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ROEFSTATION VOOR DE GROENTEN- EN FRUITTEELT ONDER GLAS,
E NAALDWIJK.

Verslag van een studiereis naar North Carolina (1960)

door:

ir.J.v.d.Ende

Naaldwijk, 1962.

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Verslag van een studiereis naar North Carolina (1960).

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Proefstation voor de Groenten- en Fruitteelt onder Glas te Maaldwijk.

VERSLAG VAN EEN STUDIEREIS NAAR NORTH CAROLINA (1960).

ir. J. van den Ende.

Het doel van de reis was de bestudering van de waterhuishouding van de plant. Daartoe werd van 11 juli t/m 6 augustus een bezoek gebracht aan P.J. Kramer van het Department of Botany van de Duke University te Durham.

Tijdens dit verblijf werd op 25 en 27 juli en 3 augustus een bezoek gebracht aan het North Carolina State College te Raleigh. Dit werd mogelijk gemaakt doordat ik kon meerijden met Kramer, die lezingen op deze universiteit moest houden.

Duke University

De Duke University heeft twee campus-terreinen (zie 1). Op elk van deze terreinen was een plantenfysioloog gevestigd: Kramer op de West Campus en A.W. Naylor op de East Campus. Met Naylor heb ik slechts vluchtig kennis gemaakt. Hij was voorzitter van de American Society of Plant Physiologists.

Op de afdeling van Kramer waren de volgende personen werkzaam:
 een assistent H. Brix (een Deen);
 een bezoeker E. Shmueli (een Israëliër);
 vijf Ph.D.-studenten... L.D. Dove, W. Lopushinsky, R.P. Pharis,
 B.V. Ratnam (een Indiër), B.R. Roberts.

Ik heb mij op de hoogte gesteld van de lopende onderzoeken van deze personen. Vooral het onderzoek van Brix trok mijn belangstelling en voorts ook dat van Shmueli. Laatst genoemde is hoofd van de Irrigation Department van het Agricultural Research Station, Rehovoeth-Beit Dagan (2).

Met Kramer heb ik verschillende door hem geschreven artikelen bediscussieerd. De in dit verband gehouden besprekingen vormden aanleiding tot het doornemen van vrij veel literatuur. Onder meer werden de Bande I t/m IV van het Handbuch der Pflanzenphysiologie doorgewerkt (zie 3a t/m 3t). De gezichtspunten die de literatuurstudie heeft opgeleverd, zullen in dit verslag ter sprake worden gebracht; voor zover zij buiten het gebied van de waterhuishouding van de plant zijn gelegen deels onder het hoofd "Duke University" en deels onder het hoofd "North Carolina State College".

Onderzoek van Brix

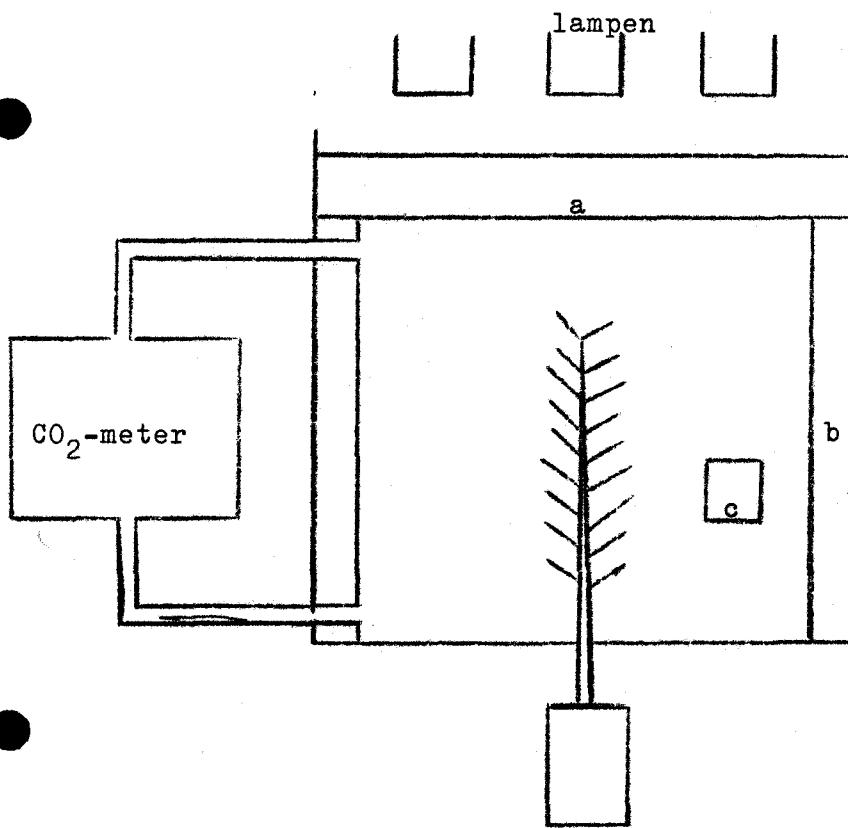
Brix heeft in 1959 aan de Agr. and Mech. College of Texas de Ph.D.-graad behaald. Zijn thesis handelt over "Some aspects of drought resistance in loblolly pine seedlings". Ook te Durham werkte hij met dit gewas. Hij bepaalde de rate of photosynthesis, de rate of respiration en de rate of transpiration bij uiteenlopende total soil moisture stress (TSMS). Tevens werden van het blad de water content, de relative turgidity (RT) en de turgor pressure (TP) bepaald; de laatste door middel van metingen van de osmotic pressure (OP) en de diffusion pressure deficit (DPD): $TP = OP - DPD$. De TSMS bij het permanent wilting point (zero TP of leaves) en de TSMS bij het ultimate wilting point (threshold for survival) zouden worden vastgesteld.

Dove zou in de proefplanten van Brix de koolhydraten — zoals zetmeel, rietsuiker en reducerende suikers — en de wel en niet in 80% aethanol op-

losbare stikstofverbindingen gaan bepalen; 80% aethanol geeft een ruwe scheiding tussen aminozuren en andere minder ingewikkelde stikstofverbinding en enerzijds en eiwitten en peptiden anderzijds. Ten tijde van mijn bezoek hield Dove zich bezig met het uitwerken van de betreffende analysemethodieken.

Meting photosynthese en ademhaling (CO_2 -meting)

Voor de meting van de photosynthese en de ademhaling werd gebruik gemaakt van de volgende opstelling:



- a. circulerend water om de warmte van de lampen weg te vangen.
- b. koelwater voor regeling van de temperatuur.
- c. thermometer.

Onderaan de container werd lucht afgezogen, die door de CO_2 -meter werd gevoerd en vervolgens bovenin weer in de container geblazen; de lucht werd voor het passeren door de CO_2 -meter eerst gedroogd (silicagel) en van stof ontdaan. Bij de meting van de photosynthese bepaalde Brix de tijd, die nodig was om het CO_2 -gehalte van het systeem met 10% te verlagen; feitelijk werd dus niet de photosynthesis bepaald maar de net photosynthesis. Bij de meting van de ademhaling werden de lampen uitgeschakeld en werd de tijd nagegaan, die nodig was om het CO_2 -gehalte van het systeem met een bepaald percentage te verhogen.

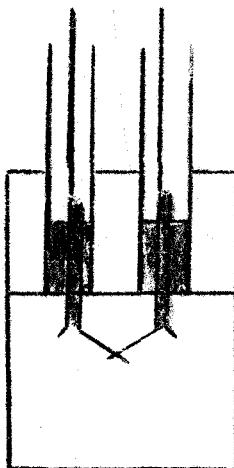
De CO_2 -meter was een door Liston-Becker (Hope Street, Stamford, Conn.) vervaardigde Beckman L/B Infrared Analyzer Model 15a. Een folder over dit instrument vermeldde onder meer het volgende. All heterocatomic gases have infra-red absorption bands which are produced by vibrations of the mole-

cular bonds. Some gases such as O_2 , N_2 , H_2 and the rare gases do not have infra-red bands and therefore cannot be analyzed by this instrument. In some analyses it is possible that some of the other gases present in the gas stream might have absorption bands that overlap the bands of the gas for which the instrument is sensitized.

De CO_2 -meting wordt zo beïnvloed door waterdamp. Door een juiste keuze van het windowmaterial kan de waterdampinterferentie echter worden weggewerkt. Bij het apparaat van Brix was dit niet gebeurd, vandaar dat hij de gasstroom vooraf moet drogen.

Meting diffusion pressure deficit

De DPD werd bepaald door middel van een dampspanningsmeting. De — met behulp van vijf evenwijdig gemonteerde scheermesjes in stukjes gesneden — needle-leaves werden hier toe in een glazen buisje gedaan, dat werd afgesloten met een stop, waarin thermokoppel was bevestigd (zie tekening).



De natte las werd bevochtigd door middel van Peltier-koeling. Deze koeling werd reeds eerder toegepast door Spanner (D.C. Spanner: The Peltier effect and its use in the measurement of suction pressure. J. Exp. Bot. 2: 145-168) en door Monteith en Owen (J.L. Monteith and P.C. Owen: A thermo-couple method for measuring relative humidity in the range 95-100%. J. Sci. Instr. 35:443-446, 1958). Zie voor andere methoden voor de meting van de dampspanning met behulp van thermokoppels bij Baldes (E.J. Baldes: Micro method of measuring osmotic pressure. J. Sci. Instr. 11:223, 1934), bij Hill (A.V. Hill: A thermoelectric method for measuring the vapour pressure of an aqueous solution. Proc. Roy. Soc. A 127:9-19, 1930), bij Townend (R.V. Townend: A new method for measuring osmotic pressure. J. Amer. Chem. Soc. 50:2958-2966, 1928) en bij Richards en Ogata (zie het Verslag van een studiereis naar Californië).

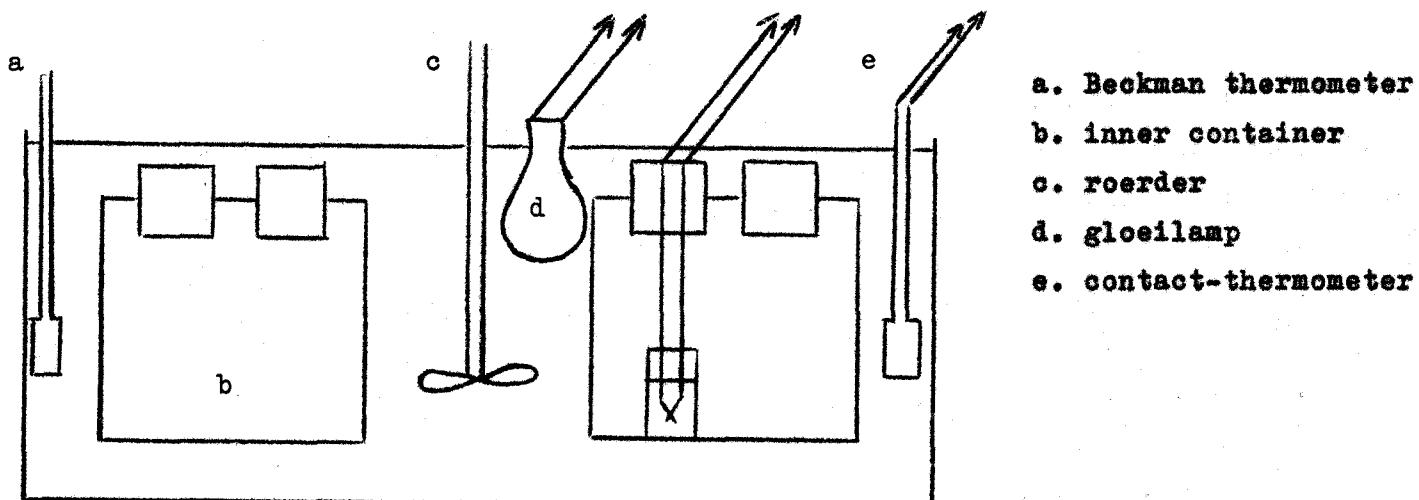
Onder het Peltier effect worden verstaan de koeling of verwarming (de laatste afgezien van de Joule-verwarming), die optreden bij doorvoeren van

stroom door een las. De stroomrichting bepaalt of zich koeling dan wel verwarming voordoet. De koelingsmogelijkheden van het Peltier effect zijn slechts beperkt. De koeling is namelijk evenredig met de stroomsterkte, terwijl de Joule-verwarming evenredig is met het kwadraat van de stroomsterkte.

De bevochtiging van de natte las door middel van de Peltier-koeling is slechts gering. Vandaar dat na het verbreken van de koelingsstroom direct de galvanometer voor de meting van het thermische voltage van de thermokoppel moet worden ingeschakeld. De kleine hoeveelheid vecht is namelijk spoedig verdampft, speciaal wanneer de DPD hoog is. Bovendien moet de galvanometer in dit verband een korte periode bezitten. Brix koelde door gedurende een minuut 20 mA door de thermokoppel te voeren. De te noteren grootste galvanometeruitslag werd ^{na} ongeveer 15 seconden bereikt.

Brix zei dat de thermokoppel per graad C. 62.5 microvolt levert; het voltage zou voor de verschillende exemplaren van de thermokoppel vrijwel niet uiteenlopen. De galvanometer zou een gevoeligheid van liefst 0.02 microvolt dienen te bezitten. Deze gevoeligheid komt overeen met ongeveer 0.0003°C . ofwel ongeveer 0.025 atm. Een oplossing met een osmotische waarde van 10 atm. zou namelijk bij 25°C . een dauwpuntsdaling bezitten van 0.124°C (met een corresponderende relatieve vochtigheid van 99.24%).

De temperatuur moet tijdens de meting zeer constant worden gehouden. Het door Brix hiertoe gebruikte waterbad is weergegeven in de volgende tekening.



Het bad vertoonde een temperatuurschommeling van $\pm 0.005^{\circ}\text{C}$. De temperatuurschommeling in de twee inner containers was ongetwijfeld geringer en in de monsterbuisjes nog weer geringer (met een totale temperatuurschommeling van 0.01°C . zou volgens het voorgaande de nauwkeurigheid niet groter

zijn dan ongeveer 0.8 atm.). In elke inner container konden zes monsterbuisjes worden geplaatst. Zij werden bij gebruik steeds met dit aantal gevuld om te voorkomen, dat er water doorheen zou circuleren. Ter water- en luchtdichte afsluiting van de monsterbuisjes werden de stoppen hiervan ingesmeerd met vaseline. De gloeilamp schijnt een zeer goed verwarmingselement te zijn; having the advantages of low heat capacity and of giving off its energy by radiaton, this latter ensuring a rapid and general rather than local heating.

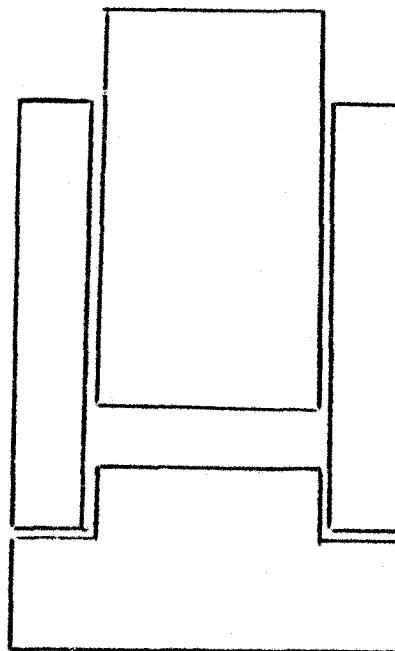
Whereas vapour-pressure equilibrium in the chamber is reached very rapidly with the leaf turgid, it becomes a slower and slower process as the leaf dries. Why this is so is a matter of conjecture, but it may be supposed that both stomatal closure and the physical state of the cell walls have a part in it. Monteith en Owen vonden bij meting van zoutoplossingen, dat het op evenwicht komen ongeveer zes uur in beslag nam, tenminste wanneer een filter paper lining in de thermokoppelkamer werd aangebracht; bij meting van vochtige grond zou het wel een week kunnen duren. Brix dacht dat het voor bladeren wel voldoende is, wanneer de monsterbuisjes twaalf uur voor de meting in het waterbad worden geplaatst (de inhoud van zijn thermokoppelkamers bedroeg ongeveer 13 ml).

Very close to saturation minute temperature fluctuations can produce condensation within the sample tube and wet-bulb depressions tend to be erratic. The upper limit of measuring is therefore a relative humidity of about 99.98% (ofwel een osmotische waarde van ongeveer 0.3 atm.).

Ik heb de indruk dat de hier besproken dampspanningsmeting minder nauwkeurig is dan de te Riverside gebezigde (zie het Verslag van een studiereis naar Californië). Een definitief oordeel over de bruikbaarheid van beide methoden zal echter pas gegeven kunnen worden na een grondige bestudering van de geciteerde literatuur of na een eigen onderzoek. Enkele gerezen vragen konden niet door Brix worden beantwoord. De voornaamste vraag was wel, waarom te Riverside zoveel sneller — binnen een half uur — evenwicht wordt verkregen (mogelijk is dit een gevolg van de zeer kleine afmetingen van de aldaar toegepaste thermokoppelkamer). Brix was overigens over de door hem gebezigde techniek zeer tevreden. Een nauwkeurigheid van 1 atm. achtte hij voor zijn onderzoek reeds voldoende.

Meting osmotische waarde

De OP werd cryoscopisch bepaald aan het persvocht van needle-leaves, die gedurende meerdere dagen in aluminium foil gewikkeld in een diepvries waren bewaard (zie ook 5).



Bij het persen werd gebruik gemaakt van een Carver press. Het persvat — zie tekening — werd in een metalen bakje geplaatst om het persvocht op te vangen. Kaasdoek werd niet gebruikt. Het persvocht was dan ook troebel. Het werd daarom gecentrifugeerd en vervolgens gefiltreerd. De hoeveelheid persvocht werd vergeleken met het vooraf bepaalde vergewicht van de needle-leaves.

De vriespuntsdaling werd gemeten met een kwikthermometer, waarvan het nulpunt was vastgesteld met behulp van smeltend ijs in een Dewarvat; het ijs was vervaardigd van water dat goed was gedestilleerd. Tijdens de meting — ook tijdens de koeling — werd het persvocht onafgebroken geroerd. De roerder bestond uit een metalen spiraal, die zich om het kwikreservoir van de thermometer bevond; zij werd op en neer bewogen.

Meting relative turgidity

De meting van de R_f wordt besproken door Kramer (4; zie ook 6). Stocke suggested that a good measure of internal water balance is the amount of water taken up by leaves or twigs that are allowed to absorb water until saturated. The leaves or twigs are weighed and their bases set in water in a saturated atmosphere until equilibrium is attained, which usually requires one or two days. The saturation deficit is calculated as follows:

$$100 \times \frac{\text{saturated fresh weight} - \text{field fresh weight}}{\text{saturated fresh weight} - \text{oven-dry weight}}$$

A variation of this method was introduced by Weatherly for measuring the RT of plant tissue. Disks of leaf tissue about 1 cm in diameter are cut out of leaves, weighed, floated on water until they attain equilibrium and their fresh weight and oven-dry weight obtained. The RT is then calculated as follows:

$$100 \times \frac{\text{field fresh weight} - \text{oven-dry weight}}{\text{saturated fresh weight} - \text{oven-dry weight}}$$

This method requires smaller samples of tissue and less time than the Stocker method and the method of calculation is more satisfactory because the smaller the uptake of water the larger the number representing RT.

The Weatherly method has been used extensively by Slatyer (zie 5). It seems that RT may be a useful measure of water balance in plants and might even be used as an indicator for irrigation. Its use is based on the assumption that the fully turgid condition is normal and desirable, but this assumption perhaps needs more study. The time of day when plants are sampled will make considerable difference in the RT observed and early-morning sampling seems best for most purposes. Unfortunately, the effect of a given RT is not the same in all species; hence, the critical level probably must be determined for each species and perhaps even for each variety (zie 5).

Brix bepaalde de RT van needle-leaves door ze in een reageerbuis met een beetje water te zetten. De reageerbuizen die niet werden afgesloten, werden weggezet in een kamer met geringe verlichting en met vrij constante en relatief lage temperatuur. Het op evenwicht komen duurde ongeveer twaalf uur. De bepaling van het drooggewicht van de needle-leaves werd gecontroleerd door van andere needle-leaves direct het drooggewicht te bepalen.

Brix berekende de RT volgens Weatherly. Zijn bepalingswijze was echter die volgens Stocker. De bepalingswijze volgens Weatherly heeft volgens hem enerzijds het nadeel van het binnendringen van water in de intercellulairen en anderzijds de moeilijkheid van het drogen na het floating.

Ratnam die zich bezig hield met de studie van de droogteresistentie van grassen, had voor deze gewassen de meting van de RT nader in onderzoek genomen. Hij ging bijvoorbeeld na, of het onder water afsnijden van een stukje van de onderzijde van de bladeren — nadat deze reeds enkele uren in een beetje water hadden gestaan — van invloed was op het saturated fresh weight.

Kennis werd gemaakt met apparaten voor de meting van de luchtvochtigheid, de instraling en de verdamping.

Luchtvochtigheid

De Hygrodynamics Inc. — 8030-8050 Georgia Avenue, Silver Spring, Maryland — levert voor de meting en de regeling van de luchtvochtigheid tal van apparaten. Er zijn vrijwel geen omstandigheden te bedenken, waarvoor niet één of meer van de apparaten geschikt zijn. De meting en de regeling kunnen desgewenst ook op grote afstand worden verricht: 300 meter en nog wel meer. In een folder van genoemde firma las ik onder meer het volgende.

The Aminco-Dunmore Sensing Element is an electrical resistor consisting of a polystyrene cylinder, a dual winding of precious metal wire, a coating of moisture-sensitive compound, plug-in contact pins and a guard that protects the element from damage. Operation of the element is based on the ability of hygroscopic film to change its electrical resistance instantly with micro-changes in relative humidity.

Instraling

Brix toonde mij een Sun Meter van de Messrs. Megatron Ltd., Fonthill Road 115 a, London. Dit apparaat wordt beschreven in de Commercial Grower van 28 March 1958. Brix had er nog geen ervaring mee opgedaan.

Verdamping

De meting van de verdamping wordt uitvoerig besproken door Maximov (7) en Miller (8). The sharp decrease in transpiration during the night is far from corresponding to the reduction of evaporation as determined by white Livingston's atmometers (7). The plant is particularly sensitive to radiation, the atmometer to wind. It was found that atmometers and plants responded unequally to changes of wind velocity but that changes in temperature and relative humidity acted upon the rate of evaporation and transpiration equally (8).

The daily march of transpiration is determined primarily by the march of solar radiation (7). The moisture deficit of the atmosphere is also one of the main factors. That wind must be relegated to the third place in order of importance is probably to be attributed to the structure of the evaporating surface of the plant. The vaporization of water takes place not on the cutinized outer surface, but on the surface of the intercellular spaces, which are protected from the wind. Thus the atmometer, with its vertical evaporating surface, is more sensitive to air movements than evaporimeters with a horizontal water surface, slightly protected from the

wind by the protruding edges of the cup. A shallow blackened copper tank must react particularly to changes in the vertical component of radiation. In comparing the rate of evaporation from such a tank with the transpiration rate it was found that the correlation coefficient ranged from 0.84 to 0.95 (8).

De laatste jaren zijn er aan de atmometer nieuwe perspektieven ontdekt. Het verschil in verdamping tussen een zwarte en een witte atmometer zou namelijk in hoge mate samenhangen met de transpiratie. Zie in dit verband Janes (B.E. Janes: Predicting need for irrigation by measuring loss of water from atmometers. Progr. Rep. Conn. agric. Exp. Stat. 42, 1960). Kramer zei dat atmometers worden geleverd door M.A. Livingston — de weduwe van de ontwerper van de Livingston's atmometer — 7908 Sherwood Avenue, Riderwood, Baltimore 4, Maryland.

Hygen (12) bespreekt de formule van Dalton:

$$V = K (F-f) \frac{760}{P} S$$

In deze formule hebben de letters de volgende betekenis: V = verdamping; K = constante; F = waterdampdruk aan het wateroppervlak; f = waterdampdruk in de atmosfeer; P = luchtdruk in mm kwik; S = oppervlakte.

Meting van de water balance van planten

The effect of water deficits on growth is discussed here in terms of cell processes (4; zie ook 5). In terms of cells, growth consists of cell division, enlargement, differentiation and maturation. Although the relations between turgor and growth are not fully understood, all of these processes are affected by water deficits and dehydration of the protoplasm. Cell division is ~~reduced even more, because some degree of turgor is essential to the expansion of cells.~~ ^{but cell enlargement is reduced} One of the first effects of water deficit is a decrease in or cessation of elongation of stems and enlargement of leaves and fruits, because these processes are dependent on a turgid condition of the cells.

The internal water balance, or turgidity, of the plant represents the integration of all the factors affecting plant water relations. Thus, we need to give more attention to the internal water balance as a measure of whether or not plants are adequately supplied with water. This approach seems to have been applied with considerable success to sugar cane in Hawaii and to various crops in Israel.

Kramer (4) bespreekt de volgende "methods of measuring or characterizing the condition of plants and plant tissues with respect to water": water

content, RT, OP, DPD, stomatal opening and other possibilities. Onder het hoofd other possibilities worden genoemd de "measuring of changes in electrical resistance by inserting electrodes into the plant tissue" en de "measurement of changes in electrical capacitance". Maximov (7) en Meyer (3n) noemen voorts metingen van schommelingen in de afmetingen van plantendelen. Deze metingen kunnen onder meer een indruk geven van de "transference of water from one part of the plant to another" (7).

Volgens Kramer (4) geven de RT en de DPD de beste karakteristiek voor de water balance. At one time, OP of sap expressed from leaves or other plant organs was used extensively as an indicator of the water conditions in plants, and this is still favored by Walter. In general, dehydration is accompanied by increase in OP and increase in water content by decrease in OP, but OP is not sufficiently sensitive to be used as an indicator of small changes in water balance.

In recent years attention has tended to shift from measuring ^{elements} of OP to measurements of DPD, because the latter is a more sensitive indicator of the degree of turgidity (zie voor commentaar op de meting van de RT de desbetreffende paragraaf van het hoofdstuk Onderzoek van Brix). Fully turgid tissue has a zero DPD and the DPD increases as the water deficit increases until it equals the OP, except that, when negative wall pressure or tension develops, it may even exceed the OP. As dehydration proceeds beyond the state such that there is zero TP in the cells of a tissue, Meyer (3 n) suggested that the water in the cell passes into a state of tension and the cell walls are subject to a strong centripetally directed pull due to the strong adhesion between the protoplast and the cell wall (5). This causes the development of negative TP and inward folding of cell walls has been observed as a result of such pressure during severe wilting. It would seem that the magnitude of the negative pressure which can develop in this manner must be limited by the degree of adhesion between the protoplast and the cell walls. For some species values up to 10 atm. have been found.

Tijdens mijn verblijf is aandacht besteedt aan de meting van de RT, de OP, de DPD en de openingstoestand van de huidmondjes. Zie voor de eerste twee de desbetreffende paragraven van het hoofdstuk Onderzoek van Brix. De laatste twee worden in de volgende paragraven besproken.

Diffusion pressure deficit

Bij de DPD-meting kan gebruik worden gemaakt van twee groepen van bepalingsmethodieken. De methodieken van de ene groep zijn gebaseerd op meting van de dampspanning van het te onderzoeken materiaal. Bij de andere groep van methodieken wordt door middel van onderdompeling in suikeroplossingen nagegaan, met welke suikerconcentratie het materiaal in evenwicht is.

De door Brix gebezigde techniek behoort tot de eerste groep (zie de paragraaf Meting diffusion pressure deficit van het hoofdstuk Onderzoek van Brix). Ook voor de door Slatyer (5) gevolgde methode is dit het geval. He determined the DPD of leaf tissue by placing disks over solutions of various vapor pressures to find at what solution^m DPD no gain or loss of water occurred (4). Een met Slatyer's methode overeenkomende bepalingswijze is die, waarbij de lengteveranderingen van oplossingen in capillairen wordt nagegaan.

Kramer (4) vermeldt over de tweede groep van methodieken het volgende. One method is to determine the concentration of sucrose or mannitol in which no change in length occurs in strips of tissue, but this is applicable only to thin tissues containing little supportive tissue. Another method is to determine the concentration of solutions in which no change in weight of pieces of tissue^m occurs, but this is applicable only to tissue, such as beet or potato, from which a number of uniform pieces of tissue can be cut. Vervolgens noemt Kramer enkele auteurs, die een meer algemeen toepasbare methode bezigden. They immersed pieces of leaf tissue in sugar solutions of various concentrations and determined the changes in concentration of the solution by measuring the change in refractive index with a refractometer.

Tijdens mijn verblijf heb ik enkele DPD-metingen verricht, waarbij het principe van laatst genoemde methode werd gevuld. Alleen de concentratieveranderingen werden op andere wijze vastgesteld. De werkwijze was als volgt.

In reageerbuisen met suikeroplossingen van 0.5, 1.0, 1.5..... atm. worden stukjes plantenmateriaal ondergedompeld; aan kleine hoeveelheden van dezelfde oplossingen wordt wat methyl blue toegevoegd. Na enkele uren wordt met behulp van een pincet aan de oplossingen in de reageerbuisen — ongeveer ter halve hoogte — een druppel van de overeenkomstige gekleurde oplossing toegevoegd. Stijging van de kleurstof wijst er op, dat het plantenmateriaal water aan de oplossing heeft onttrokken en daling dat het omgekeerde heeft plaats gevonden.

Ik heb bij mijn metingen als gevolg van de vaak geringe stijging of daling van de kleurstof geen scherp begrensde DPD kunnen vinden. Mogelijk was het gebezigde plantenmateriaal — katoenblad — weinig geschikt voor de dye method en misschien zijn de tijdsduur van onderdompeling en de verhouding materiaal/oplossing niet goed gekozen. Bij een blancoproef waarbij een kleurstofdruppel van 2.0 atm. werd toegevoegd aan oplossingen van 1.5 en 2.5 atm., trad in elk geval wel een snelle daling resp. snelle stijging van de kleurstof op.

Shmueli toonde mij later een reageerbuisje, waarmede de dye method zonder pipet kan worden uitgevoerd.



Onderin het buisje wordt suikeroplossing met plantenmateriaal gedaan. Voor de meting wordt kleurstof aan de oplossing toegevoegd, waarna in de holte wat ongekleurde oplossing wordt gebracht. Na kantelen van het buisje wordt nagegaan, of het kleurstofniveau in de holte al of niet daalt.

Openingstoestand van de huidmondjes

Kramer (6) noemt voor het gedrag van huidmondjes onder meer de volgende literatuur: Miller (8), Loftfield (J.V.G. Loftfield: The behavior of stomata. Carnegie Inst. Wash., Publ. 314, 1921) en Wilson (C.C. Wilson: The effect of some environmental factors on the movements of guard cells. Plant Physiol. 23:5-37, 1948).

Stomatal opening seems to be one of the most sensitive plant processes with respect to internal water deficits (4). A slight decrease in turgidity sometimes is accompanied by increased opening of stomata, but further reduction is nearly always accompanied by a decrease in stomatal aperture. Stomata of apple trees begin to close prematurely long before soil water falls to the permanent-wilting percentage. Decreasing soil moisture also causes premature closure in citrus. Stomata usually close earlier each day as soil water becomes less available, until finally they remain open for only a short time each morning.

Iljin (14) vermeldt echter, dat de huidmondjes soms ook zeer traag kunnen reageren, waardoor zij zelfs bij verwelkte planten nog open kunnen zijn.

Premature closure of stomata is undesirable because, in at least some species, it cuts off the supply of carbon dioxide for photosynthesis, although, in others, considerable carbon dioxide appears to enter through the epidermis (4). One effect of stomatal closure is to reduce transpiration, because by far the larger fraction of water loss occurs through the stomata. This reduction would be desirable in itself, for there is little doubt that very responsive stomata that close early in the development of an internal water deficit must materially increase drought resistance and survival; but, unfortunately, they also reduce photosynthesis by reducing the supply of carbon dioxide. For this reason it is doubtful if very responsive

stomata are desirable in crop plants, except, possibly, in plants such as tomato, which seems to manufacture most of its food before noon (het laatste is ontleend aan Went; voor het gedrag van de huidmondjes van tomaten verwees Kramer mij eveneens naar Went; zie Amer. J. Bot. 31:597, 1944).

More or less successful attempts have been made, especially in Israel, to use the closure of stomata as an indicator of developing water deficit before visible wilting occurs. For this purpose the extent of infiltration by a series of liquids of different surface tension has been used to estimate the degree of stomatal opening. If stomata are wide open, even a substance of relatively high surface tension, such as kerosene, penetrates readily; if nearly closed, only one of low surface tension will enter. Is is, of course, only an indirect indicator of water deficit, not a quantitative measure.

Shmueli had veel ervaring met de infiltration method. Bij zijn promotie-onderzoek — relation between irrigation procedures and the water balance and assimilatory activity of banana, maize and cowpea (17; zie ook 15) — heeft hij behalve deze nog drie andere methoden toegepast: direct microscopic examination, Lloyd's fixation method and collodion-film method. De methode van directe waarneming gaat volgens hem alleen goed bij dunne bladeren de bladeren die men aan de plant laat zitten — moeten hierbij sterk worden belicht en vandaar dat snel te werk moet worden gegaan. Lloyd's methode vraagt dat de epidermis gemakkelijk van het blad kan worden afgelicht. De epidermis wordt direct ondergedompeld in absolute alcohol of dioxan — voor tomaten zou dioxan het beste fixatiemiddel zijn — en wordt vervolgens bekeken onder een microscoop. Zie voor kritiek op Lloyd's methode en op de methode van directe waarneming bij Oppenheimer (10).

Shmueli found Lloyd's method satisfactory only with cowpeas, while the collodion method was best suited for bananas and maize (15, 17). Hij demonstreerde mij laatst genoemde methode. Het collodion werd met behulp van een kwastje op het blad gebracht. Het vormde zeer snel een vlies, dat van het blad werd afgelicht en werd bekeken onder een microscoop. Shmueli zei dat deze methode alleen geschikt is voor niet-behaarde bladeren (dus niet voor tomatenbladeren), waarvan de huidmondjes zich op ongeveer gelijke hoogte bevinden als de epidermis (dus niet voor bladeren met ingezonken huidmondjes). Collodion zou bestaan uit ongeveer 5% cellulosenitraat, 25% alcohol en 70% aether. Het zou worden geleverd door onder andere Pharmacie Belgique (vragen naar no. 4) en Merck.

Shmueli heeft voor mij ook de infiltrationmethode gedemonstreerd. De vloeistof werd met een knijppipet op het blad — meestal op de onderzijde — gebracht. De diverse onderzoekers hebben met elkaar reeds een groot

aantal verschillende vloeistoffen gebesigd. In de doorgenomen literatuur ben ik de volgende tegen gekomen.

Oppenheimer (9, 10): kerosene; mixture of turpentine oil and castor oil in the proportion 2:1; paraffin oil.

Oppenheimer (11): ethyl alcohol; xylol.

Hygen (12): vloeistoffen volgens Dietrich.

Alvim (13): mixtures of Nujol and xylol; mixtures of Nujol and kerosene.

Schorn (mededeling van Shmueli): mengsels van aethyleenglycol en isobutylalcohol.

Kramer (4): mixtures of Nujol and n-dodecane.

Alvim (13) schrijft naar aanleiding van zijn onderzoek het volgende. The results show that stomatal aperture decreases much before water content in the soil reaches the so-called permanent wilting point. A solution made up of 80% Nujol and 20% xylol or kerosene can apparently be used to indicate drought threshold in sugarcane and wheat. For cacao, which has smaller stoma-ta, a solution with 40% Nujol and 60% xylol or kerosene is recommended.

Shmueli noemde als volgorde van afnemende snelheid van binnendringen: xylol; kerosene en isobutylalcohol; turpentine oil en clove oil; aethyleenglycol; paraffin oil. Bij tomaten voldoet volgens hem een mengsel van 2 delen paraffin oil en 1 deel benzol zeer goed. Met behulp van Lloyd's methode heeft hij kunnen vaststellen, dat het aantal seconden — benodigd voor het binnendringen van dit mengsel — op de volgende wijze samenhang met de in procenten uitgedrukte openingstoestand van de huidmondjes (15): 2 (100%), 3 (90%), 4 (80%), 5 (70%), 6 (60%), 7 (50%), 8 (40%), 9 (30%), 10 (20%). Bij langere tijden waren niet alle huidmondjes meer open en was de volgende samenhang aanwezig: 11 (19%), 12 (18%), 13 (17%), 14 (16%), 15 (15%). Langere tijden dan 15 seconden werden niet aangehouden. Wanneer het met vloeistof bedekte deel van het blad na deze tijdsduur niet geheel gefimpregneerd was, werd genoteerd of er veel (II), weinig (I) of geen (0) gefimpregneerde plekken waren: 15 II (10%), 15 I (5%), 15 0 (0%). Zie voor de notering van de infiltratiegegevens ook bij Oppenheimer (9,10).

Zoals reeds is vermeld werkte Shmueli bij zijn promotie-onderzoek met de gewassen banana, maize en cowpea (17). Examination of stomatal opening by means of infiltration tests performed between noon and 1.00 p.m. provides reliable information concerning the response of the banana to reduction of available moisture below optimum range, i.e. below two-thirds of total available water. Thus, infiltration tests provide a useful and practical indicator to the need for renewal of irrigation. In the case of maize, the differences

in the stomatal openings as influenced by the variations in soil moisture were particularly evident between the hours 9.30 and 11.30. Ook voor cowpeas werd tussen de beschikbaarheid van het bodemvocht en de openingstoestand van de huidmondjes een bruikbare samenhang gevonden.

Transpiratie

Kramer (4) schrijft over de transpiratie onder meer het volgende. The transpiration rate of well-watered plants is controlled by such plant factors as leaf area, internal leaf structure, thickness of cutin and extent of stomatal opening, and by such environmental factors as solar radiation, humidity temperature and wind. It seems possible that more attention ought to be given to plant factors that reduce water loss, such as thickness of cutin and responsiveness of stomata. Emphasis on the idea that evapotranspiration should be potentially equal from all types of vegetation cover has led to neglect of the probability that differences in rate of water loss may exist between different kinds of plants. It seems very probable that, under identical environmental conditions, plants with thick layers of cutin and stomata that close promptly as soon as a water deficit begins to develop are likely to survive drought better than those with less responsive stomata. There is reason to doubt if evapotranspiration is the same from all types of plant cover.

Midday reduction in photosynthesis occurs in plants of many species on sunny days. This reduction is usually attributed to midday closure of stomata. It does not occur on cloudy days.

Ik vestigde Kramer zijn aandacht op het onderzoek te Silsœ, waar men bij een goede watervoorziening voor tomaten en anjers onder glas heeft gevonden, dat gedurende de zomermaanden de transpiratie wordt bepaald door de insstraling. Dit wijst niet op een sluiting van de huidmondjes, evenmin als op een "control of the transpiration by other plant factors" (aangenomen dat het gewas de grond geheel overdekt). Kramer zei dat voor glasteelten — succulente planten — de "control of the transpiration by plant factors" inderdaad wellicht van weinig belang is. Hij verwacht dat in de natuur de plantensoorten alleen dan verschillend transpireren, wanneer zij sterk verschillen in bouw (internal leaf structure, thickness of cutin, enz.). In Ohio hebben ze volgens hem over de transpiratie van tomaten veel onderzoek verricht; dit niet zozeer over korte als wel over lange perioden.

Transpiration ratio

Plant scientists have long been interested in differences in the efficiency with which plants of different species use water (4). This is usually

expressed in terms of pounds of water used per pound of dry matter produced, and is often termed the water requirement. This is an unfortunate, because there is no specific water requirement, but only a highly variable ratio of water used to dry matter produced. Since this ratio is largely controlled by transpiration, it might more accurately be termed the transpiration ratio. Miller (8) summarized much of the early work on transpiration ratio.

It has been known for many years that fertilization and other cultural practices that increase yields usually increase the efficiency of water use by crops. This is supported by extensive investigations by Arland and colleagues at Leipzig. It was claimed that increasing nitrogen supply reduced transpiration ratio, by changing the pattern of growth rather than by decreasing transpiration per unit of leaf surface.

Beregening en transpiratie

Rate of photosynthesis is rarely limited by lack of water as a reagent, but is often limited because dehydration of protoplasm reduces its photosynthetic capacity and because stomatal closure reduces the supply of carbon dioxide (4). Stocker and associates regard midday sprinkling of crops in hot weather as very beneficial by keeping leaves turgid and stomata open, preventing a midday decrease in photosynthesis. The cooling effects of sprinkling might also reduce respiration, thereby increasing net photosynthesis. Showers too light to increase soil moisture materially may be quite beneficial in decreasing internal water deficits. Irrigation by sprinkling during periods of high evapotranspiration might produce unexpectedly good results in proportion to the amount of water applied if wetting the leaves increases photosynthesis and, by its cooling effect, decreases respiration. Dew and atmospheric moisture may also increase growth far beyond the same amount of water added to the soil, because it produces direct rehydration of tissues.

Kramer (18) investigated the effect of drops of water on leaf temperatures. The leaves were exposed to the sun or to a 500 watt mazda lamp. The temperature of the leaf areas covered with water drops was 4 to 12°C. lower than the temperature of the dry areas. Wetted leaves placed a few inches from a mazda lamp remained uninjured, while dry leaves similarly exposed were killed by the heat. It was found that drops of water probably cannot cause injury by acting as lenses and concentrating the sun's rays on the leaf tissues because the focal length of such drops is usually much greater than the thickness of the leaves. It is concluded that injury to leaves from exposure to the sun while covered with water drops is much less common than popularly supposed and possibly never occurs.

Kramer (6) vermeldt dat Curtis en Clark (O.F. Curtis and D.G. Clark: An introduction to plant physiology. Mc. Graw Hill, New York, 1950) een li-

teratuurbespreking wijden aan de transpiratiekoeling. Jones vond bij een met een rapid weighing method (zie de desbetreffende paragraaf) uitgevoerde "comparison of untreated leaves and leaves sprayed with water, that the stomatal closure took place in the wetted leaves at a higher moisture content" (R.L. Jones: The effect of surface wetting on the transpiration of leaves. *Physiol. Plant.* 10:281-288, 1957).

In tegenspraak met het voorgaande schrijft Maximov (7) naar aanleiding van literatuurgegevens het volgende. The moistening of the leaf surface with water may lead to harmful consequences, as it increases the intensity of transpiration, thus accelerating the loss of water and bringing nearer the moment of wilting. This rapid drying after surface wetting is well known to practical workers; gardeners avoid watering plants when directly insolated and farmers know that grass mown when it is dewy dries better and more rapidly. Het is niet onmogelijk dat de door Maximov vermelde waarnemingen betrekking hebben op gevallen, waarin de cuticulaire transpiratie in verhouding tot de transpiratie via de huidmondjes van groot belang was. Dit zou dan een verklaring kunnen vormen voor de gesigneerde tegenspraak. Wellicht namelijk dat door bevochtiging van het blad wel de cuticulaire transpiratie wordt bevorderd, maar niet — of slechts weinig — de transpiratie via de huidmondjes. Kramer (6) vermeldt "that soybean plants subjected to water deficits developed larger amounts of lipids in their leaves, which reduced cuticular transpiration". Hij beval mij de lezing aan van Kamp (H. Kamp: Untersuchungen über Kutikularbau und kutikuläre Transpiration von Blättern. *Jahrb. wiss. Bot.* 72:403, 1930) en van Linskens (H.F. Linskens: Ueber die Änderung der Benetzbarkeit von Blattoberflächen und deren Ursache. *Planta* 41:40-51, 1952).

Boon-Long (19) vond bij een onderzoek het volgende. Evaporation from open solutions is influenced by solutes to the same degree as the lowering of the vapor pressure gradient from the solution to the air, but when a collodion membrane is between the solution and the air the rates of evaporation may be reduced more than ten times what would be indicated by the lowering of vapor pressure gradient as calculated from the vapor pressure lowering of the solution behind the membrane. Several treatments of plant parts that resulted in increasing osmotic concentration of sap also resulted in a decrease in transpiration rates. These treatments involved a direct introduction of glucose, exposure of leaves to light, etc. It was found that high osmotic concentration brought about by these methods lowers the permeability of the tissues to water as tested by a plasmotic method. When the osmotic concentration was increased by lowering the temperature, however, the hardened cabbage tissues transpired more rapidly,

as compared with the unhardened tissues. This increase in transpiration was associated with a marked increase in water permeability of the hardened tissues. These findings lead to the conclusion that the permeability of plant cells to water has an important effect on the rate of transpiration.

De resultaten van Boon-Long vormen wellicht een aanwijzing, dat de transpiratie — speciaal de cuticulaire transpiratie — inderdaad door bevochtiging van het blad kan worden bevorderd (verlaging van de OP). Van de door Kramer (31) aangehaalde resultaten van Eaton kan dit niet worden gezegd. Eaton grew six species of plants in sand cultures. The evapotranspiration from plants in chloride solutions with an OP of 6 atm. was only about one-third of that from plants in a solution with an OP of 0.7 atm., even though the gradient of OP from solution to plant was 11 atm. in both solutions. Weliswaar vond Eaton dus als gevolg van een verhoging van de OP van de voedingsoplossing — waarmede tevens de OP van het plantensap werd verhoogd — een sterke afname van de transpiratie, maar ook de groei van de planten werd door deze maatregel sterk geremd (geringe groei houdt in geringe transpiratie).

When the stomata are closed, water loss is controlled by the characteristics of the cuticle or by the waxy layer covering the leaf epidermis (4). This suggests the possibility of reducing cuticular transpiration by applying some sort of waterproof film to the leaves, and coatings of wax and latex have proved moderately successful in protecting nursery stock and other plants after transplanting. Various practical difficulties limit their usefulness at present, but they show promise for some purposes where water conservation is more important than reduction in photosynthesis.

Miller (8) geeft een uitvoerige literatuurbespreking over de invloed van ziektebestrijdingsmiddelen — speciaal Bordeaux pap — op de transpiratie. Als gevolg van deze middelen is zowel toename als afname van de transpiratie geconstateerd.

Voeding en transpiratie

Kalium wirkt quellend auf den Protoplasma, Calcium entquellend (3 s.). Das erste erschwert die Wasserabgabe, das zweite erleichtert sie. Die Natur der Pflanze wirkt sozusagen diesem das natürliche Wassergleichgewicht störenden Zustand entgegen. Die Kaliumpflanzen zeigen besonders im Haupteigenen morphologisch-anatomische Verhältnisse, die die Wasserabgabe erleichtern; die Calciumpflanzen solche ^{die} sie erschweren. Überwiegt die primäre protoplasmatische Komponente, so zeigen die Kaliumpflanzen eine geringere Transpiration als die Calciumpflanzen. In Einstalzlösungen von Nitraten von Na, K, Mg und Ca ist eine mit der entquellenden Wirkung der

Kationen zunehmende Wasserabgabe gefunden (Quellungsreihe: $\text{Na} > \text{K} > \text{Mg} > \text{Ca}$). In gefäßversuchen bewirkten Sulfate die stärkste Wasserabgabe, Chloride die geringste (Quellungsreihe: $\text{Cl} > \text{NO}_3 > \text{SO}_4$).

Mit steigenden Stickstoffgaben nimmt der Wassergehalt des Pflanzensaftes zu, der Wassergehalt im Pflanzrückstand ab. Relativer Stickstoffmangel bewirkt eine Verschiebung des Wassers in die Kolloide (Zunahme der Quellfähigkeit). Relativer Stickstoffüberschuss dagegen ruft eine Verschiebung des Wassers in den Zellsaft hervor (Abnahme der Quellfähigkeit). In denjenigen Versuchen die eine Steigerung der Transpiration bei Stickstoffernährung erkennen lassen, kommt die unmittelbare kolloidchemische Wirkung des Stickstoffs im Protoplasma zum Ausdruck.

Die physiologische Rolle des Bors beruht wenigstens zu einem Teil auf Entquellung des Protoplasmas. Mit der Annahme einer entquellenden Wirkung des Bors wäre auch die direkte Beeinflussung der Wasserabgabe und die damit gesteigerten Transpirationsleistung der borgedüngten Pflanzen in Übereinstimmung gebracht.

Wanneer het bovenstaande juist is, dan moet de conclusie worden getrokken dat "die primäre protoplasmatische Komponente" niet steeds overweegt. Als gevolg van boriumbemesting is namelijk ook wel afname van de transpiratie geconstateerd. Ook met andere elementen zijn aan elkaar tegengestelde ervaringen opgedaan. Zo nam Mothes (3 s) waar dat "Stickstoffmangelpflanzen xeromorphe Strukturen annahmen". Die absolute Transpiration zeigte keine wesentlichen Unterschiede; auf die Blattfläche bezogen transpirierten jedoch die Stickstoffhungerpflanzen mehr als die normale.

Rapid-weighing method

The simplest measure for transpiration is the rapid-weighing method, using leaves or branches cut off the plant immediately prior to the first weighing (F.W. Went: The experimental control of plant growth. Chronica Botanica no. 17. The Ronald Press Company, New York, 1957). It has been pointed out by many investigations that this use of detached leaves or branches for transpiration measurements is attended by several errors. Even if the measurements are carried out over short intervals of time, the sudden release of negative tension in the vessels may cause a temporary increase in transpiration rate which is an artifact due to the cutting. Besides, no continuous record of the transpiration rate can be obtained in this way, since the leaf or branch is destroyed after the weighings.

De rapid-weighing method is onder meer toegepast door Shmueli (15, 17), Oppenheimer (9, 10, 11) en Jones (zie de paragraaf Berekening en

transpiratie). Hygen (12) heeft haar uitvoerig onderzocht. Door wiskundige analysering van de verkregen gewichtscurven wist hij allerlei leerzame conclusies te trekken. Onder meer kan uit de curven de openingstoestand van de huidmondjes worden afgeleid (zie ook Jones).

Anwelkmethode

De Anwelkmethode van Arland (zie de paragraaf Transpiration ratio) komt nauw overeen met de rapid-weighing method. Kramer noemde mij de volgende literatuur:

Institut für Acker- und Pflanzenbau der Karl-Marx-Universität, Leipzig (Redaktion: A. Arland): Die Anwelkmethode im Dienste des Landbaues. Veb Deutscher Verlag der Wissenschaften, Berlin (1955).

A. Arland und J. Enzmann: Ein Beitrag zur Technik der Anwelkmethode. Zeitschrift für Acker- und Pflanzenbau 101:5-21 (1956).

R. Zwicker: Die Transpirationsintensität der Kartoffelpflanze unter besonderer Berücksichtigung der Beurteilung des Pflanzwertes. Wissenschaftliche Zeitschrift der Karl-Marx-Universität, Leipzig, Mathematisch-Naturwissenschaftliche Reihe 4:105-151(1954-1955).

R. Zwicker: Die Anwelktranspiration unter besonderer Berücksichtigung der Temperatur des Substrates im Hinblick auf die Ermittlung vergleich- und reproduzierbarer Versuchsergebnisse bei der Kartoffel. Die Deutsche Landwirtschaft, Januar 1956:1-4.

R. Zwicker: Die Anwelktranspiration im Blickfeld des Welkens der Pflanzen. Zeitschrift für Acker- und Pflanzenbau 101:431-452 (1956).

Plant en total soil moisture stress

There has been much argument as to the time when transpiration begins to decrease in plants in drying soil (4). Weihmeyer and Hendrickson long contended that transpiration does not decrease materially until soil moisture falls almost to the permanent wilting point, but it now seems clear that transpiration and other physiological processes are usually affected considerably earlier. Most of the controversy on this subject could have been avoided had it been realized more clearly that plant processes are controlled directly by the water content of the plant and only indirectly by the water content of the soil.

There has been much discussion as to whether photosynthesis is materially reduced before soil water approaches the permanent wilting point. It was reported that photosynthesis of apple leaves was reduced 50 per cent before wilting was visible and in wilted leaves fell to only 15 per cent of the expected rate. Similar results were reported for several forest

trees. On the other hand, no reduction in photosynthesis was observed in some other plants until the readily available soil moisture was almost entirely depleted, although the rate fell rapidly when wilting occurred. There is some evidence that rate of photosynthesis is maximum in some leaves at slightly less than maximum leaf turgor; this has been attributed to the wider stomatal apertures at slightly less than maximum turgidity. But, opposed to this view is the claim that, in at least some plants, the stomata exercise less control over photosynthesis than over water loss. It was reported that the porosity of corn leaves to gases was greatly reduced by wilting, but lack of high correlation between porosity (measured with a porometer) and photosynthesis indicated that factors in addition to stomatal closure are responsible for the reduction in photosynthesis.

Ordinarily, a decrease in water content is accompanied by a decrease in respiration, but respiration occasionally increases during dehydration. Increased respiration combined with a decreased photosynthesis, can seriously reduce the amount of food available for other processes. A decrease in leaf size from lack of turgidity is especially serious because it decreases the photosynthetic surface and production of food. According to Watson, yield of crops is more closely related to leaf area than to variations in photosynthetic efficiency per unit of leaf area.

The nature and course of various biochemical reactions are often changed by water deficits, resulting in changes in chemical composition. Best known is the decrease in proportion of starch to sugar in plants subjected to water deficits, because of increased hydrolysis of starch. In most instances, total carbohydrate reserves are decreased. In general, water deficits seem to increase nitrogen content, but this probably depends on the stage of growth at which the deficit develops and on the organ sampled.

Gates found that even moderate wilting affects plant growth and claimed that it is erroneous to suppose that plant growth is affected only after permanent wilting is reached. He found, relative to tomato plant weight, that leaf weight increase was slowed down while stem weight increase was increased, and that, after recovery from wilting, growth rates of moderately to slightly wilted plants soon increased above the growth rate of controls.

According to Slatyer (5), there is now general agreement that soil water becomes progressively less available to plants as MSMS increases. He suggested that permanent wilting occurs at a stress value such that there is zero TP in the leaf tissue. This implies that the permanent wilting point is a value determined not by any particular soil characteristic

but by the osmotic characteristics of the plants, and as a result could vary considerable from plant to plant.

Growth (as increase in total dry weight) and elongation will finally be completely inhibited by decreasing hydration, and it is logical to assume that in any one tissue growth will cease at or before a DPD exists such that there is zero TP in the cells of the tissue concerned; such a degree of dehydration should be reflected in a permanently wilted appearance of the leaves. In the results presented this hypothesis appears valid. In tomato and cotton, increases in dry matter ceased approximately at the same DPD as that at zero TP in typical adult leaves. In privet, cessation occurred at much lower stress values. This may have been due partly to sampling error and partly to the fact that the RT at zero TP was highest in privet.

Cessation of elongation in privet and cotton occurred at stress values close to those obtaining at zero TP in the adult leaves. In tomato, elongation continued until very severe stress existed and until the plant as a whole was losing dry weight. A similar result was reported for tomato by Wilson (zie 6). It is probable that in young elongating tissue most of the cells are not completely vacuolated and osmotic theory is not strictly valid. Herr and Anderson (zie 3 n) considered that imbibitional forces in developing cotton bolls enabled development to proceed at water deficits which stopped the growth of other tissues, and a similar situation possibly existed in the apical tissue of tomato.

Although Veihmeyer and Hendrickson have claimed that transpiration is unaffected by TSMS until the permanent wilting point is reached, when they consider that it virtually ceases, there is no valid physical or physiological reason why this should necessarily be so, and in general investigations of plants in their natural habitats and in containers have demonstrated continued absorption of soil water to values well below the permanent wilting point (5). In the present study these general contentions were borne out, reductions in transpiration rate first occurring at low stress values, but continued transpiration being observed, although at reduced rates, until the conclusion of the experiment, when the soil water content was 2.4 - 5.3 per cent below the value at 15 atm. TSMS. Depending on the sensitivity of stomatal closure, the effectiveness of stomatal control and on the actual rates involved, transpiration is generally ^{less} affected by low levels of soil moisture stress than is growth or metabolism, since transpiration is primarily a passive phenomenon controlled by atmospheric conditions and rate of movement of soil water to the absorbing surfaces of the roots.

At high stress levels there was strong evidence of nocturnal absorption of water directly from the atmosphere and its accumulation in the tissues of the shoots. Although a diffusion gradient appeared to exist favouring movement of water out of the plant into the soil no evidence of such movement was obtained (this is attributed to the development of discontinuity in root-soil contact). This has an interesting practical implication, as it suggests a mechanism whereby plants in dry soil could use atmospheric water for re-saturation of tissues without losing this water to the soil.

Shmueli (17) found that reduction of soil moisture below two-thirds down to one-third of total available water in the root zone resulted in a significant decrease in the water and dry-matter content of banana leaves and a decrease in the average daily stomatal opening (up to 25 per cent). In maize plants, the reduction of moisture in the root zone below 40% of available water resulted in a significant decrease in the yield grown for fodder. There was also a decrease in the average daily stomatal opening (45 per cent).

Gunstige effecten van droogte en zout

Sometimes a moderate water deficit produces desirable changes in composition (4; zie voor gunstige effecten van droogte ook het voorgaande hoofdstuk). For example, the rubber content of guayule plants is increased by a moderate water deficit (zie ook 6 en 16) and the quality of apples and of pears is improved by moderate moisture stress during the latter part of the season. In soybean leaves subjected to wilting an increase in lipids was found, which was accompanied by decreased transpiration and increased resistance to dehydration. Tobacco subjected to a moderate water deficit produces leaves with more body and aroma than does tobacco not so treated. It is said that water stress during maturation increases the protein content of wheat.

In general, water deficit hastens maturation of cells and tissues, increases the thickness of cell walls and decreases succulence. This not only decreases the size of plants and their yield, but may also decrease quality, especially in the case of pasture and hay crops. On the other hand, the increased amount of dry matter and supporting tissue produced in plants subjected to a moderate water deficit may be beneficial by increasing stem strength or resistance of fruit to injury by bruising. The increased thickness of cutin often found on plant organs matured in dry air is beneficial because it reduces cuticular transpiration.

The per cent of sugar in cane and beets was raised by increasing the

moisture stress (16). A study of the influence of soil moisture stress on various aspects of growth in Ladino clover has shown that increasing soil moisture stress decreases forage production and potential seed production, but increases the yield of harvestable seed; it holds preharvest germination of newly produced seed to a minimum by keeping dry the atmosphere around the plants.

Koffie schijnt voor het in bloei komen enigszins droog te moeten worden gehouden (P. de T. Alvim: Moisture stress as a requirement for flowering of coffee. Science 132:354, 1960).

When the molecular proportion of the salts in the solution was changed, the optimum concentration for wheat growth was between 4.5 and 5.5 instead of at 1.6 atmospheres (8).

Milieu en osmotische waarden in planten

Harris and Walter collected a large amount of data on the OP of plants growing in various habitats (3 f, 3 n, 6; zie ook H. Walter: The water economy and the hydrature of plants. Ann. Rev. Plant Physiol. 6: 239-272, 1955). Increase in OP of the plant sap occurs when the OP of the soil solution is increased, although this is not invariably true (3d; zie voor literatuur betreffende dit hoofdstuk ook 8).

Verschillende auteurs (3 c, 3 n, 3 r) bespreken de stoffen, die de OP in planten veroorzaken. Zie in dit verband ook Slatyer (5: blz. 327 en 333), Shmueli (2: blz. 230 en 236) en Bernstein (L. Bernstein: Osmotic adjustment of plants to saline media. I Steady state. Amer. J. Bot. 48: 909-918, 1961).

Volgens Mothes (3 s) is de OP in planten met stikstofgebrek groter dan in normale planten. Zie Tsui voor de invloed van zink op de OP van tomateplanten (C. Tsui: The effect of zinc on water relations and osmotic pressure of the tomato plant. Amer. J. Bot. 35: 309-311, 1948).

Shmueli (17) found that the OP of banana roots was significantly higher when soil moisture was below one-half of total available water as compared with OP prevailing under conditions of higher soil moisture content. In the leaves, the highest OP and the lowest relative water content were recorded when the soil contained approximately three-quarters of total available water. The OP of leaves was lowest when available water in the soil approaches the state of depletion. Conspicuous yellowing of leaves occurred when available water was down to one-third.

When moisture in the root zone decreased to below 50%, the OP of maize leaves rose 28% and of maize roots 69%.

Shmueli (2) found that OP of banana leaves varies very little during

the winter and is similar to the summer level. In banana leaves uninjured by frost, OP never exceeded 15 atm. However, much higher osmotic pressures of 17-18 atm. may be reached in the green bases of leaves damaged by frost. Banana leaves attained even higher osmotic pressures following the occurrence of an unusual snowfall; two days after the snow had thawed off the leaves, osmotic pressures close to 21 atm. were recorded. Sap analysis showed that the quantity of reducing sugars was approximately double the normal amount. Following chilling (chilling damage is niet hetzelfde als frost injury), changes also appear in the OP of the cell sap. These are also apparently related to increased hydrolytic activity and the resultant increase in sugar concentration. These changes do not take place immediately but develop slowly and are most pronounced about twenty days after chilling. Yet, even before this, changes in the appearance of the leaf indicate decomposition of chlorophyll and an increase in the permeability of the cell membranes.

Permeabiliteit

A high concentration of CO_2 and low temperature produce rapid decreases in permeability of the protoplasm to water (31). Respiration inhibitors and deficient aeration reduce both active and passive absorption, probably chiefly because reduction in rate of respiration reduces the permeability of the roots.

Although Brouwer concluded that decrease in root turgor, caused either by increased transpiration or by increase in OP of the substrate, increases permeability of the roots to water, this probably can be true for only a short period and for limited regions of roots. It has been demonstrated that prolonged moisture stress decreases the permeability of the roots to water, both by causing increased suberization of the root surfaces and possibly because of protoplasmic effects.

Iljin (14) vermeldt daarentegen het volgende. Studies by various workers point out the fundamental structural changes undergone by protoplasm submitted to desiccation. Viscosity is lowered and permeability is increased. Artificial shaking produces similar effects.

Schroeder found that watering the soil with cold water often caused serious injury to greenhouse grown cucumbers because at soil temperatures below 20°C water absorption was seriously reduced (31; zie ook 3 a). Kramer found that active absorption of tomato root systems, as measured by exudation from their stumps, attained a maximum at about 25°C and decreased as the soil temperature was increased.

The potassium ion with its small charge and large hydration shell

tends to increase permeability; similarly it generally increases swelling and hydration of proteins (3 e). On the other hand, the divalent calcium ion decreases permeability and likewise usually decreases swelling and hydration of proteins.

Sodium ions in a single-salt solution may penetrate protoplasm, leading to a pronounced swelling (3 k; zie ook 3 h). If, however, calcium ions are added to the solution in about $\frac{1}{10}$ the concentration of the sodium ions, swelling does not occur, because the calcium ions prevent the penetration of the sodium ions. In the unbalanced single-salt sodium solution the cell soon dies. The single-salt calcium solution, however, is non-injurious to most cells, because the calcium ions presumably decrease the permeability of the cell to themselves as well as to other ions.

Voor de invloed van de OP op de permeabiliteit wordt verwezen naar de paragraaf Beregening en transpiratie.

Chilling injury of banana leaves results in decomposition of chlorophyll and increased permeability of the cell membranes (2). Lieberman e.a. have shown conclusively that chilling damage is related to an increase in the permeability. The changes observed in the leaves of the banana following chilling suggest that chilling causes physiological changes similar to those of senescence. The hypothesis of physiological similarity between chilling damage and natural ageing is supported by the work of Sacher which established that: 1) senescence is accompanied by an increase in permeability; 2) increase of permeability and senescence can be largely prevented by the addition of auxins.

Imbibitie

De imbibitie van het protoplasma is reeds ter sprake gekomen in de paragraaf Voeding en transpiratie en in het hoofdstuk Permeabiliteit.

Biebl (3 s) geeft de volgende Quellungsreihe: $\text{Li} \lessdot \text{Na} \lessdot \text{K} \lessdot \text{Rb} \lessdot \text{Cs} \lessdot \text{Mg} \lessdot \text{Ca} \lessdot \text{Al}$. Fisher (3 i) vermeldt voor de alkalikationen de volgende Hydratationsreihe: $\text{Li} > \text{Na} > \text{K} > \text{Rb} > \text{Cs}$; deze ionen staan hierin dus in dezelfde volgorde als in de Quellungsreihe (zie ook 3 j en q). Voor enkele anionen geeft hij de Hydratationsreihe: $\text{SO}_4^2- < \text{Cl}^- < \text{Br}^- < \text{J}^- < \text{SCN}^-$ (zie ook 3 s).

Protein is the principal water binding substance of the protoplast (3 j). The cell wall is highly colloidal and presents a tremendous surface among the cellulose micelles and pectic materials. The more open the fibrillar structure, i.e. long side chains and a pH fairly distant from the isoelectric point, the more easily water will penetrate the structure and imbibition and swelling will be at maximum (zie voor het iso-elektrische punt ook 3 i en 3 q).

Eine direkte Veränderung des Quellungsgrades können Ionen nur bei solchen Kolloiden auslösen, in die sie auch einzudringen vermögen (3 q). Für die Bildung von Ionendipolen wiederum kommen unter den permeablen Ionen nur diejenigen in Betracht, die eine dem Kolloid entgegengesetzte elektrostatische Ladung aufweisen. Sofern Elektrolyte nicht zu permeieren vermögen, bewirken sie auch keinen osmotischen Ueberdruck im Kolloid; vielmehr treten sie mit diesem in Konkurrenz um dessen Quellungswasser (zie ook 3 h). Das kann mit zunehmender Elektrolytkonzentration so weit gehen, dass das Kolloid einen so erheblichen Teil seines Wassergehalts einbüsst, dass es instabil wird und ausflockt. Bei gleicher Konzentration müssen nicht-permeable Ionen demnach um so stärker entquellend wirken, je ausgeprägter ihre eigene Hydratationstendenz ist (zie ook 3 i). Das erklärt die Beobachtung, dass sich für impermeable Gele die lyotropen Ionenreihen umkehren.

Irreguläre Ionenreihen kommen sehr häufig dadurch zustande, dass Lithium und Magnesium andere Plätze einnehmen, als ihnen gemäß ihrer Stellung innerhalb der lytropen Innenreihen zukommen würden. Die beiden Ionen benehmen sich so, als seien sie schwächer hydratisiert als ihrer Hydratationswärme entspricht. So steht in vielen Übergangsreihen das Lithium zwischen dem Kalium und Natrium. Gleich häufig nimmt das Magnesium eine Zwischenstellung zwischen den Alkalien und den Erdalkalimetallen ein.

Proteine reagieren insbesondere mit mehrwertigen Ionen. Dabei werden bevorzugt Calcium-Ionen gebunden.

Op de regel dat kaliumionen de imbibitie bevorderen en dat calciumionen haar tegengaan, komen tal van uitzonderingen voor (3 i). Zo is gevonden dat bij tomatenplanten met kaligebrek het watergehalte aanvankelijk lager is dan bij controleplanten en in latere ontwikkelingsstadia hoger (zie ook de paragraaf Voeding en transpiratie).

In manchen Versuchen ist eine Viscositätszunahme des Plasmas durch Calcium- und eine Viscositätsabnahme durch Kalium-Behandlung gezeigt worden (3 h). It was noted that the chlorides of sodium, potassium and lithium lowered while the chlorides of calcium and barium raised the elastic limit or extensibility of the protoplasm (8).

The imbibitional forces of cell walls and protoplasm enable them to hold considerable water, but these forces usually tend to come into equilibrium with the osmotic forces of the vacuolar sap and therefore do not require separate consideration (3 l; zie echter ook het hoofdstuk Plant en total soil moisture stress).

Droogte- en vorstresistentie

It seems that drought resistance may depend on various characteristics occurring throughout the plants (4). These may range from depth of rooting, thickness of cutin and responsiveness of stomata, to permeability, structure of protoplasm and reaction of enzyme systems to dehydration.

Permanent wilting (accompanied by destruction of the root hairs) was observed, when the leaves had lost 40 per cent of their water content (7). On the other hand, it was found that the leaf cells themselves did not usually begin to die until they had lost 70-80 per cent of their water. Evidently the roots are injuriously affected by drought considerably earlier than the leaves and under natural conditions a plant with desiccated roots but still living leaves is doomed to perish (zie ook het hoofdstuk Permeabiliteit).

Protoplasmic properties such as permeability and viscosity are modified by water deficits, but there is no general agreement as to the nature or causes of these changes (4). We are almost entirely ignorant of the protoplasmic factors that give some plants greater resistance to dehydration than others. Some of these differences are related to cell size and shape, but there are also basic differences in protoplasmic characteristics that have not yet been adequately explained. Russell e.a. (16) noemen een aantal auteurs, die de literatuur over droogteresistentie hebben samengevat.

If dehydration is severe enough, the protoplasm may actually become rigid to the degree of brittleness (30). On transfer of plasmolyzed cells to a weaker solution, deplasmolysis may proceed only part of the way and then the rigid protoplasm layers rupture and the cells are killed. Many plants can be adapted (hardened) to more severe dehydration, if they are first subjected for several days to moderate dehydration. When hardened and unhardened cells are subjected to the same degree of dehydration, the hardened protoplasm has a lower viscosity than the unhardened and a higher permeability to water and other polar substances (zie ook het hoofdstuk Permeabiliteit). Even when exposed to more severe dehydrating forces than those capable of producing rigidity and rupture of the unhardened protoplasm, the hardened protoplasm does not become rigid and brittle. These facts indicate that the hardened protoplasm has a greater ability to hold water against dehydrating forces.

Different methods of dehydration all appear to be injurious to about the same degree (31). The hardiness of a plant can be increased in several

ways. Even simply starving the plant for nutrients such as nitrogen may be effective.

Für die Fröckenresistenz betrachtet Henckel (3 p) die einer mechanischen Zerreisung des Plasmas entgegenwirkende Elastizität als entscheidend.

Prüft man die Austrocknungsresistenz einzelner Zellen höherer Pflanzen, etwa indem man Gewebeabschnitte über Lösungen bekannten Dampfdruckes bringt, so findet man die Letalpunkte durchweg bei nahe 100% liegenden relativen Feuchtigkeiten. Die grossen Zellen der Mark- und Wassergewebe sterben schon in Luft von 99% relativem Dampfdruck, Mesophyll und Epidermiszellen von Hygrophyten bei 97-96%, solche von Xerophyten teilweise erst bei 85%. Wenn man aber die Plasmastruktur aussergewöhnlich schonend behandelt, d.h. das Austrocknen über vielfach abgestuften Lösungen von H_2SO_4 oder $CaCl_2$ vornimmt, schrittweise vorplasmolysiert und nach dem Versuch noch vorsichtiger deplasmolysiert und einquillt, so lassen sich die von Iljin untersuchten Zellen alle mindestens 2-3 Tage lang in vollständig lufttrockenem Zustand lebend erhalten (zie ook 20). Die Ursache der verschiedenen Resistenz verschiedener Zellarten sieht Iljin neben der art- und gewebespezifischen Plasmastruktur wesentlich in der Grösse der Zellen und Vacuolen. Er betont, dass die Plasmadeformation beim Austrocknen in grossen Zellen stärker ist als in kleinen und dass sie ebenso von der Menge des verdunstenden Zellsaftes abhängt, also in Zellen mit grossen Vacuolen grösser ist als in vacuolen-losen oder -armen. Dass der Trockentod der Zelle keine unmittelbare Folge des Wasserverlustes sei, sondern dadurch entsteht dass der Wasserentzug aus der Vacuole eine rein mechanische Deformation des Protoplasma herbeiführt, die sein Zerreissen verursacht, hat Iljin schon 1927 ausgesprochen.

The experiments of Iljin (20) showed that in cells of volume greater than 75.000 μ^3 the protoplasm dies if the volume is increased 1.6 to 1.8 times. If, however, the cells have a volume less than 10.000 μ^3 , they die if the volume is increased 4 to 5 times. The shape of the ~~the~~ cell is also a factor. Small cells with pronounced differences between length and width are more tolerant than are large spherical or cubical cells. The greater the volume and the less the surface area, the less tolerant is the protoplast.

Various physical agents such as pressure, swelling, blows, etc. destroy the protoplasmic structure and cause death, as Lebeschkin showed in his numerous studies (zie ook het hoofdstuk Permeabiliteit). The protoplasm suffers also very appreciable injury when repeatedly plasmolyzed and deplasmolyzed. The injury is cumulative and finally a condition is

reached when death ensues after only a slight change in turgor.

Green parenchyma tissues of leaves were placed over sulphuric acid in air of differing relative humidities. Each day the tissues were wetted and immediately returned to the same relative humidity chamber. Tissues which were wetted every day and again dried daily declined in tolerance. Presumably repeated changes in turgescence due to transpiration may produce similar loss of ability to recover.

Hoge osmotische waarden bevorderen de droogteresistentie (14). Een-deels is dit een gevolg van een kleine celafmeting (many investigators have noted that the cells of plants of dry regions are smaller than those of wet locations; zie 20) en anderdeels van de concentratie van het celsap. Cells having a sap concentration of 0.25 N may lose half of their water when placed in an atmosphere of 99% relative humidity, as this humidity corresponds with a solution of 0.5 N. Cells with an OP of 1.0 N may be expected to maintain their turgor in an atmosphere of 98% relative humidity. When 70 kinds of plants tissues were grouped according to OP of the cell sap, there was a direct correlation with tolerance to relative humidity.

The principal causes of death of cells subjected to desiccation are the structure of the cells and the presence in each of a large vacuole, which conditions the contraction and expansion of the protoplast (14). Leaf buds of some plants exhibit a striking tolerance to drying (20). The cells of their tissues either lack vacuoles or have very small ones. But during growth the vacuoles increase in size and coincidentally there is a decrease in tolerance to dehydration.

Plant tissues that have been dehydrated may conserve life for long periods, indicating that desiccation itself may not be the cause of death of the protoplasts. It would appear that there are no fundamental differences between the protoplasm of different species with respect to dehydration.

Iljin (14) vermeldt een verdrogingstheorie van Stocker, welke theorie door Levitt is bekritiseerd.

The work of Asahina (2) has advanced the understanding of the mechanism of frost damage. The damage is caused mainly by desiccation of the cells as water is withdrawn while ice is being formed. Maximow (8) believed that death from low temperatures is due to the rupturing of the protoplasm by masses of ice crystals.

Banana leaves are very sensitive to low temperatures, presumably owing to the combined effect of their morphological, anatomical and physiological properties (2). The leaves are very large and have extremely large

cells and intercellular spaces. The water content of the leaves is high and they are very sensitive to change in the degree of hydration. It has also been found that the OP is low. The banana, as like other frost tender plants, is also very drought sensitive. The OP is a good indication of its lack of hardiness.

Attempts to explain cold and drought resistance of plants as the result of a high bound water content have not been satisfactory (3 b).

Waterziek bij tomaat

Bij een gesprek met Kramer en Brix is naar voren gekomen, dat het al of niet optreden van waterziek bij tomaat wellicht samenhangt met een verschil in water stress en/of met een verschil in resistantie tegen water stress. ~~De~~ genoemde factor (directe oorzaak van het waterziek?) is aan grote dagelijkse schommelingen onderhevig, terwijl de tweede factor (maat voor de gevoeligheid voor waterziek?) slechts op langere termijn wijzigingen ondergaat.

Om een verschil in water stress te kunnen vaststellen moet de DPD van zowel blad als vrucht worden gemeten. Het verdient aanbeveling hierbij tevens de OP te meten, die wellicht als maat voor de resistantie tegen water stress kan dienen. Het zou kunnen blijken, dat bij waterige (gevoelig voor waterziek) vruchten de DPD op een gegeven moment groter is dan de OP, terwijl bij droge (niet gevoelig voor waterziek) vruchten de OP groter is dan de DPD.

Het al of niet optreden van waterziek hangt mogelijk samen met de celgrootte van blad en vrucht, met de afstand tussen de vaatbundels in de vrucht en met de cutinisering van het blad. Bij vooroemde metingen kan het van belang zijn om er op te letten, of de vaatbundels van een bepaalde vruchttros in verbinding staan met de vaatbundels van bepaalde bladeren. Kramer noemde in dit verband de boeken van Esau en Hayward (H.E. Hayward: The structure of economic plants. Macmillan Co, New York, 1938; in dit boek worden onder meer beschreven: aardappel, celery, radijs, sla, squash en tomaat).

De verdrogingstheorie van Iljin — de afsterving zou voornamelijk samenhangen met celgrootte en celvorm (zie het vorige hoofdstuk) — lijkt voor de verklaring van het optreden van waterziek zeer aannemelijk. Een verschil in resistantie tegen water stress kan wellicht met zijn methode worden gemeten. Mogelijk heeft ook Levitt op dit terrein iets te bieden.

In het vorige hoofdstuk is reeds vermeld, dat door droogte of zouten de planten kunnen worden afgeharden, waardoor zij minder spoedig last hebben van verdrogingsverschijnselen. Voor het afharden tegen waterziek is het

ene zout effectiever dan het andere. Kaliumzouten zijn in dit opzicht zeer effectief. Waterzieke vruchten bevatten relatief veel calcium. De vraag rijst of dit een gevolg is van de groeiomstandigheden die het waterziek in de hand werken, zonder dat calcium een directe invloed heeft op het optreden hiervan, of dat het laatste wel het geval is. Voor de beantwoording van deze vraag volgt hieronder een tabel, die is samengesteld uit de voorgaande drie hoofdstukken en de paragraaf Voeding en transpiratie:

	imbibitie	permeabiliteit	viscositeit
afharden	verhoging	verhoging	verlaging
calcium	verlaging	verlaging	verhoging
kalium	verhoging	verhoging	verlaging

Uit deze tabel blijkt, dat kalium en afharden de imbibitie, permeabiliteit en viscositeit van het protoplasma in dezelfde zin beïnvloeden, terwijl calcium een tegengestelde invloed uitoefent. Ook het element stikstof past in dit schema: weinig effectief voor het afharden tegen waterziek; verlaging van imbibitie (zie de paragraaf Voeding en transpiratie); stikstofgebrek kan de plant doen afharden (zie vorig hoofdstuk). Het is dus niet onmogelijk, dat de invloed van genoemde elementen op het optreden van waterziek voor een deel berust op een beïnvloeding van de eigenschappen van het protoplasma. De reeds vermelde gegegevens over de invloed die kalium en calcium uitoefenen op de elasticiteit van het protoplasma, zijn echter wellicht hiermede in tegenspraak (zie de twee voorgaande hoofdstukken).

Voedselopname, wateropname en OP van het substraat

Lopushinsky bestudeerde de voedselopname in afhankelijkheid van de wateropname. Hij werkte met wortelpruiken van de tomaat, die in een geraardeerde voedingsoplossing al of niet onder druk werden gebracht. Bij het aanbrengen van druk werd net uit de stomp van de stam stromende sap lager in concentratie. De hoeveelheid sap nam echter zodanig toe, dat ook de hoeveelheid ionen toenam; Lopushinsky had dit reeds vastgesteld voor radiaatief fosfor en de electrische geleidbaarheid en hij was bezig met calcium. De voedselopname wordt dus beïnvloed door de wateropname. De toegepaste drukken waren zodanig, dat de maximale sapstroom ongeveer de helft bedroeg van wat de transpiratie in de intacte planten kon zijn.

Zie bij Long voor het verband tussen zouttoevoegingen aan het substraat en de water- en voedselopname (E.M. Long: The effect of salt addi-

tions to the substrate on intake of water and nutrients by roots of approach-grafted tomato plants. Amer. J. Bot. 30:594-601, 1943).

Eaton (3) found that when root systems of corn and tomato were divided between solutions having osmotic pressures of 0.3 and 1.8 atm. that 1.8 times as much water was absorbed from the more dilute as from the concentrated solution. Growth of root systems left in the more concentrated solution was greatly reduced. This probably was not because of a decreased DPD gradient from solution to plant because when the OP of the environment is increased there usually also is an increase in the OP of the plant sap.

Virus

Follmann (21) onderzocht bij verschillende plantesoorten de invloed die infectie met uiteenlopende virussen heeft op de waterhuishouding van epidermiscellen van stengels en bladeren. Gegenüber Kontrollpflanzen zeigten symptomtragende Pflanzenteile bei starken individuellen Schwankungen einen signifikanten Anstieg der Zellsaftkonzentration sowie der Wasseraufnahmerate. Im Initialstadium der Viruskrankung sowie in älteren Pflanzenorganen wurden keine Unterschiede gefunden. Die Wasserdurchlässigkeit der Protoplasten gesunder Epidermis~~ellen~~ konnte in stärkeren Ausmass als die viruskranker mit Atmungsgiften gehemmt werden. Daraus darf geschlossen werden, dass sie in der gesunder Pflanzenzelle der aktiven Wasseraufnahme zufließende Stoffwechselenergie nach Virusinfektionen anderen Stoffwechselzweigen dient, während der dem höheren Spiegel an osmotisch wirksame Substanzen im Zellsaft entsprechende verstärkte Wasserbedarf durch gesteigerte passive Wasserpermeabilität gedeckt wird. Für die viruskranken Pflanzen bedeutet das eine verstärkte Anfälligkeit gegen verschiedene ökologische Einflüsse, die sich unter anderem in schnellerem Welken manifestiert.

Met betrekking tot thermotherapie van virusplanten schrijven Kassani en Posmette (22) het volgende. Therapy can be achieved either by immersing the infected plants in water at about 50°C. for several minutes or by keeping actively growing plants at about 37°C. for several days.

Groeistof

Many studies have shown that the application of auxin does not immediately alter osmotic concentration but dramatically decreases wall resistance to deformation under load (23).

An increase in the content of water-soluble carbohydrates was observed in all the plants treated either with gibberellin or with heterauxin (24)

Terminologie betreffende waterhuishouding van de plant

Kramer (3 a) used the diffusion pressure terminology of Meyer because the advantages of wide use and general familiarity seem to outweigh the objections offered by Walter and by Levitt. Broyer has proposed a mathematical treatment of cell water relations in terms of specific free energy. The rigorous mathematical treatment made possible by this approach would be more useful if the experimental data on which it is used were more accurate.

Zie voor kritiek over de handhaving van voornoemde terminologie bij Steward (6).

Literatuur

Kramer beval een abonnement op het American Journal of Botany ten zeerste aan. Hij noemt in verschillende van zijn artikelen Fortschritte der Botanik.

Vital staining

Drawert has recently summarized work by himself and others on vital staining (3 d).

Chemisch grond- en gewasonderzoek

Pharis bepaalde het calciumgehalte van gewasmateriaal vlamfotometrisch en wel volgens Jackson (M.L. Jackson: Soil chemical analysis. Prentice-Hall Inc., Englewood Cliffs, N.J., 1958).

Soil and plant water relations

Op dit terrein zijn onder meer de volgende boeken van belang:

E.C. Miller: Plant physiology (8).

M.B. Russell, coord.: Water and its relation to soils and crops (16).

F.C. Steward, ed.: Plant physiology; vol. 2: Plants in relation to water and solutes (6).

North Carolina State College

Op het North Carolina State College heb ik kennis gemaakt met een achttal onderzoekers — in het navolgende te noemen — en voorts met F.D. Cochran. Laatst genoemde is hoofd van het Department of Horticulture.

Voedingsstoffen

Für alle Kationenaustauscher gelten folgende Gesetzmäßigkeiten (3 g)

1. Der Ioneneintausch steigt mit der Wertigkeit des betreffenden Ions; innerhalb einer Wertigkeitsgruppe mit der Atomnummer.
2. Der Ionenumtausch steigt mit der Konzentration (genauer: Aktivität) der Ionen; in hohen Konzentrationen gehen die Valenzunterschiede mehr und mehr verloren (Die Donnan-Beziehung lässt erkennen, dass in physiologisch hohen Konzentrationen einwertige Ionen besser eingetauscht werden als gleichstark hydratisierte zweiwertige; umgekehrt sind mehrwertige Ionen in verdünnten Lösungen im Eintausch bevorzugt).
3. Die Differenzen zwischen dem Eintauschvermögen der einzelnen Ionen sind um so ausgeprägter, je geringer der Austauscher selbst hydratisiert ist.
4. Der Einfluss des pH-Wertes auf den Ionenumtausch an schwachen Kationen austauscher ist sehr beträchtlich; dagegen ist der Einfluss der Anionen auf den Kationenumtausch gering.

Nitrikof

In the tomato Fisher observed that an excess of nitrogen stimulated vegetative growth at the expense of flowers and fruit development (8). Murneek (32) stressed the negative correlation between vegetative development and fruiting (The rate of growth of the tomato, as measured by increments of height, declines at the exact time and in inverse proportion to the amount of fruit set and developing). He concluded that nitrogen was the immediate limiting factor effecting this correlation. Under more optimal growing conditions Arnon and Hoagland found no negative correlation between growth and fruit set.

Tiedjens and Robbins found that tomato plants grew well when nitrogen was supplied as ammonium sulphate in a medium with a pH of 8.0 and that the best growth with calcium nitrate occurred at a pH of 5.0 to 6.0 (8).

It was observed that plants which take up nitrogen exclusively as ammonium salts generally contain very distinctly higher percentages of nitrogen than other plants supplied with nitrates.

It was found that the nitrogen in ammonium compounds is in a form that can be utilized more readily by the plant in the formation of organic nitrogenous compounds than the nitrogen of the nitrates. Tiedjens and

Robbins for tomato reported that the nitrogen in the form of ammonium salt was utilized directly in the synthesis of nitrogenous compounds. Clark for tomato observed that more nitrogen accumulated in the tissues when nitrates were used than when ammonium salts were applied. He considered that this indicated that the nitrogen in the form of ammonium salts was quickly utilized and thus did not accumulate.

Gurjar noted in the case of the tomato that the carbon/nitrogen ratio may be as high as 19 and as low as 2, but that the fruiting took place between the ratios 4 and 6. Work considered that a nitrogen content of 0.5 per cent on a green basis in this plant is conducive to a vigorous vegetative growth.

Starring studied the effect of the carbohydrate/nitrogen content upon the production of roots on the cuttings of tomato and found that the best production of roots is obtained from those cuttings which have a high content of carbohydrate. Reid observed also that shoots are produced in greater number in light than in darkness. A greater quantity of roots is produced in darkness.

Fosfor

Owen noted in tomatoes that if phosphates were omitted the potassium content of the foliage was depressed and that if they were added to a medium deficient in this radical the content of potassium in the leaves was increased (8; zie voor fosfor ook onder de paragraaf Calcium).

R.J. Schramm gaf mij een tweetal references over fosfaat en wel van Eckerson (S.H. Eckerson: Influence of phosphorus deficiency on metabolism of tomato. Contrib. Boyce Thompson Inst. 3:197-217, 1931) en van MacGillivray (J.H. MacGillivray: Effect of phosphorus on the composition of the tomato plant. Journal Agr. Res. 34:97-127, 1927).

Kalium

It was reported by Gericke that the nutrient solutions which produced the best growth of wheat in the early growth phases varied with the temperatures (8). It appeared, for example, that the proportion of potassium may be less for high than for low temperatures.

Carolus in experiments with tomatoes found that a slight deficiency or excess of potassium in the plant caused a condition of physiological unbalance that resulted in both decreased growth and reduced yields, and impaired the quality of the fruit.

Stocklaza considered that in the presence of sunlight and with a sufficient supply of carbohydrate and other material, protein can be foun-

in either the presence or the absence of potassium. In the dark, however, the formation of protein occurs only in the presence of potassium, provided the necessary materials are at hand. It was considered that potassium is apparently essential either directly or indirectly for the initial stages in nitrate reduction in the plant and probably for the synthesis of proteins of meristematic tissue.

Magnesium

C.L. McCombs gaf mij een overdruk van het artikel "Heredity and nutrition in relation to magnesium deficiency chlorosis in celery" (33). The differential performance of celery varieties observed in the field was repeated when Utah 10B, a variety expressing the chlorosis, and Summer Pascal, a normal variety, were grown at different concentrations of magnesium in nutrient culture solutions. Performance of F_1 plants from a cross between a normal parent and a chlorotic parent, and the reciprocal cross indicated a dominance of the normal condition. The F_2 population resulting from a cross of a normal x a chlorotic parent produced ratios of three normal to one chlorotic plant indicating that a single gene conditioned the utilization of magnesium.

Calcium

Mynd and Fuller observed that tomato and cucumber plants which had been treated with ultraviolet radiation showed a decided increase in calcium and a decrease in phosphorus as compared to the controls (8).

In the tomato plant, Nightingale and others found that all the calcium of the fresh tissues of calcium-deficient plants was soluble.

Cowell found the calcium content of the outermost leaves of cabbage may be 20 to 30 times as great as that of the inner leaves.

Sorokin and Sommer found that plants of *Pisum sativum* grown in culture solutions without calcium usually die within 2 or 3 weeks. The death of the plants is associated with the degeneration that takes place in the protoplasts of the meristematic cells of the root tips. The absence of calcium does not have a direct effect on the disintegrating tissues due to the separation of the cells because of the absence of calcium pectate.

It was observed by Boehm that an abnormal accumulation of starch occurred in *Phaseolus vulgaris* grown in water cultures lacking calcium, an observation that has since been verified for numerous plants by many investigators. It was observed by Nightingale and others in the tomato that the calcium-deficient plant accumulated carbohydrates in large quantities apparently because absorption and accumulation of nitrates

did not take place.

It is difficult to separate the direct effects of mineral nutrients on root growth from their indirect effects on processes in the shoot which in turn affect root growth (3 m). Boron and calcium seem to have direct effects on root growth and apparently must occur in the immediate environment of roots if they are to grow. It was found when a part of a root system was grown in a complete nutrient solution and the other part in a solution lacking calcium, the part of the root system without calcium died. In the absence of boron the roots survived, but did not absorb minerals.

Zie voor de wederkerige beïnvloeding van calcium en borium bij Stiles (3 t).

M.W. Hoover bezigt 0.3% $\text{Ca}(\text{OH})_2$ — 0.18% is verzedigd — as a firming agent for canned peppers (zie 27). Cubes of slices worden onder roerend gedurende een minuut ondergedompeld om ze daarna een half uur te laten uitlekken, followed by a thorough rinse prior to heat processing. $\text{Ca}(\text{OH})_2$ zou veel betere resultaten geven dan gelijke calciumconcentraties aan CaCl_2 of CaSO_4 . Hoover denkt dat de werking van $\text{Ca}(\text{OH})_2$ berust op de vorming van calciumpectaat. Groene vruchten "firm up" beter dan rijpe vruchten. Het gehalte aan pectin neemt toe met het rijpen; de gehalten aan de andere pectineverbindingen nemen echter af. Hoover zou de resultaten van zijn onderzoek op korte termijn publiceren in Food Technology.

Borium

Zie voor de wederkerige beïnvloeding van borium en calcium bij Stiles (3 t). One of Schmucker's conclusions was that boron affected the absorption of water by protoplasm, and Gisiger in supporting this view saw in this an explanation of the favourable effect of boron in overlimed soils (zie ook de paragraaf Voeding en transpiratie en J.E. Baker, e.a.: Effects of boron on the water relations of higher plants. Plant Physiol. 31:89-94, 1956). Voor de invloed die borium op de wortels heeft, wordt verwezen naar de voorgaande paragraaf.

Miller (8) geeft over de invloed van borium op de tomaat tal van references. With tomato Reeve and Shive found that the appearance of boron deficiency symptoms was related to the concentration of potassium and calcium in the medium (3 t). McHargue and Calfee found that the varieties of leaf and head lettuce which they observed required boron for normal growth (8). A deficiency of boron caused a burning of the leaves and an early death of the growing parts.

McCombs gaf mij een overdruk van het artikel "The inheritance of susceptibility to boron deficiency in celery" (34). An inbred strain (IS)

was compared with Summer Pascal at various concentrations of boron. At concentrations lower than 0.1 ppm boron IS produced significantly lower fresh and dry weights. Progenies resulting from crosses of normal parents x IS were tested at a concentration of 0.01 ppm boron. The F₁, F₂ and backcross populations indicated that susceptibility to boron deficiency was conditioned by a single recessive gene.

Emmert (25) schrijft het volgende (zie ook E.H. Emmert: Effect of boron, dextrose and beta-naphthoxyacetic acid on fertilizer requirements and yields and fruit quality of tomatoes. Proc. Amer. Soc. Hort. Sci. 77: 494-499, 1961). When a weak hormone such as beta-naphthoxyacetic acid is activated by boron, the setting and sizing effects on tomatoes are attained without causing hollow fruits or foliage injury. Few seeds are present where the combination is used, but the locules are well filled, resulting in a solid meaty fruit. The response is greatest in periods of adverse early spring weather. It has been found that the boron-hormone can be applied as a dust.

Volgens Mc Combs heeft Emmert (zie ook voornoemde reference) kans gezien de suikeropname door tomaten te stimuleren door bij bespuitingen gebruik te maken van borated sugar. Een andere onderzoeker zou door bespuitingen met borated sugar het suikergehalte van cantaloupes hebben kunnen verhogen.

IJzer

H.J. Evans gaf mij een overdruk van zijn artikel "The biochemical role of iron in plant metabolism" (35).

Molybdeen

From a review of the role of molybdenum in plant metabolism, it is concluded that molybdenum is an essential element in the process of nitrogen fixation, and in nitrate reduction in plants when this source of nitrogen is utilized (36). It is, however, not a role which is limited to these two physiological processes, for plants grown upon combined nitrogen sources other than nitrate still require molybdenum for normal growth. The magnitude of the molybdenum requirement for nitrogen fixation and nitrate reduction is greater than that for the utilization of the reduced combined nitrogen sources. Evans gaf mij een overdruk van het artikel "Association of molybdenum with nitrate reductase from soybean leaves" (37).

Koper

The acid organic soils are normally subject to copper deficiency (31). This is well known in the Middle West, but not — apparently — in the

Eastern coastal regions with organic soils. In New York and in Michigan marked results have been obtained in increasing the yield and quality of onions and leeks by the application of copper sulfate to much soils (8).

Cobalt

Evans gaf mij een overdruk van de publikatie "Effect of cobalt on the growth of soybeans in the absence of supplied nitrogen" (38). It may be concluded that the soybean plants grown under conditions which forced them to depend on nitrogen from the symbiotic process were distinctly benefitted from small quantities of cobalt (0.1 ppb zou voldoende zijn voor een normale groei). The responses reflect the combined cobalt requirements for the soybean plant and the Rhizobia growing in the symbiotic relationship. In view of the decreased yields and apparent nitrogen deficiency symptoms of plants grown without cobalt it is suggested that this element is probably involved in some way for the adequate fixation of nitrogen for the leguminous plants.

Significant increases in the growth of rubber and tomato plants have been demonstrated with a supply of 0.005 ppm of cobalt in purified sand cultures, but no characteristic foliar deficiency symptoms attributable to cobalt were observed.

Fysiogene ziekten

Verschillende van de volgende fysiogene ziekten hangen nauw samen met calciumgebrek. Zie daarom ook de paragraaf Calcium van het voorgaande hoofdstuk.

Neusrot bij tomaat en paprika

Zowel Evans (39) als Mc Combs (40) gaven mij een publikatie over neusrot bij tomaat, van welke publikaties zij één van de schrijvers waren. Beide onderzoekers hebben zich sindsdien niet meer met het onderzoek van neusrot bezig gehouden. N.N. Winstead vertelde, dat neusrot bij tomaat in North Carolina veel voorkomt en wel als gevolg van kalkarme grond. In sommige jaren treedt echter weinig of geen neusrot op, wat volgens hem te danken is aan de goede regenval in die jaren.

In de literatuurbespreking van de publikatie van Evans (39) worden onder meer de volgende factoren bevordelijk voor het optreden van neusrot genoemd: staking of plants and maintenance of vigorously vegetative plants Went (32) reports that fruits developing in continuous high temperature produced blossom-end rot. This physiological disease was noticed to a much smaller degree in fruits developing under fluctuating temperature

conditions. McCombs (40) constateerde verschillende in rasgevoeligheid voor neusrot.

Evans (39) vond bij greenhouse tomatoes (Rutgers variety) voor neusrotte vruchten een CaO gehalte van 0.10% en voor normale vruchten van 0.13 (het CaO gehalte van met calciumgluconaat geïnjecteerde vruchten bedroeg 0.21%). Bij field tomatoes (Marglobe variety) was het CaO gehalte van de neusrotte vruchten echter iets hoger dan dat van de normale vruchten; resp 0.17% en 0.15%. It was interesting that in this case the coefficient of variation for the CaO analyses of diseased fruit was twice that of the normal. This suggests that fruits with less severe symptoms should have been selected for chemical analyses. Undoubtedly the destruction of materials caused by microorganism infection of diseased fruit introduced an error in the chemical analyses which were expressed on a dry matter basis.

McCombs (40) vond voor normale en neusrotte vruchten calciumgehalten van resp. 3.4 en 2.1 mgaeq per honderd gram drooggewicht. In a preliminary test it was found that the calcium content of fruit did not vary significantly with maturity; therefore, blossom-end-rot-affected fruits were harvested as soon as the disorder appeared and normal fruits were harvested at maturity.

The experiments of McCombs were designed to show the effects of three levels of calcium nutrition in sand culture. The incidence of blossom-end rot was decreased significantly as calcium levels were increased (bij Doublerich van 83% naar 0% en bij Rutgers van 100% naar 0%). Visible symptoms of calcium deficiency, i.e. cessation of terminal bud growth followed by complete necrosis of the growing points, were evident in the majority of plants grown at the low calcium level. There was a significant reduction in number of fruits at this calcium level. Although there were no visible manifestations of calcium deficiency on plants grown at the medium calcium level, Doublerich and Rutgers developed 1% and 26% blossom-end rot respectively. Tegenover deze gegevens staan die van een pottenproef van mij, waarbij de toppen van de planten in ernstige mate calciumgebrek vertoonden, terwijl er toch maar weinig neusrot optrad.

Evans (39) found in a greenhouse experiment that plants sprayed each week with 1 per cent CaCl_2 solution developed significantly fewer blossom-end rot fruit than comparable plants sprayed with water. Injection of fruit with 2% sterile calcium gluconate solution completely prevented the disease. A treatment where fruits were injected with water as a control should have been included.

Evans and Troxler (39; zie 40) suggest that organic acids, such as citrate or oxalate, may be effective in immobilizing calcium within the

plant. The former may act as a chelating agent within the fruit, while oxalate may precipitate calcium in the stems before it reaches the fruit.

Fruits are reported to contain lower percentages of dry matter and mineral elements but a higher percentage of citric acid than leaves or stems. They contain much lower concentrations of oxalic acid.

Some preliminary experiments were conducted in a greenhouse, where 2% sterile citric acid solution was injected into tomato fruits. Many of the injected fruits developed at the stylar end a discolaration and breakdown of the tissue which was similar to blossom-end rot symptoms.

The numerous observations that the occurrence of blossom-end rot in tomatoes parallels soil moisture conditions demand serious consideration. Lee and Sayre presented results of field experiments which show that tomato fruit grown under conditions of low soil moisture supply consistently contained higher percentages of both dry matter and organic acids than those grown with adequate soil moisture. They also reported that organic acids of fruits were highest at the beginning of the season and that high potash fertilization was associated with increased fruit acidity. These trends are certainly in agreement with the many reports that blossom-end rot is most serious during early portions of the harvest season and in periods of limited soil moisture supply. Schramm noemde mij een referance betreffende het gehalte aan organische zuren van de tomaat (A.R. Garangol, e.a.: The influence of mineral nutrition on the organic acids of the tomato. Plant Phys. 29: 29355-360, 1954).

The results of the experiments reported are in agreement with the theory that blossom-end rot is caused by an insufficient supply of calcium for the synthesis of rigid cell walls of fruit (zie echter de paragraaf Calcium van het voorgaande hoofdstuk).

Wallace and Bear have summarized the work on cation balance in plant tissues (40). Many studies have shown that individual cations may vary widely, but cation equivalent summation values tend to be constant under similar conditions. McCombs, however, found that the potassium content of fruit was not affected by variety, calcium level or the presence of blossom-end rot.

James (41) produced parthenocarpy in tomato fruits by the method of Gustafson. One per cent indole butyric and one per cent indole acetic acid have been used as growth promoting substances. A few parthenocarpic fruits were induced by pollen of *Lycopersicon peruvianum*. The fruits produced by indole acetic acid were quite small and those produced by indole butyric acid and by pollen of *L. peruvianum* were more nearly normal in size.

but still smaller than the seeded fruits.

As had been found by other investigators the reducing sugars comprised most of the soluble sugars in ripe tomato (total soluble solids were determined with an Abbé refractometer; Saywell and Crueess found this method very satisfactory). Sucrose varied from 0.1 to 0.3 per cent. Only 0.2 0.3 per cent of the ripe fruits was starch; however, in the immature fruits a large percentage of the carbohydrate was starch.

The titratable acidity in both parthenocarpic and seeded fruits was the same during all stages of development except for a short period during the ripening process, when the acid in the seeded fruits was somewhat higher (Bornträger has shown that the titratable acid of tomatoes is mainly citric and therefore the acid was calculated as citric). However, there were marked differences in the distribution of the acid in the two kinds of fruits. The parthenocarpic fruits had a rather even distribution throughout while the seeded fruits, ~~had~~ especially during the ripening process, had a low percentage of acid in the outer wall and a higher percentage in the locular region.

The percentage of starch in the parthenocarpic fruits was greater in all stages of development except for the very ripe fruits, when both kinds had a very low starch content. This difference was almost entirely located in the locular region.

As the fruits matured the percentage sugar increased in the parthenocarpic fruits faster than in the seeded ones. In the red ripe fruits each region of the parthenocarpic fruits had a higher percentage of sugar than corresponding regions of the seeded fruits.

From the fact that the differences noted are almost entirely located in the locules, it is evident that the developing seeds exert a profound influence upon the chemical composition of the fruit.

A period of hot weather caused two types of damage to the fruits. The seeded ^{fruits} developed a large amount of blossom-end rot, but of the two hundred parthenocarpic tomatoes observed all were entirely free from this injury. As a result of the rapid accumulation of water during the cool wet weather which followed the period of hot dry weather, many fruits split and cracked. This type of injury was much more prevalent in the parthenocarpic than in the seeded fruits, but did occur in both.

C.H. Miller vertelde dat neusrot bij peppers bij goede regenval weinig of niet optreedt. Hij noemde het neusrot overigens een symptoom van calciumgebrek. In North Carolina worden hem meer peppers geteeld dan tomatoes.

In een publikatie schrijft Miller (26) onder meer het volgende (zie

ook C.H. Miller: Some effects of different levels of five nutrient elements on Bell peppers. Proc. Amer. Soc. Hort. Sci. 77:440-448, 1961). In a sand culture experiment in a greenhouse, one of the more important effects on the fruit was the occurrence of blossom-end rot on a number of fruits produced by plants that were treated with low calcium, high nitrogen or high potassium solutions. In the field, it was found that the addition of gypsum to a soil initially low in calcium resulted in a significant reduction in the incidence of blossom-end rot. Neither the form of nitrogen nor the rate of nitrogen had any measurable influence on the severity of blossom-end rot. The disorder was much less severe late in the season than earlier. This was attributed to heavy rainfall during the latter part of the growing season.

Rand bij lettuce en cabbage

According to Curtis and Ivanoff, salts left on the surfaces of leaves by the evaporation of guttated water are sometimes subsequently redissolved and drawn back into the interior, causing injury (6; zie ook 31). They suggest that many instances of tip burn to succulent leaves such as lettuce are caused in this manner.

Miller vertelde dat in North Carolina de Great Lakes variety wordt geteeld. Tip burn zou niet zo veel voorkomen, maar wel brown rib (zie het "Verslag van een studiereis naar Californië" en J. Mitchell Jenkins: Brown rib of lettuce. Proc. Amer. Soc. Hort. Sci. 74:587, 1959). Miller heeft deze met rand samenhangende ziekte in onderzoek (zie ook de paragraaf Borium),

Winstead gaf mij een reference over rand bij kool (Walker and Edgington: Studies on internal tipburn of cabbage. Phytopath. 47:537, 1957). Zie ook de paragraaf Calcium.

Toppling bij gladiool

The commercial growing of gladiolus is largely confined to two sections of the state, in the West around the Hendersonville area and in the East along the Atlantic coast from Wilmington northward (42). The estimated acreage of gladiolus plantings in the state is between 3.000 and 5.000 acres, which represents a gross annual income of over five million dollars. The acreage affected by topple is located in the western part and may amount to over 1.000 acres. Topple has never been reported from plantings in the East.

Topple has first been reported by Figk. The breakdown is very much similar to topple in tulip and narcissus. It is known that applications of calcium to the soil or dilute calcium foliar sprays will prevent topple

in tulips and narcissi. The breakdown does not occur on intact floral spikes in the field but only after they have been cut for market. It usually occurs between 12 to 24 hours after cutting.

Fink found that applications of various calcium sources to the soil and also calcium nitrate sprays (2%) would reduce the incidence of disease considerably. Of the various calcium sources tested by Fink, it was found with soil additives that dolomitic limestone gave best results in reduction of topple incidence (41%). However, dilute calcium nitrate sprays (2%) applied two weeks before the flowers were harvested gave much better control than dolomitic limestone reducing the incidence to 19%.

Woltz stated that topple of gladiolus, the breaking over of spikes as they open in vases, is caused by low calcium content of the spikes and may largely be prevented by the methods used for bud-rot control. These preventive measures include: adequate liming; avoiding nutritional imbalance due to excess magnesium, potassium, sodium or nitrogen; spraying with four pounds of calcium nitrate per hundred gallons of water two to four times between the stage spikes first begin to slip and the time flower cutting starts; broadcasting 1.000 pounds of gypsum per acre before planting. These treatments have not, like those of Fink's, eliminated it entirely in the Florida plantings (zie het verslag van een studiereis naar Florida).

Additional observations on calcium deficient plants showed that the florets had a water-soaked appearance of the petals toward the base. Fink reported that in the case of topple no lesion or water-soaked area marked the place where the topple might occur. Also there were no visible breaks in the epidermis of the spike.

Woltz found an outstanding interaction between nitrogen and calcium, wherein considerably greater amounts of calcium were apparently required at higher levels of nitrogen in order to obtain normal flower production. This is ⁱⁿ accord with the findings of Gartner who found in field trials that high levels of calcium were required to reduce topple on heavily nitrogen fertilized plots.

There is a difference between topple and blossom-end rot in that topple occurs only after the flower spike is cut, whereas blossom-end rot occurs on intact, non-detached tomato fruits. Thus it may be entirely possible that since topple occurs only after the flowers are cut that in the presence of organic acid accumulations (heavily nitrogen fertilized) the activity of some kind of pectin-hydrolyzing enzyme system might be high in the susceptible plants.

It should also be noted that in the Hendersonville area it has been

found that the incidence of topple is very greatly reduced during seasons when precipitation has been excessive and high during very dry seasons. A possible explanation for this is that most growers in that area are over fertilizing with nitrogen and that during seasons of high rainfall the excess nitrogen is leached.

Legering van graan

Miller (8) geeft een uitvoerige literatuurbespreking over het legeren van graan.

Jonathan spot en soft scald

W.E. Ballinger gaf mij een overdruk van een publikatie, waarin de resultaten van een onderzoek over de bewaring van Jonathan-appels worden beschreven (43). An outstanding advantage of controlled-atmosphere storage for Jonathan apples was the control of two serious storage disorders, Jonathan spot and soft scald. Fruit damage attributable to above-normal concentrations of carbon dioxide was the only factor limiting the success of controlled atmospheres for Jonathan apples.

Tomaat

De tomaat is in de voorgaande hoofdstukken reeds tal van keren ter sprake gekomen. In dit hoofdstuk zullen de overige over dit gewas opgedane wetenswaardigheden worden vermeld.

Thermoperiodiciteit

Between 70 and 90 per cent of the daily growth of the tomato stem occurs during darkness (32). On cloudy days, when the light intensity remains low, there is no great drop in growth rate during day, nor is there a rise after sundown.

When tomato plants are grown in a constant temperature twenty-four hours per day, the optimal temperature lies well above 20° C. Plants kept warm during the day (26.5°) and cool during the night (17-20°) grow most rapidly. Approximately the same temperature relation holds for fruit development. Fruit set is abundant only when the night temperatures are between 15 and 20°; with lower and higher temperatures during the night, fruiting is reduced in amount or even absent. The temperature has to be below 20° for only part of the night to result in fruit production (by decapitating the plant above the first flower cluster, fruits set in the 26.5° greenhouse on most of the treated plants). Artificial light when applied during the cool night period completely inhibits fruit formation.

The temperature dependence as described above holds only for plants over 40 cm long. In younger plants a night temperature of 26.5° gives

consistently greater growth than one of 20° , even though coupled with day temperatures of 26.5° .

In the later development of the plants, fruit production at a constant day and night temperature of 20° overtakes that obtained at 26.5° day and 20° night temperature. This is in contrast to the situation in regard to stem elongation.

There was no indication of a decrease in growth rate due heavy fruit set. The more highly vegetative character of the plants kept at high night temperatures was expressed by the greater number of foliage leaves developing on the flower cluster.

Met betrekking tot de thermoperiodiciteit noemde Dove mij een artikel van Went en Hull (F.W. Went and H.M. Hull: The effect of temperature upon translocation of carbohydrates in the tomato plant. Plant Physiol. 24:505-526, 1949) en een artikel van Hull (H.M. Hull: Carbohydrate translocation in tomato and sugar beet with particular reference to temperature effect. Amer. J. Bot. 39:661-669, 1952).

Bodemtemperatuur

Gericke and Travernetti reported on an experiment with tomatoes that the plants in heated tanks (70° and 80° F.) began to ripen fruit about four months after transplanting, while those in an unheated tank (60° F.) did not ripen fruit until six weeks later (8).

The work of Riethmann showed that stem growth and fruit set of tomatoes, grown in the same greenhouse, largely depend upon root temperature, with an optimum at 33° C. for the Schöne von Lothringen variety (32; zie dit artikel ook voor de bodemtemperatuur bij de in de voorgaande paragraaf vermelde onderzoeken over de thermoperiodiciteit).

Suikerbespuiting

The failure to grow in prolonged darkness is due to a lack of carbohydrates, for application of sucrose will restore growth in darkness (32).

Siev and Shmueli (44) found that pre-planting sprayings with a ten per cent water solution of table sugar improved survival of the transplants. Subsequent growth in the field was enhanced, as indicated by the number of roots, the height of plants and the early yields.

Zie voor bespuitingen met borated sugar de paragraaf Borium.

Aëratie

Clark and Shive found that aeration had a more pronounced influence upon the growth of tops of the tomato than upon the growth of roots (8). The plants in the nonaerated cultures bloomed and fruited earlier than did those in the aerated cultures.

Luchtvochtigheid

Went stated that the growth rate of the tomato is not dependent upon the humidity of the air, inasmuch as a decrease in humidity causes merely a temporary decrease; an increase of the relative humidity increases the growth rate only temporarily. However, Nightingale and Mitchell found that tomatoes grown in moist soil at a constant temperature were much smaller and more woody if kept at a relative humidity of 35 per cent than when grown at a relative humidity of 70 per cent (4).

Gehalten aan voedingsstoffen

Raleigh and Chucka indicated that variation of the concentrations of nutrients had much less effect on the inorganic composition of tomato fruits than on leaves or stems (39).

Groeistof

McCombs zei dat behandeling van tomatezaad met 0.001 ppm 2-4,D wellicht gunstige resultaten zou kunnen geven. Hij verwees mij in dit verband naar California Agriculture 8: no. 2, 3 en 4.

Zie voor born-hormone sprays de paragraaf Borium.

Bodemkundig onderzoek

J.F. Lutz gaf mij een overdruk van de volgende publikaties: Intrinsic permeability of clay as affected by clay-water interaction (45); Soil physical conditions and drainage (46); Hydraulic conductivity in large channels as determined by an electric analog (47). Voor de bepaling van het vochtgehalte van grond, maakt Lutz veel gebruik van de neutronenmeter; ook de dichtheid van de grond wordt vaak op een dergelijke wijze bepaald. De betreffende bepalingsmethodieken bemevens de evapotranspiratie zijn destijds door Van Bavel te Raleigh onderzocht.

Samenstelling bodemfiltraat

Lutz and Kemper (45) calculated the thickness of water films and of the electric double layer around clay particles from pressure membrane data and from the concentration of extracted solution. Na and K clays in dilute electrolyte solution have diffuse layers of adsorbed cations extending to more than 100 Å from the particle surfaces, in accord with Gouy theory. There is a water structure of about the same thickness. In Ca clays the diffuse layer of adsorbed cations and the water structure extend to only about 10 Å.

At the lower pressures the Ca clay held only about 60 per cent as

much water as the Na and K clays. There was a sharp decrease in concentration of the solutions from the Na clay in water at about 30 Å from the π clay particle. There was no change in the concentration of the successive extracts from the Na clay in 1 N NaCl, even though the mid-point of the last fraction was only 8.6 Å from the particles. The Na clay in water held a water layer of 12.3 Å at the same pressure. Thus, the 1 N NaCl suppressed the diffuse double layer and reduced the force holding to water.

The Ca clay in water showed a slight increase in concentration of the solution extracted between 3 and 6 atm. pressure. The solution extracted between these pressures was at an average distance of about 12 Å from the particle. Apparently, this layer of greater concentration represents an accumulation of anions surrounding the diffuse layer of Ca ions.

Lutz raadde mij aan een tweetal artikelen van G.H. Bolt en R.D. Miller door te nemen (Compression studies of illite suspensions. Soil Sci. Soc. Amer. Proc. 19:285-287, 1955; Calculation of total and component potentials of water in soil. Transactions Amer. Geophysical Union 39:917-928, 1958).

Richards and Weaver measured the OP of the saturation extract and computed the OP values applicable to any soil moisture content (5).

In günstigen Fällen (Salzmarschtorfe) kann der Boden ausgepresst und der Gefrierpunkt des Preszsaftes in üblicher Weise bestimmt werden (3r).
Meting total soil moisture stress

Slatyer (5) measured TSMS directly on soil cores by equilibrating them in vapour of known vapour pressure using a modification of the method of Thomas and Edlefsen. The direct determinations made in this manner were in good agreement with the indirect estimates which combined soil moisture tension and OP determinations.

Fosfaat en structuur van de grond

Lutz zou op het internationale bodemkundige congres te Wisconsin een lezing houden over het effect van fosfaatbemesting op de structuur van de grond (zie de Congress Proceedings). Determinations by the neutron method showed that the moisture content of phosphate-treated soils was significantly higher than of no-phosphate soils (Working papers on Friday 19 August, page 6; zie het verslag van een studiereis naar Wisconsin). All rates of phosphate markedly decreased the bulk density of the soil as measured by the gamma radiation method.

Literatuur

In dit hoofdstuk zullen nog enkele onderwerpen ter sprake komen, waarover mij references werden gencemd of overdrukken van artikelen werden overhandigd.

Nemateden bij tabak

Winstead gaf mij de extension circular "Cropping systems for nematode control and tobacco production" (48). Tabak is in North Carolina een zeer belangrijk gewas. In Durham zag ik een fabriek voor Chesterfield sigaretten en een fabriek voor Pall Mall en Lucky Strike sigaretten. De eerst genoemde heb ik bezocht.

Ziekten van Cucurbita's

Winstead gaf mij de bulletin "Cucurbit diseases in North Carolina and their control" (49).

Voeding van blueberry

Ballinger hield zich bezig met het voedingsonderzoek van de blueberry (zie gemaakte kleurendia). Hij gaf mij de overdrukken van een drietal artikelen op dit terrein: Production in Michigan blueberry plantations in relation to nutrient-element content of the fruiting-shoot leaves and soil (28); Relationship between nutrient-element content of blueberry foliage and fruit (29); Soluble solids in blueberry fruit in relation to yield and nitrogen content of fruiting-shoot leaves (30).

The data suggest that a nitrogen-carbohydrate relationship may be of importance in the blueberry plant; that an excessively high nitrogen content or a large yield of fruit may effect a decrease in soluble solids content of the blueberry fruit. Conversely, an abnormally low content of nitrogen or a small yield may contribute toward a high soluble solids content.

Nadelen van grondstomen

McCombs vroeg hoe de nadelen van grondstomen — mangaanvergiftiging — kunnen worden ontgaan. Hij verwees mij in dit verband naar een artikel van Hoffman (I.C. Hoffman: Soil steaming. Ohio Farm and Home Research 1952, July-August: 54-55).

Marsh soils

Van Staveren gaf mij een overdruk van het artikel "Marsh soils in the United States and in the Netherlands" (31).

Koolzuurgas

Miller (8) geeft een uitvoerige literabespreking over de toepassing van koolzuurgas.

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