INSTITUUT VOOR BIOLOGISCH EN SCHEIKUNDIG ONDERZOEK
VAN LANDBOUWGEWASSEN
WAGENINGEN

MEDEDELINGEN
212-219

JAARBOEK 1963

with summaries

INHOUDSOPGAVE/*CONTENTS*

WOORD VOORAF

Dit jaarboek draagt ook weer geheel het karakter van aanvullend publikatiemedium, in het bijzonder bestemd voor het doen van voorlopige mededelingen. Enige grotere definitieve onderzoekverslagen verschenen onlangs of zijn bijna gereed, zodat er ditmaal minder stof voor het jaarboek bestemd werd.

Ik hoop dat ook dit kleinere aantal zaden in vruchtbare aarde zal vallen. De verzorgers hebben zich beijverd de slagingskansen zo groot mogelijk te maken. Daarvoor komt aan Mej. A. H. VAN ROSSEM en de heren A. KLEINENDORST en G. C. BEEKHOF veel dank toe. Drs. G. F. MAKKINK heeft, aangemoedigd door reacties uit diverse windrichtingen, weer voor samenvattingen in het Esperanto gezorgd.

De Directeur van het Instituut voor
Biologisch en Scheikundig Onderzoek van
Landbouwgewassen,

Prof. dr. ir. G. J. VERVELDE

Wageningen, oktober 1963

NOTICE FOR FOREIGN SCIENTISTS

As in the three preceding years a mimeographed issue has been prepared with summaries and the explanation of figures and tables in Esperanto. It will be sent on request.

AVIZO POR FREMDAJ SCIENCISTOJ

Kiel en la tri antaŭaj jaroj mimeografita kajero estas preparita kun resumoj kaj la klarigo de la figuroj kaj tabeloj en Esperanto. Ĝi estos alsendata post peto.

INSTITUUT VOOR BIOLOGISCH EN SCHEIKUNDIG ONDERZOEK VAN LANDBOUWGEWASSEN

1 JULI 1963

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Mededeling 212 van het I.B.S.

SOME PHYSIOLOGICAL ASPECTS OF THE INFLUENCE OF GROWTH FACTORS IN THE ROOT MEDIUM ON GROWTH AND DRY MATTER PRODUCTION

R. BROUWER

INTRODUCTION

As the plant takes up water and minerals from the root medium via its root system it stands to reason that this medium is of great importance for the entire plant. Normally this is the only means for a plant to obtain these essential elements necessary for its growth.

To enable this uptake the plant needs an adequately fuctioning root system. Accordingly, factors influencing this root system in any way are of great interest as well as the way in which this influence is effected. It stands to reason that the extent of the root system as well as its activity is important.

Obviously, an intricate complex of problems is involved. The purpose of this article is to throw some light on the way in which certain factors in the root medium finally affect the entire plant growth indirectly by means of a direct influence on the root system and its activities. Consecutively, attention will be payed to aeration, root temperature and suction tension. All experiments mentioned have been carried out on water culture and more detailed data on the method have been described elsewhere (2, 3, 4, 5, 6 and 7).

INFLUENCE OF AERATION

Much research has been carried out on the influence of aeration on plant growth. Due to the close relationship of aeration, water supply and structure of the soil this research has invited keen interest up to the present. The results of physiological investigations into this subject are most contradictory with regard to the direct cause of lack of aeration (carbon-dioxide accumulation or oxygen shortage) as well as to the effect on the plant. Plant roots need oxygen for their growth and functioning. The roots of some species are able to grow in oxygen-deficient media. This possibility seems to be related to the existence of conspicious air cavities in the cortex enabling a rapid diffusion of gases between the air and the root cells. Although a number of plants develop such structures when grown in oxygen-deficient media, most crops prefer well-aerated soils. Bean plants react very favourably on a good aeration (fig. 1). Non aerated plants retard during the whole period of development. Apparently, root growth is more depressed than shoot growth (fig. 2).

The problem to investigate is the origin of the depression in leaf growth. It is to be expected that either the ion or water supply is deficient. Figure 3 shows there is no difference in the ion content. It is therefore improbable that growth reduction in the non-aerated plants is due to ion deficiency. Evidently, water supply is the limiting factor. A number of facts indicate this is indeed the case.

First of all there is a difference in growth rate of the leaf in the light and in the dark period. It has been proved that non-aerated plants mainly grow at night and much

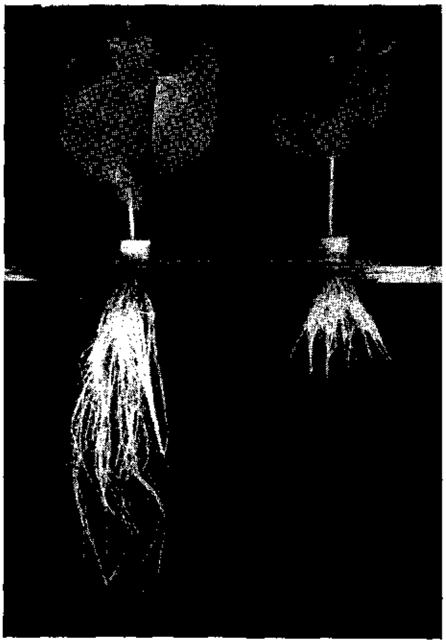


FIG. 1. A photograph of 7 days old bean plants, grown on nutrient solution with (right) and without (left) aeration.

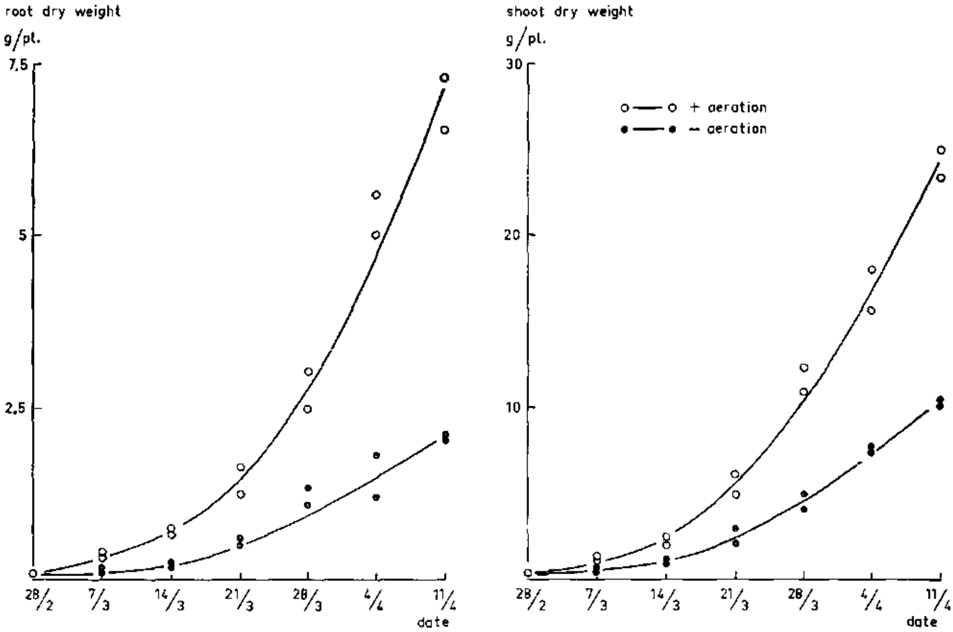
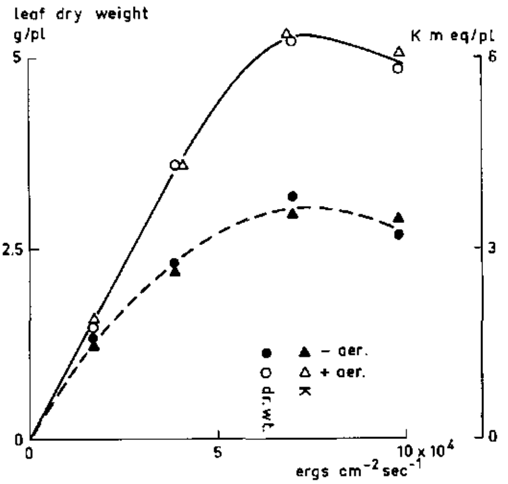


FIG. 2. Increase in dry weight of shoots and roots of bean plants with and without aeration.

FIG. 3. Dry weight and potassium accumulation in bean plants grown at different light intensities with and without aeration.



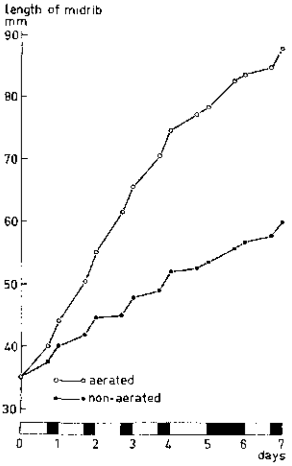


FIG. 4. Increase in leaf length of aerated and non-aerated bean plants during light and dark periods.

less or not at all in day time, especially after some days (figure 4). Evaporation is high during the light period due to incoming radiation combined with the opening of stomata. Since the absence of aeration induces a reduction of water permeability (3) in the non-aerated root system this will cause a high suction tension in the leaf cells, resulting in hampered cell elongation in the growing leaf. As it has been proved that aeration has no effect on cell division, reduced leaf growth obviously is due to inhibited cell elongation. Even in aerated plants leaf growth during the dark period appears to be somewhat more rapid than during the light period. This also is a result of the suction tension increasing by light. The same phenomenon has been described under normal growing conditions, during periods with high evaporation (LOOMIS, (16); V. D. ENDE (10)).

A second argument confirming that non-aeration affects leaf growth via the water balance in the plant is the interaction with relative air humidity and light intensity. Naturally, suction tension in the plant increases as light intensity is higher. In agreement with expectations the difference between aerated and non-aerated plants is greater according to light intensity being higher, as is shown in figure 5. The effect of aeration appears to be smaller at high relative humidity and less transpiration, than at low relative humidity and high transpiration.

The next topic of interest is whether the reduced amount of dry matter ultimately produced is due to depressed leaf growth only or to an additional decrease in photosynthesis per unit of leaf area as well (see fig. 2). Calculations in which the dry matter production in a certain period is compared to the average leaf area in the same period prove that the dry matter production per unit of leaf area is the same in both cases (fig. 6).

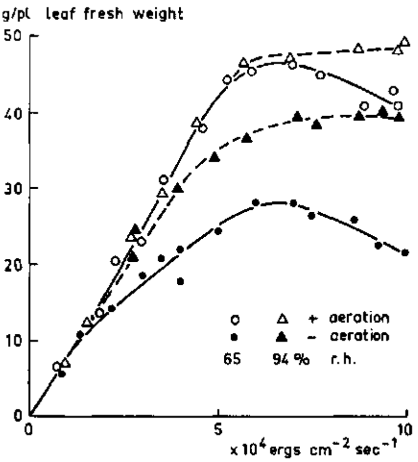


FIG. 5. Leaf fresh weight of bean plants grown at various light intensities with and without aeration at two levels of relative humidity.

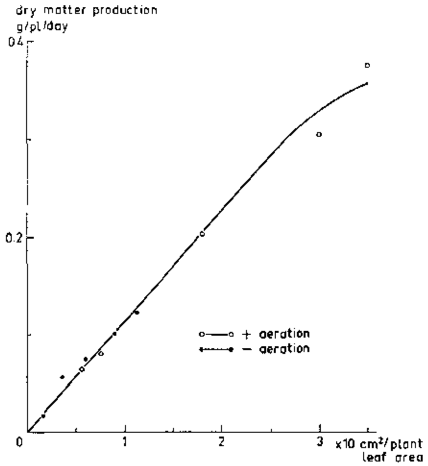


FIG. 6. Relation between leaf area and dry matter production of aerated and non-aerated bean plants

In the above mentioned it has been proved that the influence of aeration depends on light intensity and relative air humidity. Besides these, however, the plant density is of importance as well (fig. 7). When the plant density is low the amount of fresh material per unit area is proportional to the number of plants per unit area in aerated as well as in non-aerated plants. Density is such as to allow for free development of each plant without any hampering effect of its neighbour. The influence of aeration is independent of crop density and nonaeration will result in a growth reduction of about 50 per cent. Growth of the aerated plants will no longer be proportional to the number of plants if the crop density exceeds 60 plants per 25 sq.dm. Mutual shading will probably hamper the plants in development. On the same age non-aerated plants will be much smaller and thus this effect will only occur at much higher crop densities. The

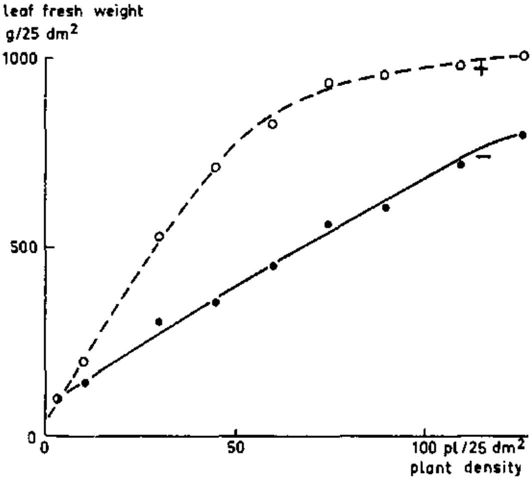


FIG. 7. Relation between leaf fresh weight per 25 dm² of pot surface and number of plants at this area with and without aeration. Age of plants at harvest time (14 days).

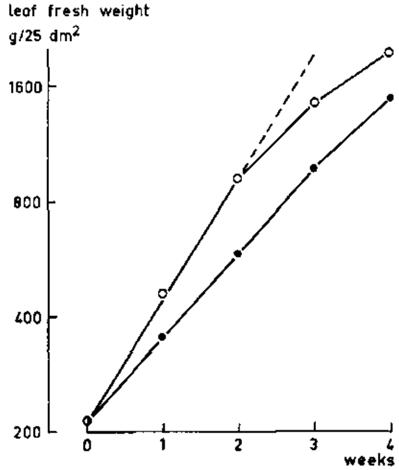


FIG. 8. Leaf production per 25 dm^2 of pot surface and a plant number of 90 with and without aeration.

result is that the influence of aeration decreases. Not so much on account of the effect of non-aeration being less severe, but because the growth rate of the control is reduced. Also the age of the plants that are harvested is essential. In figure 8 the weight of aerated and non-aerated plants has been plotted against time. Plant density in both cases was 90 plants per 25 sq.dm. The straight line (logarithmic growth) in both cases bends at the same weight. Non-aerated plants reach this weight one week later than aerated plants. Evidently, the influence of aeration decreases at higher crop densities A closed crop surface completely intercepts all incoming radiation. This also means the maximum rate of net assimilation has been reached. After this moment it seems as though it is not important whether plants are aerated or not. The experiments that have been taken up till now, however, suggest that the influence of aeration never quite disappears. It is assumed therefore that the leaves of non-aerated plants due to their position as regards light in one way or another hamper optimal photosynthesis. Briefly, non-aeration may lead to reduced root growth, with the result that not enough roots are formed, thus ruling out optimal root function. As a consequence water uptake is partially hampered, so that a considerable water deficit is formed in the plant during the light period. This water deficit gives rise to depressed leaf growth so that a smaller leaf surface is obtained which especially in the seedling stage when the crop density is low, results in a decreased dry matter production per unit of soil surface, although the rate of photosynthesis per unit of leaf area is the same. The fact that the influence of aeration does not completely disappear in a closed crop surface suggests that there is an additional factor (e.g. the position of the leaves) at issue.

As the growing root has to strike the mineral sources in the soil, contrary to those in water cultures, it should be taken into account that non-aeration of the soil may induce a mineral deficiency as well as a water deficit.

SUCTION TENSION IN THE ROOT MEDIUM

A more direct influence on the hydrature in the plant is to be expected from suction tension than from aeration. It has been proved that contrary to non-aeration there is no direct influence on root growth if suction tension is applied (fig. 9). The same holds whether suction tension is induced osmotically, as in this case with NaCl, or mechanically (KAUSCH, 13). If the suction tension in the root medium is increased the plant reacts by raising the osmotic value in the cells. In accordance with the formula of

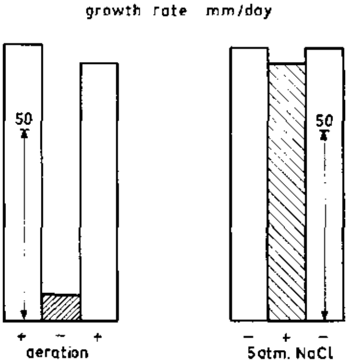


FIG. 9. Growth rate of individual crown roots of maize plants in Hoagland solution with or without an addition of 5.0 atm. sodium chloride, and with and without aeration.

URSPRUNG (22) the maximal suction tension in the plant (Z = O − W) is increased. Generally this only is a partial compensation.

Contrary to root growth, leaf growth is clearly reduced by increasing the suction tension in the root medium (figure 10). The growth depression is reversible when the suction tension is only temporarily applied for short periods. However, this is no longer the case in prolonged application. A reduced shoot/root-ratio is then found which is also general in dry soil. In fact, here too shoot growth reacts indirectly on increased suction tension in the root medium. The suction tension in the leaf cells is important. Sudden application of increased suction tension in the root medium will effect about the same increase in suction tension of the leaf cells. An increase in the osmotic value of the leaf cells leads gradually to reduced suction tension to about 2/3 of the original value. It is, however, impossible to mention a fixed ratio because suction tension in the plant is also dependent on the rate of transpiration. To wit, the difference in suction tension between leaves and roots is proportional to the rate of

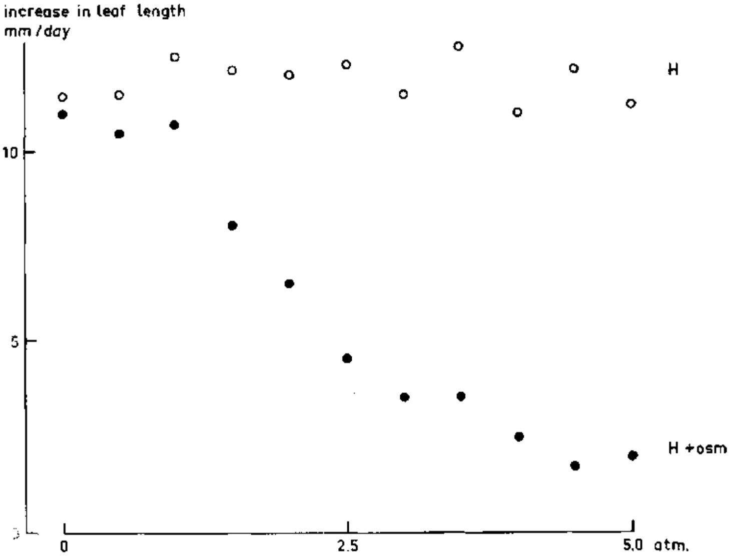


FIG. 10. Rate of leaf growth of bean plants on nutrient solution with various salt additions as compared with the growth rate on the nutrient solution the day before.

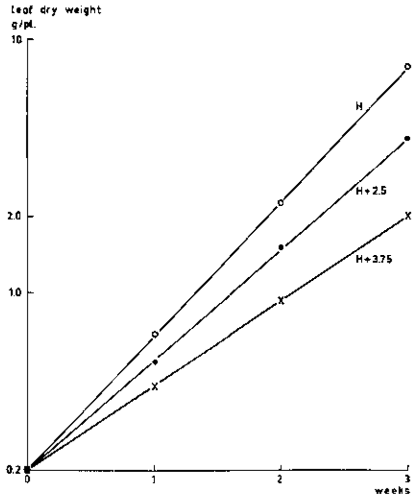


FIG. 11. Influence of the suction tension of the nutrient solution on the growth rate of the leaves of been plants in a climate room.

transpiration. Evidently here again interactions with other factors such as relative humidity and light intensity also play a role.

The growth reduction as reflected in figure 11 is derived from experiments in climate rooms. Only those suction tensions are treated here that show logarithmic growth during the whole growing period. The different suction tensions have been established by the addition of common salt. When other salts such as potassium chloride and potassium nitrate are used in high concentrations symptoms may occur resembling a kind of ion poisonning. This is because uptake is too rapid and leads to internal concentrations that are too high. The growth depression due to the suction tension induced by this limitation will be constant during the whole growing period of three weeks (figure 11). Other environmental conditions affect the influence of salt concentrations on growth rate. For the factor light intensity this has been proved by a greenhouse experiment in which bean plants were grown for three weeks after germination at different suction tensions in the root medium. Salt concentrations that have no influence in December (low light intensity) cause a very clear reduction in June (fig. 12), with all transitional stages during the months in between.

Again the water balance evidently is the growth limiting factor in these experiments since the NaCl-concentrations do not have a distinct effect on the ion uptake. Figure 13 shows that potassium and phosphorus uptake by individual crown roots of maize hardly decreases when 5 atm. of common salt is applied. Water uptake, however, is much reduced. In this case half the roots have been treated with common salt, the other half has not been treated. Water uptake in the non-treated roots increases as soon as that in the treated ones decreases due to osmotic suction in the medium. Apparently suction tension in the plant increases owing to the limited water uptake. Consequently, salt treatment has no direct influence on ion uptake, neither in prolonged application, as has been proved in our experiment with bean plants. Figure 14 shows the contents of potassium and crude protein in bean plants grown for three weeks on a normal Hoagland solution, while various common salt concentrations have been added. It is possible (WIERSUM, 23) that the ion transport to the root may be a limiting factor in desiccating soils. On the other hand, however, the root is probably involved in water uptake over its whole length, while ion uptake is mainly limited to just differentiated zones near the root apex. As long as these find enough moisture for growth they can also absorb enough ions. In view of this it is to be expected that ion supply is not the growth limiting factor under practical conditions in drought. If the ion content has been found to decrease in some cases in drought it has to be kept in mind that due to growth depression the dry matter content is increased in those cases. In relation to fresh weight the content may be normal or even somewhat higher than normal. Obviously, the content in the fresh material is the growth determining factor.

Due to the high suction tension in the root medium, resulting in increased suction tension in the plant, the stomata will remain closed during the greater part of the day. This undoubtedly will affect the dry matter production per unit of leaf area. Figure 15 shows the calculated net assimilation rate (per unit of leaf surface and time) for the experiment in May. A distinct reduction only occurs at salt concentrations of 2.5 atm. and higher. The effect is not noticeable at lower salt concentrations. These calculations have been confirmed by direct measurements of photosynthesis in the laboratory.

The experiments on photosynthesis also yielded evidence on a marked interaction between suction tension in the root medium and light intensity (figure 16). At a light intensity of 0.4 g cal cm^{-2} sec^{-1} the addition of 5 atm. NaCl to the nutrient solution will very rapidly induce a 60 per cent reduction, while there will hardly be any effect at low light intensity. The rate of photosynthesis will gradually increase again if this high suction tension in the root medium is prolonged. This adjustment is due to an increase in the osmotic value in the leaf cells which brings the turgidity of the leaves up to level

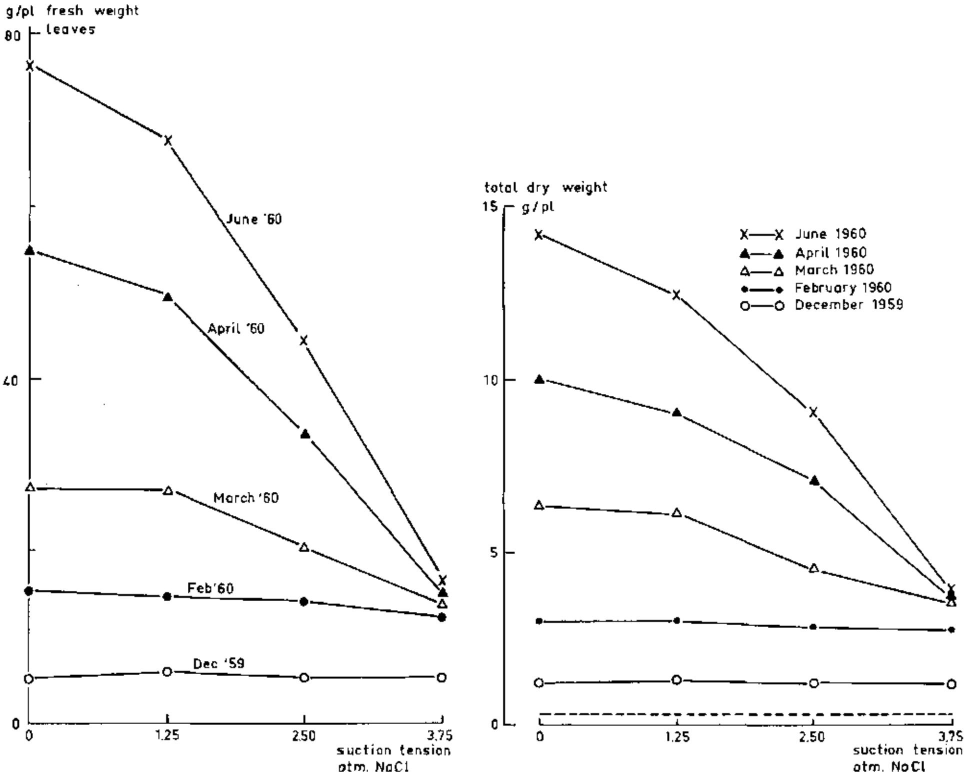
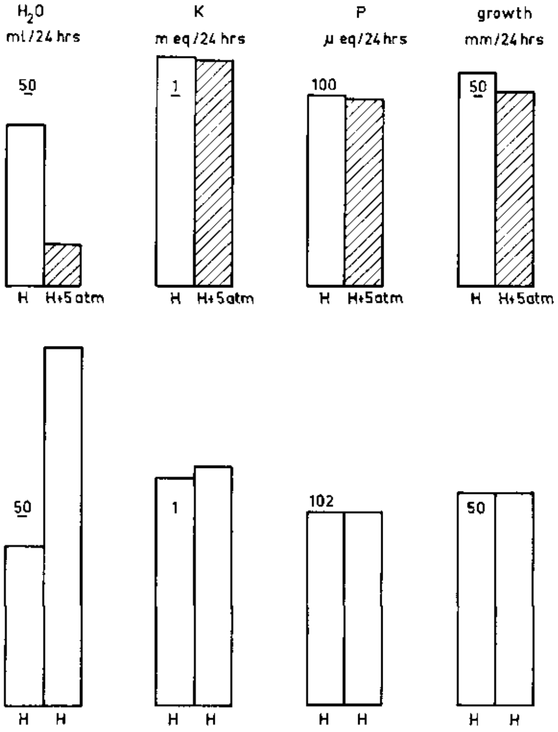


FIG. 12. Influence of the suction tension of the nutrient solution on leaf growth and dry matter production in the green house at various light conditions. All plots harvested after a growing period of 3 weeks at 20 °C air and root temperature.

FIG. 13. Influence of a 5 atm. sodium chloride addition on the water-, the potassium- and phosphate uptake of individual crown roots of maize plants. Although the waterabsorption is strongly influenced the mineral uptake does not alter.



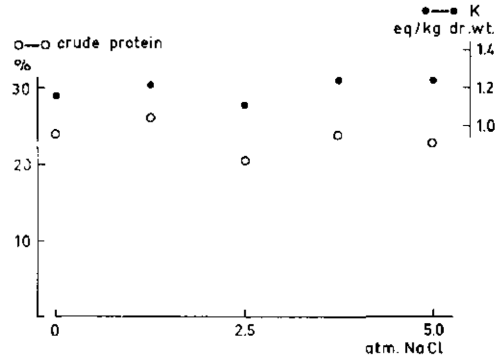


FIG. 14. Content of potassium and crude protein of bean plants grown for 3 weeks at Hoagland solutions with various sodium chloride additions.

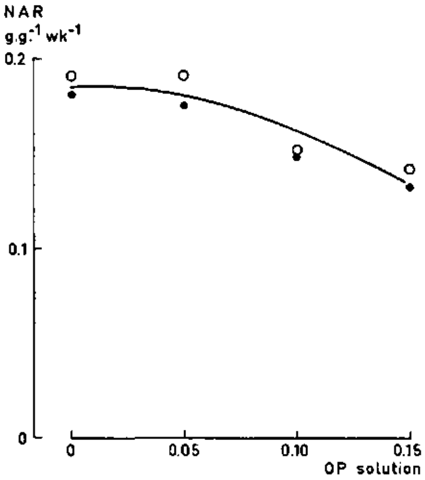


FIG. 15. Net assimilation rate (NAR) of bean plants grown for a period of three weeks at different sodium chloride additions to the basic nutrient solution.

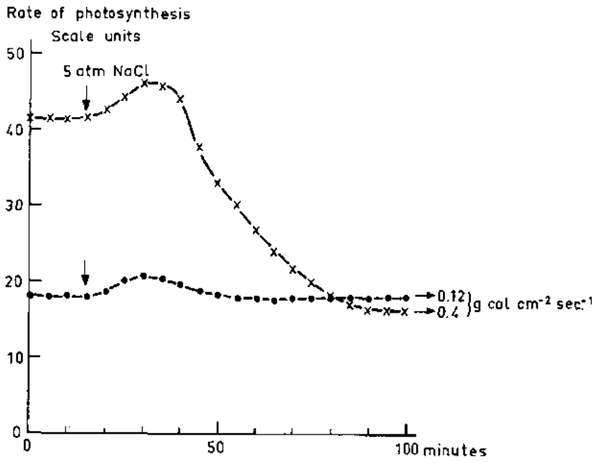


FIG. 16. Influence of sodium chloride additions to the basic nutrient solution on the rate of photosynthesis at two light intensities. Plants pregrown in a climate room at a light intensity of 4000 ergs cm^{-2} sec^{-1} on Hoagland solution.

again. The fact that an increase in suction tension in the root medium has hardly any influence in December has also been confirmed by these experiments. Obviously, light intensity is the limiting factor for growth as well as for photosynthesis.

Briefly it may be put that, an increased suction tension in the root medium hampers water uptake. The suction tension in the plant will show an upward trend, hampering leaf growth directly; only when suction tension passes the critical value at which the stomata are closed there will be a marked reduction in evaporation and photosynthesis.

By increasing its internal osmotic concentration the plant will partly compensate for this reduction in the long run. The reduction in dry matter production runs parallel to the depression in leaf growth over a certain range (constant net assimilation rate) but under severe drought conditions also the rate of photosynthesis per unit of leaf area decreases. The same factors showing interaction with aeration, as e.g. light intensity, relative humidity in the air and crop density, also influence the effect of an increased suction tension in the root medium.

INFLUENCE OF TEMPERATURE OF THE ROOT MEDIUM

There is much literature on this topic. Especially these last few years much work has been done on this subject. Yet there is no certainty as to the origin of the influence of temperature on growth. Temperature affects all processes taking place in the plant and especially chemical processes, which show a Q_{10} of 2 to 3. It stands to reason therefore that temperature in the root medium will affect root growth and activity to a great extent. However, this article will mainly treat the effect of the indirect influence via root growth on shoot growth and activity. Figure 17 shows the extent of the reaction of shoot growth on root temperature. This has been demonstrated for various other plant species as well. The curve reflecting the correlation between fresh weight and root temperature or dry matter production and root temperature generally has the same trend. Little growth at minimum and maximum temperatures with a more or less gradual change from minimum to optimum temperature, followed by a rather abrupt change from optimum to maximum temperature. According to the plant species used the level of the minimum, maximum and optimum temperatures will vary widely.

Like both preceding factors this one also has the most obvious effect on leaf growth (fig. 18). Immediately after application the growth rate of the leaves at 5°, 10° and

15 °C will be considerably retarded as compared to that at higher root temperatures. At 5 °C growth even terminates completely after two days.

The effect of a root temperature of 35 °C is remarkable; initially growth rate is high, but after a few days it decreases. This is due to the fact that the uptake by the root which has terminated growth at this high temperature is checked as a result of impermeable layers forming in the roots.

All leaves at this stage vary in length from 30 to 90 mm (figure 18) and have almost the same number of cells. The variation in the final size of the leaves accordingly is due to a difference in elongation of the individual cells. Similar as in the aeration and suction tension experiments here too water supply has apparently been the growth limiting factor.

There is more evidence that the water balance in the plant acts as a factor in these growth reactions. Thus leaf growth reacts immediately after a root temperature of 20 °C is decreased to 5° or 10 °C (fig. 19). In view of this immediate reaction it stands to reason that a factor is involved that can change rapidly. Because the ion content in water culture always is very high, the plant will have formed a reserve for some days and thus ion supply cannot be a factor of importance in this respect (BROUWER, JENNESKENS and BORGGREVE, 7). The water balance in the plant is therefore a factor of first consideration. Due to the low root temperature water conductivity in the root tissues decreases rapidly, considerably hampering water uptake. Initially evaporation continues, bringing about a high suction tension in the plant which results in growth reduction and even in complete growth stagnation at 5 °C.

This, however, does not imply that the mineral content of the plants is not affected

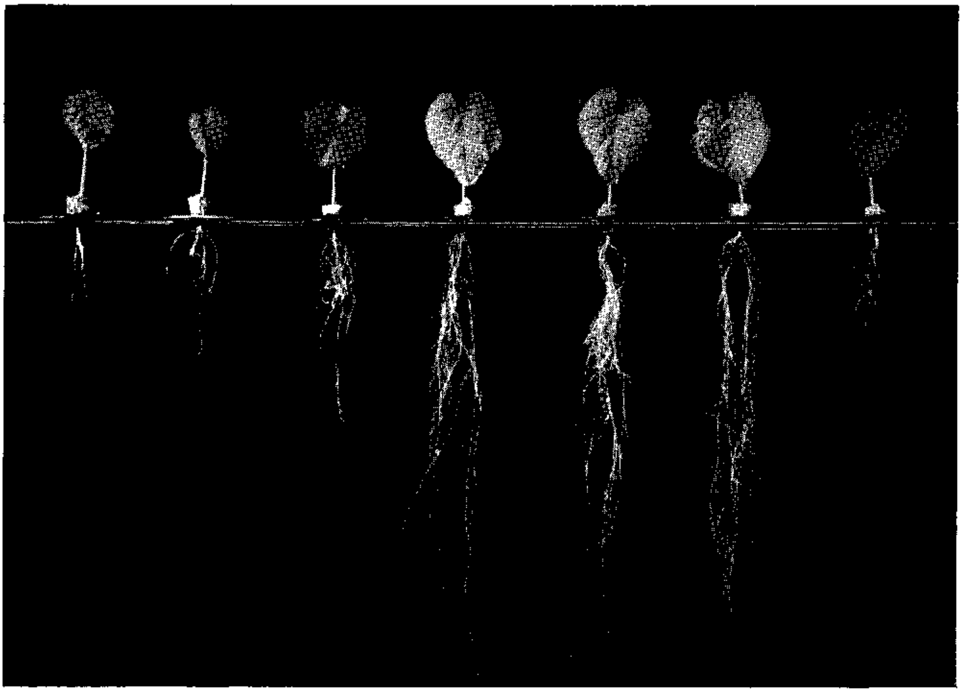


FIG. 17. A photograph of bean plants growing for 7 days on nutrient solutions of various temperatures after germination at 20 °C. For all plants the air temperature was 20 °C, the relative humidity ± 65 % and the light intensity 30000 ergs cm^{-2} sec^{-1}.

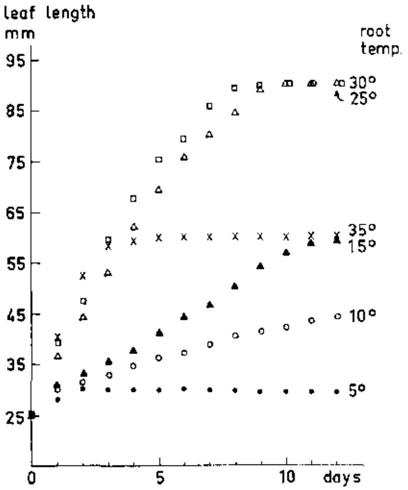


FIG. 18. Leaf growth of bean seedlings at various root temperatures.

by root temperature. GROBBELAAR (12) proved that in maize the ion content in relation to fresh weight was highest at root temperatures of 25°–35 °C, while at 20°, 15° and 10 °C this content was lower as root temperature dropped. At 5 °C the content was higher again than at 10° and 15 °C. At 5 °C no growth took place in experiments with maize and the initial content was maintained. At 10° and 15 °C, however, the content was slightly diluted by growth, because uptake could not keep pace with growth. The same happens in peas. This phenomenon is inherent to using nutrient solutions as a root medium. It is a well-known fact that in applying the normal concentrations of the most common nutrient solutions, internal mineral concentrations will be found that by far surpass those generally found in the field. Therefore, the relatively lower concentrations found at unfavourable root temperatures in comparison to field experiments always are comparatively high so that it does not seem justified to conclude on ion deficiency occurring in view of the content only. An increase in the concentration of the environment does not affect growth at lower temperatures but even increases the content somewhat (GROBBELAAR, 12). On the other hand the high content may not be used in evidence of ion uptake not being a growth limiting factor. A content that is considered as limiting in pot cultures may be much higher than a limiting content in field experiments (ULRICH, 21). The fact of an increased content having a yield increasing effect should be applied as a criterion and as this is not the case here it may be stated that another limiting factor is affecting growth; in this case, water. In soil cultures, however, this may be completely different. Various authors suggest that increasing P-treatment may partly compensate the growth depression at low root temperatures (DAVIS and LINGLE (8); LINGLE and DAVIS (14)), while others did not observe any effect of such measures. A lot will depend on the temperature range in which these experiments are carried out (compare BROUWER and VAN VLIET, 5). However, there remains an essential difference between soil and water cultures. At low root temperature root growth is very limited, more still than shoot growth. In water cultures this small amount of roots is continuously surrounded by the normal concentration of mineral solution. In soil, however, the various nutrients, as for instance phosphate, are bound. The roots can only take up the ions that are in the immediate surrounding of it. With a poorly developed root system and at low concentrations this will be an extremely small quantity. Uptake in this case is proportional to development of the root system that is the amount tapped. At higher concentrations in the action sphere of the roots, when not all is taken up, the difference between nutrient solution and soil disappears (LOCASSIO and WARREN (15)). Experiments on sand culture, in which nutrient solution is regularly passed through the sand, do not differ from water cultures.

Even after stimulating mineral uptake as much as possible by enhancing concentrations, there remains a definite effect of root temperature on growth. This effect is due to the influence of soil temperature on the water deficit in the plant and accordingly on growth of the overground parts.

In the same way as ion uptake may be influenced by changes in the concentration in the root medium, water balance may be affected by changes in evaporation conditions in the overground medium (BROUWER, 3).

Evaporation conditions change with light intensity and relative humidity. The influence of light intensity on the effect of root temperature is shown in figure 20. There is a close correspondence with figure 13. As light intensity is higher the influence of root temperature will be larger. The decreasing difference at unfavourable root temperatures is not the result of more rapid growth at these temperatures, but of reduced growth in the optimum range.

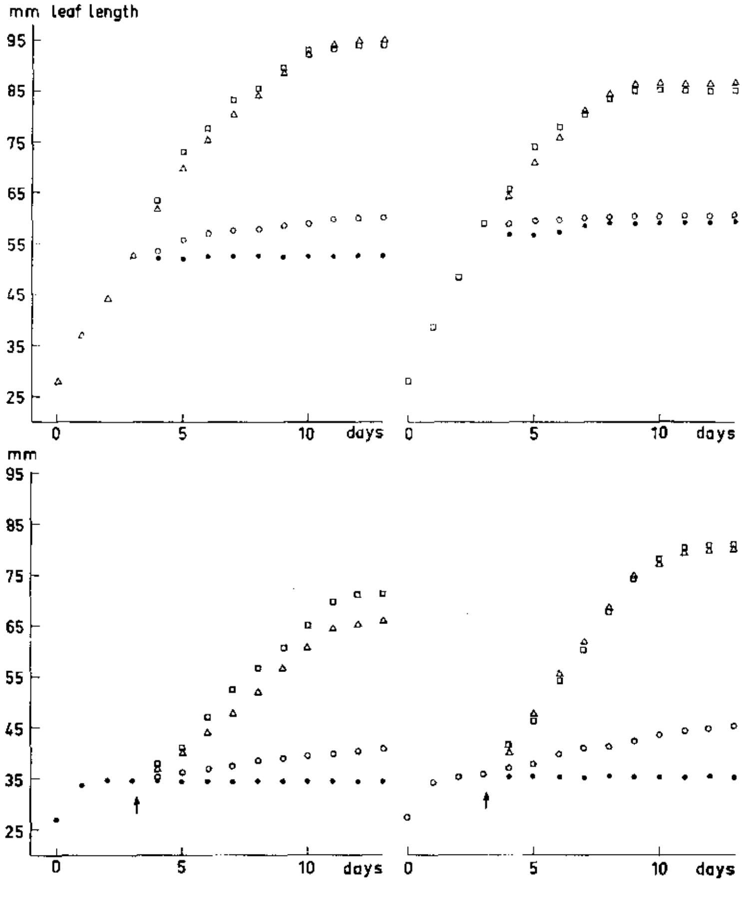


FIG. 19. Influences of changes in root temperature on the growth rate of bean leaves.

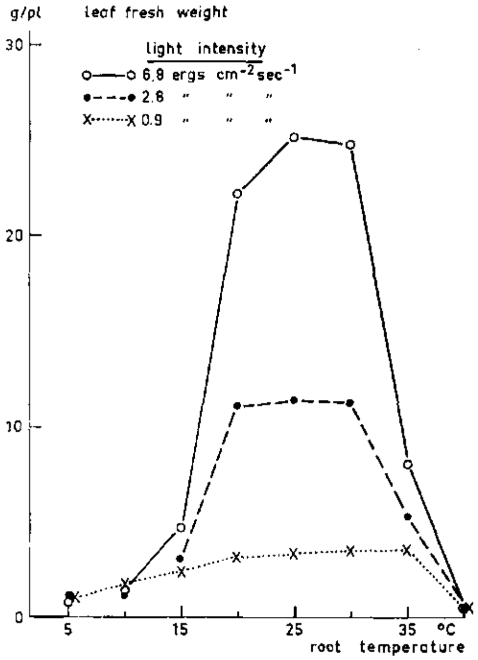


FIG. 20. Influence of root temperature on leaf growth of bean plants at three light intensities.

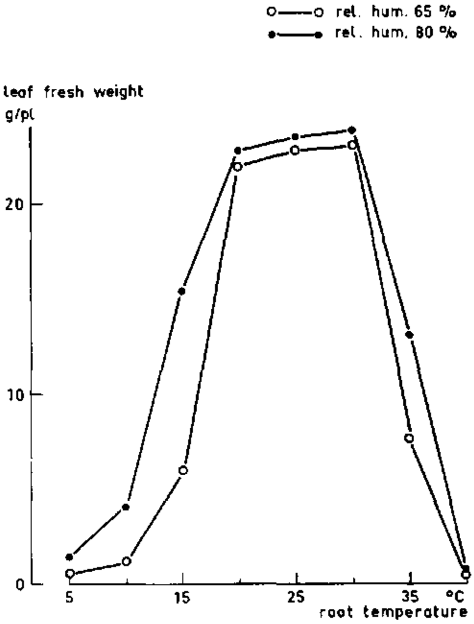


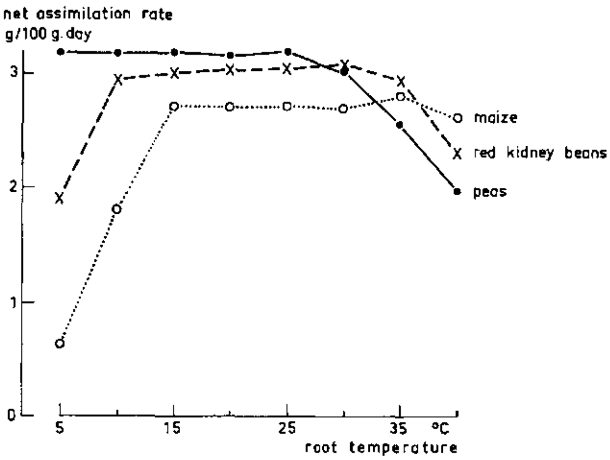
FIG. 21. Influence of root temperature on leaf growth of bean plants at two relative humidities of the air at a constant air temperature of 20 °C.

The results at various relative humidities are given in figure 21. Leaf growth has indeed improved considerably especially with root temperatures of 15° and 35 °C at higher relative humidities as compared to low relative humidity. It is apparent that the influence of root temperature has not terminated completely in this case. Perhaps it is ion uptake now that becomes more and more limiting.

The causality of the effect of root temperature on growth of the overground parts can be represented as follows. In temporarily applying low root temperatures there will be a growth depression as a result of hampered water uptake. This effect will be less obvious as evaporation is slighter. Ion uptake is immediately reduced as well, but the effects of this on growth are only visible after some time. At high root temperatures there is no immediate reaction as water and ion uptake initially continue as normal, even though root growth has terminated. However, due to cork formation in the endodermis up to the root apex the roots gradually lose their uptake ability and consequently shoot growth reacts as well. Nevertheless, it remains difficult to establish by this kind of experiment the true limiting factor in growth processes. Evidently, several processes may act as limiting factors at the same time and if not, they are anyway ready to replace each other as such.

Thus the primary effect of root temperature on shoot growth has been characterized as an influence on leaf growth and especially on cell elongation in the leaves. There is a definite effect on evaporation as well. As this is only possible if the stomata are partially closed, it stands to reason to assume that photosynthesis per unit of leaf area is also influenced by root temperature. However, this only holds for extreme root temperatures (fig. 22). These extremes are on a different level with various crops and this is not surprising. These results and those of the aeration and suction tension ex-

FIG. 22. Influence of root temperature on net assimilation rates of beans peas and maize.



periments closely correspond and justify the conclusion that leaf function is less sensitive to all kinds of condition than leaf growth. Continued photosynthesis when growth has terminated will increase the dry matter content in the plant (fig. 23). The same increase is found outside when growth conditions become more unfavourable, for instance in late autumn and winter. The increase in dry matter content is associated to an increase in the content of carbohydrates in the dry matter. Outdoor experiments with Colza, much affected by root temperatures (fig. 24), proved that mainly those plants were damaged by severe night frost that had developed at the most favourable root temperatures and consequently had the lowest dry matter content. This phenomenon is known to be of much influence in frost resistance and it has been mentioned here to prove that optimal growth need not always be advantageous.

There is rather a lot of evidence indicating a close correlation between seed yield and the assimilatory surface present at the moment of flowering (BROUWER, 1; BROUWER,

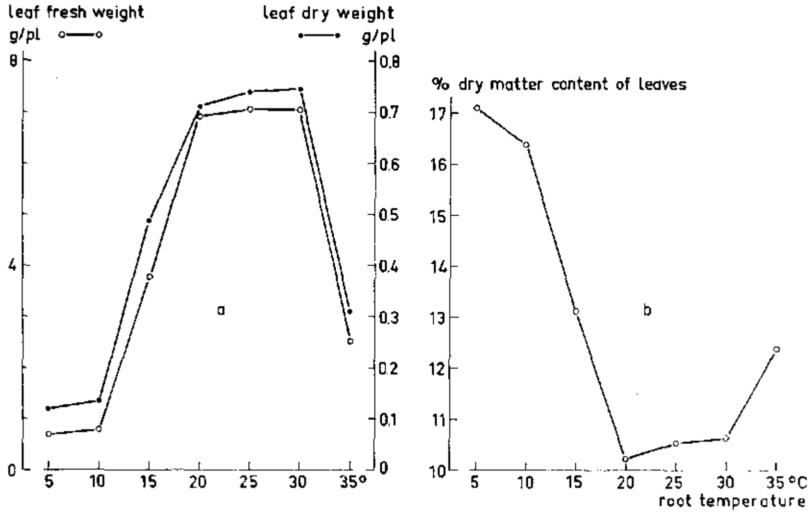


FIG. 23. Influence of root temperature on leaf fresh weight, leaf dry weight and dry matter content of red kidney beans.

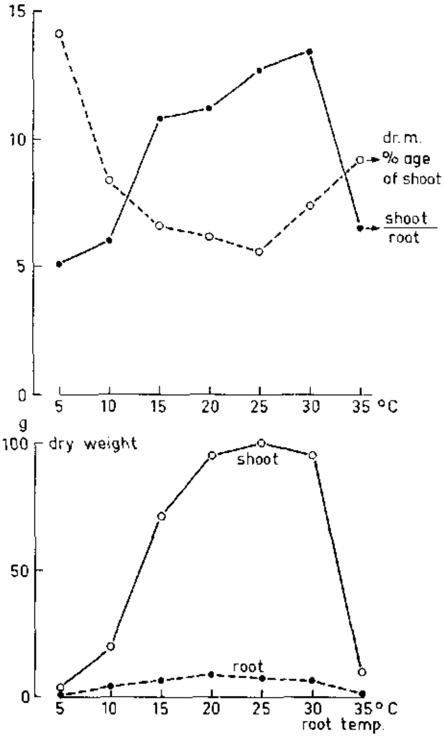


FIG. 24. Influence of root temperature on root- and shoot growth, on shoot/root ratio and on dry matter content of the leaves of colza.

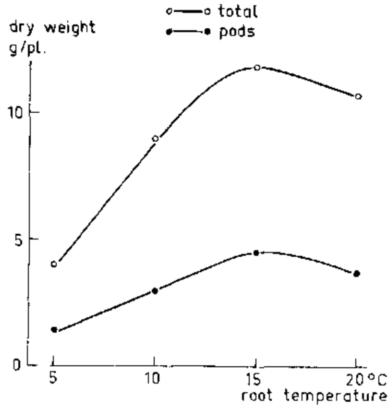


FIG. 25. Total dry weight and dry weight of pods of mature pea plants grown at different root temperatures.

4; VAN DOBBEN, 9; MEYLING, 17). Root temperature in peas does not influence the moment at which they start flowering nor fruit setting. The optimum for seed yield accordingly coincides with that for total dry matter production (figure 25). Relatively the reduction is somewhat smaller at lower root temperatures which may be due to the fact that these plants remain green slightly longer.

Strawberries, mainly consisting of water, show another picture. Optimum root temperature for fruit yield and leaf yield is indeed the same, but at lower root temperatures fruit yield as compared to optimal yield will be more depressed than leaf production (BROUWER, 4). The fruits clearly show they suffer from drought at root temperatures of 5° to 10 °C.

The change from the vegetative phase into the reproductive phase evidently is a kind of competition between vegetative and reproductive organs. It has been proved in practice that in plants with simultaneous vegetative development and fruit formation the fruit yield will be stimulated if vegetative growth is checked. The desiccation of tomatoes is an example of this. These measures should only be taken in cases of profuse vegetative growth associated to a low dry matter and sugar content.

It is possible to reduce vegetative growth by decreasing root temperature. This method offers advantages to applying osmotic substances, because no additional chemical effects will occur.

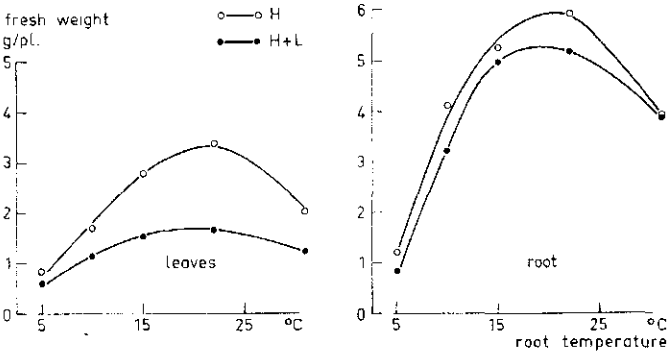


FIG. 26. Fresh weights of roots and leaves of 18 days old pea plants at various root temperatures used during the growing period after germination. Two series: H (circles), Hoagland solution throughout, H + L (dots) 3 days tap water and 3 days Hoagland solution alternately.

INFLUENCE OF THE MINERAL SUPPLY

It is a well-known fact that leaf growth also retards considerably with mineral deficiency. Shoot growth is much more sensitive in this respect than root growth. Figure 26 shows the results of an experiment with peas in which various root temperatures have been combined with two levels of ion supply. In one case (H) the nutrient solution was regularly refreshed and in the other (H+ L) nutrient solution and tap water were alternately applied in periods of 3 days. This treatment induced great differences in leaf growth, while root growth showed almost no difference.

There was no difference in dry matter production per unit of leaf area in these experiments (fig. 27). Apparently, mineral deficiency initially affects leaf growth only and an influence on net assimilation rate is only observed with extreme deficiencies

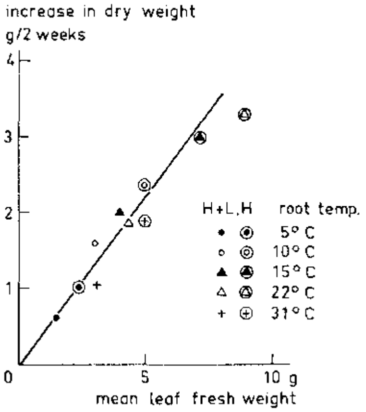


FIG. 27. The increase in total dry weight of both series (fig. 26) at different root temperatures in a fortnight plotted against the mean weight of the leaves in that period.

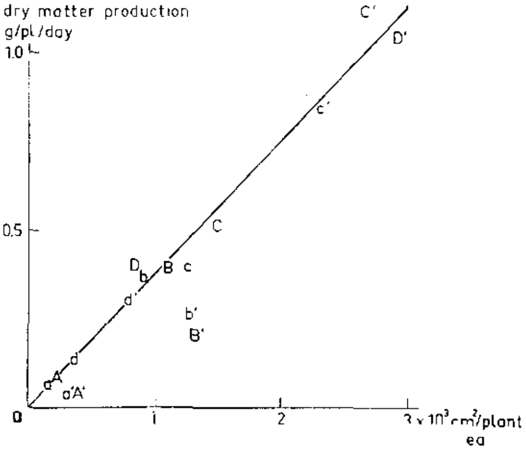


FIG. 28. The increase in total dry weight in two subsequent periods plotted against the mean fresh weight of the leaves in those periods. Experiments started with the nutrient concentration indicated. The solutions have not been renewed.

(fig. 28). These results are from an experiment with bean plants. After germination the bean plants were put on nutrient solutions of concentrations varying from tap water to a four times concentrated Hoagland solution. The solutions were not refreshed and the bean plants were harvested after 14 days and 4 weeks. In figure 30 the amount of dry matter produced in these periods has been plotted against the average leaf surface in that period. Evidently, there is no difference in net assimilation rate the first fortnight. During the second period the series on tap water and the one on $\frac{1}{4}$ Hoagland, which were soon depleted, showed a reduced net assimilation rate.

Although there were great colour differences in the groups photosynthesis was retarded in these two groups only and not until the second period. The leaves of these two groups were very much discoloured in the second period. Apparently, the intensity of the green colour has no influence until extremely low values are reached, as appears also from literature data of GABRIELSEN (11), WILLSTÄTTER and STOLL (24) and VAN DER PAAUW (18).

DISCUSSION

The preceding proves that the pattern in which much diverging soil factors affect dry matter production is closely related. The main aspect of all these factors is the influence on leaf development. In view of the fact that net assimilation rate is only clearly influenced during the most extreme conditions leaf growth is to be considered as the limiting factor for yield. This is especially so if the dry matter production of single plants is considered, as is often the case in horticulture. It has been proved that the influence on leaf growth decreases as the area covered increases. It may be assumed that the influence of soil factors terminates as soon as a closed crop cover has been formed, as from that moment onwards all incoming light is intercepted by the crop. The importance of leaf development and consequently of soil factors lies in the time in which a closed crop surface is obtained (DE WIT, DIJKSHOORN and NOGGLE (25)). Factors in the root medium affect leaf growth in the beginning of the growing period (in grassland also after cutting or grazing). In this way they determine the relative

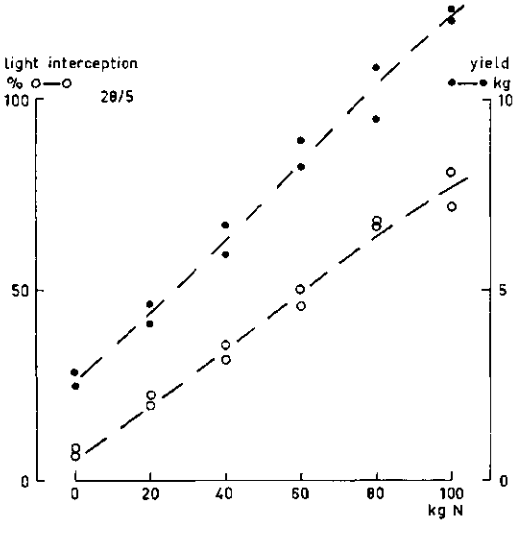


FIG. 29. Light absorption at may 28, 1962 and yield at final harvest of oats at various nitrogen applications (yield data of SIEBEN, (20).

duration of a closed crop surface. These factors are relatively more important as the time during which the crop grows on the field is shorter, accordingly more in horticulture than in agriculture, for green peas more than for beets. Fertilization effects are due to the fact that in sub-optimal fertilization the crop surface is not completely closed during a longer or shorter period. The correlation between light absorption and production of oats (fig. 29) in the „Flevopolder" at various nitrogen levels needs no explanation. Generally a more profuse crop is to be found on moist sandy soils than on clay soil. BROUWER and CLAEYS (6) have proved that this is due to the pF on clay soil being on an average higher than on sandy soil. This retards leaf growth on clay soil as compared to that on sandy soil. Accordingly, it takes longer to obtain a closed crop surface. In theory a greater plant density should be preferable on clay soils (fig. 30). Yield data of pea varieties confirm this assumption. In practice, however, the relation between yield and area covered shows an optimum (fig. 30). A crop density that is too high often gives a yield depression. Evidently, not only the period necessary for obtaining a closed crop surface is of importance for the yield, but also the amount of vegetative material which is produced after this. This extra amount in general will not increase assimilation, but it will increase dissimilation and as such it will decrease net production. Moreover, the danger of secondary effects such as lodging will increase. The optimal crop density accordingly will fluctuate with weather conditions. Ideal would be if growth could be influenced in such a way that a closed crop surface could be attained as soon as possible and that vegetative growth could be terminated after this. Much research is still needed to be able to control this completely.

It has been proved that soil conditions play an important part in reaching a closed crop surface and hardly influence net assimilation rate. This means that the process of photosynthesis cannot be considered as limiting production (VAN DER PAAUW, 18), but leaf growth is much more important as such. Water shortage and mineral deficiency are with temperature, factors determining leaf growth. Instances are even known in which there is no obvious water shortage as limiting factor, as e.g. in water cultures, while this may all the same to be the case. In practice a water shortage even though the supply in the soil is sufficient, e.g. at low soil temperature in spring or poor aeration, will act as a limiting factor. Besides in many cases nitrogen supply will limit growth.

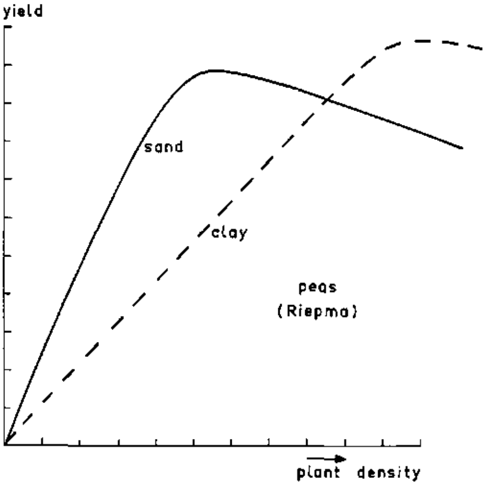


FIG. 30. Theoretical curves indicating the relation between yield and plant density of peas at sandy soil and clay soil. Derived form data of RIEPMA (19).

SUMMARY

In experiments in water culture the effect of aeration, suction tension and temperature of the nutrient solution on top growth as well as on dry matter production has been studied. It appeared that a great variety of factors in the root medium influence production mainly by their influence on leaf growth. The net assimilation rate appeared to be very insensible to soil conditions which cause distinct reductions in leaf growth. Only extremely severe conditions in the root medium also reduce the net assimilation rate.

From the interaction with light intensity and relative humidity of the air it could be concluded that even in water culture using a half strength Hoagland solution as a mineral source the process of water uptake is growth limiting.

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SOME ASPECTS OF THE EQUILIBRIUM BETWEEN OVERGROUND AND UNDERGROUND PLANT PARTS

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The shoot/root-ratio is one of many correlations between the various organs of a plant. The physiological backgrounds of these correlations are as yet not clear. In fact, the relation of growth rates is really measured in studying these correlations. In short, it may be put that the relation reflects the growth conditions of various parts.

There is a number of factors important for growth. These include carbohydrate supply, ion supply, water supply, the presence of specific substances (e.g. growth substances), oxygen supply and temperature. Each of these factors may limit growth in due time, but not necessarily for all organs at the same moment or to the same extent.

A number of the factors mentioned is regulated by special plant parts. The complete carbohydrate supply for instance is dependent on photosynthesis in the green parts. For this supply the root is entirely dependent on the shoot. Reversely the ion supply of the whole plant is dependent on ion uptake by the root system. Moreover, translocation is also of importance. It is not known to what extent this also holds for the production of the specific substances mentioned.

As far as other factors are concerned such as temperature and oxygen supply differences in the environment of the concerning organs as well as differences in the optimum level will be important in determining the relative growth rates.

Many data on the influence of various external conditions on the relation between the organs are known from literature. Some effects can be easily reproduced and are generally accepted. Nitrogen deficiency, for instance, always shows a well-developed root system as compared to the shoot. This effect is interpreted as follows. At impending nitrogen deficiency the greater part of the nitrogen taken up is used by the root system for growth, leaving only a small part to be translocated to the shoot. Due to this shoot growth is depressed earlier and to a much greater extent than root growth (CURTIS and CLARK, 10; MEYER and ANDERSON, 15). This explanation seems reasonable, but it needs testing by experiments in which the change from one situation into another is investigated. These experiments (BROUWER, 5; BROUWER 6; BROUWER, JENNESKENS and BORGGREVE 9) resulted in assuming that a kind of equilibrium is reached under all conditions. The level of this equilibrium is characteristic for the conditions prevailing. It is considered to be a functional equilibrium, because it is controlled to a great extent by activities of the various organs, such as photosynthesis of the shoot and ion uptake by the root system.

It will be interesting to see if there is indeed such an equilibrium under all conditions and how far the level of this balance is affected by various external conditions.

Many data in literature prove that the relation between the various organs is dependent on the developmental stage of the plant (BROUWER 5). Therefore, solely plants in a certain developmental stage, viz. the vegetative phase, have been used in the experiments discussed below.

There are many methods to investigate whether there is an equilibrium between root and shoot or not. One method is to remove a part of an organ and to observe the effect on various activities. Thus BIALOGLOWSKY (1) compared the transpiration of entire plants with that of plants of which different percentages of the root system had been removed. KAUSCH and EHRIG (13) removed at the same time parts of the root system and parts of the shoot. It was evident in both cases that transpiration did not decrease before 50 per cent or more of the root system had been removed. The obvious explanation seems that the plant has a reserve of roots amounting to this percentage. However, transpiration is a poor measure for the activities of the root system. Although the root is indeed one of the links in the system of water transport, this link is of minor importance in a part of the transpiration range only (BROUWER, 4). By removing a part of the roots the conductivity for water of the root system as a whole is decreased, but suction tension in the plant will increase. Due to this the rate of water transport will remain the same. Decreased transpiration by removing roots only occurs when suction tension is increased to such an extent that it passes the critical value and the stomata are closed. In fact, transpiration as such cannot determine whether there will be a functional equilibrium or not. More activities should therefore be included in the investigation.

Figure 1 shows the effect of removing different percentages of the root system on water uptake, ion uptake and leaf growth. Evidently, the results of the above mentioned authors as to water uptake are confirmed. Ion uptake and leaf growth, however, react immediately on interference in the equilibrium between root and shoot.

Generally the growth reaction to disturbing the equilibrium is to re-establish it as soon as possible. If parts of the root system are removed leaf growth will be reduced, while root growth will be accelerated. The latter is due to the fact that continued photosynthesis and reduced leaf growth (limited by water shortage) lead to an accumulation of carbohydrates in the plant. As root growth needs not to compete with shoot growth it will have a greater portion of the photosynthates available. If parts of the shoot are removed root growth will be limited (less photosynthesis and accordingly less carbohydrates) and shoot growth accelerated. The shoot has the carbohy-

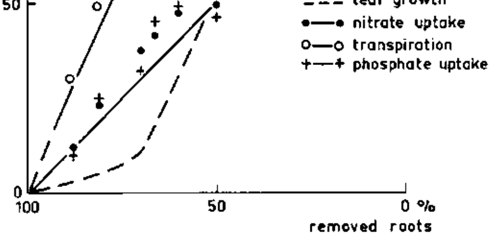


FIG. 1. Influence of removal of increasing portions of the root system of bean plants on the subsequent uptake of water, nitrate and phosphorus and on the growth rate of the leaves.

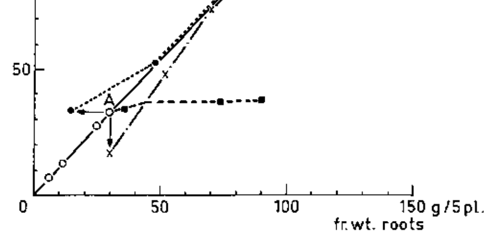
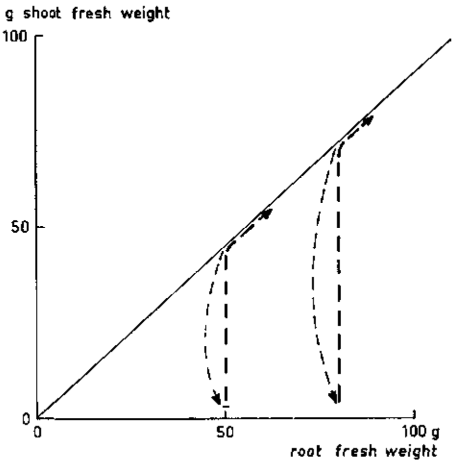


FIG. 2. Recovery to the original leaf/root ratio of bean plants (circles) after removal of parts of the leaves (crosses) and of the roots (dots). No recovery if the growing parts of the shoot have been removed continuously (squares).

FIG. 3. Recovery to the normal shoot/root ratio of perennial rye grass after mowing. (Derived from a pot experiment of ENNIK, 1962).



drates at first hand and will show good growth with the uptake by the root system (fig. 2). In practice this takes place in the regrowth of all those crops that are regularly cut. A pot experiment of ENNIK (12) with *Lolium perenne* serves as an example in figure 3. In all these cases an equilibrium may be assumed between shoot and root, one that is adjusted to the prevailing environmental conditions.

The next topic of interest is to know how environmental conditions affect this equilibrium. In considering this subject only those factors will be treated that have yielded some results in our research.

Mineral supply is one of the main factors influencing the shoot/root-ratio. Little nitrogen and/or phosphorus shows relatively much root and little shoot growth. A liberal supply of these elements will show the reverse. The equilibrium suited to a prevailing condition is reached by a kind of overshoot reaction, a fluctuation around the equilibrium. The shoot grows as the root supplies nitrogen. At ample supply the shoot will use most of the photosynthesis products formed in the leaves and little is translocated to the roots. The equilibrium shifts in favour of the shoot. Growth increases the shoot's requirement for water and nitrogen. The root, retarded in growth, cannot supply this and shoot growth will be somewhat reduced. More carbohydrates are now available to the root system and thus it will recover slightly. Figure 4 a gives an indication that this is indeed the case. It can be more emphasized by interrupting the nitrogen supply at regular intervals. In periods without nitrogen the root will have the advantage and in periods with nitrogen the shoot. It has also been proved that the presence of nitrate in the root medium is not the primary factor, but the nitrate reserve in the plant is. When the nitrate containing solution is changed for a solution without nitrate the reaction is delayed until the nitrate reserve in the plant has been depleted. At short intervals there will be no difference with the uninterrupted nitrate supply, because uptake in the period with nitrate will be ample for growth to continue at the same rate and in normal proportions during the period without.

These experiments also prove that in changing conditions, in fact, disturbing the equilibrium, the plant will react by establishing another equilibrium adjusted to the new situation (fig. 5).

Water supply mainly has the same effect as nitrogen supply. The leaf/root-ratio (on fresh weight basis) of bean plants on a Hoagland solution from just after germination to flowering will be ± 1 at a temperature of 20 °C, a light intensity of 25000 erg. cm^{-2}

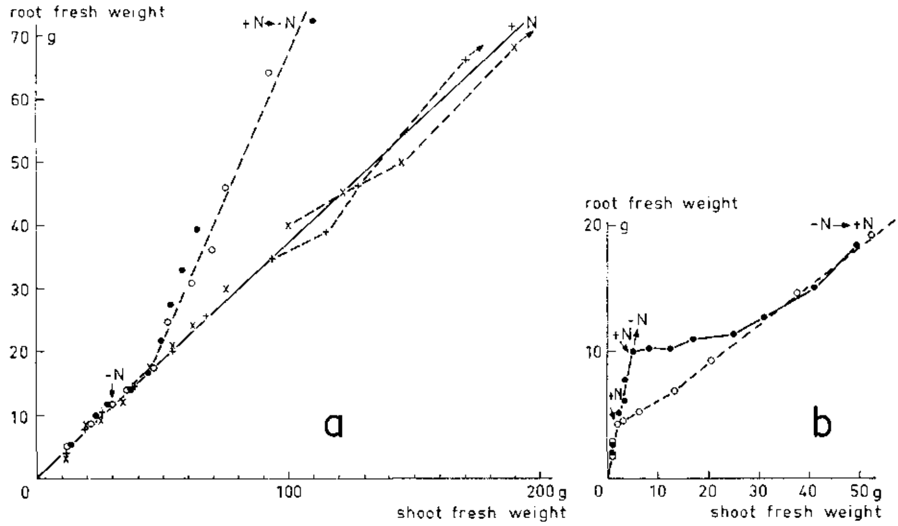


FIG. 4. Influence of changes in the nitrogen supply on the shoot/root ratio of maize seedlings. Each symbol represents the fresh weight of a single plant (vide 9).

sec^{-1} and a relative humidity of 65 per cent (fig. 6). Increasing suction tension in the root medium by raising its osmotic concentration is associated to about the same increase in suction tension in the plant (BROUWER, 8). Leaf growth is depressed at once (fig. 6), while root growth is hardly affected. Accordingly the shoot/root-ratio will decrease (fig. 6). Obviously, the influence of raising the osmotic value in the root medium closely corresponds with the effect of removing parts of the root system (compare fig. 7 with fig. 1). In both cases leaf growth is much more sensitive than transpiration. The mechanism of the change in the shoot/root-ratio in favour of the root can be explained in the same way as the nitrogen effect. An unfavourable water balance will reduce leaf growth. Photosynthesis products are accumulated in the plant and the root will profit by these. As there is a higher suction tension in the leaves

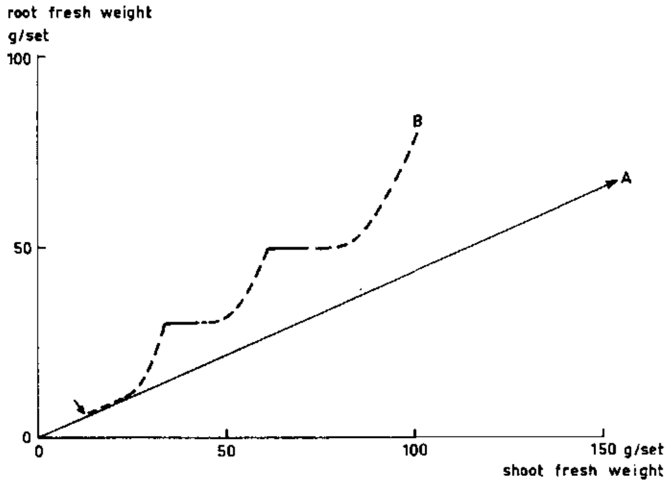
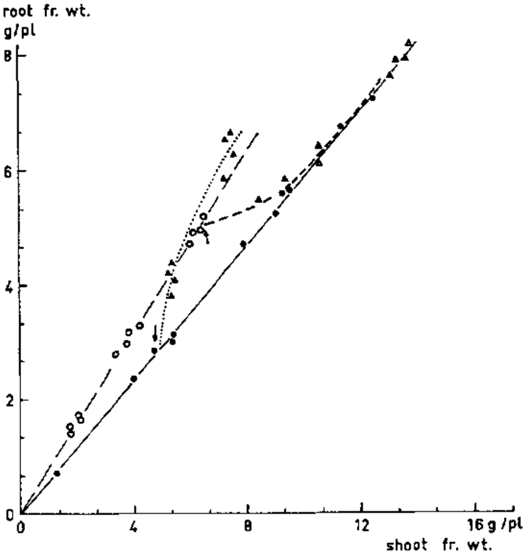


FIG. 5. Influences of changes in the nitrogen supply on the shoot/root ratio of perennial rye grass. Solid lines plants on Hoagland solution with nitrogen; dotted lines the nitrates of the nutrient solution substituted by the chlorides.

FIG. 6. Influence of changes of the osmotic concentration in the nutrient solutions on leaf growth compared with root growth (dots Hoagland throughout circles Hoagland + 2.5 atm. NaCl over to Hoagland; filled triangles from Hoagland open over to H + 2.5 atm. NaCl; turn over indicated by arrows).



than in the roots (BROUWER, 4; BERNSTEIN and HAYWARD, 2) it stands to reason that the roots will be less hampered by increased suction tension than the shoot.

The reduction in leaf growth occurring at the slightest increase of suction tension shows that even in water culture the hydrature in the plant seems to be the growth limiting factor. There are many examples to prove this in the field. LOOMIS (14) found that maize showed a growth reduction on hot days in periods of fierce sunshine. Due to high transpiration rates the water deficit in the plant under these conditions is apparently high enough to cause growth depression. VAN DEN ENDE (11) also found a growth depression due to much transpiration in cauliflower roundabout midday. This reduction was less as the day was less sunny.

There is a great difference in growth between aerated and non-aerated bean plants

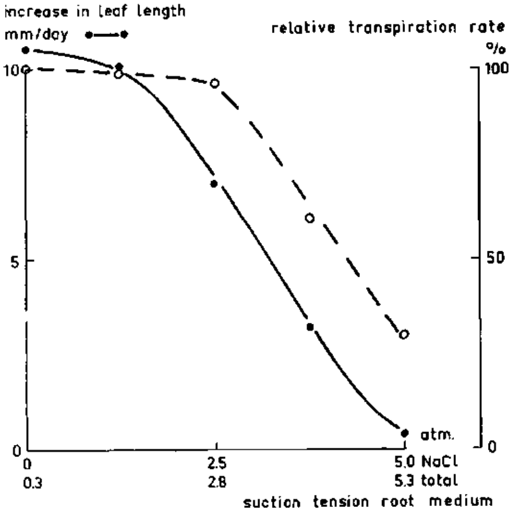


FIG. 7. Influence of increasing osmotic concentrations on transpiration and growth rate of bean leaves.

on water culture (Brouwer, 3). A growth analysis has proved that this difference in growth rate is mainly present during the day. In the dark period the difference in growth rate is less. Due to transpiration the internal water deficit will be larger by day than at night. In non-aerated plants it can reach such high values that growth stops. Even aerated plants will show a somewhat reduced growth rate in the light period. This is yet another fact proving that growth is most sensitive to the water balance.

Insufficient mineral supply as well as insufficient water supply produce relatively more roots than a sufficient supply. Uptake is a function of the amount of roots and of the presence of minerals. When these minerals are less available the amount of roots per gram of shoots should increase in order to meet the requirement of the shoot. It is therefore quite reasonable that this effect is reached. The data obtained in experiments on the influence of root temperature are not quite so easy to interprete.

In several crops there is an obvious effect of root temperature on growth (Brouwer, 5 and 6). Overground and underground parts generally will react in the same way. However, there are large quantitative differences, manifested in a change in the shoot/root-ratio. In general this will be largest at the most unfavourable root temperatures, so that it seems as though the root value is highest at these temperatures (fig. 8). This is especially so when root growth is retarded by external factors. In such cases it seems as though there is shoot growth despite the poor root system.

An experiment, in which seedlings grown at a root temperature of 20 °C have been transferred to a root temperature of 10 °C, will do to show how this effect is reached (fig. 9). Root growth terminates at once after this transfer. Shoot growth continues for a short time even though much retarded. In our experiment this continues until the leaf/root-ratio is about 3. This leaf growth mainly consists of cell division, while cell elongation is impossible due to the unfavourable water balance in the plant. As the plants remain longer in this unfavourable temperature growth will decrease gradually and will finally completely terminate, while after some time necrosis will even occur in the leaves. At a root temperature of 5 °C this effect will be enhanced. At 10 °C the root is completely at rest. Epidermis and endodermis show progressive cork formation up to the apex (Brouwer, unpublished results), but remain alive. This is proved by transferring the plants again to a more favourable root temperature later on. It will take a few days before the tops of the main and branch roots start to grow again and form a great number of fresh lateral roots. Leaf growth is resumed only when root growth is again in full progress. A large difference is to be found in plants that have remained at a root temperature of 10 °C for a shorter or longer period. Accelerated

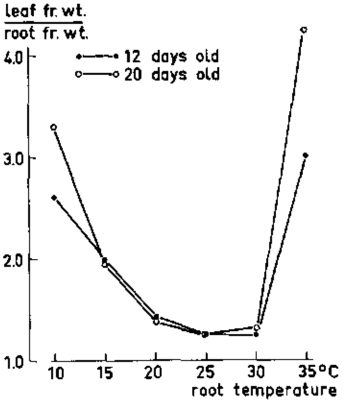
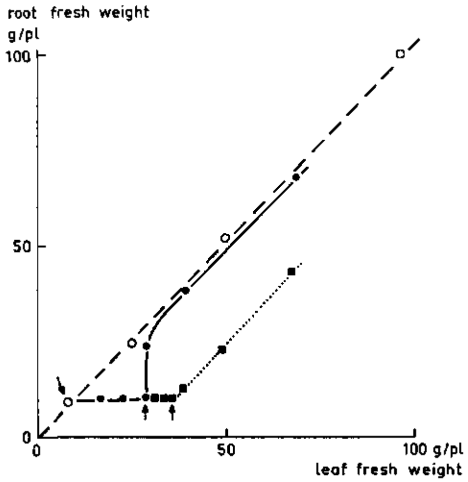


Fig. 8. Leaf root ratio of bean plants grown for 12 and 20 days on various root temperatures.

FIG. 9. Fresh weights of leaves of bean plants plotted against fresh weights of the root system at various harvest times.
Circles: plants on a root temperature of 20 °C throughout
Dots: plants over to a root temperature of 10 °C (1) and again to 20 °C (2)
Black squares: prolonged application of a root temperature of 10 °C continued to (3) and then over to 20 °C.



root growth will start immediately after transferring the plant to 20 °C if cork formation in the roots is not complete, so that the equilibrium belonging to 20 °C is soon reestablished. When cork formation in the roots is complete and there is necrosis in the leaves, root and shoot growth will only start later and in a ratio adjusted to 20 °C. Due to the ballast of the material present at the moment of transfer the total ratio will deviate however (fig. 9).

From all this it is apparent that due care should be taken in mentioning simple figures. Morphological and anatomic characteristics should be taken into account as well. However, a quantitative evaluation of these is not a simple matter. A few examples may serve to prove this.

In comparing the reaction of a plant transferred from a root temperature of 20 °C to one of 10 °C with that of a plant transferred to a root temperature of 35 °C it will be seen that root growth terminates immediately in both cases. At 10 °C leaf growth is immediately retarded as well, while at 35 °C leaf growth initially continues as normal (fig. 9 and 10). A reduction in leaf growth rate sets in only a few days later, progressing

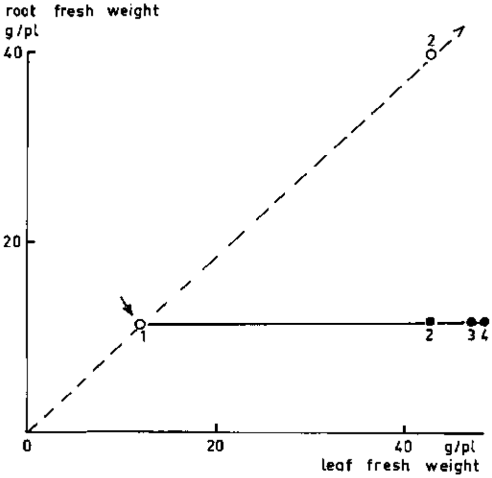


FIG. 10. Fresh weights of leaves of bean plants plotted against fresh weights of the root system at various harvest times. Circles denote plants on a root temperature of 20 °C throughout. At the time indicated by the arrow part of the plants has been transferred to a root temperature of 35 °C (dots).

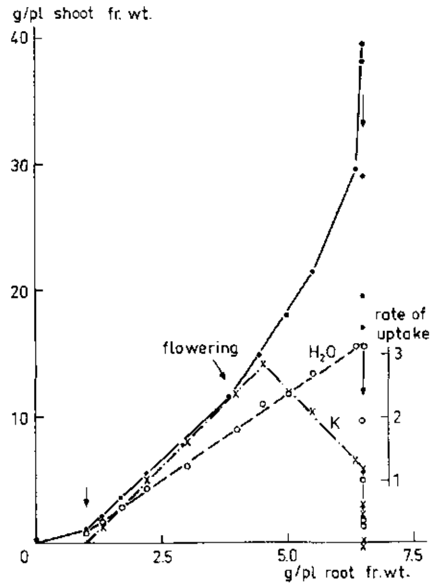


FIG. 11. Fresh weights of shoots, rate of water uptake and rate of potassium uptake of peas plotted against the fresh weight of the root system.

rapidly and terminating in an almost complete stop (fig. 10). Accordingly the difference is an instantenious reaction at 10 °C and a deferred reaction at 35 °C. Apparently, at 10 °C the activity of the root system is immediately retarded by low temperatures. This is also evident from measurements of the water and ion uptake. At 35 °C root growth terminates, but uptake continues as normal. This temperature accordingly is not unfavourable for root function initially. At prolonged application, however, water and ion uptake gradually decrease. This decrease is associated to a cork formation in the endodermis progressing towards the root apex, which gets more and more impermeable. It results in the above mentioned effects on leaf growth.

It has been proved that at 10 °C as well as at 35 °C higher shoot/root-ratio is formed, but the way in which this is affected differs somewhat. By taking into account the structural changes in the root more light will be thrown on this.

The changes in the shoot/root-ratio in the course of development is another example in which a functional equilibrium seems improbable, due to the weight relation between shoot and root. It is often observed that shoot growth is relatively more rapid than root growth during development. Especially so after flowering, because in many plants root growth retards considerably after this and sometimes terminates completely. However, it is also noticed that in many cases the leaves in sequence of formation show a more xeromorphous nature. This is evident at upright stems. The relation between these two phenomena is obvious. If the growth rate of the root system is limited the water and/or mineral supply to the shoot will be reduced. In general, especially water supply influences leaf structure. The relation between root and shoot weight changing continuously, while that between evaporation and root weight remains the same (fig. 11), is a most striking fact. In this case it probably is the non aerated medium that limits root growth. To wit, if the nutrient solution is aerated the relation between shoot and root weight as well as that between evaporation and root weight will be constant until just after flowering. Deviations will then only occur after fruit setting. It seems probable that root growth in this instance is limited by internal factors (hormonal). The effect as mentioned above is repeatedly considered to be caused by a more unfavourable competitive position of the higher leaves as compared to the basal ones. However, it looks as though it is due to a reduction in root growth by external or internal factors. It is striking that these changes in shoot growth in relation to root growth are associated to a decreased relative growth rate as well as anatomic changes. It seems likely that these anatomic changes and the decreased growth rate both are causally related to water shortage. These changes can be induced in peas by removing a part of the root system in young developmental stages. Figure 1 shows that transpiration is hardly influenced by this provided not too much is removed. However, suction tension in the leaf will be increased (BROUWER, 4) and thus growth rate will be reduced. The leaves present, but especially the newly formed ones will get more xeromorphous and the shoot/root-ratio will change.

Briefly, it may be assumed that in all probability the relation between shoot and root is regulated by activities. It may therefore be characterized as a functional equilibrium. In order to interprete this functional equilibrium correctly combined anatomic and physiological research is necessary. In many correlative researches this aspect often is completely neglected.

SUMMARY

Data on relative growth rates of shoots and roots at different conditions are summarized. The assumption is proposed that at each set of conditions a functional equilibrium exists between these parts of the plant. To understand this equilibrium data are required concerning the morphological and anatomical properties of the plant.

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THE PHYSIOLOGICAL BACKGROUND OF THE REACTION OF PEAS TO SOWING TIME

W. H. VAN DOBBEN

INTRODUCTION

It is common experience that spring crops from the temperate zone (small cereals, peas, flax) must be sown as early as possible to obtain optimal yields. All these crops ripen rather early in summer and therefore it is not immediately clear why they react unfavourably when their growth period is shifted to later part of the season. Moreover this reaction seems to be specific, for crops originating from the warm zone (maize, beans) show inverse relations.

The explanation of this phenomenon is to be found in the specific reactions of plants to the climate.

The ultimate measurements and weight of a plant are determined by development rate (length of stages) and growth rate (daily increase in weight). Both factors are influenced by temperature and light conditions independently.

The prolonged day and higher temperature of advanced spring have important specific repercussions in the final yield of a plant.

DAYLENGTH

Photoperiod has an important influence on the duration of the youth stage of long-day and short-day plants. It has been pointed out long ago (4) that optimal daylength gives small plants because of the drastical shortening of the youth phase.

This is one of the important reasons why long-day plants, including many pea varieties and all varieties of small cereals grown in Western Europe, do not reach a sufficient size when they miss the short days of early spring. The plant weight attained at the beginning of flowering is closely correlated to ultimate plant size and yield.

Spring barley is the only small cereal acceptable as a catch crop. It thanks this position partly to its moderate reaction to daylength in comparison with other species. It maintains a reasonable growth period, leaf number and plant size when sown late (2).

Maize is a short-day species and for this reason shows inverse relations in comparison with long-day cereals. The plants reach a larger size when sown later in spring (1) because the youth stage is prolonged in long days. Beans are day-neutral and this crop can also be sown with good results in late spring.

If photoperiodic reaction should be the only factor determining the reaction of yield to sowing time it might be expected that day-neutral varieties of crops from the temperate zone should be comparable to beans. There is a possibility to check this supposition with peas. Day-neutral varieties are not at all rare in this species, especially in canning-peas.

Some well-known canning peas, as Kelvedon Wonder, Gloire de Quimper and Alaska meet this condition. According to practical experience, however, the first two mentioned cannot be sown late without heavy losses in yield. This already indicates that apart from daylength other factors are involved.

INFLUENCE OF TEMPERATURE

Late sowing in spring exposes a crop to a higher average temperature.

In a previous paper (4) it has been pointed out that in crops of the temperate zone the shortening of the period from emergence until flowering caused by higher temperature results in a smaller plant size. The reduction of the period available for production is not sufficiently compensated by increased growth (daily gains in weight) in this type of crops. Crops of southern origin, as maize and beans, show a comparable (even greater) acceleration of development in high temperature but their growth is simultaniously stimulated at such a tremendous rate that the loss of time is overcompensated which results in a higher plant weight at the moment of flowering.

Reaction to temperature is a second factor as important as photoperiodicity to explain sowing-time effects.

CONCLUSION

The following properties are favourable for a plant species to reach a high weight at the moment of flowering after late sowing:

1. Short-day habit or day-neutrality
2. Low acceleration of development in high temperature
3. High acceleration of growth in high temperature

Crops of the tropical and sub-tropical zone appear to meet conditions 1 and 3 sufficiently to obtain even a higher plant weight after late spring sowing notwithstanding the fact that development is even more accelerated than in plants of the temperate zone.

Crops of the temperate zone are as a rule long-day plants. In peas day-neutrality occurs. Their weakness concerns especially condition 3. It would be interesting to know whether there are differences between varieties in respect to 2 and 3.

A COMPARISON OF PEA VARIETIES AT TWO TEMPERATURES

In the present investigations 30 pea varieties were compared to assess possible specific differences in temperature reaction.

The plants were grown in pots (6 plants per pot, 2 replications) in greenhouses at constant temperatures of 16 and 25 °C and natural light complemented to long-day (18 hours) by weak fluorescent illumination. The sowing date was September 3. The observations concern the period emergence-flowering and the plant weight at the moment of first flowering. Moreover the length of internodes was measured and the number of full-grown leaves counted.

On April 2 the varieties were again sown at 25 °C to assess the effect of an extension of natural day by weak fluorescent light on the date of flowering.

The results are recorded in table 1.

INFLUENCE OF TEMPERATURE ON DEVELOPMENT

In table 1 the pea varieties are arranged according to earliness at 25 °C. They differ very widely in this respect. The period from emergence until flowering differs from 26 to 57 days at 16 °C and from 17 to 40 days at 25 °C. From these figures it is already clear that high temperature shortens the period of development considerably.

The relative rate of acceleration calculated from the number of days at 16 °C devided by the same value at 25 °C ranges from 1.2 to 1.78 for individual varieties (fig. 5). The average is about 1.45.

TABLE 1. Reaction of several pea varieties to temperature and daylength. Recorded data:
number of days from emergence until first flowering (days)
dry shoot weight at the moment of first flowering (weight)
average length of internodes in mm (internode mm)
number of full grown leaves at the moment of first flowering (leaf nr.)

Variety (origin)	16 °C				25 °C				25 °C			
	Natural daylength (± 13 hours) prolonged until 18 hours				Natural daylength (± 13 hours) prolonged until 18 hours				Natural daylength (± $14\frac{1}{2}$ hours) prolonged until 17 hours		Natural daylength (± $14\frac{1}{2}$ hours)	
	days	weight	internode mm	leaf nr.	days	weight	internode mm	leaf nr.	days	leaf nr.	days	leaf nr.
Gloire de Quimper (Fr)**	29	625	24	8	17	368	21	8	18	8	18	8
Alaska 14 (Am)**	26	520	52	8	20	449	48	9	20	8	20	8
Kelvedon Wonder (Eng)**	31	743	37	8	20	481	23	8	19	7	18	7
Annovert (Fr)**	32	855	25	9	21	455	19	9	20	8	20	8
Zeiners Grüne Bastard (G)*	32	877	38	11	22	797	38	11	26	11	29	13
Express Karlowy (Pol)**	37	855	22	12	24	662	25	11	24	10	24	10
Elf (USA)	36	981	34	12	26	590	27	12	26	12	32	17
Jade (USA)	37	1280	42	11	26	920	34	12	26	12	27	13
Supcovert (Fr)	36	1059	40	10	26	1080	41	11	26	11	31	14
Dippe's Gelbe Victoria (G)*	40	1739	44	13	27	1326	43	14	30	16	32	17
Weitor (Sw)	39	1384	53	14	27	1170	50	14	–	–	–	–
Finette (Neth.)*	36	983	27	11	27	1060	33	11	26	11	29	11
Wando N. King (USA)*	43	1508	31	15	30	1122	29	14	31	15	33	17
Asgrow (nr. 362) (USA)	45	1194	31	15	30	1147	25	15	32	18	36	19
Mansholt 2008 (Dik Trom) (Neth.)	43	855	20	13	31	728	17	12	33	18	38	20
Doperwt v. Waveren (Neth.)	45	545	17	14	31	515	16	13	31	15	34	18
Rovar (Neth.)	43	1069	20	13	31	1053	21	12	–	–	–	–
Heralda (G)	45	2074	31	18	31	1453	30	17	31	19	35	20
Lincoln (Eng)	45	1521	28	16	32	1174	24	16	32	16	36	19
Dark Skin Perfection (USA)*	43	2200	38	16	32	1575	33	15	33	16	36	18
Finnish pea (Finl)	57	2837	40	18	32	1870	53	17	36	18	43	22
Wyola (USA)	45	1681	31	16	32	1762	30	15	32	17	36	20
G. 17 Canner Multipod (USA)	46	1368	25	16	33	1280	30	14	–	20	38	20
Cent Vert (Fr)	46	1351	28	16	33	1020	29	16	33	18	37	20
Oreste (Fr)	46	1971	29	16	33	1320	27	16	36	18	41	20
Hamlet Hunderup (Da)	51	2675	38	17	34	1845	34	17	37	19	43	20
Merida (Neth)	50	1271	23	14	34	1129	18	14	–	–	–	–
Wico (Neth)	54	1521	27	14	34	787	18	15	36	14	43	17
Pea A-100 (Canada)	48	1895	27	15	40	1873	29	16	–	–	–	–

** day-neutral varieties
in italics: varieties suffering a heavy weight reduction at higher temperature
fat print: varieties with a slight weight reduction at higher temperature

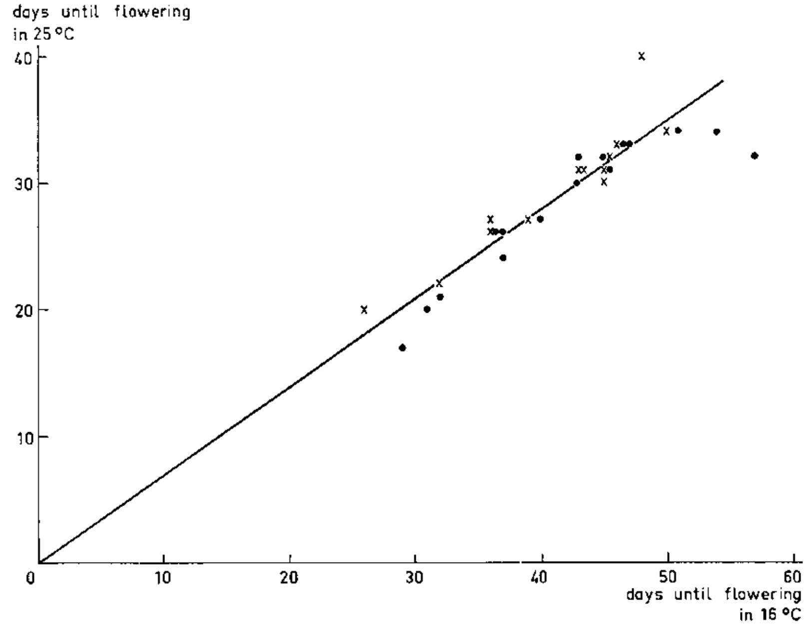


Fig. 1. Relation between the number of days from emergence until first flowering at 16 °C and 25 °C for several pea varieties. Varieties which maintain a relatively high plant weight in higher temperature are represented by (x).

If the „heat-sum" (average daily temperature times number of days until flowering) should be constant the calculated rate of acceleration should be 1.56 $\left(=\frac{25}{16}\right)$ for a zero-temperature of 0 °C or 1.7 $\left(=\frac{20.6}{11.6}\right)$ for a zero-temperature of 4.4 °C (= 40 °F.) (3)

It appears that the „heat-sum" is about constant only for a minority of varieties and that there is indeed a large variability in respect to the temperature reaction of development.

Fig. 1 gives no indication for an interaction between earliness and average relative acceleration of development at high temperature.

Early varieties therefore, generally are speeded up at the same rate as late ones.

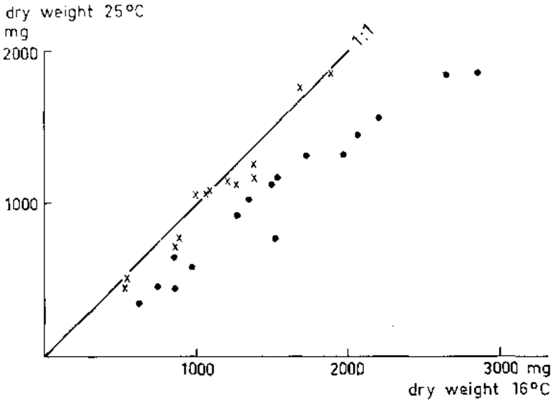
INFLUENCE OF THE TEMPERATURE ON PLANT WEIGHT

Plant weights at the moment of first flowering are plotted in fig. 2 for temperatures of 16 and 25 °C.

There are large differences in plant weight between the varieties. Early varieties generally reach much lower weights than late ones since the period available for growth is much shorter (table 1).

Only a few varieties reach the same plant weight at 16 and 25 °C. A majority shows a clear reduction at the higher temperature. Varietal differences obviously are considerable. The relative weight reduction does not show an interaction with absolute weight. This means that the reaction to temperature is not especially related to earliness.

FIG. 2. Relation between dry weight attained at the moment of first flowering at 16 °C and 25 °C for the same pea varieties as in fig. 1. Varieties which maintain a relatively high plant weight in higher temperature are represented by (x).



It is interesting to observe (table 1) that higher temperature does not significantly affect the leaf number at the moment of first flowering. Leafs, however, become smaller and the internodes generally are shorter.

RELATION BETWEEN DEVELOPMENT RATE AND DRY WEIGHT REACHED AT THE MOMENT OF FIRST FLOWERING

The relation between the length of the period until flowering and the dry weight attained at this moment is shown in fig. 3 for both temperatures. The large deviations from average values indicate considerable specific differences in growth rate.

Notwithstanding the enormous variations in weight reached by different varieties after a given number of days the average relation is clearly exponential as could be expected for widely spaced plants in pots. The 2 curves drawn in fig. 3 in fact represent average growth curves for peas at two temperatures. Fig. 4 gives for comparison growth curves for one pea variety assessed by periodical harvesting.

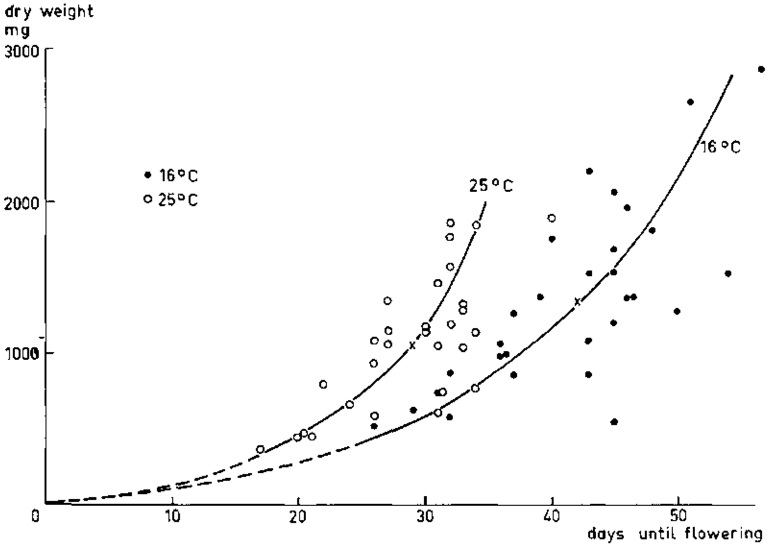


FIG. 3. Relation between the length of the period from emergence until flowering and dry shoot weight attained at this moment by several pea varieties at two temperatures. The same data as recorded in fig. 1 and 2 (x = average weight).

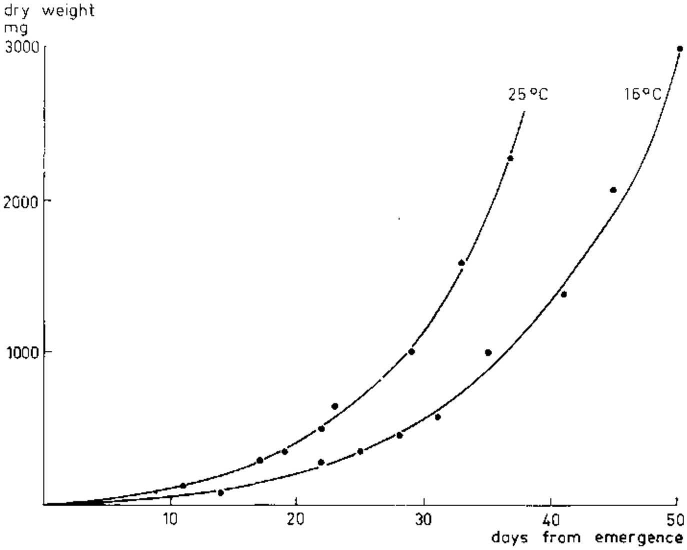


FIG. 4. Increase in dry shoot weight shown by a pea plant at 16 °C and 25 °C, assessed by means of periodical harvesting.

The much steeper trend of the 25 °C curve indicates a more rapid growth (by higher daily production). This explains why the drop in final weight caused by the rise in temperature is less than could be expected for the loss in time. At 16 °C the average period until flowering is 42 days; the average dry weight reached at this moment amounts to 1337 mg. At 25 °C the average period until flowering is 29 days. At 16 °C this period should have given an average dry weight of 550 mg, whereas actually 1056 is measured owing to increased growth.

The relation between growth rates at 16 and 25 °C may be somewhat influenced by the fact that average light conditions in the 25 °C series were slightly better than the 16 °C one due to the weakening of natural light during the experiment (September-October) which favoured the cases with the shortest period of growth. It can be observed, however, that plants receiving a higher temperature by late sowing in practice are also exposed to stronger radiation.

The data recorded in fig. 4 are taken from a glasshouse experiment in spring with simultaneous flowering of the 16 and 25 °C series at the end of April.

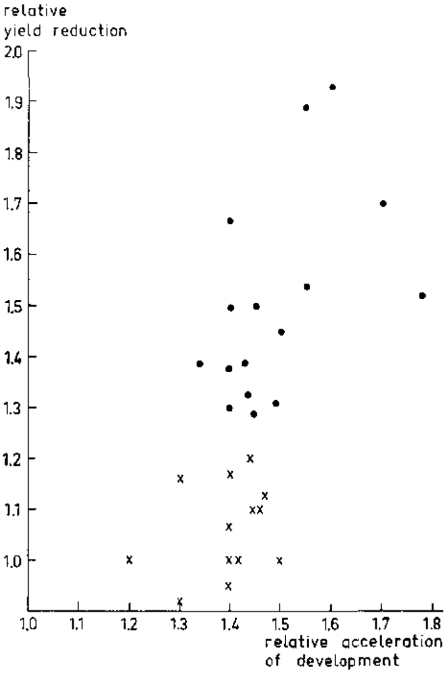
THE SPECIFIC INFLUENCE OF TEMPERATURE ON GROWTH RATE

According to expectation fig. 5 shows a positive relation between the rate of acceleration (number of days until flowering at 16 °C: the same value at 25 °C) and the rate at which plant weight is reduced (weight at flowering at 16 °C: the same value at 25 °C).

The steep slope of the regression indicates that slight differences in development rate have great repercussions in weight relations. This is in accordance with the exponential growth curve which shows a steep trend in the period just before flowering (fig. 3 and 4).

Fig. 5 also demonstrates that a group of varieties with a same acceleration of development still shows a wide variation in the reaction of plant weight to temperature. This indicates specific differences in the reaction of growth rate to temperature. These can also be shown by comparing fig. 1 and 2.

FIG. 5. Relation between the rate of acceleration of development in higher temperature (number of days until flowering at 16 °C: the same value at 25 °C) and the rate of yield reduction (shoot weight at flowering at 16 °C: the same value at 25 °C) attained by the examinated pea varieties. Varieties which maintain a relatively high plant weight in higher temperature are represented by (x).



The varieties which are only slightly reduced in weight by higher temperature are recorded in fig. 1 and 2 by (x).

It appears that they generally are above the average in maintaining a relatively long period of development at 25 °C. However not all varieties in this position maintain a good plant weight and this also indicates that there are specific differences in reaction to temperature not only in respect to development rate but also in respect to growth rate.

RESPONSE TO DAYLENGTH

In the right part of table 1 the number of days until flowering is recorded for two photoperiods. It appears that a rather large number of pea varieties does not show a significant difference. These may therefore be considered as day-neutral (*in table 1). The remaining varieties show a varying rate of delay in short day and thus behave as long-day plants.

It appears that early varieties are more often day-neutral or nearly so (*) than late varieties. This may be explained by the fact that breeding on earliness in a short-day regime will favour the selection of day-neutral types. In peas daylength reaction is only recognizable when flowering begins. The youth stage does not show differences in long and short day.¹) In short-day flower formation only begins at a higher leaf number so that the decrease in growth rate which is typical for the generative stage is postponed. As a result a higher ultimate plant yield is reached.

Tillers flower somewhat later and always have a lower leaf number than the main

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¹) In an experiment with a large difference between long day (22 hours) and short day (12 hours) the internodes were somewhat shorter and tillers more numerous in short day for long day varieties.

stem. This may cause deviations in the figures concerning leaf numbers, especially when the main stem is abortive.

DISCUSSION

The pea varieties examined in these investigations show clear differences in their response to daylength and temperature. In table 1 day-neutral varieties (**) and varieties with a slight reaction (*) are marked. Day-neutrality seems to dominate in early varieties.

Varieties maintaining a relatively high plant weight in high temperatures are printed fat (table 1). This habit does not seem to be associated with earliness.

Both qualities may be supposed to increase the suitability of a variety for late sowing, for late spring is characterized by longer day and higher temperature, both of which tend to reduce the yield of long-day crops of the moderate zone.

Among the examined varieties only a few combine a slight reaction to both daylength and temperature: Alaska 14, Zeiners Grüne Bastard and Finette. This being the most favourable constellation it would be interesting to know whether these varieties show good results in practice when sown late in spring.

According to a personal communication by Ir. P. RIEPMA (P.A.W., Wageningen) practical experience about the suitability of pea varieties for late sowing is very limited.

Kelvedon Wonder and Gloire de Quimper give poor results. In the Netherlands Finette (selection from the French Roi des Fins Verts) is preferably used for late sowings. Experience with the common Dutch pea types (Rovar, Dik Trom) is rather good.

In England and the Netherlands reasonable results are obtained with American varieties as Dark Skin Perfection, Jade and Wyola. For the most interesting Alaska experience is lacking.

A comparison of these rather scanty data with the results of our investigations gives the impression of a reasonable agreement.

Finette is outstanding both in the experiments as well as in practice. The other varieties used for late sowing do not show a strong reaction to temperature or they are rather indifferent to daylength.

The practical experience obtained with Gloire de Quimper and Kelvedon Wonder could be predicted from the glasshouse experiments. They are day-neutral but fail at high temperature.

The results suggest that it would be possible to test pea varieties in the laboratory on suitability for late sowing by way of their reaction to daylength and temperature.

The existence of a large variability among varieties to photoperiodicity and temperature opens the possibility for a breeding program aimed at varieties showing a certain independence with regard to sowing time. Such varieties are useful in spreading the harvesting season of canning peas for industrial purposes.

It seems feasible to choose the crossing parents suitable for such a breeding program by analysing their reaction to daylength and temperature and also to test the selections obtained.

SUMMARY

Pea varieties show large differences in their reaction to daylength and temperature. These reactions may be decisive for the ability of a variety to maintain a good yield after sowing late in spring.

For peas and other long-day crops of the temperate zone the long days and higher temperature of late spring lead to a decrease in plant size and final yield by shortening of the growth period, which is not completely compensated by more rapid growth per time unit.

It is supposed that the following proporties give an advantage in this respect:

day-neutrality

low acceleration of development in higher temperature

high increase of growth rate in higher temperature. There are indications that varieties which give good practical results after late sowing thank this faculty to these properties. This opens the possibility to test varieties in this respect in the laboratory.

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DETERMINATION OF FREE FATTY ACIDS AND SOAPS IN FAECES FROM CATTLE

W. B. DEIJS, H. J. IMMINK AND J. WIND

INTRODUCTION

The determination of fatty acids in human faeces according to the method of VAN DE KAMER, TEN BOKKEL HUININK and WEYERS (1) gives good results. In this method the free fatty acids and soaps are determined together. After boiling the faeces with hydrochloric acid (2.5%) the fatty acids are extracted with petroleum ether. After distilling off the petroleum ether the residue is dissolved in alcohol and titrated with 0.1 N isobutyl alcoholic KOH (indicator: thymol blue). When using this method in the analysis of faeces from cattle it was difficult to observe the equivalence point as the colour of the extract was too dark. Good results were obtained with a slightly modified method in which the equivalence point is found by potentiometric titration. Moreover the contents of free fatty acids and soaps were determined separately.

PROCEDURE

Reagents

1. NaCl solution (250 g in 1 litre of CO_2-free water)
2. Hydrochloric acid (2.5%) containing 250 g NaCl in 1 litre
3. 96% ethanol, containing 0.4% amylalcohol
4. 96% ethanol, neutralized just before use on thymol blue
5. Petroleum ether (B.P. 40–60 °C), washed with a dilute solution of KOH and finally washed with water. The distillation residue must be neutral on thymol blue.
6. Isobutyl alcoholic KOH (0.1 N). 5 litres of isobutyl alcohol are refluxed over 100 g of NaOH during 3 hours. In a litre of the distillation fraction 105–108 °C, 15 g of KOH (50%), diluted with 20 ml of methanol, are dissolved. Before use the isobutyl alcoholic KOH is standarized on 0.1 N HCl (Indicator: thymol blue).
7. 0.1 Hydrochloric acid
8. 2% Thymol blue in 50% ethanol
9. Glass tubes (30 × 4 cm) provided with ground glass stoppers and a reflux condensor.

Determination of free fatty acids

50 g of fresh faeces and 75 ml of water are mixed thouroughly during 2 min in a mixer. Of the suspension 10 g (corresponding with 4 g of fresh faeces) are weighed and rinsed into a glass tube with 30 ml of the NaCl-solution. After addition of 60 ml of ethanol (0.4% amyl alcohol) and 50 ml of petroleum ether the tube is closed and vigorously shaken for 1 min. Occasionally the tube is rotated in order to improve separation of the layers. 25 ml of the petroleum ether solution is distilled from an erlenmeyer-flask containing a small piece of filter-paper (ca. 5 × 5 mm). The residu is rinsed quantitatively into a 50 ml beaker with 25 ml neutralized ethanol and titrated

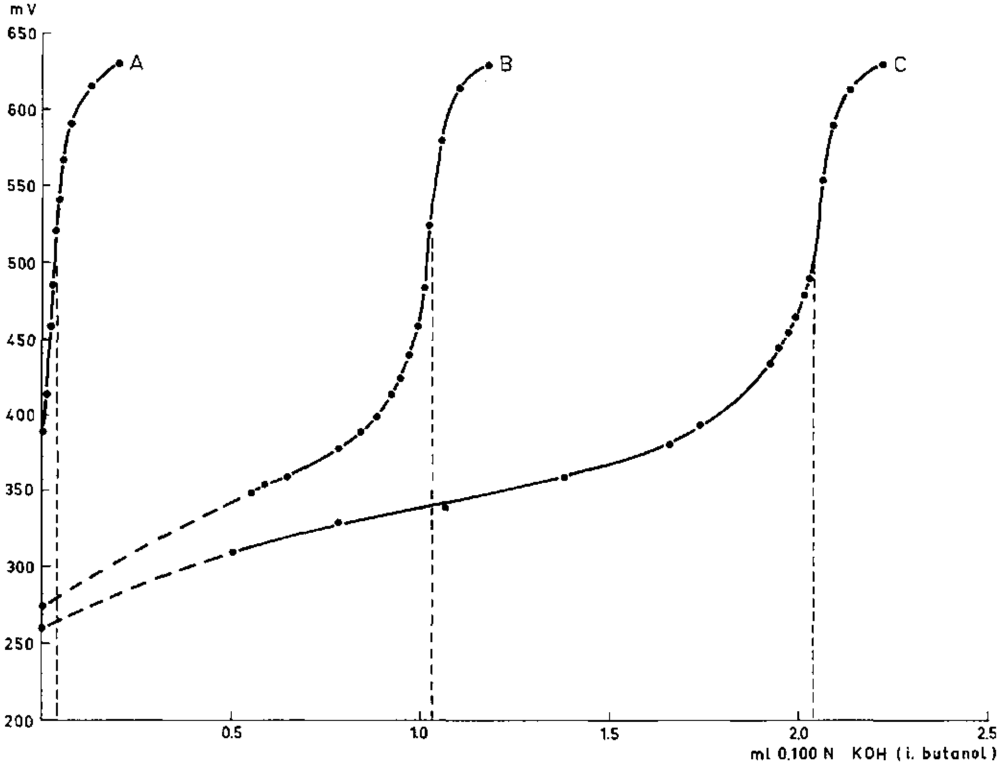

FIG. 1. Analysis of a mixture of 0.200 me. of palmitic acid and 0.200 me. of Ca-palmitate.
A = blanc.
B without boiling and without hydrochlorid acid (free fatty acid).
C after boiling with hydrochloric acid (soap + free fatty acid).

potentiometrically from a micro-burette with butyl alcoholic KOH (magnetic stirrer, glas-electrode, saturated calomel-electrode). Examples of titration curves are given in fig. 1.

Determination of free fatty acids + soaps

10 g of the faeces supension are rinsed into a glass tube with 30 ml of the NaCl containing 2.5% hydrochloric acid. After heating (reflux condensor) to boiling point the tube is cooled in ice. Then 60 ml of ethanol (0.4% amyl alcohol) and 50 ml of petroleum ether are added. After shaking (1 min) the above procedure is followed.

Blanks are carried out in the same way with 10 ml of water instead of the faeces suspension.

The results, reported in table 1, prove that it is immaterial whether the faeces suspension is boiled during 1 min with hydrochloric acid, heated until the boiling point is reached, or whether the faeces suspension is mixed with hydrochloric acid without heating. In the last case the layers separated too slowly. The results prove that storing of the faeces at 4 °C during 6 days did not alter the contents of free fatty acids and soaps.

TABLE 1. Different methods of releasing fatty acids from soaps in faeces.

Sample	HCl-treatment	Titration (ml 0.100 N KOH)	Free fatty acids+soaps (me. in 100 g of d.m.)
Fresh	boiled (1 min)	0.180	5.29
Stored at 4 °C			
2 days	not boiled	0.181	5.32
2 days	boiled (1 min)	0.175	5.15
6 days	boiled (1 min)	0.185	5.44
6 days	heated to boiling point	0.182	5.35

TESTING THE METHOD

K-palmitate, Mg-palmitate and a mixture of Ca-palmitate and palmitic acid were analysed according to the above mentioned method.

a. Starting from 2 ml of a 0.100 N alcoholic solution of K-palmitate (2) 0.004 me. free fatty acids and 0.203 me. soaps were found.

b. Mg- palmitate was precipitated from a solution of $MgSO_4$ by adding a solution of K-palmitate (see a) until phenolptalein turned pink. The precipitate was filtered off by suction, washed with water and ethanol and dried in vacuo over silica-gel. 166.20 mg of the Mg-palmitate gave after ignition 11.64 mg of MgO. Found: 4.22%, calculated for $(C_{16}H_{31}O_2)_2Mg$: 4.55% Mg. An analysis of 53.4 Mg (0.2 me.) of the Mg-palmitate according to the above mentioned method resulted in 0.004 me. free fatty acids and 0.192 me. soaps.

c. Ca-palmitate was prepared from a solution of $CaCl_2$ (see b). 136.50 mg of the Ca-palmitate gave after ignitation 13.75 mg of CaO. Found: 7.20%, calculated for $(C_{16}H_{31}O_2)_2Ca$: 7.29% Ca.

A mixture of 55.0 mg (0.200 me.) of Ca-palmitate and 51.2 mg(0.200 me.) of palmitic acid was analysed (see titration curves fig. 1).

Results: Free fatty acids 0.198 me.
Soaps 0.202 me.

d. In two other experiments the results were compared when different quantities of the faeces suspension were analysed.

Faeces sample A. Analysed 15 g of the faeces suspension (6 g of fresh faeces). Found: 0.19 me. free fatty acids and 0.37 me. soaps per 100 g of fresh faeces. With 10 g of suspension these figures were 0.18 and 0.37 respectively.

Faeces sample B. Analysed 20 g of the suspension (8 g of fresh faeces). Found: 0.37 me. free fatty acids and 0.86 me. soaps per 100 g of fresh faeces. With 15 g of suspension the figures were 0.35 and 0.88, respectively.

It is seen that the results are practically indentical.

Note. When using 20 g of the faeces suspension the petroleum ether layer separates very difficultly.

SOME RESULTS OF FAECES ANALYSIS

During one month samples of faeces from 3 cows on winter rations were analysed. The results are reported in table 2. As only one excretion of faeces per cow was sampled and not the total dayly excretion per cow, the large fluctuations in the contents may partially be due to irregular excretion of free fatty acids and soaps by the cows.

TABLE 2. Analysis of faeces.

Cow nr.	Date (1963)	me. in 100 g of dry matter	
		free fatty acids	soaps
1	9–4	10.3	11.0
	17–4	2.1	3.0
	23–4	0.8	1.4
	29–4	2.7	6.7
2	9–4	4.4	7.6
	17–4	4.5	4.8
	23–4	2.4	2.9
	29–4	4.2	6.3
3	9–4	1.3	3.2
	17–4	3.6	3.6
	23–4	1.4	2.9
	29–4	2.0	4.6

Since the pH of the faeces is usually about neutral (in our cases 6.2–6.8) and calcium and magnesium are present in excess the soaps concerned are mainly Ca- and Mg-salts (3).

The following experiment also proves that Na- and K-soaps (soluble in water) are not present. The press-juice from a sample of fresh faeces (pH 6.3, dry matter content 13.7%) was centrifuged (2500 r.p.m.). 100 ml of the clear press-juice contained only 0.02 me. of free fatty acids, and 0.09 me. of soaps. The latter figure is in the order of the solubility of Ca- and Mg-soaps in water (In me. per 100 ml: Ca-oleate: 0.13; Ca-palmitate: 0.01; Ca-stearate: 0.01; Mg-oleate: 0.08; Mg-palmitate: 0.03; Mg-stearate: 0.01).

For the total contents in 100 g of fresh faeces (containing 13.7 g of d.m. and 86.3 g of water) 0.50 me. of free fatty acids and 0.50 me. of soaps were found. This is considerably more than the values found for press-juice.

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A NOTE ON THE APPLICATION OF THE FORMALDOXIME METHOD FOR MANGANESE DETERMINATION IN PLANT MATERIAL

O. C. SPOELSTRA

In our laboratory manganese is determined by wet-ashing with nitric-perchloric acid, subsequent Ag^+ catalyzed oxydation with persulphate to permanganate and colorimetric measurement.

This method is very suitable for plant material of average Mn-content but it is somewhat time-consuming and, in the case of low Mn-content in plants and animal tissue, its lack of sensitivity sometimes is a disadvantage.

A more sensitive test on manganese is the formaldoximetest (1, 2, 3, 4). Its applicability was considerably improved when it was found that the interference of iron can successfully be removed by decomposition of the Fe-formaldoxime compound with EDTA-hydroxylamine which leaves the manganese compound intact (1). In this manner Fe up to 25 mg per litre does not interfere in the determination of manganese.

The method has been adapted to the testing of series of samples as described below. It was found that in this procedure, amounts of up to 1000 ppm Fe, 500 ppm Cu and 100 ppm Co in the dry plant material do not interfere in the determination of manganese.

2 grams of the powdered, dry sample is transferred to a 250 ml flat-bottomed flask and 15 ml of a mixture of concentrated sulphuric acid, concentrated nitric acid and water (30 : 70 : 50 v/v) is added. The mixture is heated on an electric hot plate until nitrous fuming ceases. It is removed from the plate and after some cooling a few ml of concentrated nitric acid are added. Heating is continued until nitrous vapors cease to develop and the treatment with nitric acid is repeated until the liquid turns from brown to yellow, this indicates destruction is completed. Four subsequent treatments with a few drops of nitric acid and heating are made to secure complete wet-ashing.

The flask is removed from the heating plate and after standing for a few minutes 1 ml of 20 per cent urea in water is added. Subsequently the mixture is heated, to remove nitrosyl compounds completely, until gass development ceases. Thereafter, 20 ml of water is added, the mixture is cooled and transferred to a 50 ml measuring flask, made up to volume, mixed and filtered.

25 ml of the filtrate is transferred to a 100 ml Erlenmeyer flask allowing sufficient air to enter for oxidation to mangani, and 2 ml of 20 per cent sodium citrate and 2 drops of 0.1 per cent phenolphtalein are added. Concentrated ammonia is added dropwise until the solution turns pink. Under swirling the flask 4 drops of a saturated solution of bromine in water are added and the solution becomes colourless in a few minutes. This is the test solution.

The formaldoxime reagent is prepared by dissolving 4 grams of hydroxylamine-HCl in water, adding 2 ml of 37 per cent formaldehyde solution and making up to 100 ml.

The EDTA-solution is prepared by dissolving 10 grams of hydroxylamine-HCl and 1 gram of ethylene diamine tetraacetic acid (Titriplex III, Merck) in water and making up to 100 ml.

Add 1 ml of the formaldoxime reagent to the colourless test solution. A red-brown colour slowly develops reaching its maximal intensity after ca. 2 hours. Then, add 2 ml of the EDTA-solution, transfer the liquid to a measuring flask after 10 minutes and make up to 50 ml. Mix and measure the extinction at 450 millimicron in a 1 cm cuvette.

The test solution and a blank for the chemicals used are measured against distilled water. 10 micrograms of Mn in 50 ml of the test solution gives an extinction of 0.037.

Beer's law is valid over a wide range of concentrations. The sensitivity of the formaldoxime method is about four times that of the method of oxidation to permanganate.

If the material is sufficiently low in silica (animal tissue), filtration can be dispensed with and the coloured suspension finally obtained can be used more concentrated. In this case the wet-ashing is performed with a smaller amount of the sulphuric acid-nitric acid mixture (10 ml) to avoid an excess of sulphuric acid. The residue of destruction is diluted with some water (3 ml) and made alkaline with citrate and ammonia in the destruction flask. Subsequently the above mentioned procedure is continued. Finally the coloured liquid in the flask is quantitatively rinsed into a 25 ml volumetric flask and made up to volume. In this way smaller quantities of manganese can be determined.

The following figures may serve to illustrate values found in the formaldoxime method as compared with those obtained by means of the Ag^+ catalyzed oxidation to permanganate, in the analysis applied to herbage samples of varying manganese contents. The data are given as mg Mn per kg dry material.

sample nr:	a	b	c	d	e	f	g	h	j	k
formaldoxime method:	29	29	32	42	106	116	130	133	149	160
permanganate method:	24	25	24	40	110	113	129	132	142	158

Evidently, somewhat higher values are obtained in the formaldoxime method, more in particular for samples lower in manganese. Probably, the results obtained in the formal-doxime method on samples low in manganese are more reliable due to its greater sensitivity as compared with the method to permanganate.

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ENKELE ERVARINGEN MET DROOGTE- EN VOCHTINDICATOREN BIJ VERSCHILLENDE VOCHTTOESTANDEN VAN DE GROND

with summary

J. P. VAN DEN BERGH

INLEIDING

Het is bekend dat in de natuur de plantesoorten niet willekeurig door elkaar staan, maar dat bepaalde soortencombinaties steeds weer terug te vinden zijn op plaatsen die enkele milieuëigenschappen gemeen hebben. Zo zijn er bijvoorbeeld grassoorten die alleen massaal voorkomen op droge en andere op natte standplaatsen. Het is nu de vraag waardoor dit verschijnsel veroorzaakt wordt. Indien het alleen een kwestie van verschil in opbrengstreactie op de vochtvoorziening is, lijkt deze vraag langs experimentele weg nog wel te beantwoorden. Het is echter ook mogelijk dat de grootte van de opbrengst weinig heeft uit te staan met het zich handhaven van een soort en bovendien dat andere factoren, die sterk gekoppeld zijn aan de vochtvoorziening van de grond (bijv. bodemkundige factoren of factoren die met het gebruik en de verzorging van het grasland verband houden), hierbij een belangrijke rol spelen. In dit geval is de oorzaak van het veel of weinig voorkomen van een soort niet of althans veel moeilijker aan te wijzen.

WERKWIJZE

In een kasproef werden 5 verschillende vochttoestanden van de grond gerealiseerd door in met gemengde humeuze zandgrond gevulde PVC-buizen van uiteenlopende lengten en met een diameter van 20 cm, grondwaterstanden te handhaven op diepten variërend van 10 tot 100 cm (fig. 1). In deze buizen zijn 2 droogte- en 2 vochtindicato-

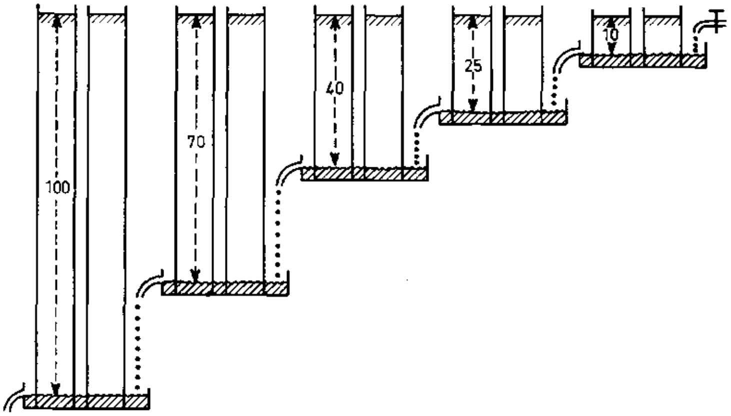

FIG. 1. Opstelling van de waterstandsproef (maten in cm).
Layout of the groundwaterlevel experiment (depth of waterlevel in cm).

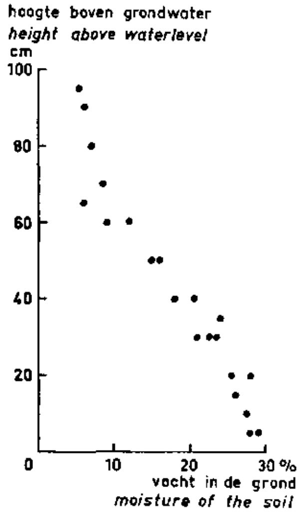

FIG. 2. Vochtpercentage van de grond op verschillende hoogten boven het grondwater.
Moisture content of the soil at different height above the waterlevel.

ren zowel in monocultuur als gemengd uitgeplant. Als droogteïndicatoren zijn genomen gewoon struisgras (*Agrostis tenuis* Sibth) en goudhaver (*Trisetum flavescens* P.B.) en als vochtindicatoren geknikte vossestaart (*Alopecurus geniculatus* L.) en mannagras (*Glyceria fluitans* R.Br). Van de drie eerstgenoemde grassoorten waren klonen beschikbaar; mannagras is aan een slootkant verzameld. Per waterstand waren 6 buizen aanwezig: 4 met mono- en 2 met mengculturen.

De planten hebben 4 maanden in deze buizen gegroeid en zijn elke maand op 5 cm hoogte geknipt. In deze 4 maanden is 2 keer bemest met een volledige voedingsoplossing. Behalve gedurende de eerste paar dagen en bij de toediening van de voedingsoplossing is van boven nooit water gegeven. De wortelstelsels van de monoculturen zijn aan het eind van de proef door spoelen op een wortelplank zoveel mogelijk in hun natuurlijke ligging gehouden. Uit de buizen van de mengculturen zijn op verschillende diepten aan het eind van de proef grondmonsters genomen voor vochtbepalingen. De uitkomsten hiervan zijn in fig. 2 weergegeven.

RESULTATEN

Zowel de dichtheid als de diepte van het wortelstelsel van de vochtindicatoren *Glyceria fluitans* en *Alopecurus geniculatus* is bij al de grondwaterstanden groter dan die van de droogteïndicatoren *Agrostis tenuis* en *Trisetum flavescens* (fig. 3). *Glyceria fluitans* met het best ontwikkelde wortelstelsel doorwortelt bij de waterstand van -10 cm het bodemvolume geheel, zowel boven als onder het freatisch vlak, terwijl zelfs bij de waterstand van -100 cm enkele wortels tot in het grondwater zijn doorgedrongen. Van *Trisetum flavescens* daarentegen is bij de waterstand van -10 cm slechts een enkel worteltje doorgedrongen tot het freatisch vlak, terwijl bij de waterstand van -100 cm de wortels niet dieper gaan dan ± 20 cm.

De totale hoeveelheid droge stof die met 4 sneden in 4 maanden tijd is geoogst, vertoont slechts gedeeltelijk overeenkomst met de mate van wortelontwikkeling (fig. 4). *Trisetum flavescens* levert ook bovengronds het minste op, maar in plaats van *Glyceria fluitans* produceert nu *Alopecurus geniculatus* verreweg het meeste, terwijl *Agrostis tenuis* bij de hoogste en laagste waterstand zelfs meer produceert dan *Glyceria fluitans*.

De sterke daling in produktie van de sterk wortelende vochtindicatoren bij de

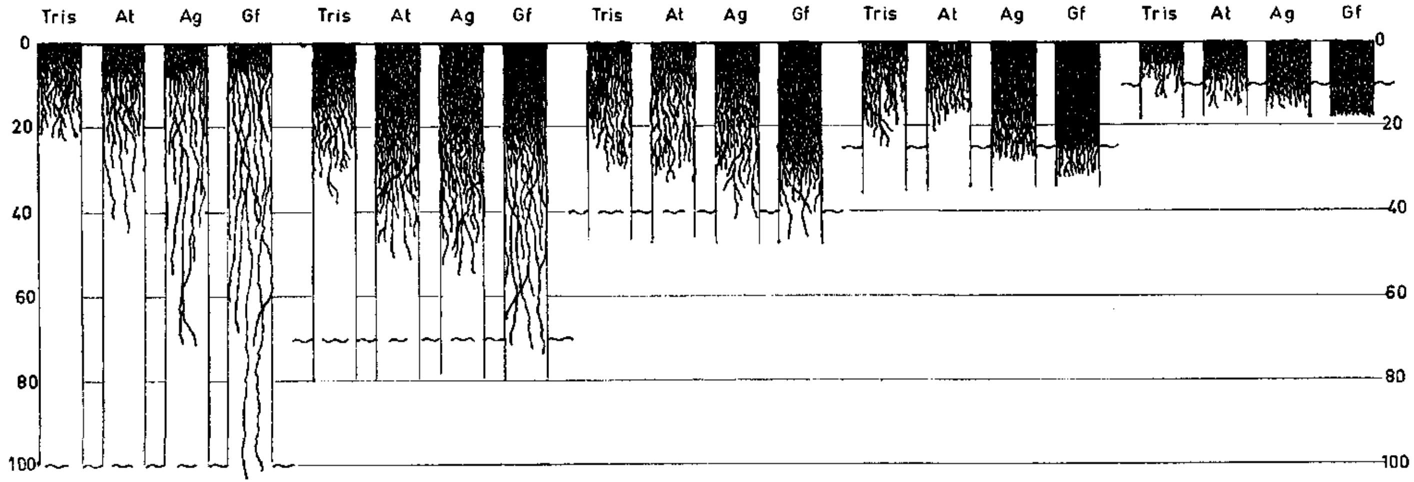

FIG. 3. Wortelontwikkeling van 4 grassoorten bij verschillende diepten van de waterstand.
Root development of 4 grass species at different waterlevels.

Tris = *Trisetum flavescens*
At = *Agrostis tenuis*
Ag = *Alopecurus geniculatus*
Gf = *Glyceria fluitans*

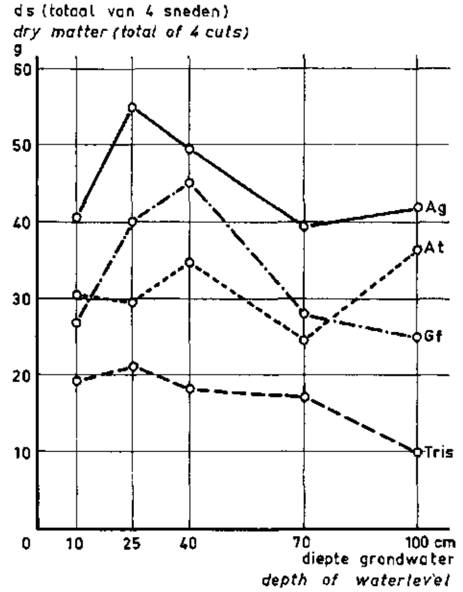

FIG. 4. Opbrengsten van de monoculturen bij verschillende waterstanden.
Yields of the monocultures at different waterlevels.

hoogste waterstand, kan het gevolg zijn van het beperkte bodemvolume aangezien daar de buizen slechts 20 cm lang zijn. Voor het onregelmatige verloop van de lijn voor *Agrostis tenuis* met het maximum bij de laagste waterstand, ontbreekt een redelijke verklaring.

In tabel 1 zijn enkele resultaten van metingen aan het blad weergegeven. De diepte van de waterstand heeft geen invloed op de vorm (lengte, breedte) van de bladeren. Bij *Agrostis tenuis* en *Trisetum flavescens* neemt het aantal ribben en bij *Glyceria fluitans* en *Alopecurus geniculatus* het aantal huidmondjes per oppervlakteëenheid toe bij diepere waterstanden.

Van de mengculturen zijn in iedere snede de drooggewichtspercentages van de afzonderlijke soorten berekend. Om de veranderingen in de gewichtsverhoudingen bij de verschillende waterstanden met elkaar te kunnen vergelijken zijn in de figuren 5 en

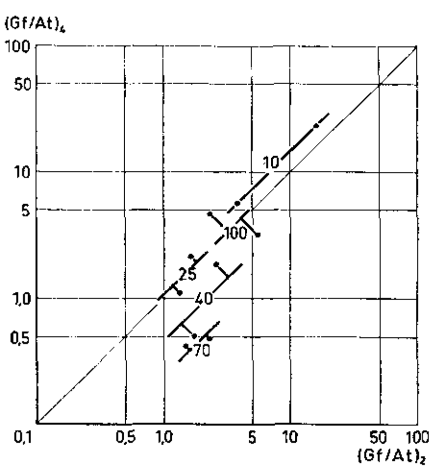

FIG. 5. De verhouding van de gewichtspercentages van *Glyceria fluitans* en *Agrostis tenuis* (in één buis) in de 4de snede $(Gf/At)_4$ uitgezet tegen die in de 2de snede $(Gf/At)_2$. De getallen in de grafiek hebben betrekking op de diepte van de waterstand. (Zie verder de tekst).
The ratio of the dry weightpercentage of Glyceria fluitans *and* Agrostis tenuis (*in the same tube*) *of the 4th cut* $(Gf/At)_4$ *plotted against this ratio of the 2nd cut* $(Gf/At)_2$*. The numbers in the graph refer to the depth of the waterlevel.* (*See text*).

TABEL 1. Enkele grootheden van volwassen bladeren van achtereenvolgens *Glyceria fluitans*, *Alopecurus geniculatus*, *Agrostis tenuis* en *Trisetum flavescens* in monocultuur bij de verschillende waterstanden.
Some measures of mature leafs of Glyceria fluitans, Alopecurus geniculatus, Agrostis tenuis and Trisetum flavescens in monoculture respectively at different waterlevels.

	Diepte waterstand *Depth of waterlevel* (cm)	Blad/*Leaf*			
		Lengte *Length* (cm)	Breedte *Width* (cm)	Aantal ribben *Number of ribs*	Aantal huidmondjes /0,3 mm^2 *Number of stomata /0.3 mm^2*
Gf	10	15,7	3,0	21	31
	25	15,5	3,3	19	32
	40	15,4	3,0	21	36
	70	15,9	3,4	21	37
	100	15,0	3,0	21	40
Ag	10	16,3	3,6	12	9
	25	17,5	3,5	13	9
	40	16,4	3,8	13	10
	70	16,6	2,5	10	12
	100	16,7	3,3	13	13
At	10	13,0	3,1	14	14
	25	13,0	3,0	17	12
	40	13,9	4,2	18	14
	70	13,9	3,8	21	11
	100	13,0	3,9	21	16
Tris	10	10,3	2,5	14	7
	25	10,3	3,0	17	9
	40	10,7	3,5	21	10
	70	10,9	2,9	19	6
	100	10,2	3,0	21	6

6 op logaritmische schalen de verhoudingen tussen de gewichtspercentages van *Glyceria fluitans* of *Alopecurus geniculatus* en *Agrostis tenuis* in de 4de snede uitgezet tegen die in de 2de snede. Door de punten van de duplo's zijn rechten evenwijdig aan de 45°-lijn getrokken, aangezien op deze lijnen de punten liggen die aangeven dat de wijziging in de gewichtsverhoudingen relatief dezelfde is. Ondanks de grote spreiding komt duidelijk tot uiting dat naarmate de diepte van de waterstand toeneemt van 10 tot 70 cm de gewichtsverhoudingen zich ten gunste van *Agrostis tenuis* wijzigen, maar dat bij de waterstand –100 cm deze wijziging t.o.v. *Glyceria fluitans* relatief weer even groot is als bij de waterstand –25 cm (fig. 5) en t.o.v. *Alopecurus geniculatus* relatief bijna even groot als bij de waterstand –40 cm (fig. 6).

BESPREKING

Met deze proefopzet is het niet gelukt het in het veld waargenomen verschijnsel der droogte- en vochtindicatie na te bootsen. In monocultuur blijken de vochtindicatoren bij al de waterstanden zowel boven- als ondergronds produktiever te zijn dan de droogteïndicatoren. In de mengculturen veranderen de gewichtsverhoudingen bij toenemende diepte van de waterstand van 10 tot 70 weliswaar steeds meer ten gunste van de droogteïndicator *Agrostis tenuis*, maar bij de diepste waterstand –100 cm is deze relatieve toename van *Agrostis tenuis* weer kleiner dan bij –70 cm.

Het is nu de vraag of deze vochtindicatoren onder omstandigheden waarbij de wa-

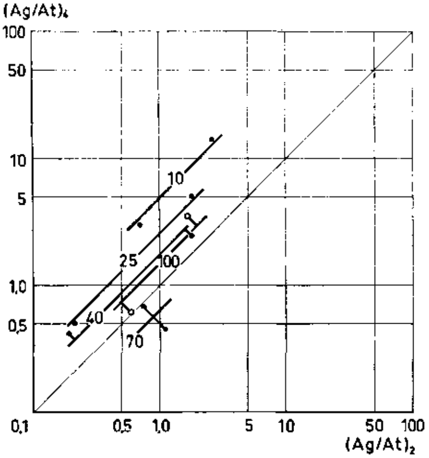

FIG. 6. Zie onderschrift van fig. 5. Lees i.p.v. *Glyceria fluitans Alopecurus geniculatus.*
See subscript of fig. 5. Read instead of Glyceria fluitans Alopecurus geniculatus.

tertoevoer voor kortere of langere tijd geheel wegvalt, het ook tegen *Agrostis tenuis* kunnen opnemen. Het is denkbaar dat de vochtindicatoren blijven doorgroeien en transpireren, verwelken en tenslotte afsterven, terwijl de droogteïndicatoren onder dergelijke omstandigheden het vermogen bezitten in een soort rusttoestand over te gaan.

Om dit na te gaan zijn monoculturen van *Alopecurus geniculatus* en *Agrostis tenuis* in mitscherlichpotten goed aan de groei gebracht, enkele malen geknipt en daarna bij gelijke hoogte van het gewas van water verstoken. Nu bleken deze grassoorten bij eenzelfde percentage vocht in de grond te verwelken. Gedurende de daarop volgende maand zijn deze monoculturen met een minimum hoeveelheid aan water in leven gehouden. Na toediening van voldoende water hervatten beide soorten hun normale groei even snel. Vervolgens is gedurende 1½ maand geheel geen water gegeven. Deze behandeling had tot gevolg dat het blad van *Agrostis tenuis* geheel bruin en verdord was, terwijl dat van *Alopecurus geniculatus* nog enigszins groen van kleur was. Watertoediening deed de groei van *Alopecurus geniculatus* weer snel herstellen, terwijl *Agrostis tenuis* na lange tijd slechts 4 nieuwe spruitjes tot ontwikkeling kon brengen.

Gezien het bovenstaande kan het verschijnsel van droogte- en vochtindicatie niet verklaard worden met verschillen in groeireactie op de vochtvoorziening tussen droogte- en vochtindicatoren. Wellicht zal naar heel andere verschilkenmerken moeten worden gezocht, bijvoorbeeld de oecologie van de kieming. Er zijn vermoedens dat voor de ontkieming van het zaad van *Alopecurus geniculatus* een vochtiger milieu vereist wordt dan voor de ontkieming van het zaad van *Agrostis tenuis.*

Zoals reeds in de inleiding is opgemerkt kan dit verschijnsel natuurlijk ook veroorzaakt worden door een complex van factoren, die in het veld sterk aan de vochtvoorziening zijn gekoppeld.

Some results with grass species indicating dry or wet circumstances growing at different moisture conditions of the soil

In a greenhouse common bent (*Agrostis tenuis* Sibth.) and golden oat-grass (*Trisetum flavescens* (L.)P.B.) (species indicating dry circumstances) and floating fox-tail (*Alopecurus geniculatus* L.) and floating sweet-grass (*Glyceria fluitans* (L.)R.Br.) (species indicating wet circumstances) are grown in plastic tubes (diameter 20 cm) of different lengths in which groundwaterlevels are realised varying from 10 to 100 cm.

At all waterlevels shoot growth as well as the depth and the density of the rootsystem of the monocultures of the species indicating wet circumstances are superior to that of the species indicating dry circumstances. In the mixtures the change after two months growth of the ratio between the dry matter production of one of the species indicating wet circumstances and *Agrostis tenuis* increases with increasing depth of the waterlevel from 10 cm to 70 cm. However at a waterlevel of –100 cm this relative increase of *Agrostis tenuis* is smaller as at the waterlevel of –70 cm (figures 5 and 6).

A second experiment in Mitscherlich pots showed that even without any watersupply during 1½ month *Alopecurus geniculatus* started to grow soon after watering, while *Agrostis tenuis* was dead.

Apperently it is not possible to explain the phenomenon of drought and moisture indication with differences in growth response on the watersupply between the species indicating wet or dry circumstances.

Probably differences between these species of a quite other nature are responsible for this phenomenon, for example the ecology of germination. It is supposed that *Agrostis tenuis* is able to germinate in a dryer environment than *Alopercurus geniculatus*. On the other hand in the field watersupply is correlated with many other factors, which altogether may determine the distribution of these species.

Ontvangen: 1 mei 1963.

Mededeling 218 van het I.B.S.

HET BOTANISCHE ONDERZOEK VAN SLOOTVEGETATIES

with summary

B. J. HOOGERS

INLEIDING

Voor het behoud van een goede afwatering en van een behoorlijke visstand is het van belang dat de plantengroei in sloten en kanalen niet te dicht wordt. Een te dichte begroeiing vermindert de stroomsnelheid van het water en verandert het biologische evenwicht zodanig, dat er 's nachts voor de vissen een tekort aan zuurstof kan optreden.

Tot de planten die belemmeringen in het water kunnen veroorzaken behoren behalve vele hogere planten ook de wieren.

Het goed functioneren van sloten en andere watergangen vereist dus een regelmatige verwijdering van het zich daarin uitbreidende plantenmateriaal en daar het mechanisch verwijderen van planten thans te kostbaar is geworden, gaat men andere methoden zoeken. De meest aangewezen weg is de bestrijding met chemische middelen. Bij de bestrijding van planten door bespuiten is het van belang te weten hoe de gehele vegetatie daarop reageert. Daar ook de wieren massaal kunnen optreden, wordt ook aan deze groep van lagere planten veel aandacht besteed.

Van grote betekenis is het voorts enigszins ingelicht te zijn over de groeicyclus, sociologie en oecologie van die waterplanten, die in sloten en andere waterlopen zodanige begroeiingen kunnen vormen dat de afwatering er ernstig door belemmerd wordt.

De beschrijving van de vegetatie vraagt een speciale methodiek die in het onderstaande nader zal worden besproken.

ORIËNTEREND ONDERZOEK

Voor de bestudering van de oecologie en sociologie en van de seizoens- en jaarlijkse schommelingen in de plantengroei was het noodzakelijk een geschikte methodiek te vinden.

Bij het bestrijden van onkruid wordt graag een eenvoudige quantitatieve maat gehanteerd waarmede de plantensamenstelling vóór en na de behandeling vergeleken kan worden. Bij het oecologische en sociologische onderzoek gaat het in de eerste plaats om het al of niet voorkomen van de soort, ofschoon de hoeveelheid niet uit het oog verloren mag worden.

Het maken van opnamen van slootbegroeiingen is niet gemakkelijk. Er zijn planten die met hun wortels in de grond verankerd zijn en omhoog groeien, terwijl anderen op het wateroppervlak drijven of op zekere diepte zweven.

Door de verschillende groeiwijze der planten is het moeilijk om hun volumen onderling te vergelijken. Een op het water drijvende plant als klein kroos (*Lemna minor* L.) kan niet vergeleken worden met een in de grond wortelende plant als riet (*Phragmites communis* Trin.) of met vele wieren die zwevend worden aangetroffen. Deze moeilijkheid wordt omzeild door de vegetatie in lagen te verdelen. Nu is het mogelijk om het volumen der planten in een bepaalde laag te vergelijken met dat in een gelijksoortige laag elders.

De vegetatie wordt door ons in de volgende drie lagen verdeeld:

1. *De waterspiegel*, een zeer dunne laag. Het onder normale omstandigheden droog blijven van bladeren of stengels die op het water liggen mag daarbij als criterium gesteld worden. Voorbeelden van planten, die tot deze laag gerekend worden, zijn o.a kroosvaren (*Azolla* Lamk.), gewoon sterrekroos (*Callitriche platycarpa* Kütz.), klein kroos (*Lemna minor* L.), bultkroos (*Lemna gibba* L.), veelwortelig kroos (*Spirodela polyrhiza* (L.) Schleiden), wortelloos kroos (*Wolffia arrhiza* (L.) Wimm.), gele plomp (*Nuphar luteum* (L.) Sm.), waterlelie (*Nymphaea alba* L.), kikkerbeet (*Hydrocharis morsus-ranae* L.), watergentiaan (*Nymphoides peltata* (Gmel.) O. Kuntze), drijvend fonteinkruid (*Potamogeton natans* L.) en het levermos watervorkje (*Riccia fluitans* L.).

Aan de oppervlakte komende plantjes van puntkroos (*Lemna trisulca* L.) worden tot deze laag gerekend, hoewel de schijfjes van deze soort grotendeels onder water blijven.

Opgekrulde bladeren alsmede de bloemen van de gele plomp, waterlelie en kikkerbeet die boven water uitsteken, worden eveneens tot de waterspiegel gerekend. Hetzelfde geldt voor dat gedeelte van de algen die blaasjes op het water vormen.

2. *De bovenwaterlaag* omvat alle planten die zich boven de waterspiegel bevinden. Ten einde een concrete maat te hebben wordt deze laag geacht zich uit te strekken tot 1 meter boven de waterspiegel. Hiervan maken o.a. de volgende planten in volwassen toestand deel uit: riet (*Phragmites communis* Trin.), grote lisdodde (*Typha latifolia* L.), grote egelskop (*Sparganium erectum* L.), zwanebloem (*Butomus umbellatus* L.), holpijp (*Equisetum fluviatile* L.), grote waterweegbree (*Alisma plantago-aquatica* L.), watertorkruid (*Oenanthe aquatica* (L.) Poir.), pijptorkruid (*Oenanthe fistolosa* L.), kleine watereppe (*Sium erectum* Huds.), grote watereppe (*Sium latifolium* L.), liesgras (*Glyceria maxima* (Hartm.) Holmb.) en mannagras (*Glyceria fluitans* (L.) R. Br.).

3. *De onderwaterlaag* omvat de planten die zich onder de waterspiegel bevinden. Voor deze laag worden o.a. genoteerd: waterpest (*Elodea canadensis* Michx.), gedoornd hoornblad (*Ceratophyllum demersum* L.), waterviolier (*Hottonia palustris* L.), puntkroos (*Lemna trisulca* L.), kransvederkruid (*Myriophyllum verticillatum* L.), gewone waterranonkel (*Ranunculus aquatilis* L.), gewoon sterrekroos (*Callitriche platycarpa* Kütz.), kamfonteinkruid (*Potamogeton pectinatus* L.), klein fonteinkruid (*Potamogeton pusillus* L.), gekruld fonteinkruid (*Potamogeton crispus* L.), glanzend fonteinkruid (*Potamogeton lucens* L.) en voorts alle wieren.

Een volwassen plant als riet die boven het water uitsteekt wordt voor alle drie lagen genoteerd. Een zeer jong exemplaar van de holpijp dat nog niet aan de oppervlakte reikt wordt alleen genoteerd in de laag waarin deze groeit, in dit geval laag 3. Een plant als het pijlkruid (*Sagittaria sagittifolia* L.) kan in verschillende stadia voorkomen. Zo zijn er exemplaren met uitsluitend lintvormige ondergedoken, met op het water drijvende en boven de waterspiegel uitstekende pijlvormige bladeren. De betreffende planten worden dan genoteerd in de lagen 3, 1, en 2. Nog heel jonge planten van krabbescheer (*Stratiotes aloides* L.) bevinden zich nog op de bodem, terwijl de volwassen exemplaren naar de oppervlakte komen en hun bladeren ver boven de waterspiegel doen uitsteken. In het eerste geval groeit de soort in de onderwaterlaag, terwijl ze in het andere geval genoteerd wordt in alle drie lagen. Het mannagras kan zeer lange lintvormige bladeren vormen die op het water drijven. Daar genoemde soort in de grond wortelt, wordt in dit geval de plant genoemd in de lagen 1 en 3. Een bloeiend exemplaar van waterviolier wordt genoteerd in alle drie lagen daar de bloeistelen ver boven de waterspiegel uitsteken.

Het bleek niet eenvoudig een exacte methode te ontwikkelen omdat men bij een slootvegetatie nu eenmaal niet op een eenvoudige wijze boormonsters kan steken, zoals dit bij een landvegetatie mogelijk is. De grote moeilijkheid is om al het door elkaar groeiende plantenmateriaal er ongeschonden uit te halen zonder het geheel te verstoren.

Voor dit soort onderzoek van slootvegetaties was men derhalve op schattingen aangewezen. Er werden verschillende methoden geprobeerd. Zij bleken echter niet bruikbaar te zijn en werden derhalve weer verlaten. Hieronder worden enkele van die methoden beschreven.

Aanvankelijk werd per laag van alle plantensoorten de bedekkingsgraad geschat. Hieronder wordt verstaan het gedeelte van het horizontale vlak dat door de loodrechte projectie van die soorten wordt ingenomen. Voor planten die op de waterspiegel drijven kan de bedekkingsgraad zonder bezwaar worden toegepast omdat die laag uiterst dun is. Voor planten echter die onder water groeien of boven de waterspiegel uitkomen gaat dit moeilijk omdat er rekening gehouden moet worden met de dikte, resp. hoogte van de plantenlaag. Voor de bedekkingsgraad maakt het geen verschil of de vegetatie in een zeer dunne of dikke laag voorkomt.

Om ook de dikte, resp. de hoogte van de vegetatie in de boven- of onderwaterlaag in het onderzoek te betrekken, werd de volgende methode gebruikt. Voor de waterplanten wordt in deze beide lagen gekeken naar het volume dat ze innemen. Speciaal voor planten die onder water groeien is dit een betere maat dan het gewicht. Een wier zal qua gewicht geen grote rol spelen, daarentegen kan het wel een belangrijk volume innemen. Van iedere soort werd in beide genoemde lagen het volume geschat en in een schaalverdeling van 1-10 aangegeven. Een plant die binnen een bepaald areaal de gehele beschikbare ruimte innam kreeg het cijfer 10. Voor planten die op de waterspiegel drijven kan de bedekkingsgraad in een schaalverdeling van 1-10 worden aangegeven. Het cijfer was lager naarmate de vegetatie ijler werd. Het geschatte cijfer werd het doorgroeiingsgetal genoemd. Om te kunnen beoordelen of een plant zijn optimale omvang heeft, is veel praktische ervaring nodig. Wanneer klein kroos de waterspiegel geheel bedekte, dan werd het cijfer 10 alleen dan gegeven als de blaadjes over elkaar heenschoven.

Aan deze getallen mag echter geen te grote waarde worden toegekend. Het schatten in de ruimte waarbij cijfers toegekend worden is zeer moeilijk en kan slechts door dezelfde persoon geschieden. Bovendien worden dit soort schattingen door allerlei factoren beïnvloed, zodat het beter bleek van deze methode af te stappen.

DE THANS GEBRUIKTE METHODEN

1. *Opnamemethodiek ten behoeve van het sociologische en oecologische onderzoek*

Bij dit onderzoek wordt er naar gestreefd om bepaalde soortencombinaties te vinden en iets te weten te komen over de oecologie. Voor dit doel is een groot aantal opnamen nodig. Op diverse plaatsen in het land worden momentopnamen gemaakt van slootvegetaties op een tijdstip dat de begroeiing goed ontwikkeld is.

Voorts is het van belang dat de schommeling in de vegetatie gedurende het jaar bestudeerd wordt. Voor dit onderzoek wordt van enkele sloten, grotendeels in de buurt van Wageningen gelegen, maandelijks een opname gemaakt. De methodiek hiervoor is als volgt:

Van een sloot waarvan de vegetatie wordt onderzocht, wordt een strook van 40 m lengte uitgezet. De vegetatie in die strook moet regelmatig over de sloot verspreid en zo homogeen mogelijk zijn. Met behulp van een op het water drijvend rechthoekig plasticraam van één m lang en ½ m breed wordt om de 2 m een opname gemaakt, zodat van de vegetatie in totaal 20 opnamen genomen worden. Door steeds gebruik te maken van dezelfde oppervlaktemaat zijn al deze opnamen met elkaar vergelijkbaar.

Om de randwerking van de oeverbegroeiing zoveel mogelijk uit te schakelen wordt het raam ongeveer 50 cm van de kant gelegd, met de lange zijden loodrecht op de oever. De opnamen worden steeds langs dezelfde oever genomen. Daar het niet om de sloot maar om de vegetatie gaat doet het er niet toe of de sloot veel breder is dan 2m, als de begroeiing maar regelmatig verspreid is.

Om georiënteerd te zijn over de verspreiding van een soort wordt per opname en per laag nagegaan of de soort al dan niet aanwezig is. Het percentage der 20 opnamen waarin de soort wordt aangetroffen wordt het frequentiepercentage (F %) genoemd. Wordt de soort in alle opnamen aangetroffen, dan is het F % 100.

Van iedere soort wordt per laag nagegaan of deze van betekenis is. Een soort wordt belangrijk geacht als deze 10 % of meer van de beschikbare ruimte inneemt.

Voorts wordt gelet op het aantal keren dat een soort procentsgewijs in een bepaalde laag het grootste deel van de ruimte inneemt. Dit wordt het dominantiepercentage (D %) genoemd. Komen er nog meer soorten voor die van belang zijn dan kan er nog een 2e en een 3e plaats toegekend worden, al naar gelang er meer of minder van de ruimte ingenomen wordt.

De mate van belangrijkheid wordt aangegeven door iedere eerste, tweede of derde plaats te honoreren met resp. 5, 3 en 1 punt(en). Van alle 20 opnamen worden de verkregen punten per soort gesommeerd. Deze som wordt de belangrijkheidsgraad (B) genoemd. Maximaal kan deze 100 bedragen. Van de niet belangrijke soorten wordt slechts de aanwezigheid genoteerd. De belangrijkheidsgraad zegt dus niets over de totale massa of het volume, maar alleen over de verhouding in volumen.

Wil men enigszins georiënteerd zijn over de werkelijk ingenomen ruimte der soorten, dan wordt de mate van dichtheid der begroeiing als volgt in een schaalverdeling aangegeven.

+	Aanwezig: t.e.m. 2 % van de beschikbare ruimte;	
1	zeer ijle begroeiing:	van 3 t.e.m. 10 %
2	ijle begroeiing:	van 11 t.e.m. 25 %
3	matige begroeiing:	van 26 t.e.m. 50 %
4	dichte begroeiing:	van 51 t.e.m. 75 %
5	zeer dichte begroeiing:	van 76 t.e.m. 100 %

Voorts worden gegevens genoteerd over de ontwikkelingstoestand der planten, de grondsoort, diepte, breedte en richting van de sloot, de helderheid van het water, of het water al dan niet stroomt, of er bomen langs de sloot groeien enz. Tevens wordt de gemiddelde hoogte van de planten die boven het water uitsteken genoteerd.

2. *Opnamemethodiek ten behoeve van de onkruidbestrijding*

Reeds eerder werd opgemerkt dat bij de bestrijding van onkruid graag gebruik gemaakt wordt van een eenvoudige quantitatieve maat waarmede de plantensamenstelling vóór en na een behandeling vergeleken kan worden. Daar het hier vaak gaat om grote oppervlakten kan hier geen gebruik gemaakt worden van een draadraam. Dit zou veel te veel tijd gaan kosten. De gehele proefsloot wordt in zijn geheel bekeken. Voor dit soort van onderzoek is men uitsluitend op schattingen aangewezen. Aan de verkregen cijfers mag derhalve geen te grote waarde worden toegekend. Ze geven min of meer een globale indruk van de vegetatie weer. De begroeiing wordt weer beschouwd in de bovenwaterlaag die zich tot 1 m boven de waterspiegel uitstrekt, de waterspiegel en de onderwaterlaag. Door langs de gehele sloot te lopen wordt per laag geschat welk percentage van de beschikbare ruimte door de planten ingenomen wordt, welk percentage dan verdeeld wordt over de aanwezige soorten.

The botanical research of ditch vegetations

As the chemical control of aquatic plants in ditches has assumed great proportions these last few years, it has become necessary to investigate the reaction of the vegetation on the diversity of various substances. In order to make effective control possible of inconvenient aquatic plants it is important to be well-informed about the ecology, sociology and growth cycle of these plants.

The most suitable survey method for a certain purpose has been discussed in this article as well.

Ontvangen: 14 mei 1963.

Mededeling 219 van het I.B.S.

AN INTERESTING SHOOT FORMATION IN GRASSES AND ITS MORPHOLOGICAL STATUS

A. A. KRUIJNE

INTRODUCTION

The morphological investigation into the shoot formation of grasses has thrown light on interesting details in the last few years. This has already been mentioned in earlier yearbooks (3, 4), and the additional purpose of these articles has been to contribute to a deeper insight in this field.

Since short, however, in foreign literature (1,2) attention is payed to a shoot formation that also frequently occurs in the Netherlands. This shoot formation has been observed since long, but in as far as we know it has as yet not been described.

It seems justified therefore to treat the general morphology of grass tillers briefly, in order to establish the exact status of this shoot formation in describing it.

THE VEGETATIVE SHOOT

Leaves are continuously formed on the main or primary tiller, all originating from the growing point. At the same time as many nodes are formed which remain closely together, however, because there is no internode elongation. All leaf-sheaths of the (vegetative) leafy shoot consequently originate almost at equal height, forming a vertical cylinder inside of which the young leaves develop.

After a few leaves have been formed the axillary bud of the first leaf begins to develop and a young secondary tiller emerges; this process is repeated in the leaves formed later (tillering). These secondary shoots may develop intravaginally or extravaginally.

In the first case the tiller develops within the leaf-sheath only to emerge at the ligule; in this way bunches (tufts) of tillers are formed which may lead to a more or less dense tussock forming.

In the second case the developing bud bursts through the base of the leaf-sheath and continues growth almost horizontally; in this case overground stolons or underground rhizomes are formed. These always show internode elongation immediately after development, in which they differ from leafy tillers with intravaginal development. Thus they are excellently equipped for the spreading of the species, as they take root in the nodes and form tertiary leafy tillers.

In this way a considerable area may rapidly be covered, especially on virgin soils (*Agrostis stolonifera* var. *prorepens* KOCH!). In grassland the space between the tussocks is filled by the over- or underground tillers, thus forming the close sward of old permanent grasslands, especially of pastures.

Species with only intravaginal shoot formation are: *Lolium perenne* L., *Festuca ovina* L., *Dactylis glomerata* L., *Poa annua* L., *Nardus stricta* L.; accordingly, these species have no stolons or rhizomes. Species with only extravaginal tiller formation are not known to us. Intravaginal formation of leafy shoots of higher order could always be established in all species examined with elaborate stolon or rhizome formation.

THE REPRODUCTIVE SHOOT

This shoot formation of which development is much more conspicuous generally than that of vegetative tillers is briefly described.

The reproductive phase sets in, naturally first in the primary shoot, when possibly required conditions of temperature and day length have been met. From that moment onwards the formation of young leaves at the growing point stops and the development of an ear primordium begins. The further development of inflorescences is associated with internode elongation, which stops again at the end of actual flowering.

VEGETATIVE SHOOTS WITH INTERNODE ELONGATION

In stolons and rhizomes internode elongation is an inherent characteristic also of vegetative shoots. Below two different types of shoot are discussed which only occur under influence of special in- or external conditions.

a. Vegetative tillers with shoot elevation

In species with intravaginal shoot development one or a few internodes just above the node concerned may start to elongate during development of a lateral shoot. In this way the older shoot is elevated out of the surrounding leaf sheaths and is placed on a bare, tough „shoot raiser" (3) which is one to some cm long. The same phenomenon may be repeated if a second lateral shoot is developing on the other side. In *Lolium perenne* this can often be clearly observed due to the moving of the coloured shoot bases.

After a few internodes have elongated the primary tiller, which has kept its vegetative character completely, will usually grow somewhat top-heavy and will take up a more horizontal position. After this the whole construction (main tiller, shoot raiser and side shoots) will greatly correspond in its appearance with overground stolons (5, 6). In addition to the differences already mentioned earlier (3) it may also be observed that a stolon always is a lateral tiller (of lower order), while shoot elevation can occur very well and even most clearly in the primary shoot.

After a primary tiller with shoot elevation has reached the flowering phase the culm will not die completely back to soil level after seed setting, but only partly. All shoots that have been formed at the nodes remain connected with the roots of the parent plant by means of green culm internodes. Regrowth in favourable autumns stimulates tiller formation in the laterals already present. The result is that bunches (tufts) of tillers are formed which extend above the grass sward (see picture in 6). Such a construction: old culm internodes, which are very firm and a bunch (tuft) of tillers, does not show any lengthwise growth anymore, as it terminates abruptly in a node. Cattle may easily sever these tufts by tearing or treading (6), and the withering material may give the pasture a most untidy appearance.

„Shoot raisers" are often to be observed in *Lolium perenne, Poa annua* and less often in *Dactylis glomerata* and *Phleum pratense* L.

b. Summer culms

Due to the much greater number of internodes involved in elongation this type of shoot completely looses its character of vegetative leafy tiller, contrary to the vegetative shoots with shoot elevation which retain their character of vegetative leafy tiller. Owing to its length and large internodes it much resembles a reproductive shoot. However, the swelling of the developing inflorescence is absent in the upper leaf-sheath and in microscopic analysis the growing cone appears to have remained vegetative. Other differences between the normal flowering culm and this culm are the greater number of leaves in the latter, since the formation of leaves continues, and the internodes shortening towards the upper part of the culm. These shoots will be called summer culms.

In all probability, and literature mentions this for *Arrhenatherum elatius* J. et C. PRESL (1), these summer culms are developed if young shoots, emerging after winter and accordingly not receiving the cold period considered necessary for flowering, are subjected to a long day illumination.

Summer culms die completely before winter, contrary to non-elongated vegetative material that hibernates almost certainly partly, in any case in perennial species. *Phragmites communis* TRIN., being a geophyte, retreats completely underground; all tillers of this species that remain vegetative in autumn are summer culms.

These summer culms which have caused so much interest recently have been found in *Elytrigia repens* NEVSKI, which may develop to 1 m high in hedges, in *Arrhenatherum elatius*, *Phalaris arundinacea* L., *Agrostis tenuis* SIBTH. and *Phragmites communis*.

In the following table some tiller numbers per dm^2 have been mentioned. These have been derived from informative countings in sward parts of various origin or (and) dates.

TABLE 1. Average number of shoots per dm^2 of some grass species.

Species	Reproductive shoots	Summer culms	Leafy shoots	Date and origin	
1. *Arrhenatherum elatius*	1	2	1	July 1962	Northern slope of the Grebbe dike
2. *Elytrigia repens*	1	7	1	July 1962	
3. *Agrostis tenuis*	22	37	10	July 1962	Border hay field I.B.S. (not cut)
4. *Elytrigia repens*	4	10	17	July 1962	
5. *Agrostis tenuis*	0	42	23	Nov. 1962	
6. *Elytrigia repens*	0	21	14	Nov. 1962	
7. *Agrostis tenuis*	2	18	7	July 1962	Hay field I.B.S. (cut in August)
8. *Agrostis tenuis*	0	9	19	Nov. 1962	
9. *Agrostis tenuis*	12	37	3	July 1962	Pasture for horses only (I.B.S.)

The number of summer culms counted in summer and autumn appears to be considerable in the species mentioned and often amounts to more than the number of leafy tillers.

If the species 3 and 5, and 4 and 6 in the table are compared the reproductive shoots present in July appear to have died by November; as may be assumed many – if not all – of the summer culms present in July, have also disappeared. Those observed in November, accordingly, must have developed after July from non-elongated material. However, as a result of this, the number of remaining vegetative tillers does not always decrease as can be seen in comparing the numbers 3 and 5.

Comparison of 7 and 8 shows that in the second counting the number of summer culms is smaller. This is due to day-length decreasing considerably after mowing, while most older leafy tillers from which the summer culm originates have been cut. Moreover, the summer culms counted in November were much shorter.

SUMMARY

A vegetative shoot formation with internode elongation has been described, the summer culm. Its morphological status is compared to other vegetative tillers, which also show internode elongation, viz. stolons, rhizomes and tillers with shoot elevation (3).

In all probability this culm-like shoot, called summer culm which sometimes may grow to 1 m high, originates from a young shoot that has developed after winter and started internode elongation under influence of long day illumination. They remain vegetative, however, and moreover differ from flowering culms by the greater number of leaves and the shortening of the internodes in the upper part of the culm.

The phenomenon has been observed in *Elytrigia repens* NEVSKI, *Agrostis tenuis* SIBTH., *Arrhenatherum elatius* J. et C. PRESL, *Phalaris arundinacea* L. and *Phragmites communis* TRIN.

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