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THE INFLUENCE OF LIGHT UPON BLUEING OF TULIP BULBS, A DISEASE OF A PHYSIOLOGICAL NATURE[1]

Met een samenvatting: Invloed van het licht op het blauwgroeien van tulpebollen

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INTRODUCTION

Although the actual nature of blueing of tulip bulbs is still unknown, a former publication suggests that it may be a physiological disorder (KAMERBEEK, 1958). The experiments described in this paper support this opinion. The true nature of the disease, however, will only have become evident after it has been shown what causes the brown necrotic spots in the parenchymatous tissue of the bulb-scale under the skin. The symptoms of the disease have been described before. It may suffice to state here, that the first symptoms to be observed are small, colourless, glassy spots in the parenchyma. These symptoms point to an infiltration of sap into intercellular spaces. Only at a later stage does the brown discoloration set in.

The extent of the disease seems to be correlated with the amount of growth made by the developing new bulbs. Even though bulbs of the same size are planted, the development of the new bulbs will not be alike and it is on the larger and heavier of these new bulbs that the disease is mainly to be found. There is a strait correlation between the disease and the weight of the bulb. The first symptoms are observed during the stage of most vigorous growth; any factors stunting growth will also check the disease (KAMERBEEK, 1958).

In the experiments the distribution of affected bulbs suggested the operation of an unknown factor, wich so far had escaped observation. There were indications that the sunlight might be responsible. For this reason field-experiments were laid out to determine to what extent shading of plants might influence the occurrence of the disorder. The distribution of the disease in the field was also investigated.

EXPERIMENTAL PROCEDURE

In normal cultivation the bulbs are planted in rows in beds 13 metres long by 1 metre wide. In the experiments tulip bulbs of the cultivars 'Korneforos' and 'Cum Laude' were used. The bulbs planted had a circumference of 9 to 10 cms. The period of planting covered the latter half of October and lifting was done in the first half of July. As the bulbs used for each experiment numbered only 400, the beds were not filled to their full length of 13 m. In the space not used for the experiments other bulbs were planted. Between the beds were paths about 45 cms wide. The groups of 10 × 40 bulbs were accordingly

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bounded by plants on two sides and were open on the two remaining sides, next to the paths. The tulips along the paths will thus have received a larger amount of light than those towards the middle of the bed, so that there should have been a light-gradient from the paths towards the middle.

An artificial reduction of light was also brought about by means of shading with screens. The screens were made of plastic wire-gauze or jute cloth. Light measurements with the spherical radiation-meter described by WASSINK & VAN DER SCHEER (1951) showed that the plastic gauze absorbed about 50% and the jute cloth about 75% of the light. Other conditions of the experiments were kept as far as possible the same for the various beds. The screens were fixed about 75 cms above the ground.

Each experiment was carefully charted, i.e. the position of each bulb in the plot was marked together with its weight and the extent of the disorder it showed on lifting. In order to ascertain this the skin had necessarily to be taken off so that possible necrotic spots on the underlying scales could be observed. A record of the various degrees of the disorder was also made by means of a series of colour slides, which provided a reference standard for each year's work.

EXPERIMENTS AND RESULTS

a. Experimental beds of normal type

Figures 1–3 give data on the distribution of the disease in the experimental beds. In figure 1, showing the situation in a normal planting, the figures for beds 1 and 2 show distinctly that a greater number of diseased bulbs occurs in the row along the path than in the rows in the middle of the beds. Towards the middle of the beds the percentage of disease decreases. The average bulb-weight diminishes also. The above-mentioned correlation between bulb-weight and disease-percentage is thus observed here. A similar edge-effect is apparant in figure 3, too, in the normal unscreened beds 1, 2, 15 and 16. The edge-effect may reach far into the bed, as is evident from figure 2, giving the results of an experiment in which the bulbs had been planted in one large plot not intersected by paths.

b. Shaded beds

In bed 3 of figure 1 and in the plot in figure 2 the effect is shown of shading the plants by means of a plastic wire-gauze screen. In the experiment of figure 3 a screen of jute tissue was used. The edges of the screen coincided with the edges on the bed. Except in the experiment of figure 2 the gauze was overhanging on the sunny side.

The results with screens go to prove that the edge-effect is if anything clearer than without screens. Moreover it can be observed that in general the disease-percentage is much lower under the screens. Similar observations have been made in other screen-experiments. In the experiments of figures 1 and 2 shading was continued during the entire season, which has had a marked effect on the average bulb-weight, as shown by the figures. On the south-west (sunny) side of the experimental beds the disease-percentage was somewhat higher than on the northeast (shady) side, notwithstanding the fact that the plants on the sunny side had an extra amount of screening because of the overhanging gauze. The experiment of figure 2 confirms the results of the experiment in figure 1.

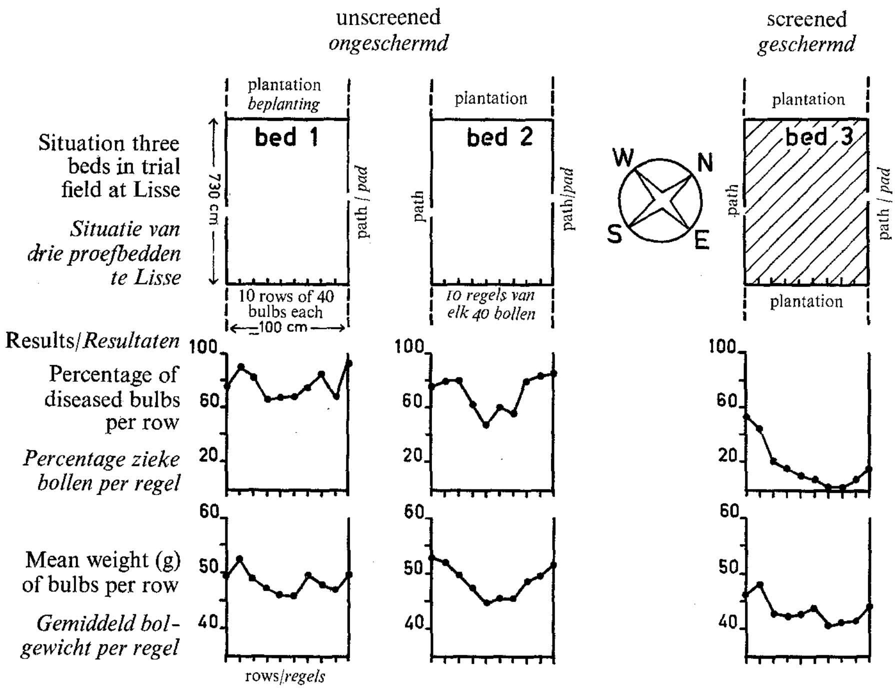

FIG. 1. Distribution of diseased bulbs in normal and shaded beds.
Spreiding van de zieke bollen in beschaduwde en onbeschaduwde bedden.
Situation of beds 1, 2 and 3 in experimental field at Lisse.
Situatie van de bedden 1, 2 en 3 in het proefveld te Lisse.
Bed 3 is shaded / *Bed 3 is beschaduwd.* Season / *Seizoen* 1957/58.
Cultivar 'Korneforos'.
Percentage of diseased bulbs and mean weight of bulbs per row.
Percentage zieke bollen en gemiddeld bolgewicht per regel.

Experiment 3 (figure 3) differs from experiments 1 and 2 in that screening of the beds was done during periods of 3 weeks only. Nevertheless each of the 16 experimental beds gave similar results.

c. Period of susceptibility to the influence of screening

There were grounds for assuming that the influence of screening was not equal throughout the period of growth; in other words, that there was a period of special susceptibility. This was confirmed by means of the following experiment (see fig. 3). Two beds at a time were screened simultaneously for 3 weeks, in such manner that the screening-periods followed and overlapped each other. The position of the beds and the screening-periods are shown in fig. 3. When two adjoining beds were being screened, the intervening path was screened, too. From the data it can be concluded that the influence of screening was at its height during the last week of April and the first two weeks of May. This result concerned an experiment at Noordwijkerhout with the cultivar 'Cum Laude', but it was fully confirmed by an experiment with the cultivar 'Korneforos' in an experimental field at Lisse. The disease-reduction at Lisse was less, to be

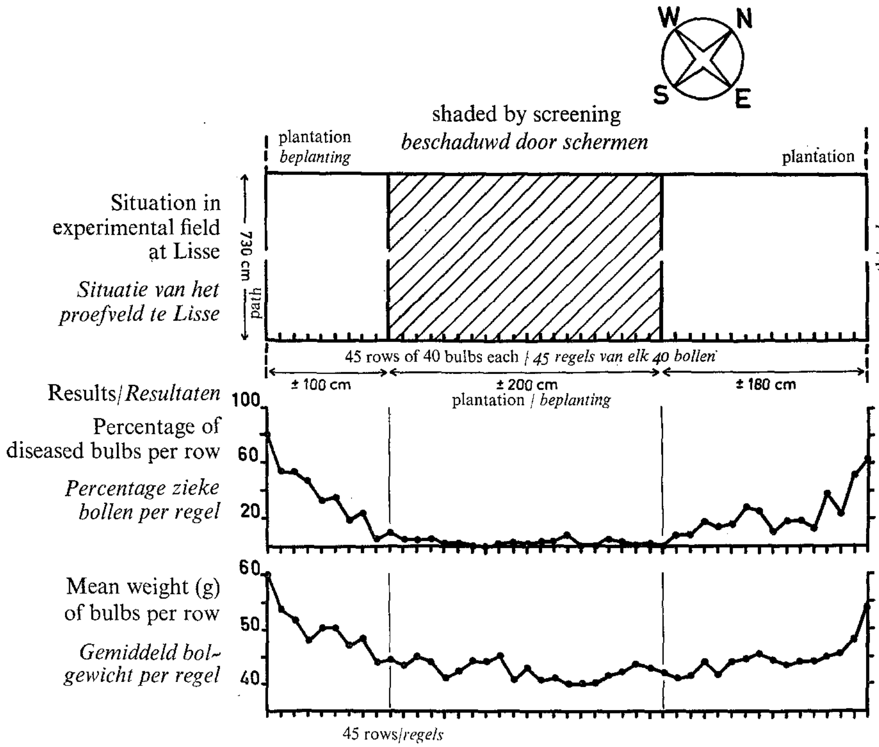

FIG. 2. Effect of shading in an experimental field at Lisse.
Effect van beschaduwing in een proefveld te Lisse.
Season / *Seizoen* 1958/59. Cultivar 'Korneforos'.
Percentage of diseased bulbs and mean weight of bulbs per row.
Percentage zieke bollen en gemiddeld bolgewicht per regel.

sure, but then the light-reduction of the screen used there was less. The edge-effect already established, was observed again in the screened beds of experiment 3 and was perhaps even intensified. The reduction of the bulb-weight was less marked owing to the limited screening periods, especially when the screening took place early in the season.

CONCLUSIONS CONCERNING EDGE-EFFECT AND SCREENING EXPERIMENTS

Though moisture and nutrients from the soil might have had an influence on the edge-effect, in view of the above results of the experiments, one is inclined to consider light as the factor having most influence on the disease in the field. Unpublished results indicate that the water content of the soil had little if any effect on the disease. Also the influence of manuring seemed to be restricted within narrow limits (KAMERBEEK, 1958). The edge-effect might thus be mainly the result of a natural lessening of light from the paths towards the middle of the beds. Screening leads to a reduction of light throughout the plots and appears to affect the incidence of the disease. Even in screened plots the edge-effect remains. The question as to the way in which light or radiation acts must

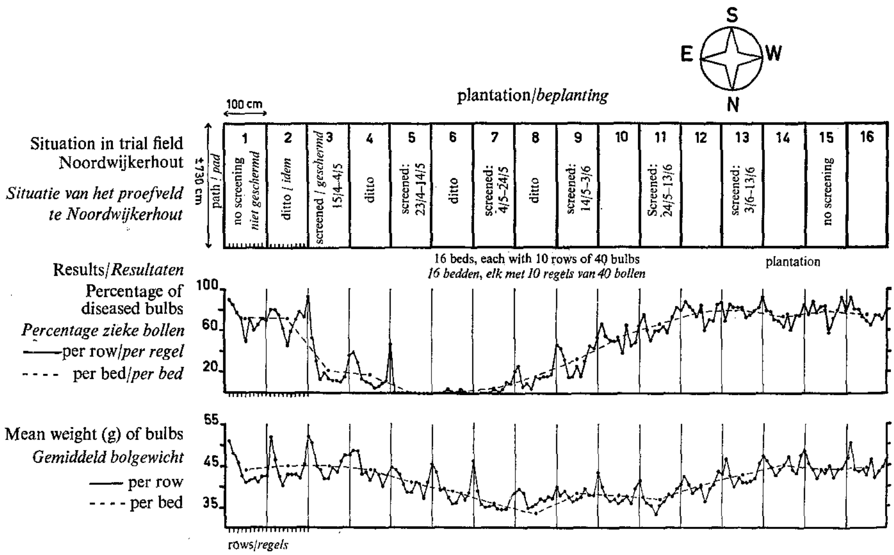

FIG. 3. Effect of shading in successive periods.
Effect van schermen in opeenvolgende perioden.
Situation of beds in trial fields and experimental results at Noordwijkerhout.
Situatie van de proefbedden en proefresultaten te Noordwijkerhout.
Percentage of diseased bulbs and mean weight of bulbs per row.
Percentage zieke bollen en gemiddeld bolgewicht per regel.
Season / *Seizoen* 1959/60. Cultivar 'Cum Laude'.

be left for later discussion. It is true that the light must be very considerably reduced in order to produce a clear effect, but the screening can be restricted to a relatively short period in the growth of the plant. In the first screening period (beds 3 and 4 of fig. 3) from 15 April till 4 May a substantial reduction in the amount of disease took place, without any very marked effect upon the bulb-weight.

Now what arguments are there for holding the light responsible? First of all there is the observation that the disease-percentage on the sunny side of the screened beds exceeds that on the shady side (fig. 1, bed 3; fig. 2). It may further be pointed out that at an earlier date it was observed that a reduction of the leaf-area caused a decrease in the disease (KAMERBEEK, 1958). The following experimental evidence is also pertinent. From an oblong experimental bed, perpendicular to the main direction of the light, a few rows parallel with the direction of the light were lifted periodically during the season. In the middle of May the first cases of disease were observed, while afterwards the numbers of diseased bulbs increased and the symptoms developed in intensity. It was expected that there would eventually be a more or less constant disease-percentage, but this proved not to be the case. It has been repeatedly observed that the disease-percentage begins to drop after reaching a maximum (see fig. 4). It is hard to assume that there could be a reduction in the necrosis. We might explain it in the following way. During the lifting procedure, as described, the shaded plants which at first had been surrounded by other plants are ex-

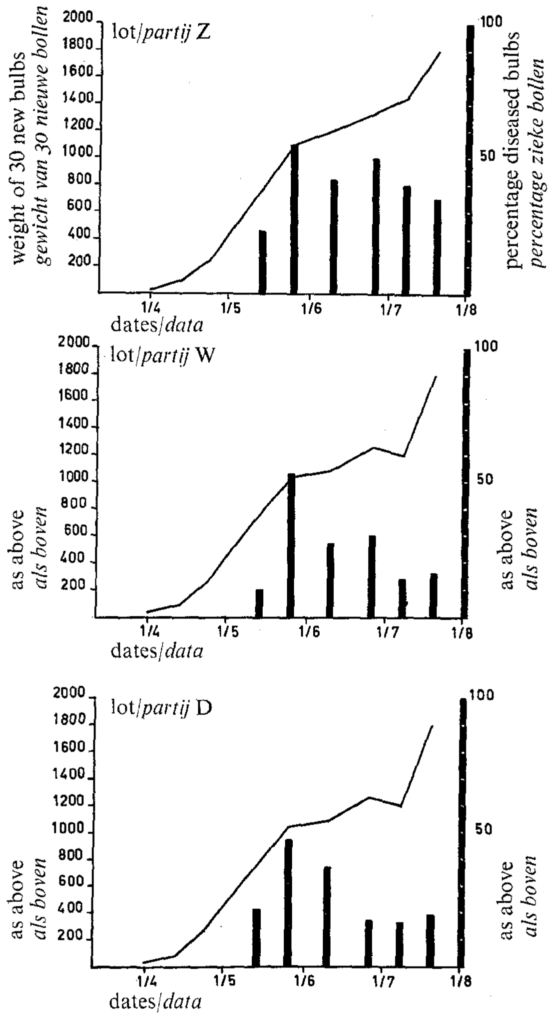

FIG. 4.
Growth curves of the new bulb (cultivar 'Korneforos') and percentage diseased bulbs at successive dates in 1959.
Groeikurve van de nieuwe bol (cultivar 'Korneforos') en percentage nieuwe bollen op verschillende data in 1959.

posed to broad sunlight. Since we know that there is a period of particular susceptibility, it is not surprising when we observe that in this period on account of an extra amount of sunlight the disease-percentage shows an upward tendency. The rows that were lifted later have been in the shade during the period of susceptibility and consequently these bulbs show a lower percentage of disease.

It was further ascertained in the experiments that with a light-reduction of about 75 per cent (experimental field Noordwijkerhout) the amount of disease was a good deal less than with a light-reduction of 50 per cent (experimental field Lisse). This might point to a quantitative effect of the light. Unfortunately this comparison rests on experiments with two different cultivars so that this argument is robbed of much of its value.

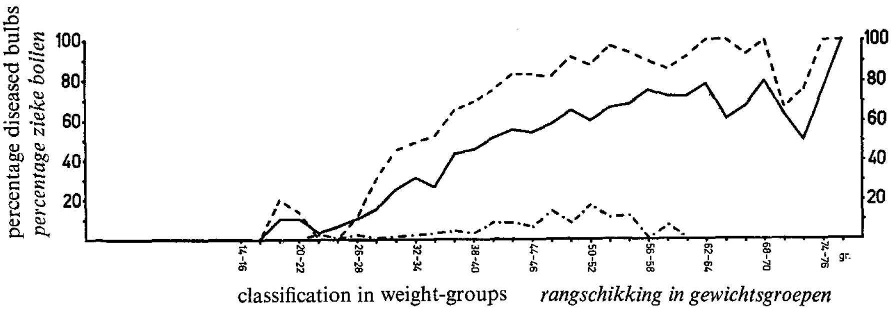

FIG. 5. Relation between weight of bulb and percentage diseased bulbs calculated from data of experiment at Noordwijkerhout (fig. 3).
Verband tussen bolgewicht en percentage zieke bollen berekend uit gegevens van proef te Noordwijkerhout (fig. 3).
—— all bulbs from experiment / *alle bollen van de proef*
------ bulbs from unshaded plants / *bollen van onbeschaduwde planten* (beds / *bedden* 1, 2, 15 and / *en* 16)
-·-·- bulbs from shaded plants in light susceptible period *bollen van planten die in lichtgevoelige periode werden beschaduwd* (beds / *bedden* 5, 6, 7 and / *en* 8)

RELATION BETWEEN BULB-WEIGHT, DISEASE-PERCENTAGE AND INFLUENCE OF LIGHT

As has been published earlier, there is a distinct relation between disease-percentage and bulb-weight. In figures 1, 2 and 3 the relation again stands out clearly. In addition, it would appear that light strongly influences the disease – but in what way does the light exert its influence? Needless to say, the amount of light received by the plant will partly determine the eventual size of the bulb and accordingly will have an indirect influence upon the disease-percentage. In this way then the light-effect could be fitted into the relation of bulb-size and disease. However, we should like to suggest that besides this there is another specific effect of the light.

In figure 5 an analysis is given of the Noordwijkerhout experiment shown in fig. 3. The disease-percentages have been calculated for the entire series of ranges of weight of the bulbs and these have been arranged in a graph. If the figures for the bulbs of screened plants are compared with those for the bulbs of unscreened plants, the curves are seen to diverge markedly. In the graph the bulbs of the four unscreened beds Nrs 1, 2, 15 and 16 have been compared with those of beds Nrs 5, 6, 7 and 8, which were screened in the period of greatest susceptibility to light. As a similar planting size of the bulbs has been assumed, the bulbs of a certain range of weight will have grown practically alike. For all that the disease-percentage of a similar range of weight varies quite distinctly. We should like to conclude from this that the light has a very specific influence upon the disease. Further information regarding the possible nature of the influence of light or radiation will be given in a discussion to follow.

POSSIBILITIES OF PRACTICAL CONTROL OF THE DISEASE

Bulbs which are obviously diseased are rejected for export. This does not hold good for those slightly affected, as the symptoms escape observation be-

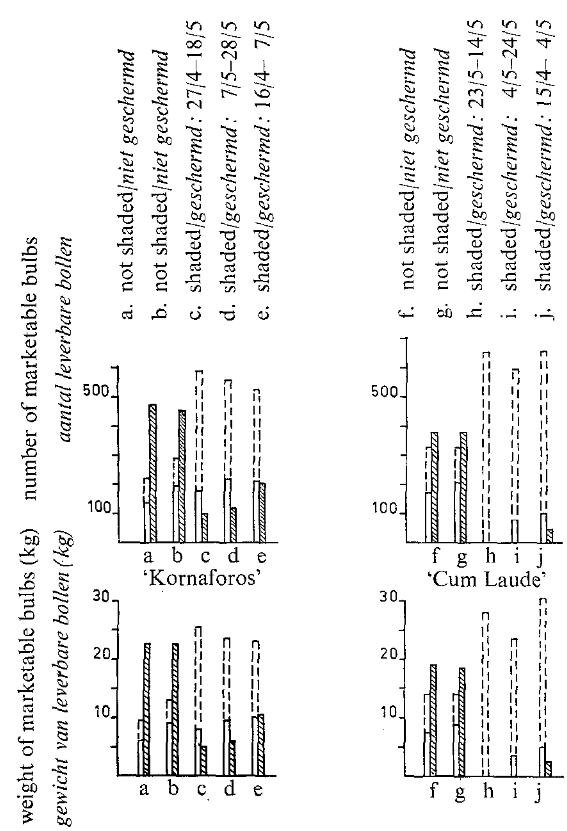

FIG. 6. Proportion of bulbs usable (blank) and unusable (hatched) from plants unshaded or shaded at various periods.
Verhouding van het bruikbare (niet gearceerde) en onbruikbare (gearceerde) deel van de bollen van planten, die al of niet beschaduwd waren.

healthy bulbs / *gezonde bollen*

slightly diseased bulbs / *licht zieke bollen*

seriously diseased bulbs / *zwaar zieke bollen*

cause of the bulb-skin. In commercial practice it is desired to obtain the greatest possible number of bulbs of a marketable size. A bulb is considered "marketable" if it measures 11 cms and upwards in circumference. Measurements showed that in the above experiments 'Korneforos' bulbs weighing 34 grams and upwards and 'Cum Laude' bulbs weighing 32 grams and upwards could be classed as "marketable". This limit being assumed, it has been calculated from the data of the experiment represented in fig. 3 and of an analogous experiment with 'Korneforos' at Lisse, what the proportion was of bulbs that because of the disease were fit and unfit for export. The results are shown in fig. 6, the "unfit" portions being hatched. From the figures it is evident that screening may prove useful. Whether it can be made commercially practicable is another story. The method is laborious and consequently expensive.

Some experiments are being made in order to find out whether covering the plants with a thin layer of straw during the susceptible period, would produce any practical effect. However, there may be a good many objections to this method.

DISCUSSION

Because the known facts about the disease are still so scanty, the following discussion should be regarded as very tentative.

The very first symptoms to be observed in blueing are small glassy spots in the bulb-scales. It seems obvious that these are small localised infiltrations of cell sap in the intercellular spaces. Possibly these infiltrations may be responsible for the subsequent necrosis of the tissue. Infiltrations of certain tissues are found with many diseases of a physiological nature; nor are they exceptional with tulips. Toppling of tulip stems and analogous phenomena in tulip leaves may be mentioned in this connection. Moreover, as with blueing, a distinct relation has been found between toppling of the stem and the growth of cells (ALGERA, unpublished).

Should one consider further the relation between blueing and special physiological activities, then three things, it seems, will have to be kept in mind:

1. There should be a relation with infiltration processes.
2. There should be a relation with growth.
3. It should be possible for the intensity of light or radiation to play a part.

If we wish to define our view, taking the infiltration process or a possible excretion process as our starting-point, we may avail ourselves of the following data from the literature. FREY-WYSSLING (1939) has been able to show that the number of hours sunshine on a given day was decisive for guttation appearing on the following day. The plant must be in an active stage of growth (FREY-WYSSLING, 1941). This writer explains the phenomenon through the influence of the sun upon the temperature of soil and air. The results of a high soil-temperature in the daytime and high air-humidity and low-temperature during the night, seem to be ideal for guttation to occur. The condition of the field early in May, when blueing starts, will come close to the conditions stipulated by FREY-WYSSLING. However, a certain degree of caution must be used, for guttation is not the same as infiltration (see ROBBINS, 1937).

Considering, on the other hand, whether the infiltrations may be due to excretion-processes, we may refer to the following data. There is some reason for choosing this view as a starting point, since PINKHOF (1929) and others have shown that sugar-containing liquid can leave the cells in the tulip stem. (For a survey of toppling see KAMERBEEK & ALGERA, in the press). When blueing occurs, the young growing bulb is in the very phase when large quantities of assimilates are in process of being transferred from the leaves. Thus there may arise a situation in which there is a surplus of assimilates to leak from the cells. SHUAL (1952) points to a relation between radiation from the sun and the amount of sugar secreted by nectaries. WYKES (1952) has shown that the concentration of the sugar-containing solution offered to the nectaries is decisive for the amount of sugar secreted. Also toppling in tulips is promoted by an increased supply of sugar (PINKHOF, 1929; ALGERA, unpublished). Thus the influence of light on blueing could possibly be explained by the amount of sugars formed by photosynthesis. With some hesitation GESSNER (1956) mentions experiments of KLEIN who has established that an excretion of glucose by the leaves of water-plants can take place under conditions of strong photosynthetic activity.

Other suppositions can be made concerning the origin of infiltrations. VAN DER PAAUW (1935, 1950) observed that leaves and also leafy shoots under conditions excluding transpiration appeared to be able to take up water for several successive days. This water got into the intercellular spaces. The cause of this phenomenon was the appearance of slight pressure-deficits in the intercellular spaces as a result of the dissimilar solubility of the oxygen taken up by the respiration process and the carbonic acid gas evolved (SEN & BLACKMAN, 1933). The suggestions made by VAN DER PAAUW as to the environmental conditions favouring the phenomenon, show the same tendency as those made by FREY-WYSSLING for guttation.

Through the effect of radiation, light can raise the temperature of the leaves well above the temperature of the air, which would promote transpiration via the leaf. The temperature of the soil can also rise considerably as a result of irradiation. Owing to this the transpiration might increase to such an extent that a water-deficit in the bulb may result. It has been pointed out by KRAAIJENGA (1960) that in the event of pronounced transpiration relativily large quantities of water can be temporarily abstracted from the bulb to such an extent that even the circumference of the bulb becomes smaller in the middle of the day. It is not beyond the bounds of possibility that this could cause infiltrations, for a loss of water causes an increase of the osmotic value of the cell sap and this will possibly further the excretion of cellular liquid. The above theories concerning water-deficit and excretion accordingly need not be contradictory.

It is obvious that our knowledge is still too slight for us to approach the fundamental problem of blueing otherwise than hypothetically. Future experiments will have to indicate the lines to be followed.

SUMMARY

The blueing of tulip bulbs is a physiological disease resembling in some ways physiological diseases of other plants. Recent experiments indicate that sunlight influences blueing. By shading the plants the extent of the disease was considerably reduced or even eliminated. The influence of light was found to apply only during a certain period of the season, the most susceptible period being in the last week of April and the first two weeks of May.

A hypothesis has been developed concerning the origin of the necrotic spots in the bulb, which may also hold good for toppling of tulips. It is assumed that cell sap, possibly together with sugars, are excreted from the cell into the intercellular spaces of the parenchymatous tissue, thus bringing about a necrosis.

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Samenvatting

Het blauwgroeien van tulpebollen is een fysiologische ziekte, die in bepaalde opzichten overeenkomst vertoont met fysiologische ziekten bij andere gewassen.

Nadat vroeger werd aangetoond, dat er een duidelijke correlatie bestaat tussen de bolgrootte en het percentage zieke bollen en dat de groei van de bol waarschijnlijk verband houdt met de ziekte (fig. 4), is door recente veldproeven duidelijk geworden dat het zonlicht of de straling een grote invloed op het blauwgroeien heeft. De verspreiding van de zieke bollen in de bedden op het veld is niet willekeurig. Er is een duidelijk randeffect waar te nemen, d.w.z. dat de bollen in de regels aan de padkant verhoudingsgewijs een groter aantal zieke bollen hebben dan de bollen in de regels midden in de bedden (zie fig. 1–3). Dit randeffect werd in hoofdzaak toegeschreven aan de werking van het zonlicht. Door het gewas te beschaduwen met een scherm van plastic horregaas (lichtabsorptie ongeveer 50%) of van jute doek (lichtabsorptie ongeveer 75%) kon de ziekte sterk worden verminderd of zelfs geheel worden geëlimineerd. Door periodiek te schermen kon in veldproeven een bij uitstek gevoelige periode, wat de lichtinvloed betreft, worden aangetoond. Deze periode viel ongeveer in de laatste week van april en in de eerste twee weken van mei (fig. 3). Het afschermen van het gewas tijdens de gevoelige periode zou met het oog op de ziekte het bruikbare deel van de geoogste bollen aanzienlijk vergroten (fig. 6). Het bolgewicht wordt door deze periodieke afscherming slechts matig ongunstig beïnvloed. Of deze maatregel met het oog op de kosten ook economisch verantwoord is, valt te betwijfelen.

Behalve het feit dat het licht effect zal hebben op de groei en de grootte van de bol en daarmede het ziektepercentage zal beïnvloeden, kon worden aangetoond dat het licht of de straling een zeer specifieke werking op de ziekte heeft (zie fig. 5). Welke werking het zonlicht of de straling heeft, is niet geanalyseerd. In de discussie zijn over het ontstaan van de necrotische plekken in de bol suggesties gedaan, die echter bij gebrek aan nadere gegevens een speculatief karakter dragen. Als basis voor verder onderzoek wordt aangenomen, dat analoog aan wat zich bij het kiepen van tulpen voordoet, een excretie van vloeistof (celinhoud) in de intercellulaire ruimten van het parenchymweefsel plaats heeft, die een necrose zou veroorzaken.

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