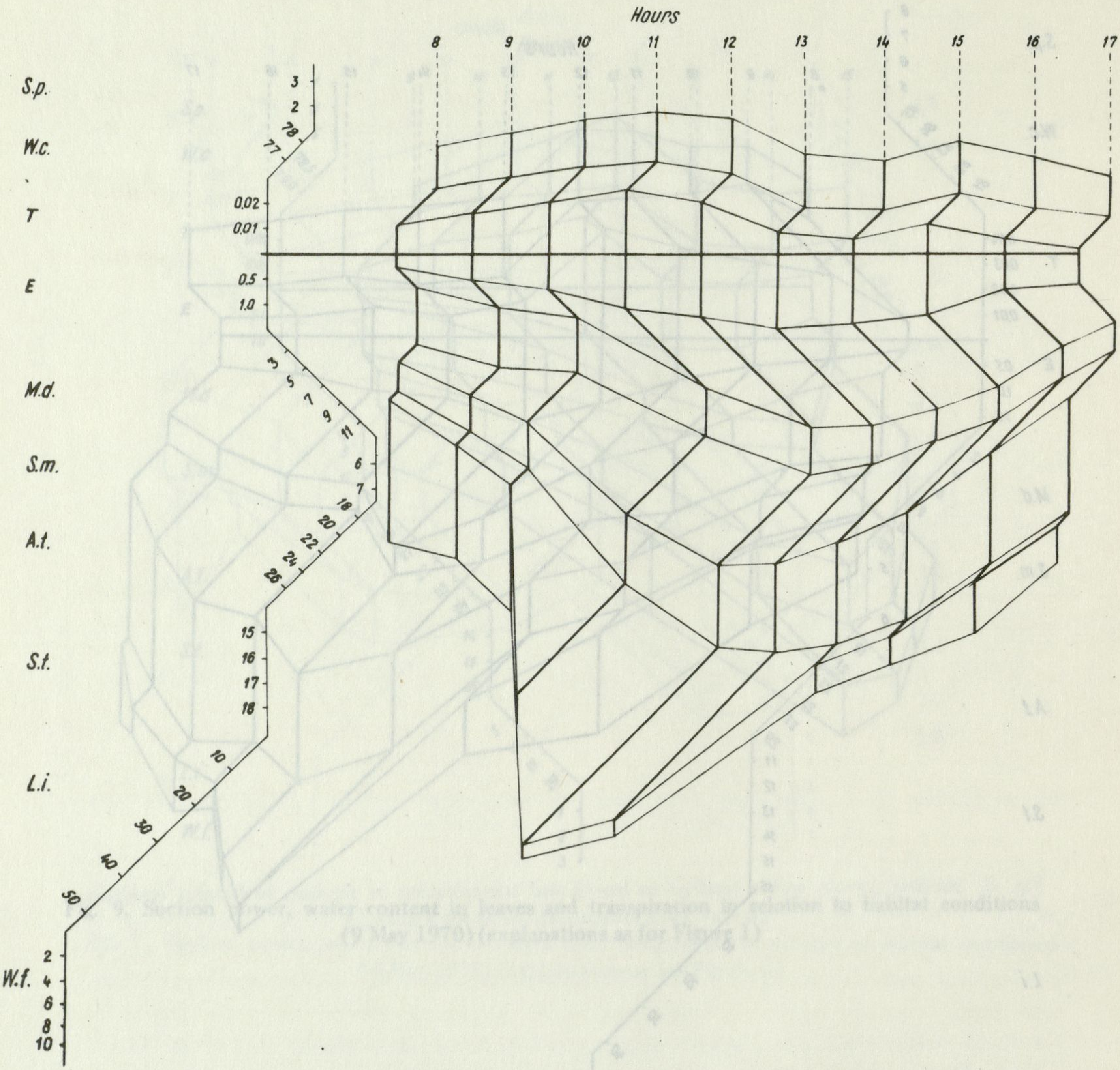

Fig. 11. Suction power, water content in leaves and transpiration in relation to habitat conditions (16 May 1971) (explanations as for Figure 1)

5. CONCLUSIONS

The results of the studies lead to three basic conclusions:

1. The low values of transpiration, suction power and the easy transition of *Spergula vernalis* into a state of water deficit indicate that it belongs to the group of mesophytes, with only certain xeric characters.

2. Despite the unusually dry biotopes with which the occurrence of *Spergula vernalis* is connected, its tolerance to periodical water deficiency is slight.

3. The fundamental adaptation of *Spergula vernalis* to life on dry dune biotopes consists in its short life cycle, limited to autumn and spring, when the soils are relatively well supplied with water.

I am greatly indebted to Professor Dr. K. Zarzycki and Dr. J. Wilkoń-Michalska for their valued advice and guidance during the preparation and editing of this paper.

6. SUMMARY

The paper contains the results of studies on basic aspects of the water economics of a dune species, *Spergula vernalis* Willd., taking into consideration transpiration, suction power of leaves and water content in leaves over the course of 24 hours and also in the ontogenesis of the plant, in relation to several habitat factors. The state of maximal hydration of tissues and wilting point were also determined for the early stage of the plant's development, and also during the blooming stage. The results are given in the form of diagrams drawn up by B a r n e r ' s (1965) method, in Figures 1–11.

The studies show that the values of transpiration and suction power of the leaves are low, that the plant easily lapses into a state of water deficit, and that it has a weakly developed root system, all of which suggest, despite appearances, that *Spergula vernalis* should be considered a mesophyte, with only certain xeric characters. The results obtained suggest in addition that the fundamental adaptation of this plant to life on outstandingly dry and infertile biotopes consists in its life cycle, occurring during the autumn and spring period, when the soil is relatively well supplied with water.

7. POLISH SUMMARY (STRESZCZENIE)

Praca zawiera wyniki badań podstawowych zagadnień gospodarki wodnej wydmowego gatunku *Spergula vernalis* Willd. Uwzględniono w nich transpirację, siłę ssącą liści i zawartość wody w liściach, w przebiegu dziennym oraz ontogenezie rośliny, na tle kilku czynników środowiskowych. Oznaczono także stan maksymalnego uwodnienia tkanek i punkt trwałego więdnięcia we wczesnym stadium rozwoju rośliny oraz w okresie kwitnienia. Wyniki podano w postaci wykresów (fig. 1–11), sporządzonych metodą B a r n e r a (1965).

Stwierdzone w tych badaniach niskie wartości transpiracji i siły ssącej liści, łatwość popadania rośliny w stan deficytu wodnego a także słaby system korzeniowy, pozwalają, wbrew pozorom, uznać *Spergula vernalis* za mezofit, z pewnymi tylko cechami kseryzmu. Wyniki badań sugerują ponadto, że podstawową adaptacją rośliny do życia na wybitnie suchych i jałowych siedliskach jest jej cykl życiowy, przypadający na okres jesieni i wiosny, kiedy gleba jest stosunkowo zasobna w wodę.

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