*Acta Botanica Neerlandica* **12** (1963) 248–261

# THE INFLUENCE OF THE SUCTION TENSION OF THE NUTRIENT SOLUTIONS ON GROWTH, TRANSPIRATION AND DIFFUSION PRESSURE DEFICIT OF BEAN LEAVES (PHASEOLUS VULGARIS)

R. BROUWER

(*Instituut voor Biologisch en Scheikundig Onderzoek van Landbouwgewassen, Wageningen*)

(*received January 4th*, 1963)

ABSTRACT

The rate of leaf growth of seedlings of *Phaseolus vulgaris* at different osmotic concentrations of the root environment has been measured. Even a small increase of the concentration gives a distinct reduction in growth. This reduction is the more important the higher transpiration is. The relationship between rate of growth, transpiration rate, osmotic value and diffusion pressure deficit has been determined.

Application of the suction tension during 24 hours only has resulted in a fully reversible inhibition.

## INTRODUCTION

Most investigators agree that plant growth is often reduced by water deficits. Too little is known, however, about the mechanism of such reductions. KRAMER (1959) states that little attempt has been made to correlate the numerous studies on soil, atmospheric and plant water conditions and to use them in explaining plant growth behaviour. The most important factor in this respect seems to be the internal water balance influencing the rates of various physiological processes underlying the quantity and quality of plant growth.

The internal water balance depends on the water supply from the root medium and the water loss into the atmosphere. There may be a direct effect of water deficit on cell extension as suggested by many authors (LOOMIS 1934, BROUWER 1960). The exact nature of this effect, however, is unknown (KRAMER 1959). A few investigations have been performed on the correlations between diffusion pressure deficit (D.P.D.) and the growth of an organ (VAN DEN ENDE 1953, SLATYER 1957).

The relation between D.P.D. in the plant and suction tension in the root medium is a complex one depending on light intensity, relative humidity of the air, shoot/root ratio, soil temperature, soil aeration, etc. Many of these factors, however, may influence growth without intervention of the water balance.

In this paper the influence of suction tension in the root medium on the D.P.D. of leaves, on leaf growth and on transpiration is described.

## METHODS

Young seedlings of *Phaseolus vulgaris* have been used in the experi-

ments. By the time the primary leaves unfolded the plants were placed on an aerated Hoagland solution. Light intensity was kept at 40.000 ergs $cm^{-2}$ $sec^{-1}$, temperature at 20° C and relative humidity at $\pm$ 65 %. High pressure mercury vapour lamps with a fluorescent outher bulb were used.

The suction tension of the root medium was raised by addition of sodium chloride.

The growth of the leaves was measured daily as an increase of the length of the midrib. As a rule the average value of 5 plants (10 leaves) was taken.

At intervals of 2 or 3 days samples of 5 plants were harvested and the leaf area was measured. At the same time trips were taken from the lower epidermis and the stomatal density was determined microscopically. The total number of stomata per leaf was calculated from leaf area and stomatal density. Since the number of stomata and number of cells are closely correlated these data give a measure of cell extension.

If required the D.P.D. of leaves was measured according to the leaf strip method of URSPRUNG (1921).

Strips of 5 $\times$ 0.5 cm were taken from the tissue between the major veins and were kept in sugar solutions of different concentrations for two hours.

Transpiration was determined by weighing the pots after a correction for losses due to aeration.

## RESULTS

*Continuous application of various sodium chloride concentrations during the growth of the first leaves.*

At the start of the experiments the leaves had a length of about 25 mm. Right away from the first application of the salt solutions a decreased growth could be observed. The higher the concentration the more important growth reduction was (Fig. 1). The same holds for the intensification of the green colour. A concentration of 1.25 atm. had no significant effect. The shape of the leaves was not affected by the treatment but the leaves at the higher concentrations tended to be somewhat thicker.

The reduction of leaf growth caused by the salt solutions depended on light intensity (Fig. 1). At the two light intensities used, leaf growth rate on the Hoagland solution did not differ during the first four days whereas the reduction by the sodium chloride solutions was smaller at the lower light intensity. At the higher light intensity the growth of the first leaves tended to be finished somewhat earlier than at the lower light intensity. This may be due to inhibition caused by the appearance of the following leaves which emerge earlier at higher light intensity.

*Cell division and cell extension at the continuous salt treatments*

The great differences in leaf size between plants on the various concentrations may be due to differences in cell division and/or cell

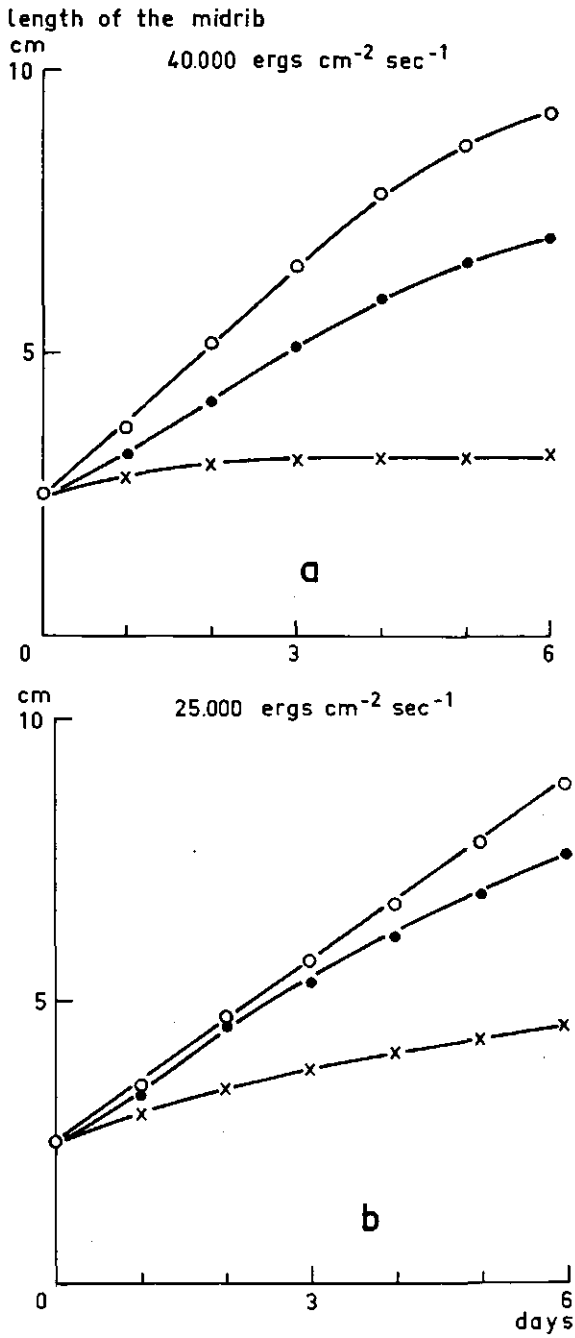


Fig. 1. Increase in leaf length at different suction tension of the nutrient solution and two light intensities.
circles : Hoagland solution
dots : Hoagland solution + 2.5 atm. NaCl
crosses: Hoagland solution + 5.0 atm. NaCl.

extension. A correlation between the number of epidermal cells and the number of stomata could be established also in this material (cf. TUMANOV 1921, BROUWER 1960).

According to this the number of stomata per unit of leaf area was counted.

TABLE I

Number of stomata per leaf (lower epidermis)

| | 1st | 2nd | 3rd | 4th | 5th | 6th day after starting |
|---|---|---|---|---|---|---|
| H . . . . . | 66,4 | 96,0 | 88,9 | 97,9 | 90,0 | 100,3 |
| H + 2,5 atm. . . . | 66,4 | 83,8 | 91,4 | 93,2 | 98,5 | 97,3 × $10^4$ |
| H + 5,0 atm. . . . | 66,4 | 79,2 | 96,8 | 87,8 | 93,6 | 95,8 |

The number of stomata per leaf increased during the first two days only. Thereafter this number (about a million per leaf in the lower epidermis) remained constant and was not greatly affected by the treatment (Table I). During the first two days the share of cell divisions in the total increase in leaf area was more important than later on. It appears from these experiments that the concentration of salt solution had no influence on cell division. At continued application the emergence and unfolding of new leaves is retarded. However, also in this case the reduction in cell extension remains the most important factor in reducing leaf area.

TABLE II

Number of stomata per 0.8 mm² on the lower epidermis

| Nutrient Solutions | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 days after starting |
|---|---|---|---|---|---|---|---|---|
| Hoagland . . . . . | 123 | 100 | 57 | 48 | 30 | 22 | 20 | 21 |
| Hoagland + 2,5 atm NaCl . | 123 | 107 | 68 | 59 | 51 | 43 | 39 | 39 |
| Hoagland + 5,0 atm NaCl . | 123 | 110 | 80 | 71 | 78 | 70 | 72 | 70 |

The number of stomata per unit of leaf area (Table II) is a measure of cell extension. The size of the cells of the leaves on a Hoagland solution is 3 or 4 times as large as with addition of 5 atm. sodium chloride. The lower concentrations gave intermediate results.

The enhanced suction tension of the root medium, therefore, resulted in reduced cell extension, whereas the number of cells was not or only slightly affected.

*Interrupted application of different sodium chloride concentrations*

In these experiments the plants were placed alternately 24 hours on the Hoagland solution and 24 hours on this solution with addition of various amounts of sodium chloride. Leaf growth was measured during the subsequent 5 days (Fig. 2). It can be seen that growth rate was reduced during the sodium chloride treatment, whereas during the intermediate days on the Hoagland solution growth rate was normal (between treatments with 5 atm. NaCl) or somewhat enhanced

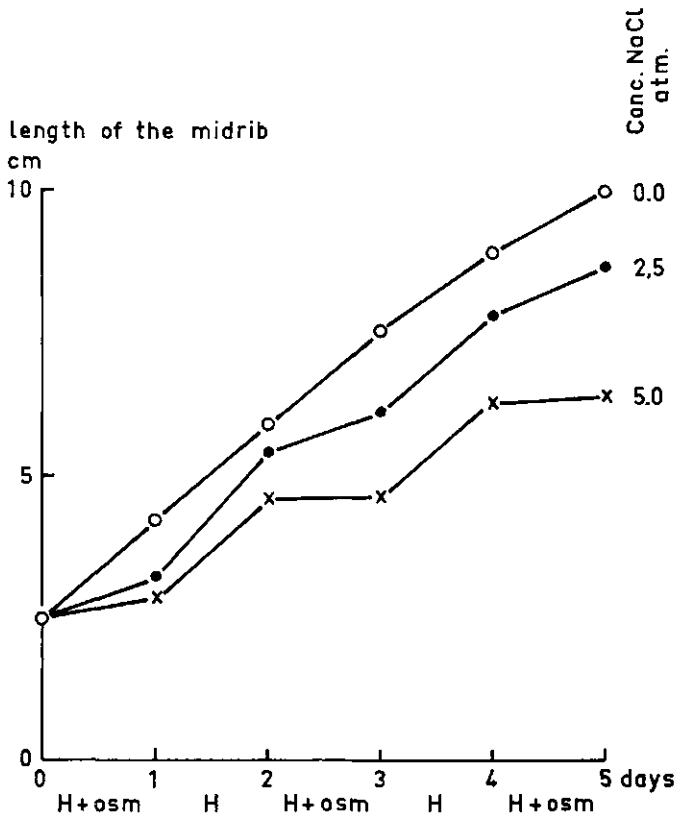


Fig. 2. Leaf growth on Hoagland solution with and without sodium chloride up to the concentrations indicated.

(between treatments with 2.5 atm. NaCl). This compensation after the lower salt concentrations was always found in these experiments (Fig. 3) and was nearly complete with 0.625 and 1.25 atm. The growth rate of the treated plants during the days on Hoagland solution did not appear to be smaller in any case than the growth rate of the controls.

This resumption of the normal growth rate after treatment not only occurred after a treatment of one day but even after a treatment of 3 days (Fig. 4), although in the latter case a delay could be established.

It appears that leaf growth is reversibly inhibited by the 24-hours' treatment and it may be assumed that this inhibition is caused by a diminished availability of water for the growing cells.

It seems to be an osmotic effect only, because of the fact that potassium chloride, potassium nitrate and sodium nitrate give comparable results (Fig. 5).

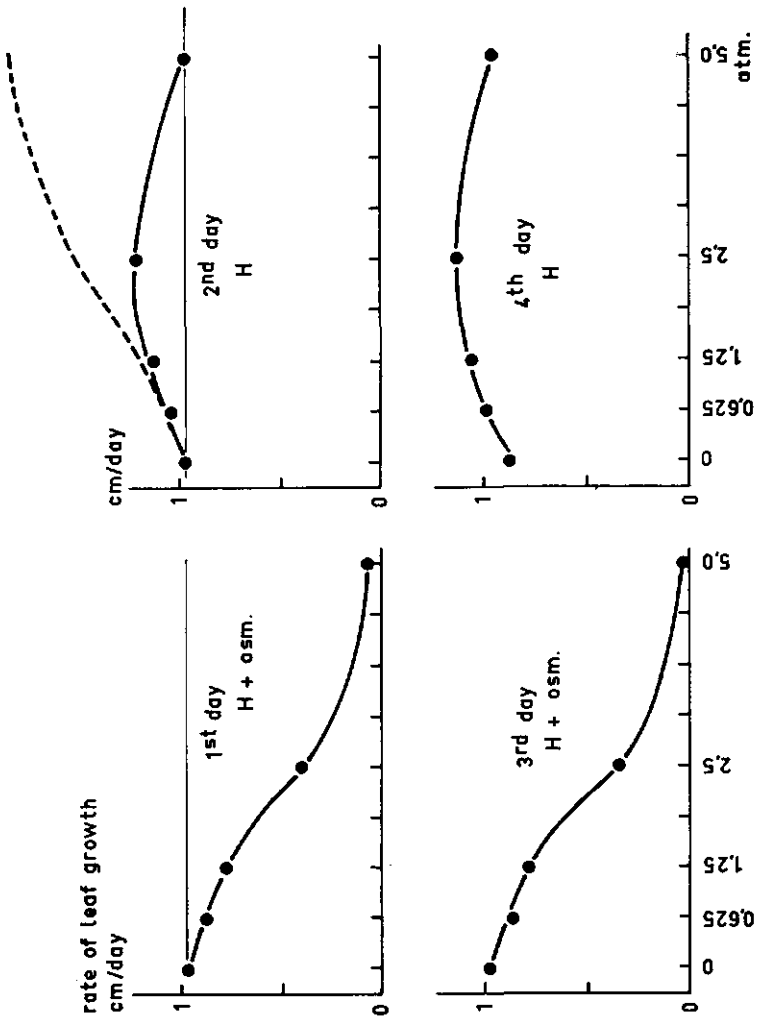


Fig. 3. Rate of leaf growth at 4 subsequent days in an experiment similar to that of figure 2 but with four sodium chloride concentrations. Dotted line expected rate of leaf growth with full compensation during the day on Hoagland.

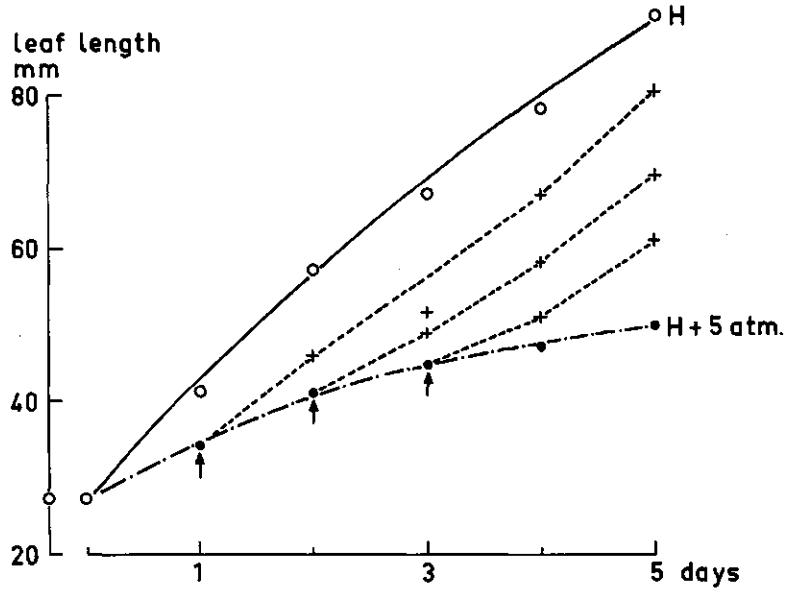


Fig. 4. Recovery of leaf growth after an application of 5 atm. sodium chloride during 1, 2 or 3 days.

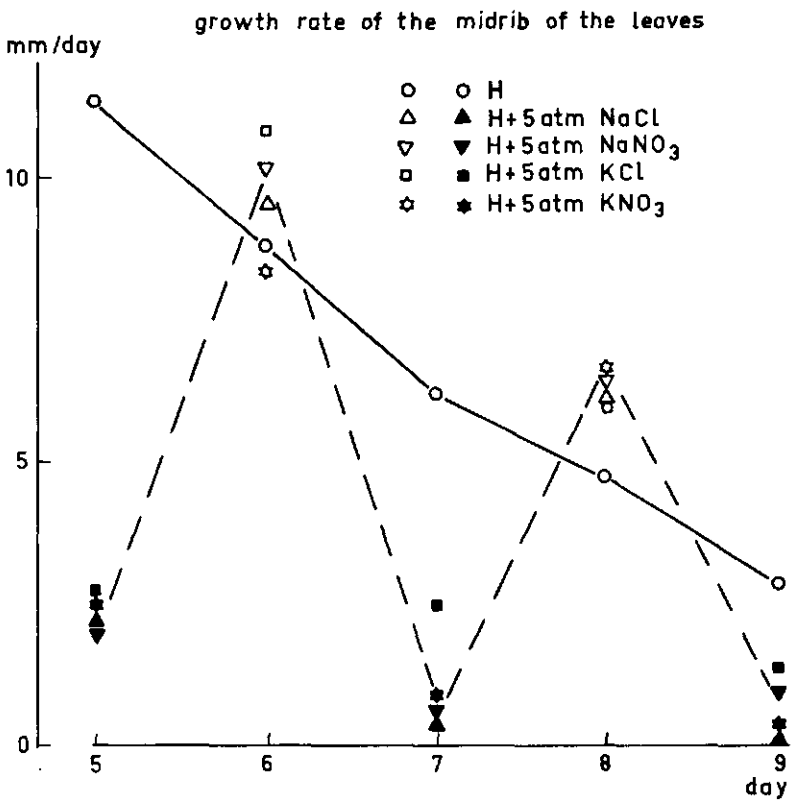


Fig. 5. Rate of leaf growth at 5 subsequent days using different salts in the outer solution, all with the same suction tension (5 atm.). Days with salt additions alternate with days without addition (filled and open symbols respectively).

*Diffusion pressure deficit, osmotic value, leaf growth and transpiration*

It is obvious that leaf growth in the first place is dependent on the D.P.D. of the leaf cells. This value depends only indirectly on the D.P.D. of the root medium and the relation between these two magnitudes is rather complex (BROUWER 1961).

The plants used in the determination of growth, D.P.D. and transpiration were grown on Hoagland solution. During the experimental period the plants were divided into five groups of five plants each. The groups received nutrient solution with addition of sodium chloride to amounts corresponding with 0, 1.25, 2.5, 3.75 and 5.0 atm. The treatment performed on the fourth day after starting the culture lasted 24 hours, started in the middle of a light period and ended in the middle of the next light period. Leaf growth and transpiration during this whole period were measured, whereas the D.P.D. values were determined at the end of the treatment only. The D.P.D. determinations, accomplished according to the method of Ursprung, showed in the control plants a difference of about 2.0 or 2.5 atm. Within the groups (Fig. 6) the differences were smaller in most cases.

Fig. 7 shows the D.P.D. values of the leaves when different salt concentrations of the root medium were used. The D.P.D. of the leaves increases about rectilinearly with the increasing D.P.D. of the nutrient solution and to about the same extent.

In Fig. 8 the rates of leaf growth during the 24-hours' period of applying the sodium chloride, previous to the measurement of the

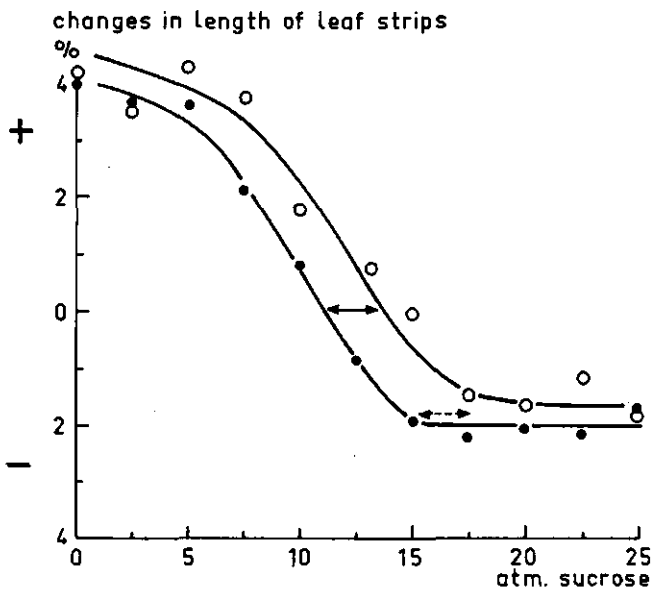


Fig. 6. Percentual changes in length of leaf strips taken from the primary leaves between the main veins and immersed during 4 hours in the sucrose solution indicated. The outmost values of one of the control groups.

D.P.D., have been plotted against the D.P.D. values found. Rate of leaf growth decreased according as the D.P.D. value increased. Between the D.P.D. values 8.0 to 10.0 atm. the decrease was rather small, whereas a rapid decrease could be observed between the D.P.D. values

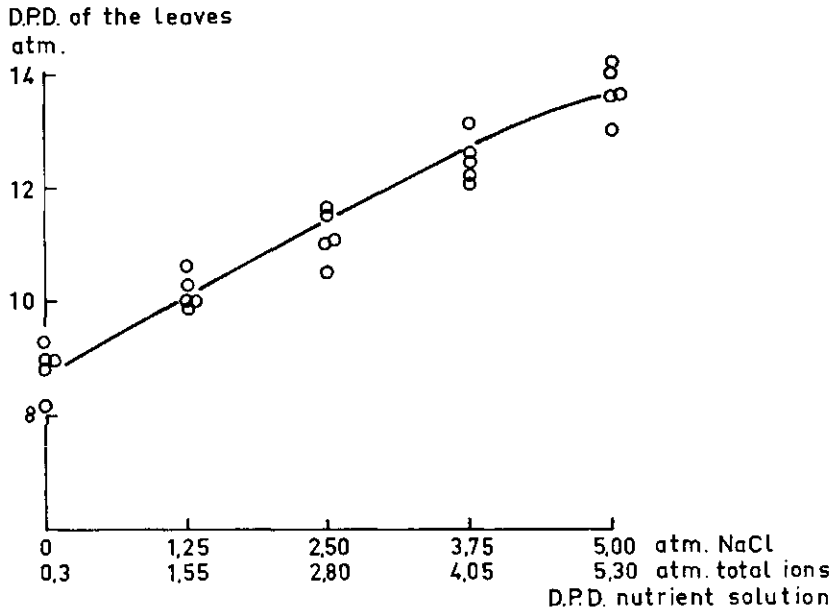


Fig. 7. Diffusion pressure deficits of the leaves of plants grown on Hoagland solution and transferred to the sodium chloride solution indicated for 24 hours previous to the determinations.

10.0 to 12.5 atm. At higher values growth actually stopped. No visible wilting occurred. Even at the highest D.P.D. values a positive turgor pressure of 0.5–1.0 atm. could be estimated. The values of turgor pressure which are the differences between D.P.D. and O.P. (distance between full drawn arrow and dotted arrow in Fig. 6) suffer from fairly large errors, however, and an accurate estimation is not possible.

The curve of figure 8 fairly resembles curves obtained in plasmolysis experiments. This may indicate that growth of a leaf stops as soon as all growing cells have lost their turgidity. In that case it can also be assumed that growth rate is not influenced at all before incipient plasmolysis and that it is not dependent on the magnitude of the turgor pressure.

There was only a small rise in osmotic value of the leaf cells due to the 24 hours' application of sodium chloride in the root medium (Fig. 10). BERNSTEIN and HAYWARD (1958) report an increase of about 3 atm. in bean plants after prolonged treatment with 5 atm. sodium chloride, whereas BERNSTEIN (1962) shows an increase in O.P. to the same extent as the enhancement in O.P. of the nutrient solution.

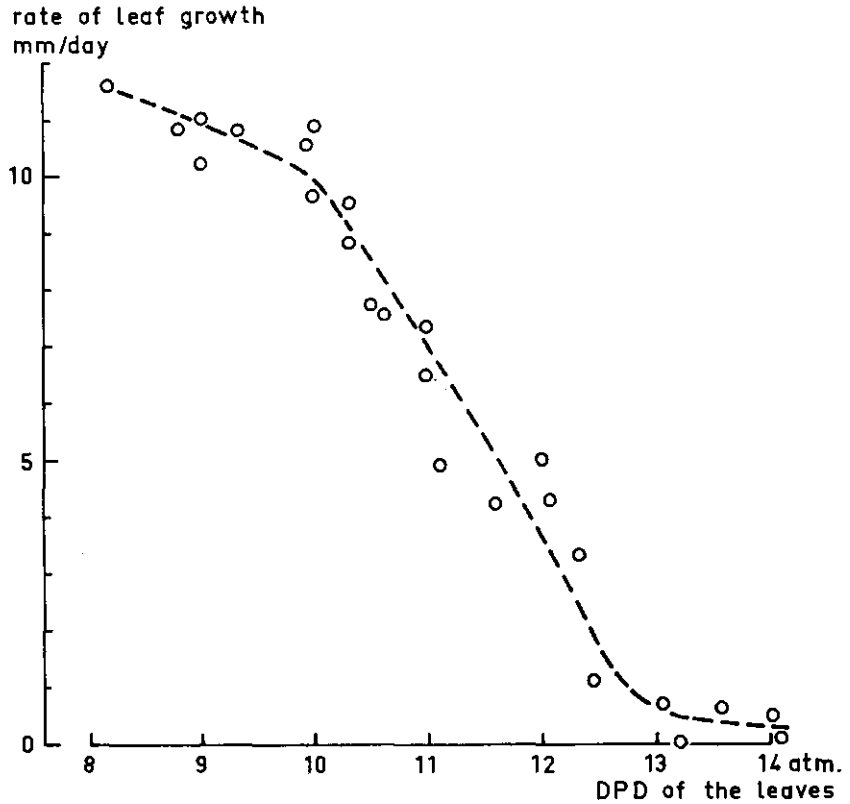


Fig. 8. Rate of leaf growth plotted against the D.P.D. of the leaves (comp. fig. 7).

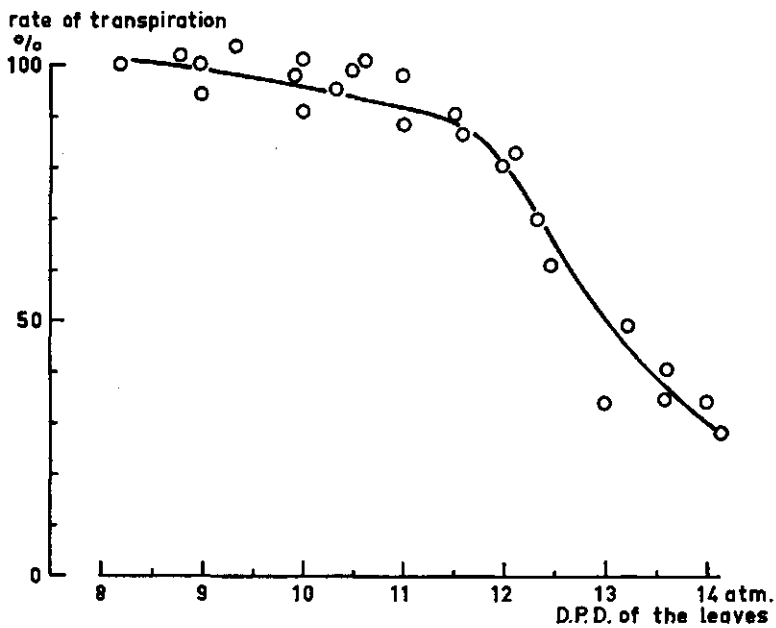


Fig. 9. Relative transpiration rate plotted against the D.P.D. of the leaves.

Obviously, the treatment here is too short to get considerable accumulation of the salt in the leaf cells.

The transpiration of plants, determined at the same time as growth measurements, is plotted in Fig. 9. It can be seen that transpiration slowly decreases with D.P.D. increasing from 8.0 to 11.5 atm. after which it decreases rapidly. This rapid decrease will be due to a partial closure of the stomata. The level of pure cuticular transpiration apparently has not been reached in these experiments. It should be kept in mind, however, that transpiration in this case is the sum of an 8 hours' dark transpiration and a 16 hours' light transpiration.

In Fig. 10 the rates of leaf growth and transpiration and the values of D.P.D. and osmotic concentration have been plotted against the sodium chloride concentration in the nutrient solution. Each point represents the average of 5 plants (10 leaves). It is clear that the process of growth is more sensitive than the process of transpiration. This is a general feature which has been found in all the experiments.

In addition it may be stated that, so far as quantitative relations are concerned these results cannot be generalised. Plants grown under conditions differing in light intensity, relative humidity and tempera-

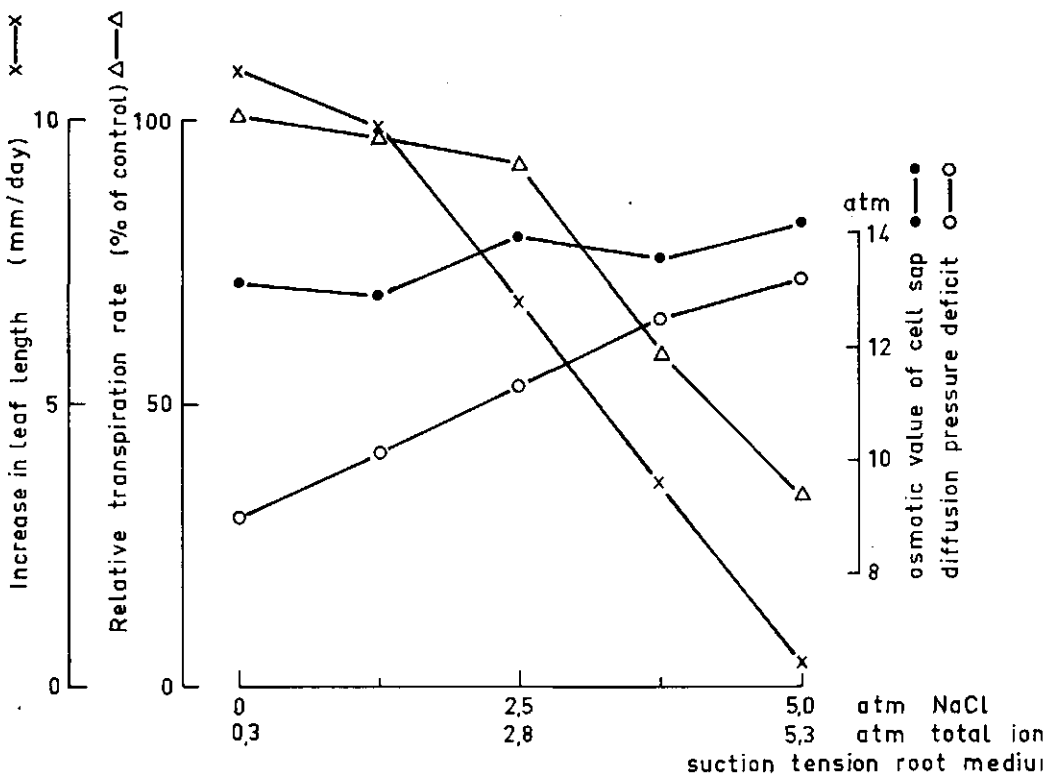


Fig. 10. Osmotic value, D.P.D. of the leaves, rate of leaf growth and rate of transpiration plotted against the osmotic suction tension of the root environment.

ture may quantitatively show other reactions. Their D.P.D. and osmotic concentrations differ from those mentioned above. The pre-conditioning of the plants plays an important role and it is worthwhile to investigate this in detail.

## Discussion

The results described above demonstrate that rather small increases in suction tension of the root environment may have distinct influences on the growth of plants. In so far as leaf growth is considered only an indirect relation between this phenomenon and suction tension of the nutrient solution may be expected. It seems more likely that the rate of leaf growth is only directly dependent on the water holding forces of the tissue from which the growing cells have to obtain their water. In this case the D.P.D. of the leaf will be the most usefull magnitude.

The relationship between D.P.D. of the leaves and D.P.D. of the solution is very complicated depending on many factors inside and outside the plant. A theoretical treatment built on conceptions of Gradman (1928) and Van der Honert (1948) leads to the assumption that an increase in the osmotic concentration in the nutrient solution results in about the same increase in the D.P.D. of the leaves (Brouwer 1961). Conditions favouring transpiration enlarge the gradient between leaves and solution as compared with low transpiration. This holds for all concentrations of the root environment. The result is that the D.P.D. of the leaves and, therefore, also the risk of growth inhibition (Fig. 1) (vide also Brouwer and Jaspers 1962) is higher at high transpiration than at low transpiration.

From the viewpoint of growth a number of data presented here are of interest. In the first place the reversibility of temporary inhibition of leaf growth by rather low suction tensions in the nutrient solution. Up to a concentration of 5 atm. sodium chloride this inhibition only occurs during the time of application. Immediately after removing the salt solution the rate of growth will be normal (5 atm.) or even increased (lower concentrations).

Obviously there are two influences working at the same time. The first is an inhibition of cell extension due to insufficient supply of water although the turgor pressure of the leaf as a whole appears to be positive in all cases. This inhibition will be the stronger as the suction tension in the root medium is higher and resembles the influence of mannitol concentrations on the growth of wheat roots as described by Burström (1953) in the range of hypotonic solutions. Whereas for wheat roots only the elastic extension may have been reduced, in the case of these leaves things seem to be more complicated. After removing the salt solution a fully compensatory extension of the cells, inhibited during treatment, only occurs at the lower concentrations up to 1.25 atm. (Fig. 3). In those cases it may be assumed that the decrease in cell extension was only due to temporarily decreasing elastic extension caused by the higher D.P.D. of the medium which supplies the growing cells with water, in this case the mature leaf tissue and the water conducting elements.

A harmfull influence of the sodium and/or chloride ions absorbed cannot fully be excluded. The observation, however, that the osmotic value has not been increased does not seem to be in favour of this supposition, no more than the quite similar results with other salts (Fig. 5).

Another interesting point follows from the relationship between growth rate and D.P.D. The growth measured here is the summation of the growth of individual cells. In the leaves different stages of maturation can be adjacent to each other (ESAU 1953). It is assumed, therefore, that different osmotic values occur. At increasing suction tension of the nutrient solution the D.P.D. values of the leaves increase and it is obvious that gradually a greater number of growing cells reach a state of incipient plasmolysis. Then, the extension of these cells stops. With this assumption the form of the curve of figure 9 may be explained. The growth curve than is similar to the curve of the osmotic values. It remains an open question in how far this also means that the rate of growth of the individual cells does not depend on the magnitude of the turgor pressure. Otherwise the shape of the curve may be the result of a gradually decreasing number of growing cells and of a gradually decreasing rate of growth of these cells at increasing D.P.D. values.

## REFERENCES


BERNSTEIN, L. and H. E. HAYWARD. 1958. Physiology of salt tolerance. Ann. Rev. Pl. Phys. **9**: 25–46.

————, 1961. Osmotic adjustment of plants to saline media I. Steady state. Am. J. Bot. **48**: 909–918.

BROUWER, R. 1960. De invloed van de aëratie van het wortelmilieu op de groei van bruine bonen. Jaarb. I.B.S. **1960**: 11–21.

————, 1961. Water transport through the plant. Jaarb. I.B.S. **1961**: 11–24.

————, and C. P. JASPERS. The influence of the suction tension of the root medium on growth and dry matter production of red kidney beans at various climatological conditions. (*In preparation*).

BURSTRÖM, H. 1953. Studies on growth and metabolism of roots. IX Cell elongation and water absorption. Phys. Plant **6**: 262–276.

ENDE, J. VAN DEN. 1954. Groeiafwijkingen die samenhangen met de waterhuishouding in de plant. Meded. Dir. v.d. Tuinb. **17**: 615–636.

ESAU, K. 1953. Plant Anatomy. John Wiley and Sons. Inc. New York pp. 411–462.

GRADMAN, H. 1928. Untersuchungen über die Wasserverhältnisse des Bodens als Grundlage des Pflanzenwachstums. Jahrb. wiss. Bot. **69**: 1–54.

HONERT, T. H. VAN DEN. 1948. Water transport in plants as a catenary process. Disc. Far. Soc. **3**: 146–153.

KRAMER, P. J. and M. B. RUSSELL. 1959. Plant-water relations. Adv. Agron. **11**: 51–77.

LOOMIS, W. E. 1934. Daily growth of maize. Am. J. Bot. **21**: 1–6.

SLATYER, R. O. 1957. The influence of progressive increase in total soil moisture stress on transpiration growth and internal water relationships of plants. Austr. J. Biol. Sci. **10**: 320–336.

TUMANOV, J. J. 1927. Ungenügende Wasserversorgung und das Welken der Pflanzen als Mittel zur Erhöhung ihrer Dürreresistenz. Planta **3**: 391–480.

URSPRUNG, A. 1925. Einige Resultate der neuesten Saugkraftstudien. Flora **118–119**: 566–599.