Water relations and keeping-quality of cut Gerbera flowers
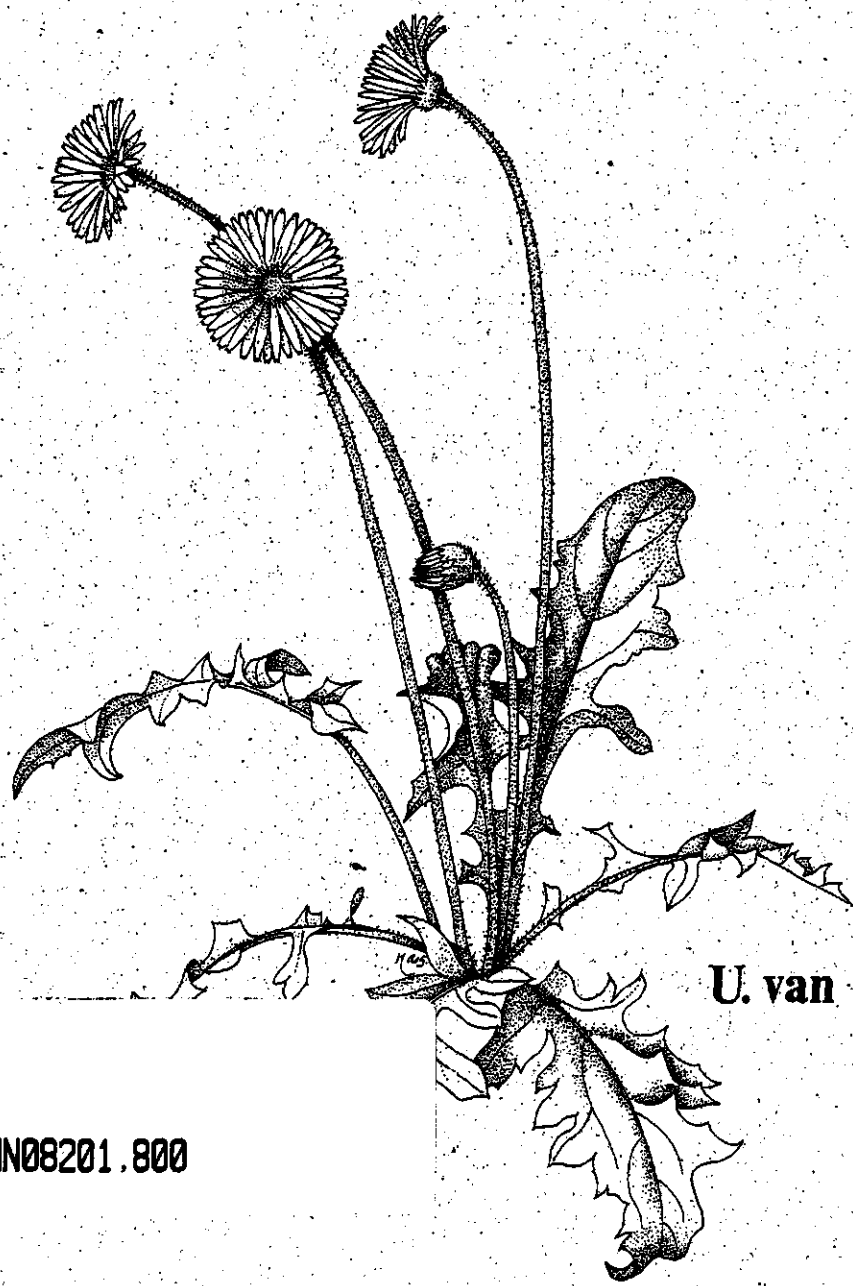

U. van Meeteren

WATER RELATIONS AND KEEPING-QUALITY OF CUT GERBERA FLOWERS

U. van Meeteren

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STELLINGEN

I

De turgor potentiaal van bloembladeren bepaald aan bloemen die zich na af-
snijden van de plant hebben kunnen vol zuigen met water, is een goede indi-
catie voor de potentiële houdbaarheid van de betreffende bloemen.

    Dit proefschrift.

II

Bij de veredeling van gerbera's moet het optreden van holle bloemstengels
als een positieve eigenschap worden beschouwd.

    Dit proefschrift.

III

Het hoeft geen verbazing te wekken, dat veranderingen in hormoonhuishouding
en in enzymactiviteiten in bloembladeren als gevolg van een watertekort,
eveneens worden waargenomen bij bloembladeren die verouderen.

IV.

De conclusie van Kleinendorst dat bij de tulp de watervoorziening van de
bloem niet van invloed is op de houdbaarheid wordt onvoldoende door zijn
onderzoeksresultaten ondersteund.

    A. Kleinendorst. Bedrijfsontwikkeling 9(10), 932-934 (1978).

V

Dat bij bloembladeren van anjers het niet de veranderingen in permeabiliteit
zijn die leiden tot een stijging in de ethyleenproduktie wordt door Mayak,
Vaadia en Dilley niet bewezen.

    S. Mayak, Y. Vaadia en D.R. Dilley. Plant Physiol. 59, 591-593 (1977).

VI

Een vergelijking van het aantal personen welke zich bezig houden met fundamenteel gericht onderzoek op het gebied van 'post-harvest' fysiologie van bloemen tussen Nederland en enige andere landen geeft reden te verwachten dat de aanduiding "Blumen aus Holland" over enige tijd beter achterwege kan blijven.

VII

Het gebruik van de term "assimilatie-belichting" om de bijbelichting bij de teelt van lelies gedurende de wintermaanden aan te duiden is voorbarig en wellicht zelfs foutief.

VIII

Voor het goed kunnen functioneren van een proefstation is enige ruimte voor meer fundamenteel gericht onderzoek aldaar noodzakelijk.

IV

De reclame-leuze "Vlees mevrouw, u weet wel waarom" wekt de foutieve suggestie dat de consument op de hoogte zou zijn met de voor- en nadelen van het eten van vlees.

X

Het gebruik van "kringloop-papier" zou zeker bij een instelling als de Landbouwhogeschool bevorderd moeten worden.

XI

Van alle soorten bloemen zijn kunststof bloemen de enige die aan bijna alle eisen die gesteld worden door teler, handelaar en consument voldoen.

U. van Meeteren
Wageningen, 18 april 1980

VOORWOORD

Hierbij wil ik allen die hebben meegewerkt aan het tot stand komen v&
proefschrift hartelijk bedanken. In het bijzonder gaat mijn dank uit naar
promotor, prof.dr.ir. J.F. Bierhuizen, voor zijn enthousiasme en waardevol
suggesties.

Alle medewerkers van de vakgroep Tuinbouwplantenteelt LH dank ik voor
prettige werksfeer. Vooral de medewerkers van het fysiologisch laboratoriu
de vakgroep ben ik dankbaar voor hun prettige samenwerking. Veel dank ben
schuldigd aan Annie van Gelder.

De vakgroep Veevoeding LH ben ik erkentelijk voor de gastvrijheid die
mij gedurende een jaar in de kelder van haar gebouw heeft verleend.

De heren F.L. Arens, H. Haalboom en A. Super hebben altijd uitstekenc
zorgd voor de planten. De figuren in dit proefschrift zijn getekend door &
H.H.W. van Lent en gefotografeerd door de heer R. Jansen, waarvoor mijn da
type-werk is uitstekend verzorgd door de dames G.M. van Dam-van Haren, G..
Haar-de Bruin en C. den Hartog. Mariet de Geus heeft de omslag van dit boe
verzorgd.

Veel enthousiasme ging altijd uit van de leden van de N.R.L.O.-conta
"Houdbaarheid snijbloemen".

Mijn ouders ben ik dankbaar, dat zij mijn studie aan de Landbouwhoge:
mogelijk hebben gemaakt.

Tenslotte ben ik zeer veel dank verschuldigd aan Margriet en Ewoud, (
vele uren buiten de normale werktijden hebben moeten missen.

INHOUD

GENERAL INTRODUCTION

During the last 20 years, there has been a boost in the production (
flowers in the Netherlands, as shown in table 1. Also the export of cut :
increased to a large extent.

Table 1. Some data about production and export of cut flowers in the Netl

Year	Area of cut flowers under glass (ha)	Production value of flower crops (x f1000.000)	Value of export: flowers (x f100(
1960		132	57
1965	770	300	139
1970	1445	550	344
1975	2608	1394	928
1976		1516	
1977	2739		1117

[1] Source: Groenewegen, 1978.

The increase in production value of this commodity strenghthened at
time the requirement to achieve a good keeping-quality of cut flowers. T
quality can vary to a large extent, probably due to growing-conditions,
influences, post-harvest handling, cultivar, harvest-stage and external
during vase life. Till now, relatively little has been published on post
physiology and handling of cut flowers as compared to fruits and vegetab
first review on post-harvest physiology of flowers was given by Aarts (1
Recently reviews were given by Rogers (1973), Carow (1978) and Halévy an
(1979).

In case more is known regarding the background of keeping-quality a
straightforward breeding-program for keeping-quality can be obtained, es
when simple methods to measure keeping-quality can be given.

Rogers (1973) wrote in his review among other thhings: "If we can p

assign greater importance to any one of the vital needs of the cut flower, maintenance of turgidity would have highest priority. A high level of turgidity is necessary for development of flower buds to full-bloom maturity. It is also necessary for the continuance of normal metabolic activity in the cut flower". Many flower species show a decline in fresh weight after a vase life of some days (Aarts, 1957). Knowledge about water relations of cut flowers, however, is still limited. Till the beginning of this study, data about pressure potential (= turgor potential) of flower petals were completely lacking in literature. Recently, Acock and Nichols (1979) published data of pressure potential of petals of carnation flowers.

To obtain more information on water relations of cut flowers in relation to keeping-quality, research on this subject was carried out with inflorescences of Gerbera ("Inflorescence" defined as the capitulum with the florets borne on it). The flower head of Gerbera was chosen because the scape has no leaves which could complicate the problem. Besides, plants flower nearly all the year round and inflorescences have a great number of ray-florets making it possible to carry out many measurements with petals of the same inflorescence. Moreover, different cultivars are available, which vary in their keeping-quality of cut flowers. The economical importance of Gerbera in the Netherlands increased during the last years, as is demonstrated by the growth of the area from 40 ha in 1973 to 92 ha in 1977 and the rise in the supply to the auctions from 3.000.000 flowers in 1960 via 14.000.000 flowers in 1970 to 88.000.000 flowers in 1977 (Groenewegen, 1978).

Since "stem break", a sudden bending of the stem, interferes with research on internal water relationships and occurs in many Gerbera cultivars, the series of investigations presented here was started with an investigation of this phenomenon. The results of this and some possibilities to prevent stem break are given in part I. The water balance, which is the result of transpiration and absorption of water, during ageing of cut flowers in a vase is described in part II. In part III data about water content of ageing petals and the relationships between water content on the one hand and ion leakage and dry weight on the other hand are given. In part IV studies on the internal water relations of ageing petal-tissue are reported because of the fact that petals of inflorescences ageing in a vase show a decrease in water content, while this decrease was absent with inflorescences ageing on the plant. In part V results are presented about cytokinin activity of ageing petals, and of the possible role of cytokinins on changes of ion leakage. Aspects of the role of pressure potential for keeping-quality are reported in part VI. The presentation is accompagnied by a general discussion and summary, and by a Dutch summary.

References

Aarts, J.F.Th., 1957. Over de houdbaarheid van snijbloemen. Meded. Landbouw-
     hogesch., Wageningen, 57(9): 62 pp.

Acock, B. and Nichols, R., 1979. Effects of sucrose on water relations of cu
     senescing, carnation flowers. Ann. Bot., 44: 221-230.

Carow, B., 1978. Frischhalten von Schnittblumen. Verlag Eugen Ulmer, Stuttga

Groenewegen, C.A.M., 1978. De produktie en afzet van snijbloemen in cijfers.
     Consulentschap in algemene dienst voor de bloemisterij, Aalsmeer.

Halevy, A.H. and Mayak, S., 1979. Senescence and postharvest physiology of c
     flowers. Part I. Hortic Rev., 1: 204-236.

Rogers, M.N., 1973. An historical and critical review of postharvest physiol
     research on cut flowers. Hort Science, 8(3): 189-194.

WATER RELATIONS AND KEEPING-QUALITY OF CUT GERBERA FLOWERS. I. THE CAUSE OF STEM BREAK

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ABSTRACT

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Experiments were performed to find out the cause of stem break in some Gerbera cultivars. In cut flowers fresh weight decreased sharply 3 days before stem break occurred, and this was accompanied by a decline in absorption of water by the flowers. The petal water potential (ψ) decreased in these flowers whereas it remained constant in flowers without stem break. Stem break could be prevented by pretreatment of the stems with sodium hypochlorite or silver nitrate, by adding silver nitrate or dichlorophen to the vase water, and by handling the stems in such a way that water could enter into the cavity of the stem.

In 1 of the 4 cultivars used, the percentage of stem break varied strongly between summer- and winter-grown flowers.

It is suggested that there are 2 different pathways for water uptake: a direct one through the xylem vessels at the cut surface and an indirect one through the cavity in the stem. Only the direct water uptake is strongly inhibited by growth of bacteria in the vase water. Stem break occurs when the direct water uptake is inhibited by bacterial activity and the indirect uptake is hampered.

INTRODUCTION

Knowledge about internal water relations of cut flowers, as affected by growing-conditions, post-harvest handling, age and external conditions during vase life, is still limited. There are only a few papers in which some aspects of internal water relations are discussed (Horie, 1962; Mayak and Halevy, 1974; Mayak et al., 1974; Halevy, 1976).

To gain information on these relationships and their significance for the keeping-quality of cut flowers, research on this subject was undertaken. The flower head of Gerbera was chosen because the scape has no leaves which could complicate the problem. For the sake of convenience hereafter the term "flower" is used for the complete inflorescence, including its stem.

Stem break, a sudden bending of the stem (like "bent neck" in cut roses), occurs in many Gerbera cultivars and is a practical problem affecting the sale

of the flowers. Data from literature (Wilberg, 1974) and some preliminary experiments, suggested that the water balance influences its occurrence, as it does with bent neck in roses (Burdett, 1970; Sacalis, 1974). Since stem break interferes with research on internal water relationships, this phenomen was studied and methods to prevent it were developed.

MATERIAL AND METHODS

Plant material. — Plants of *Gerbera jamesonii* H. Bolus were raised in a glasshouse. Unless otherwise specified, the cultivar 'Wageningen Rood' was used. The plants were grown in 10-litre plastic containers. The flowers were taken from the plants at the commercial stage of harvest (when the stamens of about 2 circles of bisexual disc florets were ripe). The plants were 1.5—2 yes old. The stems were usually cut to a length of 30 cm and in specific experiments either through or below the hollow part in the centre of the stem. All experiments were done with at least 10 flowers per treatment and were repeated several times.

Fresh weight. — Immediately after harvest the flowers were placed in deioni water at 5°C in a bucket sealed with polyethylene film for 4 hours. Thereaft the stem was blotted with a piece of filter paper and the flowers were weigh The fresh weight during the course of the experiments is given in percentage of this initial weight.
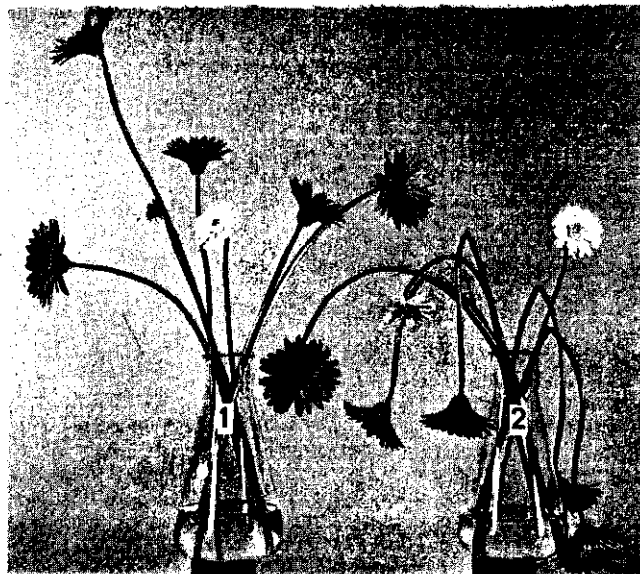

Fig. 1. Flowers without (1) and with (2) stem break. Situation 6 days after flowers were placed in deionised water at 23°C.

Water uptake, transpiration and stem break. — The experiments were carried out in a conditioned room at a temperature of $23 \pm 1°C$, a relative humidity of $60 \pm 5\%$, and constant irradiance of 7.8 Wm^{-2} at flower height, obtained from Philips TL57 fluorescent tubes. During the experiment the flowers were placed in 250 ml Erlenmeyer flasks filled with either 100 ml deionised water or a solution. Each flask contained 1 flower of which the absorption and transpiration rate were determined. The top of the Erlenmeyer flask was sealed with a piece of parafilm to prevent evaporation. In those cases where only the percentage of stem break was analysed, 5 flowers were placed in 1 flask. The weight of the Erlenmeyer flask, with and without flower, was determined daily. From the change in weight between 2 successive measurements, divided by the number of hours during that interval, the rate of absorption in gram h^{-1} flower^{-1} (weighings without flower) and the rate of transpiration (weighings with flower) were calculated. Stem break starts as a bending of the stem, which in most flowers is followed by a real break (Fig. 1). The term stem break as used in this paper also includes flowers where bending of the stem surpassed $90°$.

Water potential. — Water potential was measured in 1 of the outer petals of each flower by using a pressure chamber (Boyer, 1967; Slavík, 1974).

Percentage of "hollowness" of the stem. — The stem volume was measured by submerging the stem in a graduated tube filled with water. Thereafter, the stem was cut lengthwise and submerged again. The difference in volume represents the volume of the cavity. Dividing this volume by the volume of the intact stem and multiplying by 100, the percentage of hollowness was obtained.

Chemicals used. — A 1% solution of sodium hypochlorite was made from a household solution containing 10% of the chemical. The solutions of dichlorophen were made by diluting a technical 40% solution of the sodium salt of dichlorophen ("Panacide 40", BDH Ltd.). In all experiments deionised water was used.

RESULTS

Water balance. — Figure 2 shows the variation in fresh weight, water absorption rate, transpiration rate and petal water potential (ψ) of 4 flowers, 2 of which showed stem break. About 2—4 days before symptoms of stem break became visible, a sharp decline in fresh weight occurred. This decrease in fresh weight was a result of a decline in the absorption rate, while the transpiration rate remained nearly constant. During the decline in fresh weight ψ decreased, whereas in cut flowers without stem break ψ remained more or less constant.
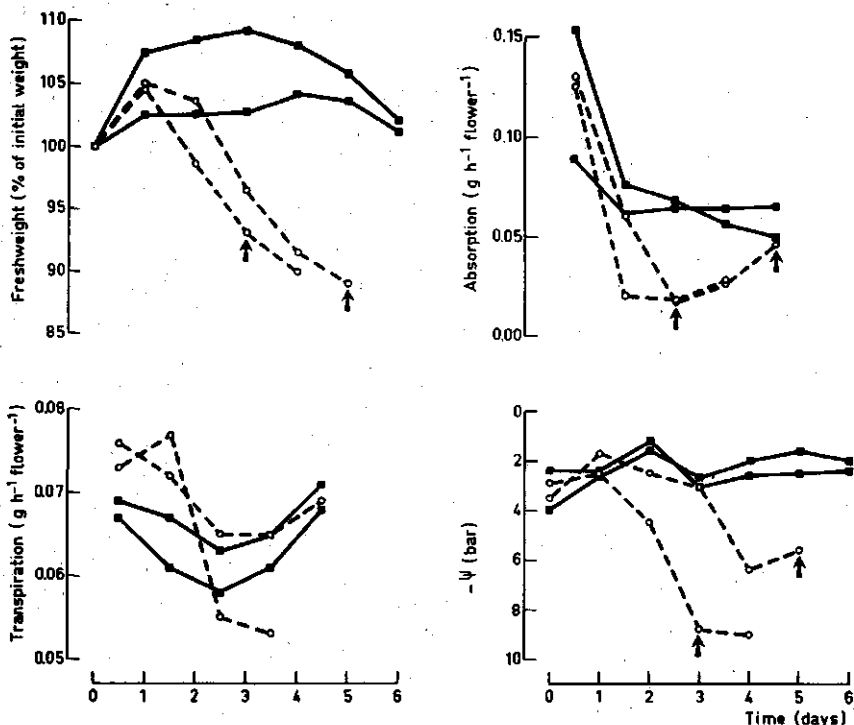
Fig. 2. Time courses of fresh weight, absorption rate, transpiration rate and petal water potential (ψ) of 4 Gerbera flowers cv. 'Wageningen Rood' of which 2 flowers showed stem break. ■—■ flowers without stem break; - - o - - o - flowers with stem break. Arrows indicate the stage at which stem break occurred.

Bactericides. — The susceptibility to stem break was greatly reduced by a pretreatment with NaOCl + Tween 20 or a high concentration of $AgNO_3$ (Table 1), and by just one addition of $AgNO_3$ or dichlorophen to the vase water (Table 2).

A minimum concentration of 20 p.p.m. $AgNO_3$ prevented stem break completely. When a sample from the vase water was applied to a nutritious agar medium ("CASO-agar"; Merck) at 27°C, this threshold concentration of 20 p.p.m. $AgNO_3$ was also the minimum concentration to inhibit complete the growth of bacteria. The minimum concentration of dichlorophen (55 p.p.m.) which resulted in a 100% inhibition of the growth of bacteria was harmful to Gerbera stems.

Stem cavity. — Numerous Gerbera cultivars show a cavity in the centre of the stem, which is formed during stem elongation. Wilberg (1974) observed that stem break decreased when the stem was cut through this cavity (at the cut surface this cavity is seen in the centre of the stem). This was confirmed with 4 different cultivars (Table 3).

TABLE 1

Influence of a pretreatment of the stem on the occurrence of stem break. After the pretreatment the stems were placed in deionised water. No cavity was visible at the cut surface. Cultivar 'Wageningen Rood' was used.

Pretreatment	% of flowers with stem break on						
	Day						
	0	1	2	3	4	5	6
No pretreatment	0	0	50	70	100	100	100
0.1% NaOCl + 0.1% Tween 20 (1 min)	0	10	10	30	30	30	30
1.0% NaOCl + 0.1% Tween 20 (1 min)	0	0	0	0	0	0	0
1.0% NaOCl (1 min)	0	40	50	50	80	80	80
1200 p.p.m. AgNO$_3$ (10 min)	0	0	0	0	0	0	0

TABLE 2

Influence of a bactericide in the vase water on the occurrence of stem break. No cavity was visible at the cut surface. Cultivar 'Wageningen Rood' was used.

Bactericide	% of flowers with stem break on						
	Day						
	0	1	2	3	4	5	6
None	0	0	60	100	100	100	100
AgNO$_3$ (20 p.p.m.)	0	0	0	0	0	0	0
Dichlorophen (10 p.p.m.)	0	0	20	80	100	100	100
Dichlorophen (20 p.p.m.)	0	0	0	10	20	50	80
Dichlorophen (40 p.p.m.)	0	0	0	10	10	30	50

TABLE 3

Influence of cutting the stem through or below the cavity, on the occurrence of stem break. Stems were placed in deionised water. No pretreatment.

Cultivar	Cutting through/ below the cavity	% of flowers with stem break on								
		Day								
		0	1	2	3	4	5	6	7	8
'Wageningen Rood'	Below	0	0	0	80	80	80	90	90	90
	Through	0	0	0	0	20	20	20	20	20
'Mandarin'	Below	0	0	0	30	50	100	100	100	100
	Through	0	0	0	0	0	0	0	0	0
'Mini Wit'	Below	0	10	60	80	80	90	90	100	100
	Through	0	0	0	0	0	0	0	0	0
'Citronella'	Below	0	0	20	40	60	90	100	100	100
	Through	0	0	0	0	0	0	0	0	0

It seems likely that stem break is caused by a decline in water absorption which is due to the development of bacteria at the cut end (to be detailed i the discussion). Since stem break occurs far less often, or not at all, when a is made through a cavity, it is plausible that water can also be taken up via the side walls of such a cavity. To confirm this hypothesis, water was inject into the stem cavity while the flowers were in a vase without water. The va life of these flowers was the same as that of flowers with a visible cavity at the cut surface, placed in water. In a separate experiment red coloured wat ("Ecoline"; Talens) was injected into the hollow part of the stem. A few hours later the stem was cut lengthwise. The red dye was visible in the vess of the stem and in that part of the cavity where it had been injected origin; ly.

When the stem was cut through the cavity and a little hole was made in : stem (about 15 cm above the cut surface), an increase in water height in th vase prolonged the period during which the flower remained at 100% or m of its initial fresh weight (Fig. 3). In this experiment transpiration of the st was prevented by winding a piece of parafilm around the stem. This prever water height from influencing the transpiring area. The relationship shown Fig. 3 is valid only when a small hole in the stem has been made as an air outlet from the cavity and when no bactericide has been added to the vase water.
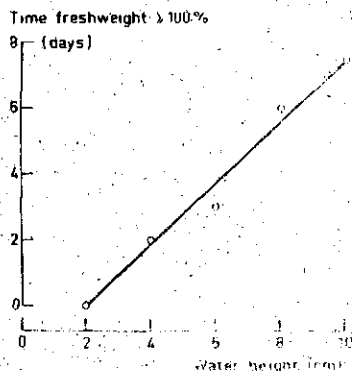

Fig. 3. Number of days during which fresh weight of the Gerbera flowers cv. Wageningen Rood' is 100% or more of the initial weight, as influenced by the water height in the va Cavity in the centre of the stem was visible at the cut surface.

Season and developmental stage. The season had a strong influence on t occurrence of stem break in the cultivar 'Wageningen Rood'. In winter ste break was rare, but in summer it occurred in 90 to 100% of the flowers. Th "percentage of hollowness" of the stem was also influenced by the season and by the stage of development of the flower (Fig. 4). The cultivars 'Mandarin', 'Mini-Wit' and 'Citronella' have a hollow stem all in a year roun

TABLE 1

Influence of a pretreatment of the stem on the occurrence of stem break. After the pretreatment the stems were placed in deionised water. No cavity was visible at the cut surface. Cultivar 'Wageningen Rood' was used.

Pretreatment	% of flowers with stem break on						
	Day						
	0	1	2	3	4	5	6
No pretreatment	0	0	50	70	100	100	100
0.1% NaOCl + 0.1% Tween 20 (1 min)	0	10	10	30	30	30	30
1.0% NaOCl + 0.1% Tween 20 (1 min)	0	0	0	0	0	0	0
1.0% NaOCl (1 min)	0	40	50	50	80	80	80
1200 p.p.m. AgNO$_3$ (10 min)	0	0	0	0	0	0	0

TABLE 2

Influence of a bactericide in the vase water on the occurrence of stem break. No cavity was visible at the cut surface. Cultivar 'Wageningen Rood' was used.

| Bactericide	% of flowers with stem break on						
	Day						
	0	1	2	3	4	5	6
None	0	0	60	100	100	100	100
AgNO$_3$ (20 p.p.m.)	0	0	0	0	0	0	0
Dichlorophen (10 p.p.m.)	0	0	20	80	100	100	100
Dichlorophen (20 p.p.m.)	0	0	0	10	20	50	80
Dichlorophen (40 p.p.m.)	0	0	0	10	10	30	50

TABLE 3

Influence of cutting the stem through or below the cavity, on the occurrence of stem break. Stems were placed in deionised water. No pretreatment.

Cultivar	Cutting through/ below the cavity	% of flowers with stem break on								
		Day								
		0	1	2	3	4	5	6	7	8
'Wageningen Rood'	Below	0	0	0	80	80	80	90	90	90
	Through	0	0	0	0	20	20	20	20	20
'Mandarin'	Below	0	0	0	30	50	100	100	100	100
	Through	0	0	0	0	0	0	0	0	0
'Mini Wit'	Below	0	10	60	80	80	90	90	100	100
	Through	0	0	0	0	0	0	0	0	0
'Citronella'	Below	0	0	20	40	60	90	100	100	100
	Through	0	0	0	0	0	0	0	0	0

It seems likely that stem break is caused by a decline in water absorption which is due to the development of bacteria at the cut end (to be detailed i the discussion). Since stem break occurs far less often, or not at all, when a is made through a cavity, it is plausible that water can also be taken up via the side walls of such a cavity. To confirm this hypothesis, water was inject into the stem cavity while the flowers were in a vase without water. The va life of these flowers was the same as that of flowers with a visible cavity at the cut surface, placed in water. In a separate experiment red coloured wat ("Ecoline"; Talens) was injected into the hollow part of the stem. A few hours later the stem was cut lengthwise. The red dye was visible in the vess of the stem and in that part of the cavity where it had been injected origin: ly.

When the stem was cut through the cavity and a little hole was made in stem (about 15 cm above the cut surface), an increase in water height in th vase prolonged the period during which the flower remained at 100% or m of its initial fresh weight (Fig. 3). In this experiment transpiration of the st was prevented by winding a piece of parafilm around the stem. This prever water height from influencing the transpiring area. The relationship shown Fig. 3 is valid only when a small hole in the stem has been made as an air outlet from the cavity and when no bactericide has been added to the vase water.

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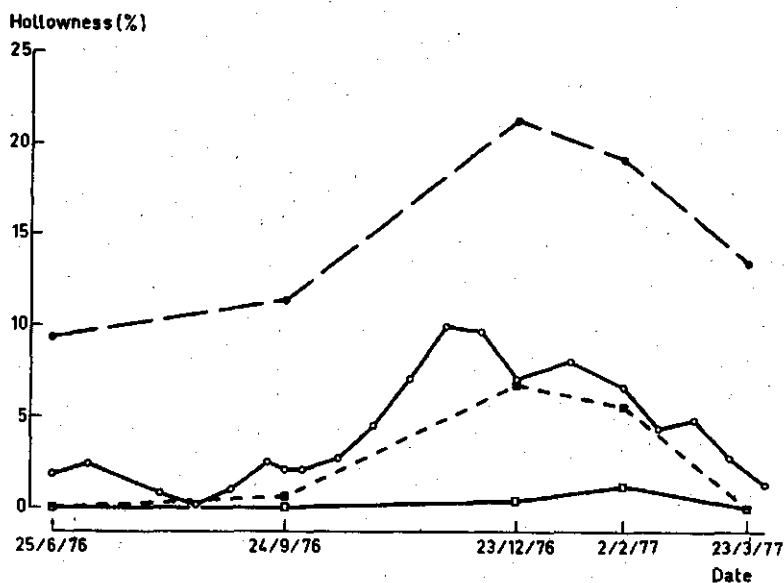
Fig. 4. Influence of season and developmental stage on percentage of stem hollowness in cv. 'Wageningen Rood'. Stage 1 (—□—□—): ray florets are red coloured, unfolded, the first female disc florets are flowering; Stage 2 (-■--■-): all female disc florets are just flowering; Stage 3 (—○—○—): stamen of 2 circles of bisexual disc florets are ripe (commercial stage of harvest); Stage 4 (-●--●-): all disc florets are just flowering.

DISCUSSION

Since the occurrence of stem break is preceded by a decline of the fresh weight of the flower and of the water potential of the petals (Fig. 2), it seems reasonable to assume that stem break is caused by water stress, like "bent neck" in cut roses (Burdett, 1970; Sacalis, 1974, 1975). The part of the Gerbera stem where the break occurs has the highest water content and the greatest cell elongation of the entire stem (Sachs, 1968; Wilberg, 1974). When water stress was induced in Gerbera flowers with and without a stem, the water content (as a percentage of dry weight) and the ψ of the petals of the flowers without a stem decreased much quicker than that of the flowers with a stem (own unpublished result). This suggests that the petals can withdraw water from the stem. Consequently the first visible symptom of water stress is stem break and not wilting of the petals.

The water balance of the flower is the result of water uptake and transpiration. After cutting, the transpiration rate remains nearly constant, while the absorption rate declines continuously (Fig. 2). The absorption rate is determined by the water potential gradient and by the resistance to water flow from the vase to the petals. The decline of the absorption rate may be ascribed

either to a decrease of the potential gradient or to an increase of the flo·
resistance. Figure 2 showed that the ψ of flowers with stem break decre
The gradient thus increases because the ψ of the vase water remains app
imately 0. Therefore, the decline of the absorption rate is caused by a c(
siderable increase of the flow resistance. This increase in resistance with
is known for many flower species (Aarts, 1957; Durkin and Kuc, 1966;
Marousky, 1969, 1972; Gilman and Steponkus, 1972; Rogers, 1973).

Stem break could be prevented in various ways, such as a pretreatmer
the stem with some chemicals (sodium hypochlorite, silver nitrate, Tabl·
adding of chemicals (silver nitrate, dichlorophen) to the vase water (Tab
and bringing water in the cavity of the stem (Table 3). The only thing tl
the 3 chemicals used in the first 2 methods have in common, is that the
prevent the growth of bacteria in the vase water (Aarts, 1957; Sykes, 19
Kofranek and Paul, 1972; Nichols, 1973). This is in agreement with the
experience that commercial preservatives, which always contain a bacte
prevent stem break (Sytsema and Barendse, 1975). Aarts (1957) showec
bacteria in the vase water cause a direct plugging of the vessels by filtera
substances. After some time non-filterable, heat-labile substances are fo
which also induce plugging of the vessels. The plugging by bacteria start;
the cut surface (Dansereau and Vines, 1975). Therefore it is possible to
obtain a recovery by recutting the stem as soon as it loses its turgidity. I
(1976) reported that spray-applied silver ion is a potent anti-ethylene ag
but Halevy and Kofranek (1977) recently showed with carnations that
benefits from the basal treatment with silver nitrate are related to its
bactericidal, and not to its anti-ethylene, effect. The third way to prevei
stem break could be explained by assuming 2 distinct pathways for wat(
uptake by a Gerbera stem (Fig. 5): (1) a direct one at the cut surface, o1
the vase into the vessels, and (2) an indirect one from the cavity of the s
via adjacent tissue into the vessels.

Bacteria in the vase water will inhibit direct water uptake very quickl
When an indirect uptake of water is possible, the inhibition of the direc·
uptake is not harmful to the flower. An indirect water uptake is only pc
if there is a cavity in the centre of the stem, and this depends on cultiva
season and developmental stage (Fig. 4), and if the stem is cut through t
cavity. This explains the strong influence of the season on the occurren(
stem break in 'Wageningen Rood'. When testing the usefulness of bacter
for the keeping-quality of cut Gerbera flowers, it is imperative to prever
direct water uptake, otherwise the effect of bactericides on growth of b.
in the vase water cannot be detected.

The water height in the vase can influence the number of days during
the fresh weight of the flowers is 100% or more of the initial weight (Fi
due to the fact that water height in the vase affects water height in the (
and thus water flow resistance. At a given water potential gradient, this
influence the absorption rate. Besides, it seems likely that the plugging
starts at the cut surface will move upwards in the vessels with time. If th
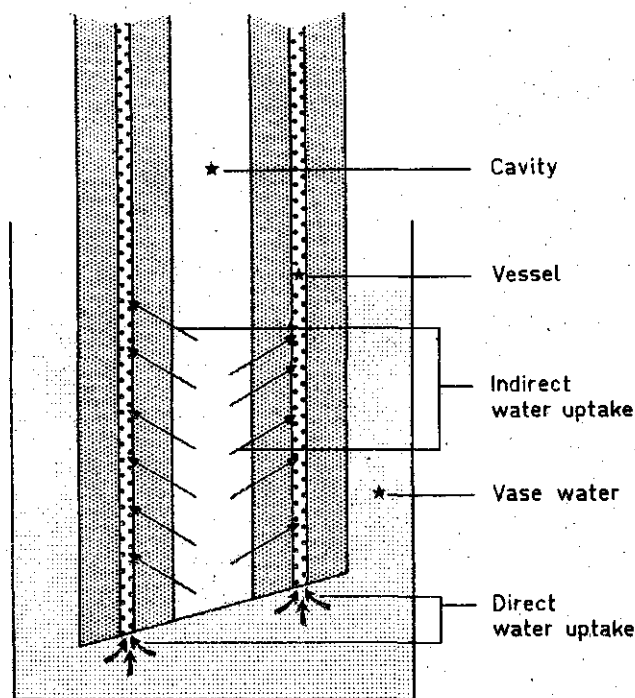
Fig. 5. The lower part of a Gerbera stem with cavity and the 2 possible ways for water uptake.

vessels are plugged above the water level in the cavity, the indirect uptake is not possible any more. Aarts (1957) suggested that placing stems in deep water inhibited the physiological stem-plugging that occurs even under aseptic conditions, because this is of an oxidative nature. The present study shows that in Gerbera, water height can also have a great influence on water uptake when bacterial stem-plugging is the most important reason for water-stress.

REFERENCES

Aarts, J.F.Th., 1957. Over de houdbaarheid van snijbloemen. Meded. Landbouwhogesch., Wageningen, 57(9): 62 pp.
Beyer, E. Jr., 1976. Silver ion, a potent antiethylene agent in cucumber and tomato. HortScience, 11: 195—196.

Boyer, J.S., 1967. Leaf water potentials measured with a pressure chamber. Plant Phys 42: 133—137.

Burdett, A.N., 1970. The cause of bent neck in cut roses. J. Am. Soc. Hortic. Sci., 95(4): 427—431.

Dansereau, B. and Vines, H.M., 1975. In-stem movement, isolation and identification c two bacteria and their antibiotic sensitivity. Acta Hortic., 41: 183—197.

Durkin, D. and Kuc, R., 1966. Vascular blockage and senescence of the cut rose flowe Proc. Am. Soc. Hortic. Sci., 89: 683—688.

Gilman, K.F. and Steponkus, P.L., 1972. Vascular blockage in cut roses. J. Am. Soc. H Sci., 97(5): 662—667.

Halevy, A.H., 1976. Treatments to improve water balance of cut flowers. Acta Hortic., 223—230.

Halevy, A.H. and Kofranek, A.M., 1977. Silver treatment of carnation flowers for redu ethylene damage and extending longevity. J. Am. Soc. Hortic. Sci., 102: 76—77.

Horie, K., 1962. Studies of the flowering of *Tradescantia reflexa* with special reference petal behaviour. Mem. Hyogo Univ. Agric. (Jpn.), 14: 1—54.

Kofranek, A.M. and Paul, J.L., 1972. Silver impregnated stems aid carnation flower lor Grower, 78(25): 1278—1279.

Marousky, F.J., 1969. Vascular blockage, water absorption, stomatal opening and resp tion of cut 'Better Times' roses treated with 8-hydroxyquinoline citrate and sucrose J. Am. Soc. Hortic. Sci., 94(3): 223—226.

Marousky, F.J., 1972. Water relations, effects of floral preservatives on bud opening, a keeping quality of cut flowers. HortScience, 7(2): 114—116.

Mayak, S. and Halevy, A.H., 1974. The action of kinetin in improving the water balanc and delaying senescence processes in cut rose flowers. Physiol. Plant., 32: 330—336

Mayak, S., Halevy, A.H., Sagie, S., Bor-Yoseph, A. and Bravdo, B., 1974. The water ba cut rose flowers. Physiol. Plant., 31: 15—22.

Nichols, R., 1973. Senescence of the cut carnation flower: respiration and sugar status Hortic. Sci., 48: 111—121.

Rogers, M.N., 1973. An historical and critical review of postharvest physiology researc cut flowers. HortScience, 8(3): 189—194.

Sacalis, J.N., 1974. Inhibition of vascular blockage and extension of vase life in cut ros with an ion exchange column. HortScience, 9(2): 149—151.

Sacalis, J.N., 1975. Vascular blockage and its inhibition in cut rose flowers. Acta Horti 41: 159—170.

Sachs, R.M., 1968. Control of intercalary growth in the scape of Gerbera by auxin and gibberellic acid. Am. J. Bot., 55(1): 62—68.

Slavik, B., 1974. Methods of studying plant water relations. Springer-Verlag, Berlin, 449 pp.

Sykes, G., 1965. Disinfection and sterilization. 2nd edition, Spon, London, 486 pp.

Sytsema, W. and Barendse, L., 1975. Verhoging kwaliteit door verbeterde houdbaarhei (5). Vakbl. Bloemisterij, 30(50): 12—13.

Wilberg, B., 1974. Physiologische Untersuchungen zur Ursache des Knickens im Blüter schaft von *Gerbera jamesonii*. Schultze, Hamburg, 66 pp.

WATER RELATIONS AND KEEPING-QUALITY OF CUT GERBERA FLOWERS. II. WATER BALANCE OF AGEING FLOWERS

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ABSTRACT

Meeteren, U. van, 1978. Water relations and keeping-quality of cut Gerbera flowers. II. Water balance of ageing flowers. *Scientia Hortic.*, 9: 189—197.

Time course of fresh weight (F.W.), water content as percentage of dry weight of petals (W.C.), maximal water content after saturation of petals (W.C.$_{max}$), relative water content of petals (R.W.C.), absorption rate (abs.), transpiration rate, water potential of petals (Ψ), stem flow resistance (R$_{stem}$) and flower developmental stage of cut Gerbera flowers in solutions with chemicals were determined. In a solution with silver nitrate, an increase of R$_{stem}$ was evident after 4 days, resulting in a decrease of abs., F.W., W.C., R.W.C. and Ψ. A constant pH of the vase water of 3.5 could prevent this increase in R$_{stem}$. The pH of the vase water was influenced by the flower itself.

When the increase of R$_{stem}$ was prevented, the absorption rate was higher than the transpiration rate during the first 5 days after cutting, which resulted in an increase of F.W., W.C. and R.W.C. After day 5, absorption was lower than transpiration, the F.W., W.C., W.C.$_{max}$ and R.W.C. decreased, while Ψ remained steady. It is suggested that the water deficit—water potential relationships of the petals change with age, resulting in a lower water-holding capacity of the petals.

INTRODUCTION

Cutting of the flower will influence various processes involved in the water-, energy- and hormonal balance. When a cut flower is placed in water, the resistance to the water flow through the stem may increase with time (Rogers, 1973; Moncousin, 1976). This increase in resistance ("blockage" or "stem plugging") can be caused by the activity of microorganisms in the vase water or by an unknown physiological reaction of the flower (Aarts, 1957). In roses, it was demonstrated that the increase in resistance was not associated with a natural senescence of flowers, since the resistance did not change with age when the flowers remained on the plant (Mayak et al., 1974).

Water potential (Ψ) is a direct parameter which reflects water deficit in plant tissue (Barrs, 1968). There are only a few papers in which Ψ of flower petals are discussed (Mayak et al., 1974; Meeteren, 1978). In these papers,

however, stem plugging was not prevented. The present paper describes changes in various parameters concerning the water balance of cut Gerbera inflorescences during ageing, while growth of microorganisms during the va life of the cut flower was prevented by silver nitrate, and "physiological" s plugging was influenced by the pH of the vase water.

For the sake of convenience the term "flower" is used for the complete inflorescence, including its stem.

MATERIALS AND METHODS

Plants of *Gerbera jamesonii* H. Bolus cultivar 'Wageningen Rood' were u: Details of cultivation, the treatment of the flowers, and the determination fresh weight, water uptake, transpiration and petal water potential have be given in a previous paper (Meeteren, 1978). All experiments were done witl at least 10 flowers per treatment and were repeated several times.

The flowers were placed in 250 ml erlenmeyer flasks filled with 100 ml c one of the following solutions:
A. silver nitrate (20 mg/l);
B. silver nitrate (20 mg/l) and citric acid (75 mg/l);
C. silver nitrate (20 mg/l), citric acid (150 mg/l) and $Na_2HPO_4 \cdot 2H_2O$ (50 n renewed every 3 days;
D. silver nitrate (20 mg/l) and $Na_2HPO_4 \cdot 2H_2O$ (25 mg/l), brought to pH 6.$ by phosphoric acid and renewed every 3 days.

The solutions were prepared with deionised water. The flasks were placed i: an air-conditioned room at a temperature of $23 \pm 1°C$, a relative humidity c $70 \pm 5\%$, a Piche evaporation of 0.11 ml h^{-1} and an irradiance of 7.8 Wm^{-2} flower height. The irradiance was obtained from Philips TL 57 fluorescent tubes during a photoperiod of 24 h.

Water content (W.C.) of the petals was expressed as percentage of dry weight and as relative water content (R.W.C.). Dry weight was determined a 24 h exposure of the petals at 80°C. The R.W.C. of the petals was calculat by a modified method of Barrs and Weatherley (1962), using complete pet instead of punched discs. The maximal water content after saturation (W.C was obtained by placing the cut surface of the petals in distilled water for £ at 23°C. A jar was placed over the petals and the walls were lined with wet filter paper in order to prevent transpiration.

The resistance to the water flow (R_{stem}) between the vase and the petals was calculated using the equation

$$R_{stem} = \frac{\Psi_{vase} - \Psi_{petal}}{abs.}$$

where Ψ_{vase} and Ψ_{petal} are the water potential of the vase water and that o the petals (in bars), respectively, and abs. is the rate of water absorption (ir g h^{-1} flower^{-1}). Ψ_{vase} is assumed to be 0. Equation (1) is valid only when fo

abs. precautions to prevent stem transpiration are taken and corrections for stem elongation are made. Transpiration from the stem was prevented by twisting a piece of parafilm around the stem. The measured values of abs. were corrected for the increase in stem volume by assuming that for an increase of 1 ml, 1 ml of water is necessary. The stem volume was determined daily by dipping the stem in a calibrated tube and observing the displacement of water. Because abs. is a mean value of 24 h, Ψ_{petal} was taken as an average between that at the beginning and that after 24 h.

The percentage of flower development (F.D.) is given by

$$\text{F.D.} = \left(1 - \frac{r_2^2}{r_1^2}\right) \times 100 \tag{2}$$

where r_1 is the radius of the total disc of bisexual disc florets and r_2 is the radius of the non-flowering part of the disc.

RESULTS

For flowers placed in solution A, during the first 3 days after cutting absorption was higher than transpiration, resulting in an increase in F.W. (Fig. 1). It should be noticed that an increase in F.W. is due both to the increased water content and to growth. After the third day transpiration was higher than absorption, and F.W. and Ψ decreased. As the Ψ of the vase water remained constant, the potential gradient between vase water and petals increased. Since absorption did not increase, and even appeared to decrease, the resistance of the stem (R_{stem}) increased. The flowers did not show "stem break" during the experiment, which was a result of the application of silver nitrate (Meeteren, 1978). The decrease of Ψ could not be prevented by a daily recutting of the stem.

Figure 2 shows the change in R_{stem} and Ψ and that in pH of the vase water of flowers during 8 days in the 4 different solutions A, B, C and D. In solution A, an increase of R_{stem} and a decrease of Ψ with time occurred similar to that of the previous experiment. Adding citric acid (75 mg/l) to the vase water (solution B) decreased the initial pH from 5.5 (solution A) to 3.5. R_{stem} and Ψ remained the same during the first 4 days. Thereafter, the pH and R_{stem} increased, and Ψ decreased. A constant pH of 3.5 (solution C), however, prevented any change in R_{stem} and Ψ. The constant value of R_{stem} and Ψ was caused by the low pH and not by Na_2HPO_4 or by changing the vase water, as shown with solution D. The occurrence of physiological stem plugging was not accompanied by visible symptoms.

Using solution C makes it possible to investigate the water balance of cut Gerbera flowers as influenced by ageing without stem plugging (Fig. 3). For the non-destructive measurements of F.W., F.D., abs. and transp. the same 10 flowers were used throughout the experimental period of 12 days. For the determination of R.W.C., $W.C._{max}$, W.C. and Ψ, however, a parallel group of 10 flowers was analysed. The first 5 days after cutting, absorption rate was
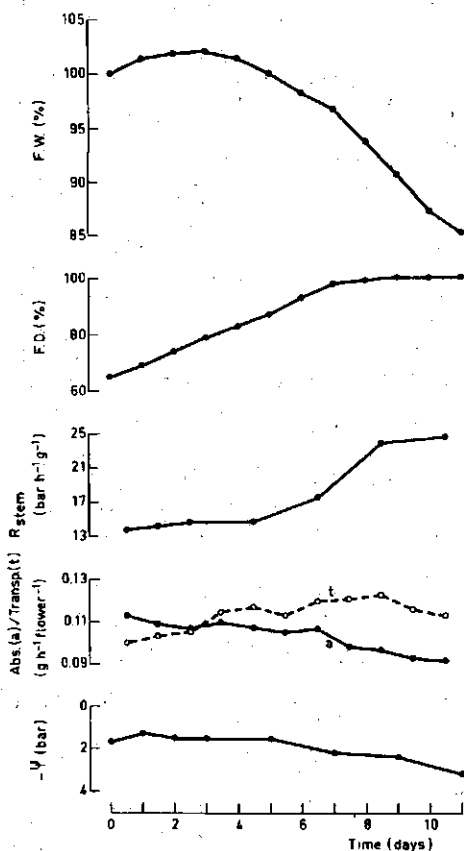
Fig. 1. Time courses of fresh weight (F.W.), flower developmental stage (F.D.), stem flow resistance (R_{stem}), absorption rate (abs.), transpiration rate (transp.) and water potential of petals (Ψ) of Gerbera flowers with their stem bases placed in a solution of silver nitrate (20 mg/l).

higher than transpiration rate. As a result of this an increase occurred in R.W.C., F.W. and W.C. Transpiration increased slightly, while climatic conditions were held constant. At day 5 the rate of absorption was equal to that of transpiration. Thereafter, transpiration remained the same, while absorption declined continuously with time, through which R.W.C., F.W. and W.C. decreased. The maximal water content after saturation (W.C.$_{max}$) also decreased after day 5. However, during the 12 days of the experiment Ψ remained constant. Although various parameters in the water balance were affected to a large extent by the composition of the vase water, the development of the flowers (F.D.) was not influenced (Figs. 1 and 3).
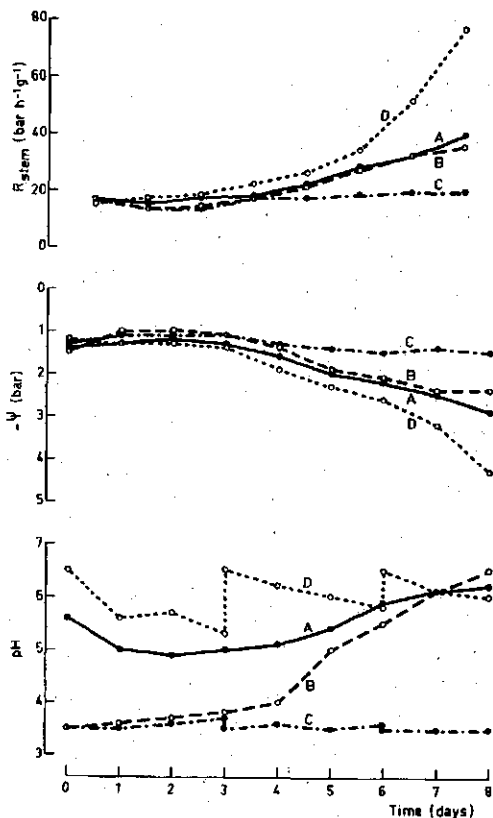
Fig. 2. Changes in time of stem flow resistance (R_{stem}), water potential of petals (Ψ) and pH of the vase water of Gerbera flowers with their stem bases placed in: A. silver nitrate (20 mg/l); B. silver nitrate (20 mg/l) + citric acid (75 mg/l); C. silver nitrate (20 mg/l) + citric acid (150 mg/l) + $Na_2HPO_4 \cdot 2H_2O$ (50 mg/l), renewed every 3 days; D. silver nitrate (20 mg/l) + $Na_2HPO_4 \cdot 2H_2O$ (25 mg/l) with a pH of 6.5 (obtained by phosphoric acid), renewed every 3 days.

DISCUSSION

When Gerbera flowers cultivar 'Wageningen Rood' were placed in water with silver nitrate (20 mg/l), the Ψ of the petals decreased after 3—5 days, due to an increase of the resistance to the water flow through the stem (Fig. 1). This increase in the resistance of the vessels ("stem plugging") was not caused by microbial activity in the vase water, as the growth of microorganisms was inhibited by silver nitrate. Recutting the stem could not prevent this phenom-enon. In a previous publication (Meeteren, 1978) it was demonstrated that "stem break" due to stem plugging of the lower part of the vessels was prevent-
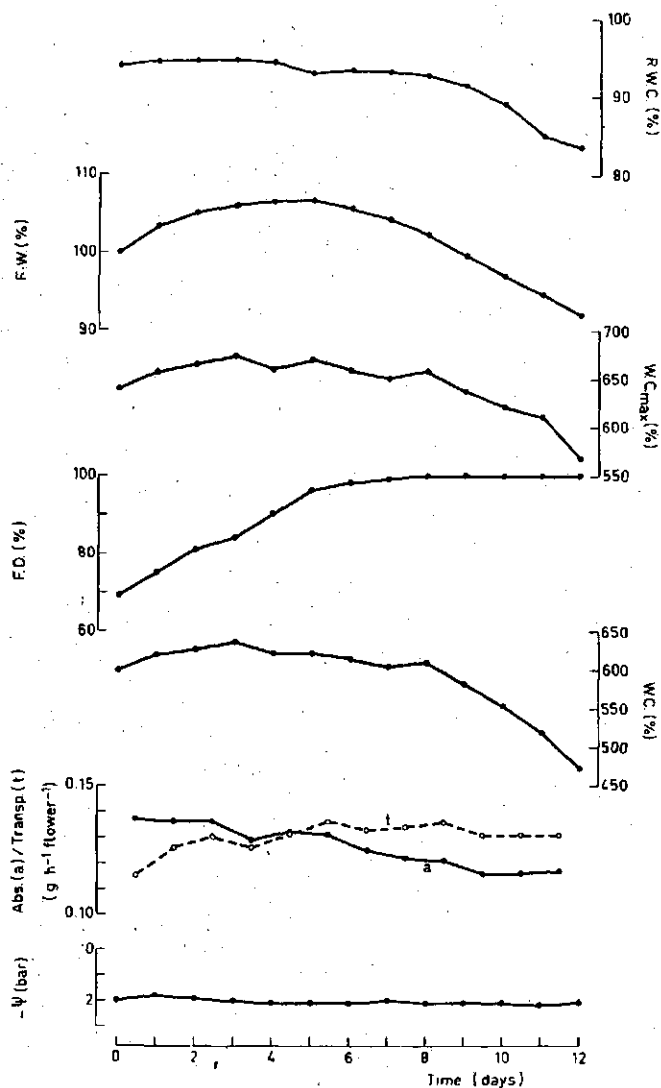
Fig. 3. Time courses — left scales — of fresh weight (F.W.), flower developmental stage (F.D.), absorption rate (abs.), transpiration rate (transp.), and water potential of petals (Ψ); — right scales — relative water content of petals (R.W.C.), maximal water content after saturation of petals (W.C. $_{max}$), and water content as percentage of dry weight of petals (W.C.), of Gerbera flowers with their stems in a solution of silver nitrate (20 mg/l) + citric acid (150 mg/l) + $Na_2HPO_4 \cdot 2H_2O$ (50 mg/l), renewed every 3 days.

ed by the addition of silver nitrate or by recutting the stem. The present results suggest that stem plugging, not caused by microbial activity, exists in the upper part of the vessels.

By means of staining-reaction, general appearance and location of occurrence in the stem profile, Lineberger and Steponkus (1976) demonstrated very clearly 2 types of vascular occlusion in stems of roses held in distilled water. A basal occlusion due to bacterial contamination was restricted to the lowest 2.5 cm of the stem, while the second type of occlusion, carbohydrate in nature, occurred above the solution level on the stem.

Aarst (1957) showed that stem plugging can be caused by an unknown physiological reaction of oxidative nature as a consequence of substances secreted by disorganised cells of the flower. He observed that this "physiological" plugging is strongly prevented by a low pH of the vase water. Influence of pH on vase life of cut flowers has also been demonstrated by Marousky (1971) and by Camprubí and Aquilá (1974). In many investigations a low pH of the vase water was achieved by using citric acid (Aarts, 1957; Penningsfeld and Forchthammer, 1966; Kofranek and Kubota, 1972; Kofranek et al., 1975). With Gerbera flowers, citric acid did not prevent the increase in stem resistance as compared with the control (Fig. 2). This increase was accompanied by an increase in pH of the vase water and occurred after approximately 4 days. The change in pH is probably due to substances leached out of the flower stem. Even a weak buffer of citric acid (150 mg/l) and $Na_2HPO_4 \cdot 2H_2O$ (50 mg/l) could not prevent this increase of the pH. Only by replacing the buffer solution every 3 days was it possible to hold the pH between 3.5 and 3.7. In this case the increase of the stem resistance (R_{stem}) and the decline of water potential (Ψ) was prevented (Fig. 2, solution C). Using solution D in Fig. 2, it was demonstrated that neither the replacement of the solution nor the application of $Na_2HPO_4 \cdot 2H_2O$ prevented stem plugging. It can be concluded from these results that pH is the most important factor in affecting non-microbial stem plugging, which is in agreement with the findings of Aarts (1957) for other flowers.

Physiological stem plugging was not accompanied by visible symptoms. When the water transport through the stem of cut Gerbera flowers is impaired by microbial activity in the vase water, stem break occurs (Meeteren, 1978). Physiological stem plugging, which also induces a water stress, does not cause stem break. There are several explanations possible for this apparent discrepancy:

(a) The sensitivity for stem break decreases when the flower becomes older (Wilberg, 1974). As in the case of microbial plugging, Ψ of petals starts to decrease after about 2 days (Meeteren, 1978), while in the case of non-microbial plugging it starts to decrease after 4 days (Fig. 1), and in the latter case the flower will be less sensitive to stem break.

(b) With microbial plugging, the Ψ of the petals decreases much quicker than with non-microbial plugging, viz. 3 bars/day (Meeteren, 1978) versus 0.2 bars/day (Fig. 1).

(c) Stem break occurs when there is a water stress in the stem. The Ψ of the petals reflects the water balance of the petals. As discussed before, microbial plugging starts at the cut surface, while physiological plugging exists in the upper part of the stem. So it is unknown if there is a water stres in the sensitive part of the stem.

Although Ψ of the petals is different in flowers with or without physiolog stem plugging, there were no externally visible differences between these pet We have to keep in mind, however, that the climatic conditions during the experiment were mild (relative humidity was 70%). It cannot be excluded th under circumstances with higher evaporative demand visible symptoms will occur.

While R.W.C., F.W., $W.C._{max}$ and W.C. of the petals decreased with time, of the petals remained constant, when microbial and non-microbial stem plugging were prevented (Fig. 3). It is likely that these changes are a result o ageing.

From a re-examination of the results of Mayak et al. (1974) in roses, it wა obvious that after 3 days the water content decreased, while the water poter of petals remained constant for at least 6 days. Aarts (1957) also found that many flower species decreased in fresh weight after some time when stem plugging was prevented with a solution of chemicals. This suggests that the decrease of water content as a result of ageing is a common phenomenon in cut flowers.

As a correlation between water content and Ψ will exist, the decrease of W.C. and R.W.C. in time without an appreciable change in Ψ suggests that this correlation changes with age, as is known for leaves (Jarvis and Jarvis, 1963; Knipling, 1967). The R.W.C. was 93.6% at a water potential of -2.0 b on day 0, but only 83.4% at the same water potential on day 12 (Fig. 3). Th indicates that the adaptation of Ψ to changes in water content becomes less when the petals are ageing. Also the decrease of $W.C._{max}$ suggests that the capacity of the petals to hold water becomes less with age. As all experimenl were conducted with cut flowers, we cannot conclude if this phenomenon is associated with a natural senescence of flowers. Probably the ageing of cut flowers will be influenced by their altered hormonal and energy balance. Cătský (1965) noted that R.W.C. of most of the leaves on plants growing in moist soil was rather similar. As the soil dried, however, the R.W.C. dropped more rapidly in old leaves than in young ones. The internal water relations of the petals will be discussed in more detail in a following paper in this seri๕

Taking together the results of the previous paper and of this one, we conclude that there can be 3 different causes for a decrease of the water conten of petals of a cut Gerbera flower placed in water:
1. microbial activity in the vase water: Ψ of the petals decreases, stem break occurs;
2. "physiological" stem plugging: Ψ of the petals decreases, stem break is absent;
3. ageing of the petals: Ψ does not change, stem break is absent.

REFERENCES

Aarts, J.F.Th., 1957. Over de houdbaarheid van snijbloemen. Meded. Landbouwhogesch. Wageningen, 57(9): 62 pp.

Barrs, H.D., 1968. Determination of water deficits in plant tissues. In: T.T. Kozlowski (Editor), Water Deficits and Plant Growth. Vol. I. Academic Press, New York, pp. 235—368.

Barrs, H.D. and Weatherley, P.E., 1962. A re-examination of the relative turgidity technique for estimating water deficits in leaves. Aust. J. Biol. Sci., 15: 413—428.

Camprubí, P. and Aquilá, J.F., 1974. Studies directed towards prolonging the life of the cut flower in the mediterranean varieties of *Dianthus caryophyllus*. Acta Hortic., 43(2): 307—318.

Cătský, J., 1965. Water saturation deficit and photosynthetic rate as related to leaf age in the wilting plant. In: B. Slavík (Editor), Water Stress in Plants. Yunk, The Hague, pp. 203—208.

Jarvis, P.G. and Jarvis, M.S., 1963. The water relations of tree seedlings. IV. Some aspects of the tissue water relations and drought resistance. Physiol. Plant., 16: 501—516.

Knipling, E.B., 1967. Effect of leaf ageing on water deficit — water potential relationships of dogwood leaves growing in two environments. Physiol. Plant., 20: 65—72.

Kofranek, A.M. and Kubota, J., 1972. More experiments on bud-opening solutions for carnations. Grower, 78: 919—920.

Kofranek, A.M., Halevy, A.H. and Kubota, J., 1975. Bud opening of chrysanthemums after long term storage. HortScience, 10(4): 378—380.

Lineberger, R.D. and Steponkus, P.L., 1976. Identification and localization of vascular occlusions in cut roses. J. Am. Soc. Hortic. Sci., 101(3): 246—250.

Marousky, F.J., 1971. Inhibition of vascular blockage and increased moisture retention in cut roses induced by pH, 8-hydroxyquinoline citrate and sucrose. J. Am. Soc. Hortic. Sci., 96(1): 38—41.

Mayak, S., Halevy, A.H., Sagie, S., Bar-Yoseph, A. and Bravdo, B., 1974. The water balance of cut rose flowers. Physiol. Plant., 31: 15—22.

Meeteren, U. van, 1978. Water relations and keeping-quality of cut Gerbera flowers. I. The cause of stem break. Scientia Hortic., 8: 65—74.

Moncousin, Ch., 1976. La conservation des fleurs coupées. Pépinièristes, Horticulteurs, Maraîchers, 172: 29—35.

Penningsfeld, F. and Forchthammer, L., 1966. Silbernitrat verbessert die Haltbarkeit geschnittener Gerbera. Gartenwelt, 1966(9): 226—228.

Rogers, M.N., 1973. An historical and critical review of postharvest physiology research on cut flowers. HortScience, 8(3): 189—194.

Wilberg, B., 1974. Physiologische Untersuchungen zur Ursache des Knickens im Blütenschaft von *Gerbera jamesonii*. Schultze, Hamburg, 66 pp.

WATER RELATIONS AND KEEPING-QUALITY OF CUT GERBERA FLOWERS. III. WATER CONTENT, PERMEABILITY AND DRY WEIGHT OF AGEING PETALS

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ABSTRACT

Meeteren, U. van, 1979. Water relations and keeping-quality of cut Gerbera flowers. III. Water content, permeability and dry weight of ageing petals. *Scientia Hortic.*, 10: 261—269.

The semipermeability of petal cells of cut Gerbera inflorescences changed with age, as was demonstrated by an increase of ion leakage. The date at which ion leakage increased depended on the cultivar and coincided with the decrease in water content of the petals. Temperature and cytokinin treatments affected water content and ion leakage, but not their coincidence. Inflorescences left on the plant showed neither an increase in ion leakage, nor a decrease in water content.

Regression curves of water content on ion leakage and dry weight of petals are given. The consequences of the type of curves are discussed.

INTRODUCTION

The water balance of cut flowers can be disturbed by a blockage of the stem vessels (Aarts, 1957; Marousky, 1972; Rogers, 1973), but even when the resistance to the water flow through the stem remains constant, the petal-water-content of cut Gerbera inflorescences changes with time, because of the altered water-holding capacity of these petals with age (Meeteren, 1978b).

It is likely that membrane properties of petal cells are affected by ageing, as has been demonstrated for *Tradescantia reflexa* (Horie, 1962), carnations (Nichols, 1968), roses (Borochov et al., 1976) and *Ipomoea tricolor* (Beutelmann and Kende, 1977). Petal dry weight of cut roses also depends on ageing (Weinstein, 1957). Changes in the semipermeability of cytoplasm and in dry matter content will modify the water content of cells.

The present paper describes changes of water content, permeability characteristics and petal dry weight of ageing Gerbera inflorescences. For the sake of convenience the term "flower" is used for the complete inflorescence, including its stem.

MATERIALS AND METHODS

Plant material and experimental conditions. — Plants of *Gerbera jamesonii* H. Bolus were raised in a glasshouse. Unless otherwise specified, the cultivar 'Wageningen Rood' was used. Details on cultivation and treatment of the flowers have been given in a previous paper (Meeteren, 1978a). Each flower was placed in a 250-ml Erlenmeyer flask filled with 100 ml of a solution, containing silver nitrate (20 mg/l) + citric acid (150 mg/l) + $Na_2 HPO_4 \cdot 2H_2 O$ (50 mg/l) in deionised water. The solution in the Erlenmeyer flasks was renewed every 3 days. In this way, stem plugging is prevented (Meeteren, 1978b). The top of each Erlenmeyer flask was sealed with a piece of parafilm to prevent evaporation. The experiments with cut flowers were carried out in a conditioned room at a temperature of $23 \pm 1°C$, a relative humidity of $70 \pm 5\%$, a Piche evaporation of 0.11 ml h^{-1}, and a constant irradiance (400—700 nm) of 7.8 Wm^{-2} at flower height, obtained from Philips TL57 fluorescent tubes. When cut flowers were compared with flowers still attached to the plant, the environmental conditions were: day/night temperatures of $23/21 \pm 1°C$, relative humidity of $70 \pm 5\%$, and irradiance (400—700 nm) of 58 Wm^{-2} at flower height, obtained from high pressure sodium lamps (Lucalox 400, Gen. Electric), during a 12-h photoperiod. The plants were watered until field capacity every other day at the beginning of the photoperiod. Samples were taken from the flowers 3.5 h after the watering.

Water content, dry weight and flower developmental stage. — Water content of the petals (W.C.) as a percentage of dry weight, dry weight of the petals (D.W.) and flower developmental stage (F.D.) were determined as described earlier (Meeteren, 1978b).

Ion leakage. — The leakage of ions (I.L.) from petal tissue was determined using a modified method of Weinbaum and Muraoka (1976). Three discs (ϕ 7 mm) from one outer petal were floated on 2 ml 2% (w/v) mannitol solution during 24 h at $23°C$. In the case of the cultivar 'Mini Wit' 2 discs were used. Thereafter the electric conductivity of the solution (c_1) was measured with a direct-reading conductivity meter. Following 2 cycles of freezing ($-20°C$) and thawing of the discs (to destroy all membranes) together with the solutions on which they were floating, and equilibration for 24 h at $23°C$, the conductivity was measured again (c_2). Dividing c_1 by c_2 and multiplying by 100 gave the percentage of ion leakage.

Treatments with cytokinin. — At the beginning of the experiment, flower heads were immersed in a solution of 6-benzyl-adenin (Fluka AG) (10^{-4} Mol) + Tween 20 (0.1 ml/l) for 2 min. Controls were treated with deionised water + Tween 20. These treatments were performed at room temperature. After the dipping, the petals were allowed to dry in the air.

RESULTS

In a series of experiments emphasis was mainly on the relation between water content (W.C.) and ion leakage (I.L.) and on that between W.C. and dry weight (D.W.) of ageing petals. Some additional studies on permeability will be mentioned in the discussion.

Figure 1 shows the effect of age in days after cutting on W.C. and I.L. of petals of cut flowers of 'Wageningen Rood', 'Citronella' and 'Mini Wit'. The W.C. increased and subsequently decreased rapidly after approximately 6 days with 'Wageningen Rood' and 'Citronella', and after 16 days with 'Mini Wit'. In all 3 cultivars the decrease of W.C. was accompanied by a simultaneous increase of I.L. With 'Citronella' and 'Mini Wit' the stage of maximum flower development (F.D.) (85% and 100%, respectively) was achieved before W.C. decreased and I.L. increased, while in the case of 'Wageningen Rood', F.D. reached 100% after the onset of the decrease of W.C. and increase of I.L., as is shown by the arrows in Fig. 1.
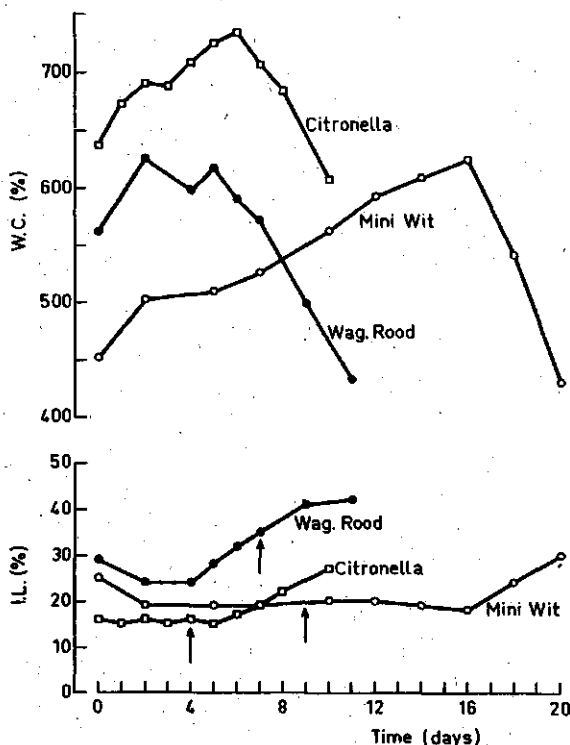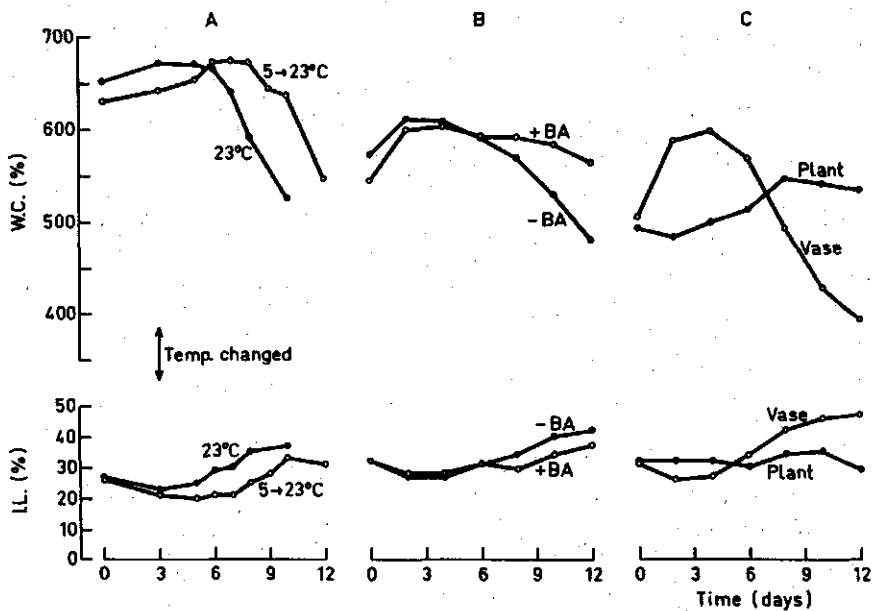

Fig. 1. Time courses of water content of petals (W.C.) as a percentage of dry weight and ion leakage from petals (I.L.) of 3 Gerbera cultivars. Each point is a mean value of 10 flowers. Arrows indicate date of maximum flower development (100% for 'Wageningen Rood' and 'Mini Wit', and 85% for 'Citronella').

In another series of experiments, time courses of W.C. and I.L. were measured when: (a) a low-temperature treatment of 5°C during the first 3 days after cutting was applied; (b) a pretreatment of the petals with 6-benzyl-adenin was given; (c) cut flowers were compared with intact flowers on the plant. A temperature of 5°C during the first 3 days of the vase life delayed the onset of the decrease in W.C. by 3 days. Also, the increase of I.L. occurred 3 days later (Fig. 2A). Immersing the petals immediately after harvest in 6-benzyl-adenin for a short time, retarded the decrease of W.C. and also the increase of I.L. (Fig. 2B). When the flowers remained on the plant, no sharp decrease of W.C. occurred, and I.L. remained steady (Fig. 2C).

Fig. 2. Time courses of water content of petals (W.C.) as a percentage of dry weight and ion leakage from petals (I.L.) of Gerbera flowers cultivar 'Wageningen Rood', as influenced by: (A) temperature during the first 3 days of the experiment; (B) pre-treatment of the flower head with benzyl-adenin (BA); (C) either cutting the flowers (vase) or leaving them on the plant (plant). Each point is a mean value of 10 flowers.

There was a highly significant linear regression of W.C. on I.L. for 'Wageningen Rood'. However, a quadratic term significantly improved the regression model. Quadratic regressions of W.C. on I.L. also existed for 'Citronella' and 'Mini Wit' for the period of increasing I.L. (after 5 and 16 days, respectively). These curves are given in Fig. 3.

The W.C. of petals of young flowers decreased rapidly when the flower heads were exposed to 23°C without water supply, whereas I.L. remained the same (Fig. 4).
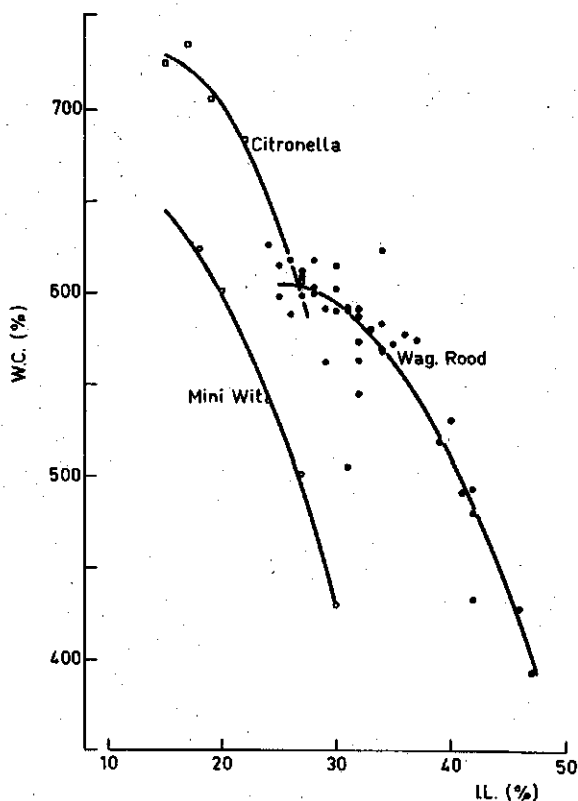
Fig. 3. Changes in water content (W.C.) in relation to ion leakage (I.L.) of petals of 3 Gerbera cultivars. Each point is a mean value of 10 flowers. The regression equations are: 'Wageningen Rood' (whole vase period), W.C. = $350 + 20.5 (I.L.) - 0.41 (I.L.)^2$ ($n = 41$, $r^2 = 0.835$, $P < 0.001$); 'Mini Wit' (after day 16), W.C. = $688 + 4.0 (I.L.) - 0.42 (I.L.)^2$ ($n = 5$, $r^2 = 0.9998$, $P < 0.001$); 'Citronella' (after day 5), W.C. = $558 + 23.9 (I.L.) - 0.83 (I.L.)^2$ ($n = 5$, $r^2 = 0.983$, $P < 0.025$).

Figure 5 shows the effect of age on petal dry weight (D.W.) of the 3 cuvars. D.W. appeared to decrease continuously with time. With 'Mini Wit', dD.W./dt was less than that of the other 2 cultivars. However, this differe was only significant at a 1% level with 'Citronella'.

With 'Citronella' and 'Mini Wit', W.C. was closely related to D.W. durir the first period of vase life (5 and 16 days, respectively), when I.L. remai more or less constant (Fig. 6).

For the entire experimental period, correlations between W.C., I.L. an D.W. were: W.C. = $871 + 43.6 (I.L.) - 1.36 (I.L.)^2 - 54.4 (D.W.)$ ($r^2 = 0.884$, $n = 10$, $P < 0.005$) for 'Citronella', and W.C. = $667 + 40.1 (I.L.) - 1.20 (I.L.)^2 - 46.1 (D.W.)$ ($r^2 = 0.816$, $n = 19$, $P < 0.001$) for 'Mini Wit' In the case of 'Wageningen Rood', the regression of W.C. on I.L., as given in Fig. 3, was not significantly improved by adding D.W. to the formula.
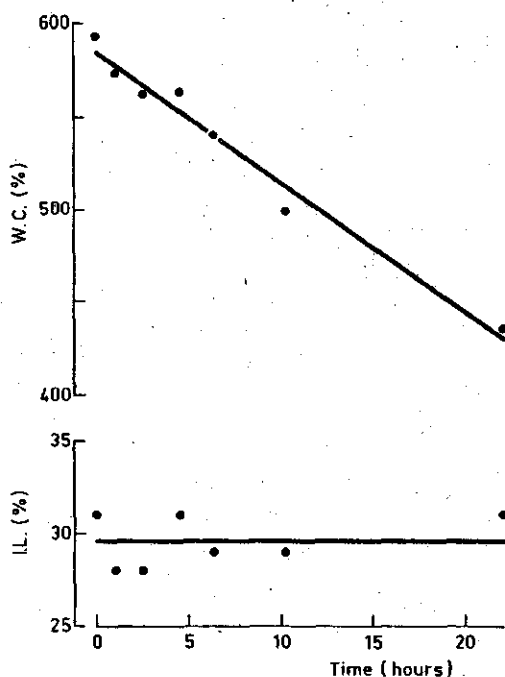
Fig. 4. Changes of water content (W.C.) and ion leakage (I.L.) of petals of Gerbera cultivar 'Wageningen Rood', exposed to 23°C, without stem and water. The experiment was carried out after the flowers had been in a vase for 1 day. Each point is a mean value of 5 petals.

DISCUSSION

The increase in W.C. of petals of cut Gerbera flowers during the first day of their vase life was followed by a sharp decrease when the flowers aged (Fig. 1). During all experiments the flowers were placed in solutions which prevented stem plugging. In a previous paper (Meeteren, 1978b), it was suggested that this decrease of W.C. was caused by a decrease of the water-holding capacity of the petals. The onset of the decline in W.C. depended on the cultivar and was associated with an increasing I.L. (Fig. 1). With 2 cultivars the flowers reached their maximal development before the onset of the decrease of W.C. and increase of I.L., while in the third cultivar sharp decrease of W.C. and increase of I.L. started before the maximum F.D. was reached. This suggests that there is no correlation between F.D. and W.C. or I.L.

Changes in the rate of ion leakage from tissue samples are supposed to demonstrate changes in membrane permeability (Baur and Workman, 1964; Bir and Bramlage, 1973). Tissues with normal permeability properties can retain solutes taken up by active uptake, despite a washing of the tissue.
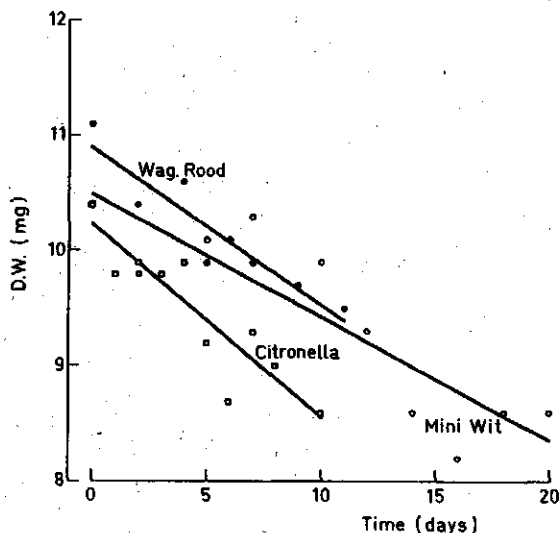
Fig. 5. Time courses of dry weight (D.W.) of petals of 3 Gerbera cultivars. Each point is a mean value of 10 petals (from 10 flowers). The regression equations are: 'Mini Wit', D.W. = $10.51 - 0.1095\ T$ ($n = 10$, $r = 0.891$); 'Wageningen Rood', D.W. = $10.89 - 0.1388\ T$ ($n = 8$, $r = 0.926$); 'Citronella', D.W. = $10.22-0.1662\ T$ ($n = 10$, $r = 0.907$). T = number of days after cutting.

The washing removes only those solutes which penetrate the discs passively (diffusion), whether into the cell-wall region or into protoplasts which have become free space owing to changes of permeability (Sacher, 1966). In some preliminary experiments with 'Wageningen Rood' a decrease in the active uptake of Cl^--ions after 4—6 days was observed. This suggests that the permeability changes, as was already indicated with the ion leakage. These changes in permeability were confirmed by the rapid uptake of mannitol by old petals as compared with young ones, as well as the ability of old petals to absorb the big molecules of polyethylene glycol 1500 (own results, unpublished).

Ageing-effects on semipermeability were observed in other flowers also. The first visible feature demonstrating the initiation of fading of flowers of *Tradescantia reflexa* is the infiltration of cell sap into the intercellular spaces (Horie, 1962). In these flowers, the plasmolysis time was least in the cells near death. Nichols (1968) with carnations and Sacalis (1975) with roses, demonstrated an increase in leakage of ions from petals when the flowers aged. However, they did not measure the total ion concentrations of the intact cells, so it is not known if this increase in leakage is caused by a change in concentration of ions in the cells or by a change in permeability. Beutelmann and Kende (1977) reported that the content of membrane lipids of ageing flower-tissue of *Ipomoea tricolor* declined rapidly.
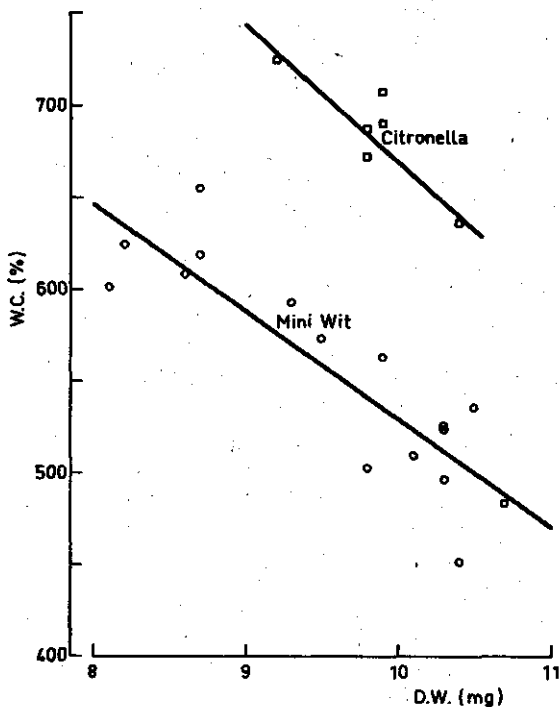
Fig. 6. Changes in water content (W.C.) in relation to dry weight (D.W.) of petals of Gerbera cultivars 'Mini Wit' and 'Citronella'. Each point is a mean value of 10 flowers. The regression equations are: 'Mini Wit' (until day 16), W.C. = 1116 − 58.6 (D.W.) (n = 16, r = 0.873, P < 0.001); 'Citronella' (until day 5), W.C. = 1361 − 68.6 (D.W.) (n = 6, r = 0.750, P < 0.05).

Time courses of W.C. and I.L. were influenced by different treatments such as temperature and cytokinin dip of petals. However, the increase of the ion leakage started at the same time as the decrease of the water content (Figs. 2A and B). When the flowers remained on the plant, there was no sharp decrease of W.C. Also, the increase of I.L. was absent (Fig. 2C). So the changes in W.C. and I.L. are not caused by a natural senescence process of the flowers, but correlated with ageing of flowers that have been cut. The close coincidence of decrease and increase of W.C. and I.L., respectively, strongly suggested the existence of a relationship between water content and ion leakage. For 'Wageningen Rood' a highly significant correlation was found (Fig. 3). When a quadratic term is included in the regression curve, only changes of I.L. above I.L. values of 30% will cause dramatic changes of W.C.

For 'Citronella' and 'Mini Wit' the same type of correlation was demonstrated only during the last part of the vase life (Fig. 3), because during the

first days after cutting I.L. did not change with these cultivars (Fig. 1).

As induced changes of W.C. in petals of the same age did not influence I.L. (Fig. 4), it is likely that changes in the selective permeability influenced the water content and not the reverse.

With 'Citronella' and 'Mini Wit', it is clear that the increase in W.C. during the first days of vase life could not be explained by changes in ion leakage (Fig. 1), but by the decrease of D.W. (Figs. 5 and 6).

The results with the 3 cultivars used suggested that for petals of cut Gerbera flowers which aged without stem plugging, water content is correlated with ion leakage and petal dry weight as given by the formula: W.C. = $a + b$ (I.L.) $- c$ (I.L.)$^2 - d$ (D.W.). The fact that for 'Wageningen Rood' the best regression formula did not include D.W. could be explained by the early start of changes of I.L. with this cultivar, which overruled the effect of D.W., and the fact that variation in D.W. between petals was large.

REFERENCES

Aarts, J.F.Th., 1957. Over de houdbaarheid van snijbloemen. Meded. Landbouwhogesch. Wageningen, 57 (9): 62 pp.
Baur, J.R. and Workman, M., 1964. Relationship between cell permeability and respiration in ripening banana fruit tissue. Plant Physiol., 39: 540—543.
Beutelmann, P. and Kende, H., 1977. Membrane lipids in senescing flower tissue of Ipomoea tricolor. Plant Physiol., 59 (5): 888—893.
Bir, R.E. and Bramlage, W.J., 1973. Assessing ion leakage from apple fruit tissue. HortScience, 8 (3): 175—176.
Borochov, A., Halevy, A.H. and Shinitzky, M., 1976. Increase in microviscosity with ageing in protoplast plasmalemma of rose petals. Nature (London), 263 (5573): 158—159.
Horie, K., 1962. Studies of the flowering of Tradescantia reflexa with special reference to petal behaviour. Mem. Hyogo Univ. Agric. (Jpn.), 14: 1—54.
Marousky, F.J., 1972. Water relations, effects of floral preservatives on bud opening, and keeping quality of cut flowers. HortScience, 7 (2): 114—116.
Meeteren, U. van, 1978a. Water relations and keeping-quality of cut Gerbera flowers. I. The cause of stem break. Scientia Hortic., 8: 65—74.
Meeteren, U. van, 1978b. Water relations and keeping-quality of cut Gerbera flowers. II. Water balance of ageing flowers. Scientia Hortic., 9: 189—197.
Nichols, R., 1968. The response of carnations (Dianthus caryophyllus) to ethylene. J. Hortic. Sci., 43: 335—349.
Rogers, M.N., 1973. An historical and critical review of postharvest physiology research o cut flowers. HortScience, 8 (3): 189—194.
Sacalis, J.N., 1975. Sucrose: Patterns of uptake and some effects on cut flower senescence. Acta Hortic., 41: 45—55.
Sacher, J.A., 1966. Permeability characteristics and amino acid incorporation during senescence (ripening) of banana tissue. Plant Physiol., 41: 701—708.
Weinbaum, S.A. and Muraoka, T., 1976. The use of electrolytic conductance to assess differential sensitivity of french prune fruit to applied ethylene. J. Am. Soc. Hortic. Sci., 101 (4): 418—422.
Weinstein, L.H., 1957. Senescence of roses. I. Chemical changes associated with senescence of cut 'Better Times' roses. Contrib. Boyce Thompson Inst., 19: 33—48.

WATER RELATIONS AND KEEPING-QUALITY OF CUT GERBERA FLOWERS. IV. INTERNAL WATER RELATIONS OF AGEING PETAL-TISSUE

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ABSTRACT

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The relationship between relative water content (R.W.C.) and water potential (Ψ_{total}) of Gerbera petals was studied when cut inflorescences aged in a vase. The regression of sap osmotic potential (Ψ_{osm}), matric potential (Ψ_m) and pressure potential (Ψ_{press}) on R.W.C. appeared to be the same for young and old inflorescences.

Computing Ψ_{press} as the difference between Ψ_{total} measured with a pressure chamber and $\Psi_{osm} + \Psi_m$ gave erroneous results for old cut inflorescences because of the increasing leakage of ions from petal cells. As there existed a correlation between Ψ_{press} and the bending of petals (B) caused by a small weight, it was possible to obtain time courses of Ψ_{press} by measuring B.

Time courses of Ψ_{osm} and Ψ_{press} of petals were completely different when inflorescences aged on the plant as compared to ageing in a vase. For inflorescences ageing in a vase without stem plugging, Ψ_{osm} increased during the first 6 days, followed by a decrease, and Ψ_{press} decreased during the entire vase period. When inflorescences were left on the plant, Ψ_{osm} was steady during the first 6 days and increased thereafter, whereas Ψ_{press} was steady until day 6 and then decreased. A hypothesis to explain the difference between inflorescences in the vase and on the plant is given.

INTRODUCTION

During vase life of cut Gerbera inflorescences, the water content of petals changes continuously. A few days after cutting, an increase of the water content occurs, due to a decrease of dry matter content (Meeteren, 1979). When the inflorescences reach a certain age, the water content suddenly decreases as a result of a decreasing water-holding capacity (Meeteren, 1978b). This decline coincides with changes in permeability characteristics of the petals (Meeteren, 1979). When stem-plugging is prevented, the changes in water content are not accompanied by changes in the water potential (Ψ) of the petals measured with a pressure chamber (Meeteren, 1978b), indicating that

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the correlation between water content and Ψ changes with age of the cut florescences.

It is likely that changes in water content will cause changes in osmotic and pressure potential (= turgor potential). Processes in a plant tissue are probably more influenced by the different components of Ψ, such as pres osmotic and matric potential, than by the Ψ value itself (Hsiao, 1973). Al though loss of turgor pressure is directly responsible for wilting of flower petals, data on pressure potential of flower petals are lacking in the literat

Investigations were carried out to establish the relation between water content and water potential and measurements were made of the osmotic pressure and matric potential of Gerbera petals of different ages. As in the previous papers in this series, the term "flower" is used for the complete inflorescence, including its stem.

MATERIALS AND METHODS

Plant material and experimental conditions. — In all experiments flowers a *Gerbera jamesonii* H. Bolus cultivar 'Wageningen Rood' were used. Details cultivation and treatment of the flowers after cutting were the same as de scribed elsewhere (Meeteren, 1978a). The experimental conditions have b given in a previous paper (Meeteren, 1979). Each flower was placed in a 250-ml Erlenmeyer flask filled with 100 ml of a solution containing silver nitrate (20 mg/l) + citric acid (150 mg/l) + $Na_2HPO_4 \cdot 2H_2O$ (50 mg/l) in deionised water. The solution in the Erlenmeyer flasks was renewed every 3 days. In this way, stem plugging was prevented (Meeteren, 1978b).

A stronger buffer solution could be used without regular renewing of th vase water, but the high salt concentration of such a solution would influe the potential components to be investigated.

Water potential. — Water potential (Ψ_{total}) was measured in one of the ou petals of each flower by using a pressure chamber (Slavík, 1974).

Osmotic potential of petal juice. — One outer petal of each flower was pla in a deep freeze ($-20°C$). After thawing, the petals were squeezed for extr tion of sap. In order to obtain enough sap, petals of 5 flowers were squee together. The osmotic potential (Ψ_{osm}) of the sap was measured by cryos using a Vogel osmometer.

Matric potential. — Matric potential (Ψ_m) of petals was measured accordir to Behboudian (1977), using a Wescor HR-33 Dew Point Microvoltmeter i conjunction with the Wescor C-52 sample chamber.

Water content. — Water content of the petals was expressed as a percentag of dry weight (W.C.) or as relative water content (R.W.C.). Determination were made as described earlier (Meeteren, 1978b).

Ion leakage. — The leakage of ions (I.L.) from petal cells was determined as described in a previous paper (Meeteren, 1979).

Rigidity of petals. — To investigate the rigidity of the petals, 1.5 cm of the base of a petal was horizontally fastened between 2 slides. Then the bending (*B*) of the petals caused by a weight of 286 mg was measured with a protractor. The weight was fastened at the tip of the petal.

RESULTS

In Fig. 1 the changes in Ψ_{total}, Ψ_{osm}, Ψ_m and W.C. during a vase life of 12 days have been given. Pressure potential (Ψ_{press}) (= turgor potential), calculated as $\Psi_{total} - (\Psi_{osm} + \Psi_m)$ is also shown in the figure. As in previous experiments (Meeteren, 1978b, 1979), W.C. increased during the first days, followed by a quick decrease, while Ψ_{total} was steady during the entire
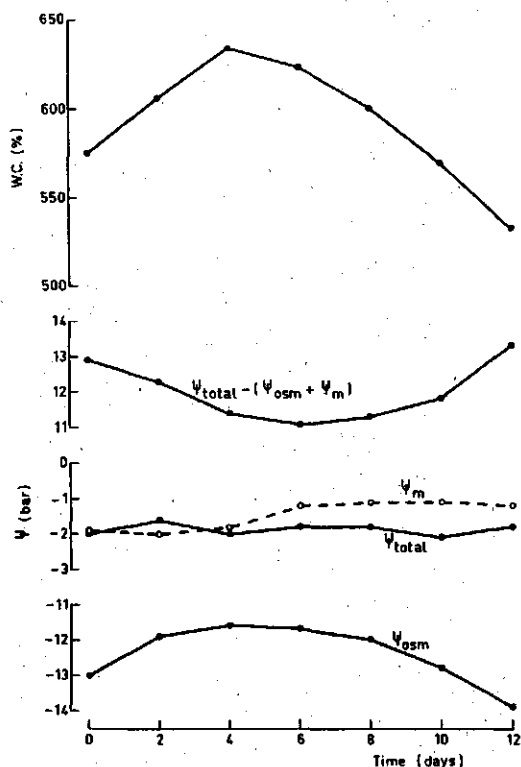

Fig. 1. Time courses of sap osmotic potential (Ψ_{osm}), matric potential (Ψ_m), water potential (Ψ_{total}), $\Psi_{total} - (\Psi_{osm} + \Psi_m)$ and water content (W.C.) as a percentage of dry weight of Gerbera petals. Each point is a mean value of 10 flowers.

period. Ψ_{osm} became less negative until the fourth day and decreased there-after. Ψ_m appeared to increase somewhat; however, this increase was not co firmed in other experiments. Ψ_{press} showed a decrease during the first days the experiment, followed by an increase. This increase of Ψ_{press} during the last 6 days was unexpected.

In a subsequent experiment, Ψ_{total}, Ψ_{osm}, Ψ_m and R.W.C. of the flower petals of 2 different ages (1 and 11 days of vase life) were determined at
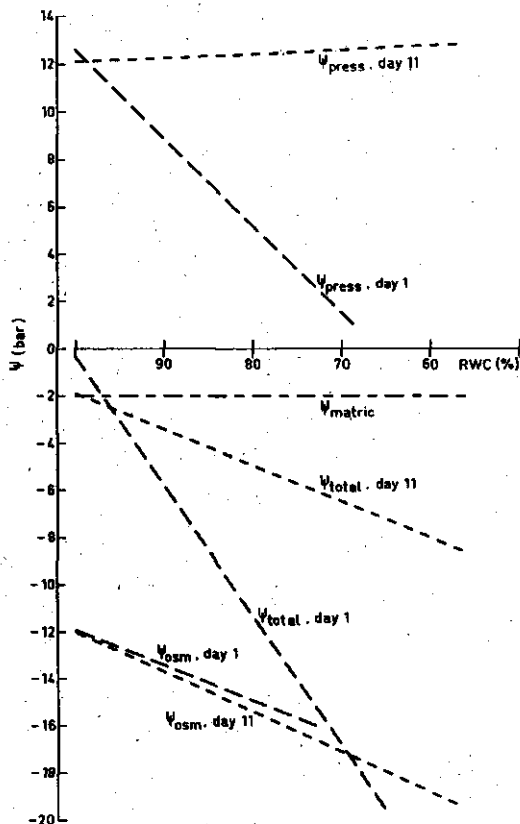

Fig. 2. Changes in water potential (Ψ_{total}), sap osmotic potential (Ψ_{osm}), matric poten (Ψ_m) and pressure potential ($\Psi_{press} = \Psi_{total} - (\Psi_{osm} + \Psi_m)$) in relation to relative wate content (R.W.C.) of Gerbera petals after a vase life of 1 and 11 days. The regression equa tions are

Day 1: Ψ_{total} = 0.55 R.W.C. − 55.6 ($n = 40$, $r = 0.89$)
        Ψ_{osm} = 0.15 R.W.C. − 26.9 ($n = 4$, $r = 1.00$)
        Ψ_{matric} = −2 bar
Day 11: Ψ_{total} = 0.15 R.W.C. − 17.0 ($n = 36$, $r = 0.56$)
        Ψ_{osm} = 0.17 R.W.C. − 29.0 ($n = 4$, $r = 0.9967$)
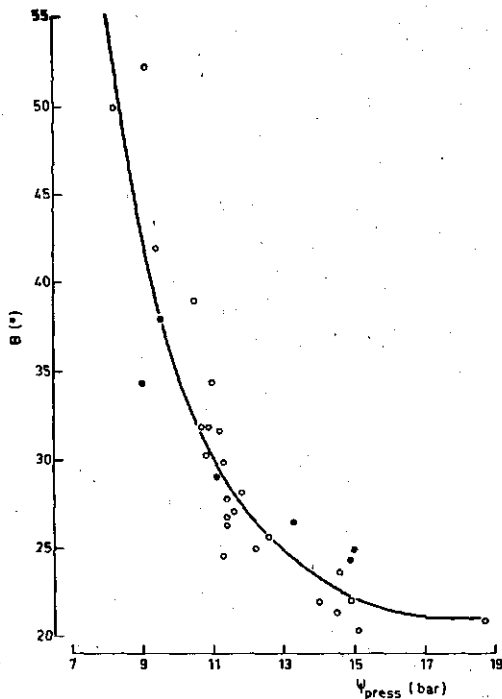 Ψ_{matric} = −2 bar

Fig. 3. Changes of B in relation to pressure potential (Ψ_{press}) of Gerbera petals. $\circ$ = cut flowers, after a vase life of 1 day; $\bullet$ = flowers of different ages, aged on the plant. Each point is a mean value of 10 petals. The regression equation is

$$\frac{1}{B} = -0.049 + 0.0108\ \Psi_{press} - 0.00030\ \Psi^2_{press} \quad (n = 29,\ r = 0.925)$$

regular intervals. The flowers were exposed to 23°C without a stem and without water. The regression curves of Ψ_{total}, Ψ_{osm} and Ψ_m on R.W.C., and also of Ψ_{press} as $\Psi_{total} - (\Psi_{osm} + \Psi_m)$ were calculated (Fig. 2). The curve of Ψ_{total} of old petals (day 11) was far less steep than that of young ones (day 1). The regression of Ψ_{osm} on R.W.C. was not affected by flower age. Ψ_m was influenced neither by R.W.C. nor by the flower age. The increase of Ψ_{press} of old petals found with decreasing R.W.C. was unrealistic, as the petals lost their turgidity when their water content decreased.

The results shown in Figs. 1 and 2 created doubts regarding the method of calculating Ψ_{press} from $\Psi_{osm} + \Psi_m$ and Ψ_{total} for old flowers. The next experiments were performed to investigate Ψ_{press} of ageing petals by another method.

The rigidity of a petal is determined by the structural strength and the turgor pressure of the cells. So, one could expect a correlation between Ψ_{press} and the rigidity of petals. The rigidity was measured as the bending (B) of

the petals, caused by a small weight, as described in "Materials and Methods". To investigate the correlation, Ψ_{press} was calculated as the difference between Ψ_{total} and Ψ_{osm} (Ψ_m was neglected as it was influenced neither by water content nor by age) of petals of young flowers with induced changes in water content and of flowers ageing on the plant. These flowers have a low leakage of ions (Meeteren, 1979). Figure 3 shows that there was a good correlation between Ψ_{press} and B. This relation was almost the same for both kinds of flowers.

In the next experiment, Ψ_{total} and Ψ_{osm} of ageing petals were measured again, and also B (Fig. 4). Measurements were done with flowers ageing in the vase and flowers still attached to the plant. With flowers on the plant, turgor pressure decreased after 6 days, as demonstrated by an increasing B as well as a decreasing $\Psi_{total} - \Psi_{osm}$. The decreasing turgor pressure was accompanied by a decrease in Ψ_{total} and an increase in Ψ_{osm}. The behaviour of Ψ_{total} and
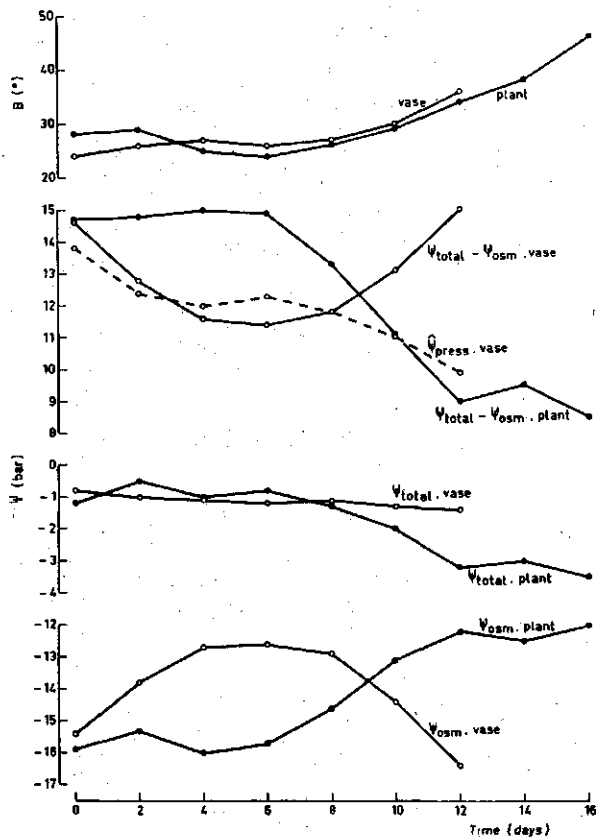

Fig. 4. Time courses of B, $\Psi_{total} - \Psi_{osm}$, $\hat{\Psi}_{press}$, Ψ_{total} and Ψ_{osm} of Gerbera petals, aged in the vase or on the plant. Each point is a mean value of 10 flowers.
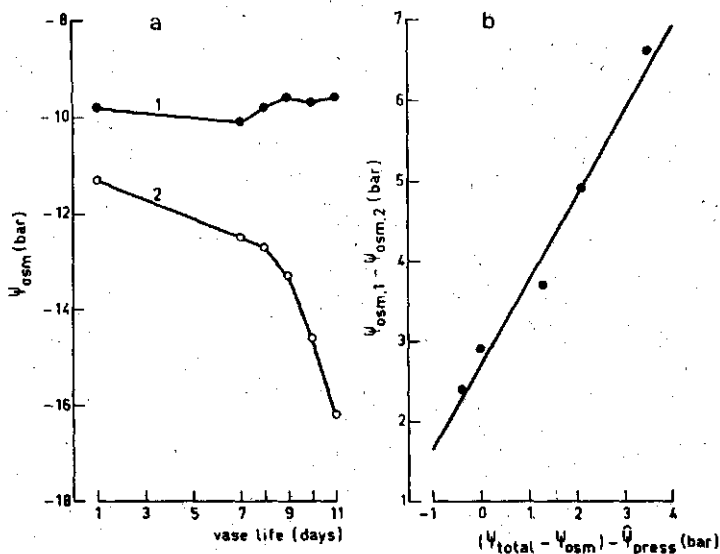
Fig. 5. (a) Sap osmotic potential (Ψ_{osm}) of fully turgid Gerbera petals after different periods of vase life. Petals were saturated in 2 different ways: (1) with their cut surfaces in water; (2) in humid air (for more details see text). (b) Correlation between $\Psi_{osm,1}$ − $\Psi_{osm,2}$ (from Fig. 5a) and (Ψ_{total} − Ψ_{osm}) − $\hat{\Psi}_{press}$ (from Fig. 4) after a vase life of 7 days and more. The regression equation is

$$\Psi_{osm,1} - \Psi_{osm,2} = 1.05 \,((\Psi_{total} - \Psi_{osm}) - \hat{\Psi}_{press}) + 2.7 \quad (n = 5, \; r = 0.99)$$

Each point is a mean value of 10 petals.

Ψ_{osm} of cut flowers ageing in the vase was the same as in Fig. 1. For the cut flowers, pressure potential was calculated by subtracting Ψ_{osm} from Ψ_{total} as well as by using B together with the regression of Fig. 3 ($\hat{\Psi}_{press}$). Ψ_{total} − Ψ_{osm} decreased during the first 6 days, followed by an increase, while $\hat{\Psi}_{press}$ decreased during the entire experimental period. $\hat{\Psi}_{press}$ of flowers on the plant (not shown in the figure) was almost the same as Ψ_{total} − Ψ_{osm}. The behaviour of Ψ_{osm} of flowers in the vase was completely different from that on the plant.

The discrepancy between $\hat{\Psi}_{press}$ and Ψ_{press} calculated as Ψ_{total} − Ψ_{osm} for aged cut flowers could be ascribed to a decrease of the osmotic potential in the xylem vessels, due to an increase in leakage of ions out of the cells into the free space of the petal tissue. To analyse this hypothesis, Ψ_{osm} was determined of petals saturated in 2 different ways:

(1) Petals were placed with their cut surfaces in distilled water for 24 h at 23°C. A jar was placed over the petals and the walls were lined with wet filter paper.

(2) Petals were placed on nylon gauze above 3 layers of wet filter paper in a petri dish (ϕ 5 cm) for 24 h at 23°C. The cover of the dish was lined with wet filter paper.

In the first method, ions could leak out of the cells into the free space o the petals and subsequently diffuse from the petal into the water. In the second method, ions leaking out of the cells remain in the petal tissue. Ψ_{os} of petals saturated in the first way ($\Psi_{osm,1}$) remained the same during vase life. When the petals were saturated in the second way, the sap osmotic potential ($\Psi_{osm,2}$) decreased when the flowers aged (Fig. 5 a). The regressi curve of $\Psi_{osm,1} - \Psi_{osm,2}$ on ($\Psi_{total} - \Psi_{osm}$) $- \hat{\Psi}_{press}$ after day 6, was a straight line with an angle of 45° (Fig. 5 b).

It is likely that a correlation exists between ion leakage (I.L.) and (Ψ_{tot} Ψ_{osm}) $- \hat{\Psi}_{press}$, when the latter is influenced by the concentration of ions the xylem. This was confirmed in some other experiments (Fig. 6 a). Also, water content will influence the ion concentration of the xylem sap. This been shown in Fig. 6 b, in which R.W.C. values of flowers after 8 days of v life and more (Meeteren, 1978b, Fig. 3) were plotted against ($\Psi_{total} - \Psi_{os}$ $- \hat{\Psi}_{press}$ of flowers of the same age, obtained from Fig. 4.
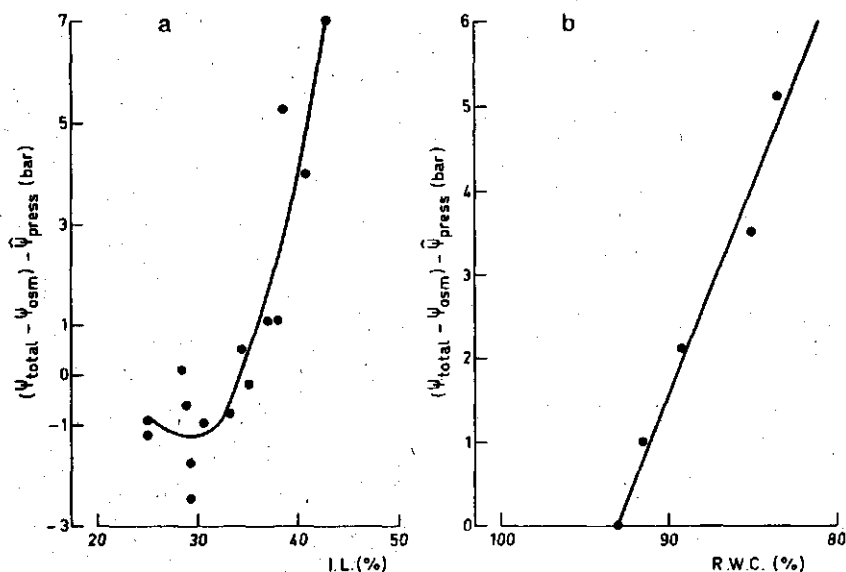

Fig. 6. (a) Correlation between ($\Psi_{total} - \Psi_{osm}$) $- \hat{\Psi}_{press}$ and ion leakage (I.L.) of Gerb petals from ageing cut flowers. ($\Psi_{total} - \Psi_{osm}$) $- \hat{\Psi}_{press}$ = 31.1 $-$ 2.29 (I.L.) + 0.04 (I. (n = 15, r = 0.93). (b) Changes in ($\Psi_{total} - \Psi_{osm}$) $- \hat{\Psi}_{press}$ in relation to relative water content (R.W.C.) in Gerbera petals after a vase life of 8 days and more.

($\Psi_{total} - \Psi_{osm}$) $- \hat{\Psi}_{press}$ = -0.50 R.W.C. + 46.4 (n = 5, r = 0.99)

Each point is a mean value of 10 petals.

DISCUSSION

Water potential of plant cells consists of osmotic, matric and pressure potentials as given by $\Psi_{total} = \Psi_{osm} + \Psi_m + \Psi_{press}$ (Slatyer, 1967, p. 145). The osmotic potential of petal juice (Ψ_{osm}) of cut Gerbera flowers increased during the first days of vase life (Fig. 1). After 4—6 days, the increase was followed by a decrease. The course of Ψ_{osm} paralleled that of W.C. As Ψ_{total} and Ψ_m were constant, Ψ_{press} decreased during the first days, followed by an increase after Day 6. The increasing W.C. during the first days of vase life, causing an increasing Ψ_{osm} and thereby a decreasing Ψ_{press}, was the result of a decrease of dry matter content (Meeteren, 1979). The decrease of W.C. after Day 4, and in addition the decrease of Ψ_{osm} of petal juice, was brought about by an increase of leakage of ions from the petal cells (Meeteren, 1979). When cells are losing the ability to retain solutes, they will also lose their turgor pressure. The increase of Ψ_{press} (calculated as $\Psi_{total} - (\Psi_{osm} + \Psi_m)$) after Day 6 was unexpected and might be the result of an incorrect determination.

In a previous paper (Meeteren, 1978b), it was suggested that the water deficit—water potential relationships of petals change with age. This suggestion was confirmed by the results shown in Fig. 2. The adaptation of Ψ_{total} to changes in water content was less for flowers after 11 days of vase life as compared with flowers after 1 day of vase life. The relation of Ψ_{osm} of petal juice to R.W.C. was not influenced by age. For leaves of cucumber, tomato and sweet pepper, Behboudian (1977) demonstrated a decreasing Ψ_m when water content decreased. In our case, however, Ψ_m showed no significant changes with changes in W.C. (Fig. 1) or R.W.C. (Fig. 2). In the next experiments Ψ_m was neglected, as is done by many authors (Gardner and Ehlig, 1965; Hsiao, 1973; Slavík, 1974). In that way, the values of Ψ_{press} will be lower than the actual ones, but the changes in Ψ_{press} will not be affected. The regression curve of Ψ_{press} on R.W.C. (Fig. 2), obtained for old flowers by subtracting $\Psi_{osm} + \Psi_m$ from Ψ_{total}, was unrealistic as pressure potential increased with decreasing R.W.C. Because the pressure chamber method measures the pressure necessary to raise the potential of water in the petal cells to the point at which it equals the potential of the xylem sap at atmospheric pressure, the method estimates the non-osmotic component of the xylem water potential (Boyer, 1967). As there is a leakage of ions from petal cells (Meeteren, 1979), there will always be some error by calculating Ψ_{press} as the difference between Ψ_{total} measured with the pressure chamber and Ψ_{osm}, due to the fact that the osmotic potential in the xylem is neglected. When the flowers age in a vase, the error becomes too high because of an increase in the ion leakage. Comparisons of Ψ_{press}, obtained as $\Psi_{total} - \Psi_{osm}$, are only useful when the ion leakage does not change and remains low, or when Ψ_{total} is corrected for the osmotic potential of the water in the xylem vessels. Attempts to collect solution out of the xylem vessels of petals were unsuccessful.

By measuring the bending (B) of the petals caused by a small weight, it

was possible to determine Ψ_{press} in another way (Fig. 3). When flowers aged without changes in ion leakage (as was the case with flowers that aged on the plant (Meeteren, 1979)), the relation between B and Ψ_{press} was not influenced by age (Fig. 3). When B is less than $26°$, this method is not an accurate way to calculate Ψ_{press}.

When cut Gerbera flowers aged in a vase, Ψ_{press} decreased during the entire vase period, as indicated for the first 6 days by $\Psi_{total} - \Psi_{osm}$ and later on by B. This decrease was caused by a decrease of dry matter content and an increase after Day 6 in ion leakage (Meeteren, 1979). The decreasing Ψ_{press} was accompanied by a constant Ψ_{total} and an increasing Ψ_{osm} during the first 6 days, thereafter by a decreasing Ψ_{osm}. When Gerbera flowers aged on the plant, however, Ψ_{press} was steady during the first 6 days; thereafter Ψ_{press} decreased. This decrease was accompanied by a small decrease in Ψ_{total} and an increase in Ψ_{osm}. As the decrease in Ψ_{press} was accompanied by an increasing Ψ_{osm}, it seems likely that this decrease was caused by a decrease in dry matter content. Previous experiments (Meeteren, 1979) showed that ion leakage from petals was not influenced by age when flowers aged on the plant. Some other experiments with intact flowers (unpublished) showed a small increase in petal dry weight during the first 6 days, followed by a quick decrease which might be due to transport from the flower to the plant. Such transport at the beginning of senescence was also demonstrated for *Ipomoea purpurea* (Winkenbach, 1971).

Figures 5 and 6 supported the idea that the discrepancy between pressure potential calculated as $\Psi_{total} - \Psi_{osm}$ and via B for old cut flowers, was caused by substances in the xylem fluid which influenced the osmotic potential of this fluid and thereby Ψ_{total} measured with a pressure chamber. The water potential of the petal cells can be estimated by $\Psi_{osm} + \hat{\Psi}_{press}$. As Ψ_{osm} and $\hat{\Psi}_{press}$ decreased after Day 6 (Fig. 4), the water potential decreased.

Assuming that the relationship between R.W.C. and $(\Psi_{total} - \Psi_{osm}) - \hat{\Psi}_{press}$ for desiccating flowers after 11 days of vase life, will be the same as in Fig. 6b obtained by flowers of different ages, it is possible with the regression of Ψ_{total} on R.W.C. from Fig. 2, to compute the relationship between R.W.C. and petal water potential for aged cut flowers. This relationship was about the same as that between R.W.C. and Ψ_{total} for young flowers (Fig. 2). As a result of this, the relationship between R.W.C. and turgor potential is also the same for flowers after 1 day and after 11 days of vase life.

The time courses of Ψ_{osm} of cut Gerbera flowers, as shown in Figs. 1 and 4, seem to contradict results for carnation flowers recently published by Mayak et al. (1978). They concluded that osmotic concentration in petals decreased, i.e. Ψ_{osm} increased. However, with their results the possibility cannot be excluded that Ψ_{osm} decreased after 5 days of vase life (that is 2 days before the development of wilting-symptoms). Also, they measured the osmotic concentration of water-saturated petals and not the actual osmotic concentration, as the petals were immersed in distilled water for 90 min before determination.

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REFERENCES

Behboudian, M.H., 1977. Water relations of cucumber, tomato, and sweet pepper. Meded. Landbouwhogesch., Wageningen, 77(6), 85 pp.

Boyer, J.S., 1967. Leaf water potentials measured with a pressure chamber. Plant Physiol., 42: 133—137.

Gardner, W.R. and Ehlig, C.F., 1965. Physical aspects of the internal water relations of plant leaves. Plant Physiol., 40: 705—710.

Hsiao, T.C., 1973. Plant responses to water stress. Ann. Rev. Plant Physiol., 24: 519—570.

Mayak, S., Kofranek, A.M. and Tirosh, T., 1978. The effect of inorganic salts on the senescence of Dianthus caryophyllus flowers. Physiol. Plant., 43: 282—286.

Meeteren, U. van, 1978a. Water relations and keeping-quality of cut Gerbera flowers. I. The cause of stem break. Scientia Hortic., 8: 65—74.

Meeteren, U. van, 1978b. Water relations and keeping-quality of cut Gerbera flowers. II. Water balance of ageing flowers. Scientia Hortic., 9: 189—197.

Meeteren, U. van, 1979. Water relations and keeping-quality of cut Gerbera flowers. III. Water content, permeability and dry weight of ageing petals. Scientia Hortic., 10: 261—269.

Slatyer, R.O., 1967. Plant—water relationships. Academic Press, London, 366 pp.

Slavík, B., 1974. Methods of studying plant water relations. Springer-Verlag, Berlin, 449 pp.

Winkenbach, F., 1971. Zum Stoffwechsel der aufblühenden und welkenden Korolle der Prunkwinde Ipomoea purpurea. I. Beziehungen zwischen Gestaltwandel, Stofftransport, Atmung und Invertase aktivität. Ber. Schweiz. Bot. Ges., 80: 374—390.

WATER RELATIONS AND KEEPING-QUALITY OF CUT GERBERA FLOWERS.

V. ROLE OF ENDOGENOUS CYTOKININS.

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ABSTRACT

Meeteren, U. van, and Van Gelder, H., 1980. Water relations and keeping-qua of cut Gerbera flowers. V. Role of endogenous cytokinins. Scientia Hortic. press).

The objective of the present work was to investigate if differences in internal water relations, due to differences in membrane permeability, betw Gerbera petals of inflorescences ageing in a vase and on the plant could be ascribed to differences in cytokinin activities. Moreover, cytokinin activi in petal-extracts of 3 cultivars, differing in their keeping-quality, were pared.

Cytokinin activities ("free" and "bound") in petals decreased during t first 6 days of the experiment (both in the vase and on the plant). On day very high activity was found in almost all the R_f-fractions of the chromato After day 8, the activity decreased again. For young inflorescences, develo on the plant, a peak level was reached for "free" cytokinins at a very earl stage and for "bound" cytokinins when the petals were just fully expanded. were no correlations between petal cytokinin activities at day of harvest (Gerbera cultivars and their keeping-quality.

It is concluded that changes in membrane permeability, which occur during ageing of petals of cut Gerbera inflorescences, are not triggered by changes in cytokinin activities.

INTRODUCTION

The petal-water-content of cut Gerbera inflorescences ageing in a vase, suddenly decreases when the inflorescences reach a certain age, due to changes in the semi-permeability of the petal cells (Meeteren, 1979a). Petals ageing on the plant do not show this phenomenon. This different behaviour in semi-permeability causes completely different time courses of osmotic and pressure potential between both kinds of petal tissue (Meeteren, 1979b).

Ageing of leaves is hastened by excising and can be retarded by exogenous cytokininis (Richmond and Lang, 1957; Sugiura et al., 1962; Letham, 1967; Goldthwaite, 1972; Tung and Brady, 1972) or by rooting of the leaves (Letham, 1967; Simon, 1967). Roots are known to be sites of cytokinin synthesis (Letham, 1967; Sitton et al., 1967; Engelbrecht, 1972), and it is now generally accepted that root-synthesized cytokinins are transported to the shoots (Van Staden and Davey, 1976; Wareing et al., 1977). However, de-rooted shoots of *Solanum andigena* and detached leaves of sunflowers have been reported to synthesize cytokinins (Wareing et al., 1977). Endogenous cytokinin levels of leaves increase after rooting (Engelbrecht, 1972) and in many cases decrease during senescence (Hewett and Wareing, 1973; Oritani and Yoshida, 1973; Even-Chen et al., 1978). In leaves of *Ginkgo biloba* L. (Van Staden, 1976) and lemon (Ilan and Goren, 1979), however, senescing leaves contained considerably more cytokinins than young ones.

Also, the ageing of cut flowers is retarded by application of cytokinins, as demonstrated for carnations (Heide and Øydvin, 1969; Eisinger, 1977), roses (Mayak and Halevy, 1970, 1974), irises (Wang and Baker, 1979) and Gerbera (Meeteren, 1979a). Cytokinin activity in young rose petals is higher than in old ones. The content of endogenous cytokinins in petals of a short-lived rose cultivar is lower than in a long-lived one (Mayak and Halevy, 1970; Mayak et al., 1972).

In the present study, we attempted to follow the changes in cytokinin activity in petal-extracts of Gerbera inflorescences ageing in a vase or on the plant, and to compare cytokinin activities in petal-extracts of 3 cultivars. The term "flower" is used for the complete inflorescence, including its stem.
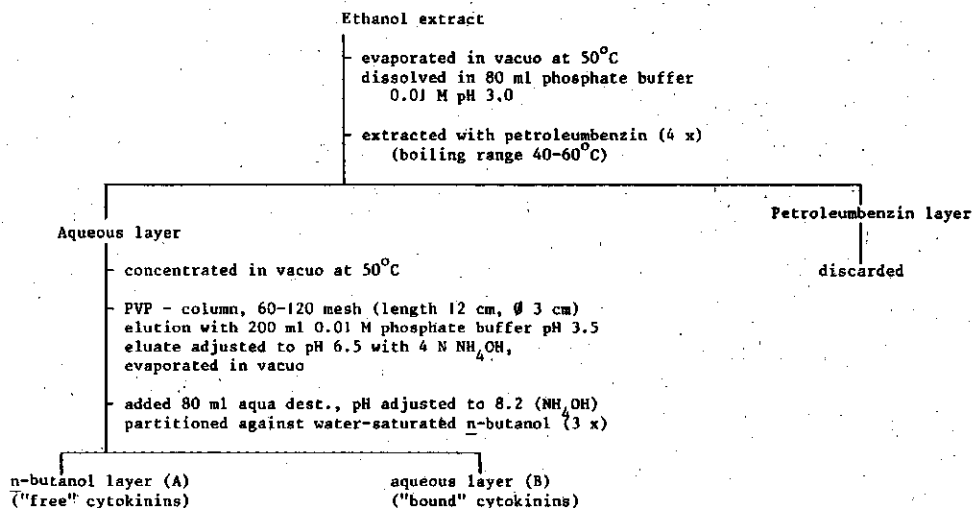
MATERIALS AND METHODS

Plants of *Gerbera jamesonii* H. Bolus were raised in a glasshouse.
Unless otherwise specified, the cultivar 'Wageningen Rood' was used. De
of cultivation and treatment of the flowers after cutting were the sam
described elsewhere (Meeteren, 1978a). Cut flowers were placed in a sol
of silver nitrate (20 mg/l) + citric acid (150 mg/l) + $Na_2HPO_4.2H_2O$ (50
in deionised water, which was renewed every 3 days. In this way, stem p
ging is prevented (Meeteren, 1978b). The experiments were carried out i
conditioned room at day/night temperatures of $23/21 \pm 1^{O}C$, relative hum
of $70 \pm 5\%$, and irradiance (400-700 nm) of 58 Wm^{-2} at flower height, ob
from high pressure sodium lamps (Lucalox 400, Gen. Electric), during a
photoperiod. The plants were watered to field capacity every other day
the beginning of the photoperiod. Samples were taken from the flowers 3
after watering.

Petals of at least 10 flowers (one outer petal of each flower) wer
used for cytokinin extraction. After sampling, all material was frozen
$-20^{O}C$ until analyzed. The petals were homogenized in 80% ethanol. The h
genate was extracted 3 times with 50 ml of 80% ethanol for 15 minutes a
centrifuged at 1.000 x g for 10 min. at room temperature. The supernata
fractions were combined and fractionated by the procedure of page 46.

Fraction B ("bound" cytokinins) was treated with alkaline phosphat
(Vonk, 1974). The resulting hydrolysate was extracted with water-satura
n-butanol at pH 8.2. The butanol layers containing the "free" cytokinin
(fraction A) and "bound" cytokinins after hydrolysis were evaporated at
$50^{O}C$ under reduced pressure and chromatographed on Whatman No. 3 filter
paper, using a solvent of n-butanol: 25% NH_4OH (4: 1 v/v). The chromato
grams were divided into 10 equal strips and eluted with 50% ethanol. Af
evaporation of the ethanol of the different fractions under reduced pre
at $50^{O}C$, the *Amaranthus* bio-assay was used (Biddington and Thomas, 1973

RESULTS

Each other day, petals were taken from flowers ageing in a vase
(= "Vase") or on the plant (= "Plant"). Histograms of the cytokinin act
ties of the petal-extracts are shown in Fig. 1. Cytokinin activities we
present in both n-butanol ("free" cytokinins) and aqueous ("bound" cyto
kinins) phases during ageing of the flowers. The figures of "free" and

Ethanol extract

- evaporated in vacuo at 50°C
  dissolved in 80 ml phosphate buffer
    0.01 M pH 3.0

- extracted with petroleumbenzin (4 x)
    (boiling range 40-60°C)

Petroleumbenzin layer

Aqueous layer

discarded

- concentrated in vacuo at 50°C

- PVP - column, 60-120 mesh (length 12 cm, ∅ 3 cm)
  elution with 200 ml 0.01 M phosphate buffer pH 3.5
  eluate adjusted to pH 6.5 with 4 N NH_4OH,
  evaporated in vacuo

- added 80 ml aqua dest., pH adjusted to 8.2 (NH_4OH)
  partitioned against water-saturated n-butanol (3 x)

n-butanol layer (A)   aqueous layer (B)
("free" cytokinins)   ("bound" cytokinins)

Flow diagram for purification of cytokinins
of Gerbera petal-extracts.

"bound" cytokinins of "Plant" and "Vase" were about the same.
There was a decrease in cytokinin activity until day 6. On day 8,
very high activities were found over the whole chromatogram but
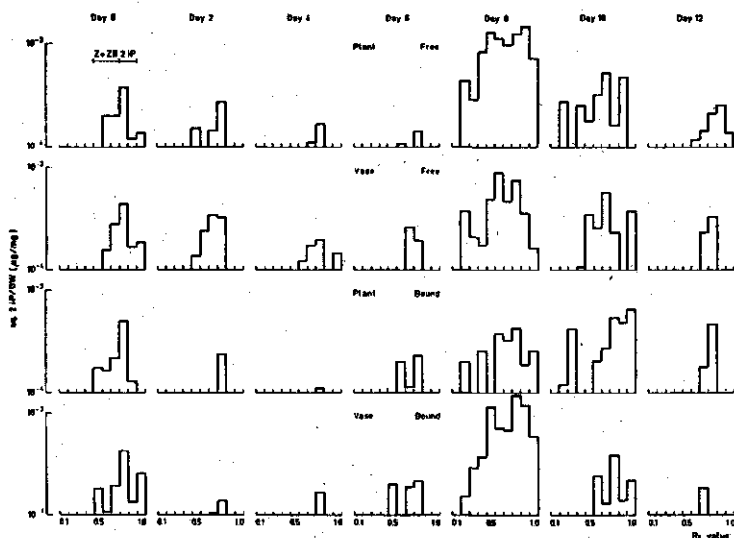thereafter the activities decreased again.

Fig. 1. Histograms of cytokinin activities ("free" and "bound") in
Gerbera petal-extracts cv. 'Wageningen Rood' of flowers ageing in a vase
("Vase") or on the plant ("Plant"). Cytokinin activities are given in
equivalents of 2iP on a dry-weight basis on a logarithmic scale. With
the number of petals and bioassay used, 10^{-4} µg 2iP per mg dry weight
was the threshold sensitivity. Values are mean values of 3 experiments,
each experiment with at least 10 flowers. Cytokinin standard: Z = zeatin,
ZR = zeatin riboside, 2iP = 6- (γ,γ-dimethylallylamino)purine.

As the cytokinin activity of flowers ageing on the plant decreased
immediately after the beginning of the experiment, it was interesting to
analyse the cytokinin activity in earlier stages of flower development.
Therefore, cytokinin activities were determined of petals of flowers take
from the plant at 4 developmental stages (Fig. 2). There was a small decr
in the "free" cytokinin activity during the flower development from stage
to stage D. The level of the "bound" cytokinins reached a peak when the
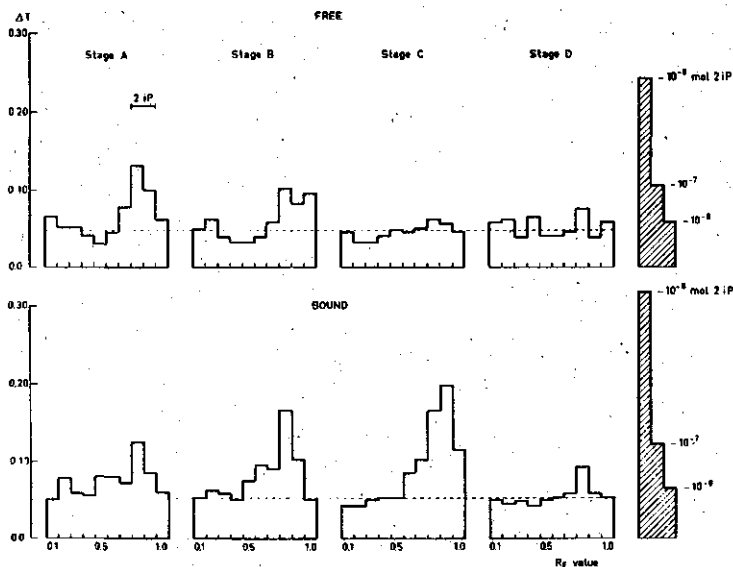petals were just expanded (stage C).

Fig. 2. Histograms of the *Amaranthus* bioassay of Gerbera cv. 'Wageningen Rood' petal-extracts of 4 flower-developmental stages:
A. Buds with a mean diameter of 16.4 mm. The ray florets were not visible and were enclosed by the bracts and not yet above the central disc.
B. Buds with a mean diameter of 21.4 mm. The ray florets were about 3 mm above the bracts and green coloured.
C. Ray florets were red coloured, unfolded; all female disc florets were just flowering.
D. Stamen of 2 circles of bisexual disc florets were ripe (commercial stage of harvest = developmental stage on day 0 in Fig. 1).
Flowers were allowed to develop on the plant. Extracts were made of 1 gram of fresh weight. Ordinate: ΔT 620-542 nm. Abscissa: R_f value in n-butanol: 25% NH_4OH (4:1 v/v). Values are mean values of 2 experiments. Cytokinin standard: 2iP = 6-(γ,γ-dimethylallylamino)purine. Dotted line represents control (zero value).

Table 1 shows total cytokinin activities of petals of 3 cultivars at the commercial stage of harvest. In the n-butanol phase ("free" cyto-kinins) 'Citronella' had the lowest activity. 'Wageningen Rood' had the highest activity of the aqueous phases ("bound" cytokinins). The zones of the chromatogram with cytokinin activity were the same for the cultivars used, suggesting that there were no qualitative differences.

Table 1.   Total cytokinin activity of Gerbera petals of 3 cultivars at
          commercial stage of harvest. Activity expressed as equivalents
          2iP per dry weight or per petal. Values are means of 9 experiment
          for 'Wageningen Rood', 3 for 'Citronella' and 5 for 'Mini Wit';
          each experiment with at least 10 flowers.

| cultivar | 2iP equivalents x 10^3 | | | |
| | per dry weight ($\mu g \cdot mg^{-1}$) | | per petal (μg) | |
	"free	"bound"	"free"	"bound"
'Wageningen Rood'	1.5	1.1	19.5	13.2
'Citronella'	0.3	0.4	3.9	5.9
'Mini Wit'	1.3	0.4	13.3	3.7

DISCUSSION

The development of Gerbera flowers, both on the plant and in the vase,
was accompanied by a decrease in cytokinin activities ("free" and "bound")
of petal-extracts from day 0 (= commercial stage of harvest) until day 6
(Fig. 1). On day 8, however, very high activities were present in nearly
all fractions of the paper chromatogram. From day 8 until day 12, the acti-
vities decreased again. Ageing of rose petals is accompanied by a decrease
in cytokinin activity (Mayak and Halevy, 1970). Also, the cytokinin content
of many leaves were demonstrated to decrease during ageing (Hewett and
Wareing, 1973; Oritani and Yoshida, 1973; Even-Chen et al., 1978).

The very high activities on day 8 are questionable. Although roots are
known to be sites of cytokinin synthesis (Letham, 1967) and root-synthesize
cytokinins are transported to the shoots (Van Staden and Davey, 1976), cytc
kinin synthesis by leaves cannot be excluded (Wareing et al., 1977). Possit
flower petals or other flower parts can produce cytokinins also. In cymbidi
flowers, production of cytokinins by the anthers is likely (Van Staden, 197
In phloem exudate of the inflorescence stalk of *Yucca flaccida* Haw. zeatin-
and isopentenyl adenine nucleotides are present (Vonk, 1974, 1978). Another
source of the high cytokinin activities on day 8 could be breakdown product
of t-RNA. The cytokinin groups present in certain species of t-RNA (Vreman
et al., 1972; Murai et al., 1975) are liable to be released during RNA
degradation (Wareing et al., 1977). On day 8, senescing processes are
progressed, as indicated by ion leakage and water content for cut flowers
(Meeteren, 1979a) and by pressure potential for flowers on the plant
(Meeteren, 1979b).

Although cytokinin activity decreased immediately after cutting in tobacco leaves (Even-Chen et al., 1978), there were no differences in cytokinin activities between petals of cut Gerbera flowers developing in a vase and flowers still attached to the plant (Fig. 1). Leakage of ions and decrease of water content started on day 6 for cut flowers, while there were no changes found in ion leakage and water content for flowers senescing on the plant (Meeteren, 1979a). This indicates that for Gerbera petals no correlation exists between cytokinin activity and membrane permeability.

The decrease in cytokinin activities in petal-extracts from intact flowers had already started at the beginning of the experiment (Fig. 1), suggesting that on day 0 there was no net import of cytokinins from the roots to the petals. Fig. 2 shows that the activity of "free" cytokinins had already decreased from a very young bud stage (stage A) of the Gerbera flowers, while the aqueous phase ("bound" cytokinins) had the highest activity when the petals were just fully expanded (stage C). In petals of rose flowers, the cytokinin level reached a peak as the flower started to open (Mayak et al., 1972). The detaching-experiments of Even-Chen et al. (1978) with tobacco leaves were done with actively growing leaves. The reason that cytokinin activities of Gerbera petals were not influenced by cutting the flower from the plant (Fig. 1) may be due to the fact, that the flowers were cut when the peak level of cytokinins was already passed.

With 'Wageningen Rood' and 'Citronella' ageing phenomena, as indicated by leakage of ions and decrease of water content, had already started after 4-6 days, while with 'Mini Wit' they did not start until after 16 days of vase life (Meeteren, 1979a). The activity of "free" cytokinins in petal-extracts of 'Mini Wit' was higher than those of 'Citronella'. However, petal-extracts of 'Wageningen Rood' showed about the same "free" cytokinin activity as 'Mini Wit' (Table 1). The activity of "bound" cytokinins was highest for 'Wageningen Rood'. The correlation found in roses between keeping-quality of 2 cultivars and their petal cytokinin content at day of harvest (Mayak and Halevy, 1970; Mayak et al., 1972) could be due to a "lucky hit" of the 2 cultivars or could be caused by the fact that roses are cut in a bud stage (before the top level in cytokinin content is reached), while Gerbera flowers are cut when the petals are fully expanded (after the top level in cytokinin content is reached).

The present results strongly suggest that no correlation exists betwee
cytokinin activities of Gerbera petals and ageing phenomena such as increas
ion leakage and decreasing water content. Recently, Ilan and Goren (1979)
concluded that their results with lemon leaves could not be regarded as
supporting the hypothesis that leaf senescence is brought about, at least
partially, by a decrease in the level of its cytokinins.

REFERENCES

Biddington, N.L. and Thomas, T.H., 1973. A modified Amaranthus betacyanin
    bio-assay for the rapid determination of cytokinins in plant extracts.
    Planta, 111: 183-186.

Eisinger, W., 1977. Role of cytokinins in carnation flower senescence.
    Plant Physiol., 59: 707-709.

Engelbrecht, L., 1972. Cytokinins in leaf-cuttings of *Phaseolus vulgaris*
    L. during their development. Biochem. Physiol. Pflanzen, 163: 335-343.

Even-Chen, Z., Atsmon, D. and Itai, C., 1978. Hormonal aspects of senescence
    in detached tobacco leaves. Physiol. Plant., 44: 377-382.

Goldthwaite, J., 1972. Further studies on hormone-regulated senescence in
    Rumex leaf tissue. In: D.J. Carr (Editor), Plant Growth Substances.
    Proc. 7th Int. Conf. Plant Growth Subst., Canberra, 1970.
    Springer-Verlag, Berlin, pp. 581-588.

Heide, O.M. and Øydvin, J., 1969. Effects of 6 benzylamino-purine on the
    keeping-quality and respiration of glasshouse carnations. Hortic.
    Res., 9: 26-36.

Hewett, E.W. and Wareing, P.F., 1973. Cytokinins in *Populus x rubusta*:
    Qualitative changes during development. Physiol. Plant., 29: 386-389.

Ilan, I. and Goren, R., 1979. Cytokinins and senescence in lemon leaves.
    Physiol. Plant., 45: 93-95.

Letham, D.S., 1967. Chemistry and physiology of kinetin-like compounds.
    Annu. Rev. Plant Physiol., 18: 349-364.

Mayak, S. and Halevy, A.H., 1970. Cytokinin activity in rose petals and
    its relation to senescence. Plant Physiol., 46: 497-499.

Mayak, S. and Halevy, A.H., 1974. The action of kinetin in improving the
    water balance and delaying senescence processes of cut rose flowers.
    Physiol. Plant., 32: 330-336.

Mayak, S., Halevy, A.H. and Katz, M., 1972. Correlative changes in phyto-
    hormones in relation to senescence processes in rose petals. Physiol.
    Plant., 27: 1-4.

Meeteren, U. van, 1978a. Water relations and keeping-quality of cut
    Gerbera flowers. I. The cause of stem break. Scientia Hortic. 8: 65-74.

Meeteren, U. van, 1978b. Water relations and keeping-quality of cut Gerber flowers. II. Water balance of ageing flowers. Scientia Hortic. 9: 189

Meeteren, U. van, 1979a. Water relations and keeping-quality of cut Gerber flowers. III. Water content, permeability and dry weight of ageing pe Scientia Hortic., 10: 261-269.

Meeteren, U. van, 1979b. Water relations and keeping-quality of cut Gerber flowers. IV. Internal water relations of ageing petal-tissue. Scienti Hortic. 11: 83-93.

Murai, N., Armstrong, J. and Skoog, F., 1975. Incorporation of mevalonic acid into ribosyl zeatin in tobacco callus ribonucleic acid preparati Plant Physiol. 55: 853-858.

Oritani, T. and Yoshida, R., 1973. Studies on nitrogen metabolism in crop plants. XII. Cytokinins and abscisic acid-like substances levels in r and soyabean leaves during their growth and senescence. Proc. Crop. S Soc. Japan, 42(3): 280-287.

Richmond, A.E. and Lang, A., 1957. Effect of kinetin on protein content ar survival of detached *Xanthium* leaves. Science, 125(3249): 650-651.

Simon, E.W., 1967. Types of leaf senescence. In: H.W. Woolhouse (Editor), Aspects of Biology of Ageing. Univ. Press, Cambridge, pp. 215-230.

Sitton, D., Itai, C. and Kende, H., 1967. Decreased cytokinin production i the roots as a factor in shoot senescence. Planta, 73: 296-300.

Sugiura, M., Umemura, K. and Oota, Y., 1962. The effect of kinetin on prot level of tobacco leaf disks. Physiol. Plant., 15: 457-464.

Tung, H.F. and Brady, C.J., 1972. Kinetin treatment and protein synthesis detached wheat leaves. In: D.J. Carr (Editor), Plant Growth Substanc Proc. 7th Int. Conf. Plant Growth Subst., Canberra, 1970. Springer-Verlag, Berlin, pp. 589-597.

Van Staden, J., 1976. Seasonal changes in the cytokinin content of *Ginkgo biloba* leaves. Physiol. Plant., 38: 1-5.

Van Staden, J., 1979. The effect of emasculation on the endogenous cytoki levels of cymbidium flowers. Scientia Hortic., 10: 277-284.

Van Staden, J. and Davey, J.E., 1976. Cytokinin translocation in xylem sa of herbaceous plants. Z. Pflanzenphysiol., 77: 377-382.

Vonk, C.R., 1974. Studies on phloem exudation from *Yucca flaccida* Haw. XIII. Evidence for the occurence of a cytokinin nucleotide in the exudate. Acta Bot. Neerl., 23(4): 541-548.

Vonk, C.R., 1978. Formation of cytokinin nucleotides in a detached inflorescence stalk and the occurence of nucleotides in phloem exudate from attached *Yucca* plants. Physiol. Plant., 44: 161-166.

Vreman, H.J., Skoog, F., Frihart, C.R. and Leonard, N.J., 1972. Cytokinins in *Pisum* transfer ribonucleic acid. Plant Physiol., 49: 848-851.

Wang, C.Y. and Baker, J.E., 1979. Vase life of cut flowers treated with rhizobitoxine analogs, sodium benzoate, and isopentenyl adenosine. HortScience, 14(1): 59-60.

Wareing, P.F., Horgan, R., Henson, I.E. and Davis, W., 1977. Cytokinin relations in the whole plant. In: P.E. Pilet (Editor), Plant Growth Regulation. Proc. 9th Int. Conf. Plant Growth Subst., Lausanne, 1976. Springer-Verlag, Berlin, pp. 147-153.

WATER RELATIONS AND KEEPING-QUALITY OF CUT GERBERA FLOWERS.

VI. ROLE OF PRESSURE POTENTIAL.

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ABSTRACT

Meeteren, U. van, 1980. Water relations and keeping-quality of cut Gerbera
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The increase of ion leakage (I.L.) of Gerbera petal cells during agei
was hastened by lowering the pressure potential of excised petals. Increas
pressure potential by placing flower stems in KNO_3-solutions delayed the
increase of I.L.

It is suggested that differences in time curves of I.L. for cut and
intact flowers are initiated by differences in pressure potential.

It is discussed that determinations of pressure potential, water cont
per dry weight and dry weight per area of petals will give a good indicati
for selection on potential keeping-quality.

INTRODUCTION

   The osmotic and pressure potential of Gerbera petals is greatly
influenced by cutting the inflorescences from the plant (Meeteren, 1979b).
Ageing of cut inflorescences in a vase is accompanied by an increasing
leakage of ions from petal tissue. This increase in ion leakage is absent
when inflorescences remain on the plant (Meeteren, 1979a). As discussed
in a previous paper in this series (Meeteren and Van Gelder, 1980), it
seems unlikely that endogenous cytokinins are responsible for the difference
in semi-permeability between petal cells of cut and intact inflorescences.
   Cutting will separate the inflorescences from their sources of carbo-
hydrates. Petal dry weight of cut Gerbera inflorescences decreases during
ageing (Meeteren, 1979a). Feeding flowers with sugars extends longevity
of many species (Aarts, 1957; Coorts et al., 1965; Marousky, 1969; Larsen
and Frolich, 1969; Nichols, 1973; Bravdo et al., 1974; Paulin et al., 1975).
In some own preliminary experiments was found that also keeping-quality of
cut Gerbera inflorescences was improved by external sucrose, either as a
short pulse or as a continuous additive to the vase water. However,
Weinstein (1957) demonstrated with roses, that during the initial stages
of senescence, while petal and receptacle tissues still contained a
relatively high level of glucose, proteolysis went on at a fairly constant
rate. Thereafter many authors discussed that the end of vase life is not
due to substrate limitations (Nichols, 1973; Mayak et al., 1975; Kaltaler
and Steponkus, 1976; Borochov et al., 1976; Halevy and Mayak, 1979).
With carnations pretreatment of the flowers with NH_4NO_3, KNO_3 and KCl
promotes the water uptake and extends the longevity. The beneficial effect
of "pulsing" with mineral salts is only slightly smaller than that observed
with sucrose (Halevy, 1976). Mayak et al. (1978) demonstrated that placing
carnation flowers continuously in solutions of KNO_3, KCl, K_2SO_4, $Ca(NO_3)_2$
and NH_4NO_3 extend their keeping-quality. They suggested that senescence
processes are closely linked to changes in osmotic concentration.
   The purpose of the present study was to evaluate the effect of pressure
potential on ageing of cut Gerbera inflorescences. As in all papers in this
series, the term "flower" is used for the complete inflorescence, including
its stem.

MATERIALS AND METHODS

Plant material and experimental conditions. -Unless otherwise specif
flowers of *Gerbera jamesonii* H. Bolus cultivar 'Wageningen Rood' were use
Details of cultivation and treatment of the flowers were the same as desc
elsewhere (Meeteren, 1978a). Each flower was placed in a 250-ml Erlenmeye
flask filled with 100 ml of a solution of silver nitrate (20 mg/1) + citi
acid (150 mg/1) + $Na_2HPO_4 \cdot 2H_2O$ (50 mg/1) in deionised water. This solutic
was renewed every 3 days. In this way stem plugging was prevented (Meetei
1978b). The experiments were carried out in a conditioned room at a tempe
of 23 ± 1^oC, a relative humidity of $70 \pm 5\%$, a Piche evaporation of 0.11
ml h^{-1}, and a constant irradiance (400-700 nm) of 7.8 Wm^{-2} at flower heiß
obtained from Philips TL 57 fluorescent tubes.

Water content. - Water content of the petals (W.C.) as a percentage
dry weight was determined as described earlier (Meeteren, 1978b).

Ion leakage. - The leakage of ions (I.L.) from petal tissue was meas
according to a previous paper (Meeteren, 1979a).

Water potential. - Water potential (Ψ_{total}) was measured in one of
outer petals of each flower by using a pressure chamber (Slavík, 1974).

Osmotic potential. - Osmotic potential of petal juice (Ψ_{osm}) was
measured by cryoscopy (Meeteren, 1979b).

Rigidity of petals. - To investigate the rigidity of the petals, the
bending (B) of the petals caused by a small weight was measured
(Meeteren, 1979b). B gives a good indication of changes in Ψ_{press}.

Specific petal weight. - For determination of the specific petal we
(S.P.W.) of a flower, the total area of all petals of the flower was est
by an optical planimeter (Technical Physical Service of Agricultural
University at Wageningen 66-2014). Thereafter the dry weight of the same
petals was determined. Dividing the dry weight by the petal area gave th
S.P.W.

RESULTS

To investigate the effect of different pressure potentials on ion l
of isolated petals during ageing, petals were brought upon nylon gauze a
3 layers of filter paper (Whatman No. 3) in a petri dish (Ø 5 cm) at 23°
The filter papers were saturated with a solution of potassiumchloride,
various concentrations of which were used in order to obtain a series of
relative air humidities above the solutions. In this way different press

potentials of the petal tissues will be obtained. In each petri dish
5 petals were placed. Each other day the ion leakage of 15 petals (from
3 dishes) per treatment were determined. Fig. 1 shows the time curves of
ion leakage for 3 different concentrations of potassiumchloride. It is
obvious from the figure that an increase in the concentration of potassium-
chloride (decrease in pressure potential of the petal tissue) increased
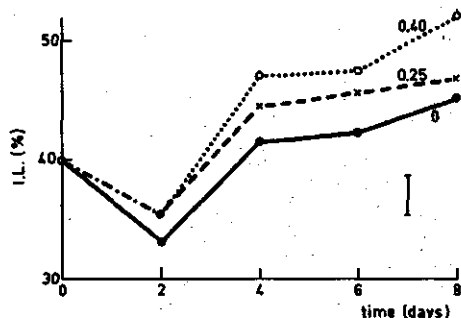the ion leakage.

Fig. 1. Time curves of ion leakage (I.L.) of excised Gerbera petals above
different KCl-solutions (for more details see text). Each point is a mean
value of 15 petals (from 15 flowers). Vertical bar represents L.S.R. at 5%.

In another series of experiments an increase in the pressure potential
of petals was obtained by bringing potassiumnitrate into the petal cells via
the vase water of the flowers. Potassiumchloride could not be used, because
of the silver nitrate in the vase water. Placing the stems during the first
24 h of vase life in solutions of 2.5 and 5% potassiumnitrate (= 251 and
509 mMol, respectively) was unsuccessful. There were no differences between
the petals of untreated and treated flowers in water content, sap osmotic
potential and ion leakage. With the 5% treatment, exudation of a brown sap
occurred after some days on the lower part (3-12 cm) of the stem. This part
of the stem was heavily damaged by the 5% treatment, even when the basal 4 cm
of the stem (height of KNO_3-solution was 2 cm) was removed immediately after
the pretreatment. Potassiumnitrate caused softening of carnation stems
(Mayak et al., 1978) unless it was combined with 5 mMol Ca $(NO_3)_2$. Placing
Gerbera flower stems 24 h in a solution of 500 mMol KNO_3 + 5 mMol $Ca(NO_3)_2$,
cutting 4 cm from the stem base after this pretreatment and adding
5 mMol Ca $(NO_3)_2$ to the vase water during the remaining vase period, influenced
water content and osmotic potential of the petals, without damage of the stems.
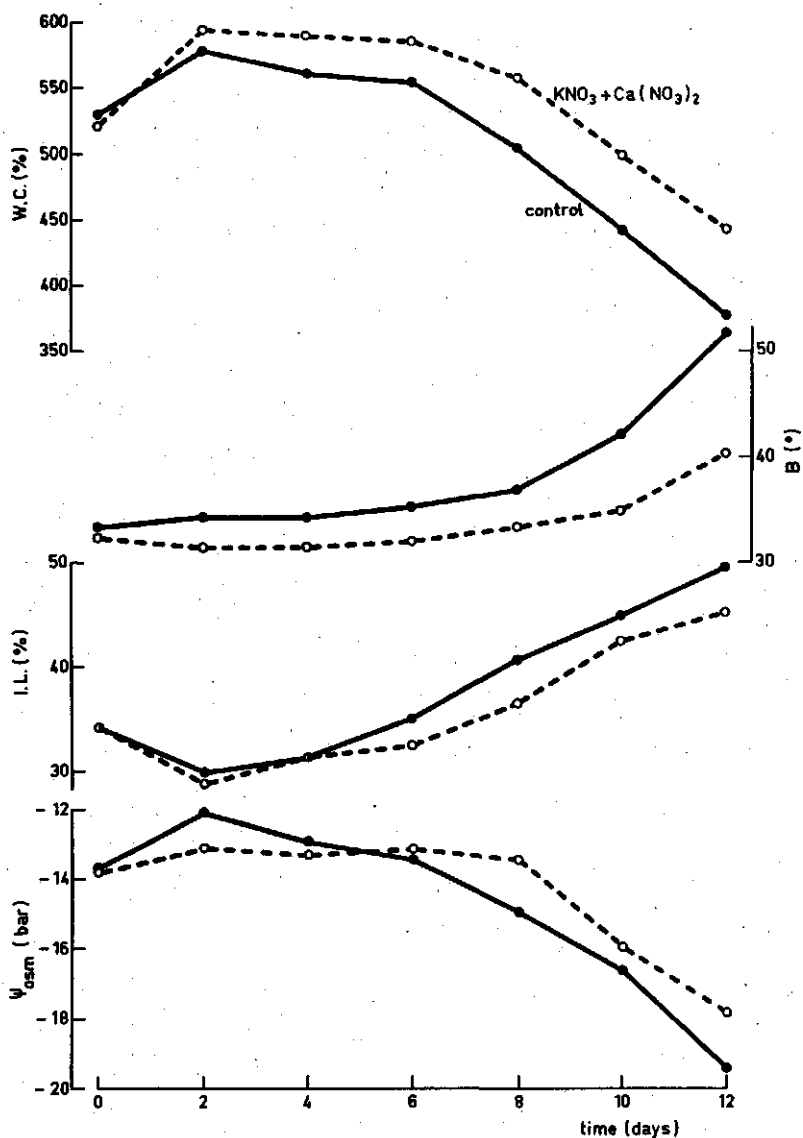Adding 30 mMol KNO_3 to the vase water after this pretreatment enhanced the effect.

Fig. 2. Time curves of water content (W.C.) as a percentage of dry weight, rigidity (B), ion leakage (I.L.) and sap osmotic potential (Ψ_{osm}) of petal of untreated (control) and treated flowers. Flower treatment: stem bases 24 h in 500 mMol KNO_3 + 5 mMol $Ca(NO_3)_2$, thereafter 4 cm from the stem base cut and stems placed in 30 mMol KNO_3 + 5 mMol $Ca(NO_3)_2$. Number of flowers was 19 for the control and 16 for the KNO_3 + $Ca(NO_3)_2$-treatment. Differences in I.L. were significant at 5% on day 6 and at 1% on day 8 according to Students t-test.

Placing flowers continuously in a solution of 120 mMol KNO_3 (or more)
+ 5 mMol $Ca(NO_3)_2$ was harmful to the petals. Adding 5 mMol $Ca(NO_3)_2$ alone
to the vase water was without any effect. Time curves of water content
(W.C.), bending (B), ion leakage (I.L.) and sap osmotic potential (Ψ_{osm})
of petals of untreated (control) and treated (as described above) flowers
are given in Fig. 2. W.C. was increased by the KNO_3 + $Ca(NO_3)_2$-treatment.
As dry weight was not influenced by the treatment (data not given in the
figure), this means that there was more water per petal cell in the treated
flowers. This will enhance the pressure potential, as confirmed by the curves
of B, lower values of B meaning less bending of the petals, indicating a
higher pressure potential. The treatment retarded the increase in I.L. by
about 2 days. Ψ_{osm} of the treated flowers was lower than the control during
the first days, due to the uptake of the ions. After about 6 days, however,
the control flowers had the lowest Ψ_{osm}, due to the higher I.L. of these
flowers as compared with the treated ones, which will hasten the decrease
of W.C. (Meeteren, 1979a).
In a previous paper in this series (Meeteren, 1979a) was shown, that I.L. of
the cultivar 'Mini Wit' started to increase about 12 days later than that of
'Wageningen Rood' and 'Citronella'. As pressure potential influences
time curves of I.L., it was interesting to compare the pressure potentials
(Ψ_{press}) of young flowers of the 3 cultivars. Therefore, after a vase
life of 1 day,
Ψ_{total} and Ψ_{osm} were determined at regular intervals of petals of flower
heads, exposed to 23°, without water supply. Ψ_{press} (calculated as
Ψ_{total} - Ψ_{osm}) was plotted against Ψ_{total}. At all waterpotentials Ψ_{press}
of 'Mini Wit' was higher than that of 'Wageningen Rood' and 'Citronella' (Fig. 3).

Differences in Ψ_{press} between the 3 cultivars can be caused by different
wall-properties of the petal cells, cell size or by a different dry-matter
content per cell. Specific petal weight (S.P.W. = dry weight per petal area)
will give some indication on cell size, dry-matter content per cell or petal
thickness. Table 1 shows, that on the day of harvest, S.P.W. of 'Mini Wit'
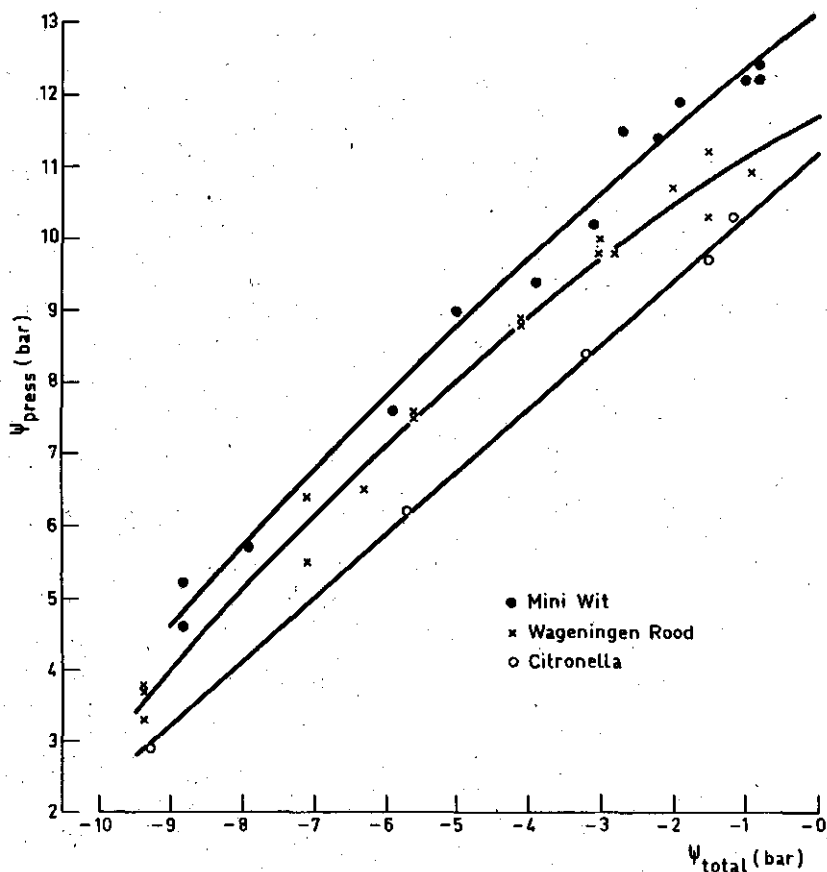was higher than that of the 2 other cultivars.

Fig. 3. Changes in ψ_{press} in relation to ψ_{total} for young petals of 'Mini 'Wageningen Rood' and 'Citronella'. Each point is a mean value of 10 flowe Regression coefficients were for 'Mini Wit' r^2= 0.988, 'Wageningen Rood' r^2= 0.987 and 'Citronella' r = 0.999.

Table. 1. Specific petal weight (S.P.W. = dry weight per area) on day of harvest of 3 Gerbera cultivars. Values followed by different letters are significantly different at the 1% level.

Cultivar	S.P.W. (mg.cm^{-2})
'Wageningen Rood'	4.0a
'Citronella'	3.5a
'Mini Wit'	6.0b

Another way to retard the increase in I.L. is a pretreatment of the flower
heads with the cytokinin 6-benzyl-adenin (BA) (Meeteren, 1979a). However, it
was unlikely that endogenous cytokinin activity influences I.L. (Meeteren and
Van Gelder, 1980). Fig. 4 shows that immersing the petals immediately after
harvest in Ba (10^{-4}Mol) + Tween 20 (0.1 ml/1) for 2 minutes retarded the
decrease of dry weight of the petals and thereby probably also the decrease
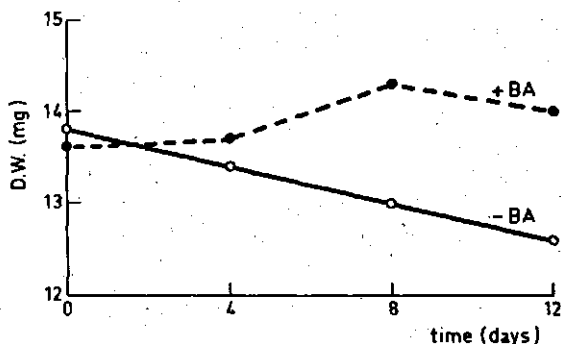in pressure potential.

Fig. 4. Time curves of petal dry weight (D.W.) as influenced by a pretreatment
(2 min) of the flower head with 6-benzyl-adenin (BA) (10^{-4}Mol) + Tween 20
(0.1 ml/1). Each point is a mean value of 45 petals from 15 flowers.

DISCUSSION

Lowering water potential and thereby pressure potential of excised Gerbera
petals during ageing hastened the increase of I.L. (Fig. 1). Increasing pressure
potential by uptake of potassiumnitrate via the vase water, delayed the increase
of I.L. (Fig. 2). Time courses of I.L. are greatly influenced by cutting the
flowers from the plant; however, also the time curves of osmotic and pressure
potential are greatly influenced (Meeteren, 1979b). Hence, it seems likely that
changes in pressure potentials of Gerbera petals can induce changes in I.L.
In giant algal cells there is convincing experimental evidence for the direct
interference of pressure potential with membrane transport and the electrical
properties of the membrane (Zimmermann, 1978). Halevy (1976) and Mayak et al.
(1978) demonstrated with carnations that uptake of NH_4NO_3, KNO_3, KCl, K_2SO_4
and $Ca(NO_3)_2$ by the flower stems can extend their keeping-quality. Mayak et al.
(1978) showed an osmotic adjustment in the petal tissue in response to the
KNO_3-treatment. They suggested that senescence processes are closely linked

to changes in osmotic concentrations. However, when water potentials of p
are decreased, the osmotic concentration will be enhanced, while this tre:
ment increased I.L. (Fig. 1). So, it seems rather likely that senescence
processes are more linked to changes in pressure than in osmotic potentia

With Gerbera flowers, placing the stems just in a solution of KNO_3 w:
harmful to the flower stems. As water content, sap osmotic potential and
leakage of the petals were not influenced by this treatment, and exudatio:
sap occurred on the lower part of the stem, it seems likely that the tran:
of KNO_3 through the stem was very slow. For Ca^{2+} (Biddulph et al., 1961;
Bell and Biddulph, 1963; Ferguson and Bollard, 1976), Cd^{2+} (Petit and Van
Geijn, 1978), and Ag^+ (Veen and Van de Geijn, 1978) is demonstrated that
transport through the xylem vessels has the characteristics of a chromato;
exchange transport rather than a mass flow. Probably also the movement of
assium in the xylem is an exchange process. In that case Ca^{2+} will act as
competitive cation and will promote the transport of K^+. Also carnation s
were damaged when they were held in solutions of KNO_3, except when 5 mMol
Ca $(NO_3)_2$ was added to the solutions (Mayak et al., 1978).

The keeping-quality of the cultivar 'Mini Wit' and its increase in I
differed greatly (both in a favourable sense) from that of 'Wageningen Ro
and 'Citronella' (Meeteren, 1979a). As Fig 3 showed, young flowers of 'Mi:
had the highest pressure potential of the cultivars used, at all water
potentials. Wall properties, cell size and number of osmotically active
substances per cell will influence pressure potential. Table 1 showed tha
petals of 'Mini Wit' have the highest dry weight per area of the 3 cultiv.
Assuming petal thickness is about the same, this will indicate that the c
size of 'Mini Wit' is the smallest and/or the dry-matter content per cell
the highest. Smaller cells should maintain pressure potential to lower va
of water potential than larger cells (Cutler et al., 1977). Also dry weig
per cell is positively correlated with pressure potential. For cotton pla
was shown (Cutler and Rains, 1978) that leaves hardened by several cycles
water stress are less sensitive to water deficits, due to the fact that t
leaves of conditioned plants had less water per unit dry weight than did
of controls. As shown in a previous paper (Meeteren, 1979a), petal-water
of 'Mini Wit' was much lower than that of 'Citronella' at the same dry we

A pretreatment of the flower heads with 6-benzyl-adenin (BA) retarde
the increase in I.L. (Meeteren, 1979a). Although it cannot be excluded th
BA influences directly membrane properties, it also retarded the decrease
dry weight of the petals (Fig. 4) and thereby the decrease in pressure po

When rose flowers were held in a kinetin solution, the decrease in dry weight of petals was retarded (Mayak and Halevy, 1974). So, a part of the cytokinin effect on ageing of cut flowers could be an indirect effect via pressure potential.

CONCLUSIONS

Changes in pressure potential of Gerbera petal cells can induce changes in the leakage of ions from the cells. Taking steps to increase pressure potential will enhance keeping-quality. Differences in time courses of ion leakage between cut and intact flowers could be initiated by differences in pressure potential.

It seems worthwhile to investigate whether correlations exist between potential longevity of petals on the one hand and pressure potential, water content per dry weight or dry weight per area on day of harvest on the other hand.

REFERENCES

Aarts, J.F.Th., 1957. Over de houdbaarheid van snijbloemen. Meded.
    Landbouwhogeschool, Wageningen, 57 (9): 62 pp.

Bell, C.W. and Biddulph, O., 1963. Translocation of calcium exchange
    versus mass flow. Plant Physiol., 38: 610-614.

Biddulph, O., Nakayama, F.S. and Cory, R., 1961. Transpiration stream
    and ascension of calcium. Plant Physiol., 36: 429-436.

Borochov, A., Mayak, S. and Halevy, A.H., 1976. Combined effects of
    abscisic acid and sucrose on growth and senescence of rose flowers.
    Physiol. Plant., 36: 221-224.

Bravdo, B., Mayak, S. and Gravrieli, Y., 1974. Sucrose and water uptake
    from concentrated sucrose solutions by *Gladiolus* shoots and the effect
    of these treatments on floret life. Can. J. Bot., 52 (6): 1271-1281.

Coorts, G.D., Gartner, J.B. and McCollum, J.P., 1965. Effect of senescence
    preservative on respiration in cut flowers of *Rosa hybrida* 'Velvet
    Times'. Proc. Amer. Soc. Hortic. Sci., 86: 779-790.

Cutler, J.M. and Rains, D.W., 1978. Effects of water stress and hardening
    on the internal water relations and osmotic constituents of cotton
    leaves. Physiol. Plant., 42: 261-268.

Cutler, J.M., Rains, D.W. and Loomis, R.S., 1977. The importance of cell
    size in the water relations of plants. Physiol. Plant., 40: 255-260.

Ferguson, I.B. and Bollard, E.G., 1976. The movement of calcium in woody
    stems. Ann. Bot., 40: 1057-1065.

Halevy, A.H., 1976. Treatments to improve water balance of cut flowers.
    Acta Hortic., 64: 223-230.

Halevy, A.H., and Mayak, S., 1979. Senescence and postharvest physiology
    of cut flowers. Part I. Hortic. Rev., 1: 204-236.

Kaltaler, R.E.L. and Steponkus, P.L., 1976. Factors affecting respiration
    in cut roses. J. Amer. Soc. Hortic. Sci., 101 (4): 352-354.

Larsen, F.E. and Frolich, M., 1969. The influence of 8-hydroxyquinoline
    citrate, N-dimethylamino succinamic acid, and sucrose on respiration
    and water flow in 'Red Sim' cut carnations in relation to flower

Marousky, F.J., 1969. Vascular blockage, water absorption, stomatal opening, and respiration of cut 'Better Times' roses treated with 8-hydroxyquinoline citrate and sucrose. J. Amer. Soc. Hortic. Sci., 94: 223-226.

Mayak, S. and Halevy, A.H., 1974. The action of kinetin in improving the water balance and delaying senescence processes of cut rose flowers. Physiol. Plant., 32: 330-336.

Mayak, S., Kofranek, A.M. and Blanc, G., 1975. The involvement of sugar in the development and senescence of cut flowers. HortScience, 10 (3): 318.

Mayak, S., Kofranek, A.M. and Tirosh, T., 1978. The effect of inorganic salts on the senescence of *Dianthus caryophyllus* flowers. Physiol. Plant., 43: 282-286.

Meeteren, U. van, 1978a. Water relations and keeping-quality of cut Gerbera flowers. I. The cause of stem break. Scientia Hortic. 8: 65-74.

Meeteren, U. van, 1978b. Water relations and keeping-quality of cut Gerbera flowers. II. Water balance of ageing flowers. Scientia Hortic. 9: 189-197.

Meeteren, U. van, 1979a. Water relations and keeping-quality of cut Gerbera flowers. III. Water content, permeability and dry weight of ageing petals. Scientia Hortic. 10: 261-269.

Meeteren, U. van, 1979b. Water relations and keeping-quality of cut Gerbera flowers. IV. Internal water relations of ageing petal-tissue. Scientia Hortic. 11: 83-93.

Meeteren, U. van, and Van Gelder, H., 1980. Water relations and keeping-quality of cut Gerbera flowers. V. Role of endogenous cytokinins. Scientia Hortic., in press.

Nichols, R., 1973. Senescence of the cut carnation flower: respiration and sugar status. J. Hortic. Sci., 48: 111-121.

Paulin, A., Bureau, J.M. and Souter, D., 1975. Action exercée sur le métabolisme azoté de la fleur coupée d'*Iris germanica* L. par l'apport exogène de glucose ou de cycloheximide. Physiol. Vég., 13 (3): 501-515.

Petit, C.M. and Van de Geijn, S.C., 1978. In vivo measurement of cadmium (^{115m}Cd) transport and accumulation in the stems of intact tomato plants (*Lycopersicon esculentum* Mill.) I. Long distance tranport and local accumulation. Planta,138: 137-143.

Slavík, B., 1974. Methods of studying plant water relations. Springer-Verlag, Berlin, 449 pp.

Veen, H. and Van de Geijn, S.C., 1978. Mobility and ionic form of silver as related to longevity of cut carnations. Planta, 140: 93-96.

Weinstein, L.H., 1957. Senescence of roses. I. Chemical changes associated with senescence of cut 'Better Times' roses. Contrib. Boyce Thompson Inst., 19: 33-48.

Zimmerman, U., 1978. Physics of turgor- and osmoregulation. Annu. Rev. Plant Physiol., 29: 121-148.

GENERAL DISCUSSION AND SUMMARY

The aim of the present investigation is to study the internal water relations of ageing Gerbera inflorescences and their consequence on keeping-quality of cut inflorescences. As in all parts of this paper, the term "flower" will be used to describe an inflorescence with its supporting stem.

A great problem during vase-life of cut Gerbera flowers is "stem break", a sudden bending of the stem. As described in part I, this phenomenon was caused by a water shortage in the flower. The water-stress was a result of a decline of the absorption rate, due to an increase of the resistance to the water flow between the vase and the petals. In roses (which show a similar phenomenon) a water deficit in the flower-neck occurs because of competition between the various organs when the water supply is limiting (Zieslin et al., 1978). Also in the Gerbera flower there seems to be a competition for the available water, between flower head and stem.

The increase in flow resistance causing stem break, was a result of microbial activity in the vase water. "Stem-plugging" by bacteria can be considerable already after 2 days for many flower species (Aarts, 1957). Silver-ions can extend keeping-quality of cut carnation flowers by their anti-ethylene effect (Halevy and Kofranek, 1977; Veen and Van de Geijn, 1978). However, the prevention of stem break by silver nitrate in the vase water is related to its bactericidal effect, as the mobility of silver supplemented as silver nitrate, is very low in flower stems (Veen and Van de Geijn, 1978; Nowak, 1979). Moreover, a pretreatment (1-24 h) of Gerbera stems with silver nitrate does not counteract the detrimental effect of etephon (Nowak, 1979). Mayak et al. (1977) demonstrated, that a pretreatment of the carnation stem with silver nitrate reduced the microbial population of the vase solution by the release of silver from the impregnated stem. They found that another important beneficial effect of such a pretreatment of the stem base is to decrease the toxic effect of metabolites produced by bacteria. So, the use of silver nitrate as a short pretreatment immediately after cutting will have advantages above other bactericides.

There are 2 different pathways for water uptake by a Gerbera stem: a direct one through the xylem vessels at the cut surface and an indirect one through the cavity in the stem. Only the direct water uptake is strong inhibited by bacterial activity in the vase water. Stem break can be pre- vented therefore without the use of chemicals by cutting the stem through the cavity in its center. The beneficial effect of this treatment could be improved by making a small hole in the stem as an air outlet from the cavity, together with a high water level in the vase in order to promote the rise of water inside the cavity.

Stem stiffness consists of the strength from turgor of the cells and that of the structural elements. Gerbera cultivars with structurally stron stems do not show the phenomenon of stem break when a water deficit develo (De Jong, 1978). Breeding for flowers with structurally strong stems only will prevent stem break, however, not the water stress caused by microbial activity in the vase water. It is worthwhile therefore to select flowers not only with a structural strong stem, but also with a hollow one all the year round from an early stage of development.

When Gerbera flowers were placed in water with silver nitrate, there was still a gradual increase in the resistance for water flow through the stem ("physiological plugging") causing a decrease of water potential of the petals (part II). This decrease of petal water potential, however, was not accompanied by stem break. Possible explanations for this apparent dis crepancy are discussed in detail in part II. The calculated resistance of the flower stem was obtained without induced pressure differences between 2 sides of a cut stem piece, so the results could not be due to artifacts caused by artificial pressures as suggested by Carpenter and Rasmussen (19 for roses. The physiological plugging could be prevented by a constant low pH of the vase water.

Even when the stem resistance for water flow remained constant at a low pH, water absorption of the cv. 'Wageningen Rood' became lower than transpiration after 5 days, resulting in a decrease of flower fresh weight and petal water content (as a percentage of dry weight and as relative water content). The water potential of the petals, however, remained stead which seems a rather conflicting result. It should be realised, that the pressure chamber method used for estimating petal water potential, actuall measures the non-osmotic component of the xylem water potential. As there are no semi-permeable membranes between petal xylem elements and vase wate

it is an accurate value for calculating stem flow resistance, but not for the actual water potential of the petal cells. This problem is discussed in more detail later on.

Ageing petals of cut Gerbera flowers without stem plugging (part III) showed that the water content (W.C.) as a percentage of dry weight was correlated with ion leakage (I.L.) and with petal dry weight (D.W.) as given by the formula: W.C. = a $+'$ b(I.L.) - c(I.L.)^2 - d(D.W.). The increase in W.C. during the first days of vase life of cut flowers was due to a decrease of dry weight, while the sudden decrease in W.C. after some days of vase life was correlated with an increase in I.L., indicating a change in the semi-permeability of the membranes. Flowers ageing on the plant did not show the sharp decrease of W.C., whereas also the increase of I.L. was absent. The date at which I.L. of cut flowers increased depended on the cultivar and was affected by temperature and cytokinin treatments. The influence of temperature on the onset of the decrease of W.C. and increase of I.L. showed the importance for keeping-quality of a low temperature during storage and transport of the flowers.

In part IV is demonstrated that the internal water relations of ageing petal-tissue were influenced to a large extent when flowers were separated from the plant. Sap osmotic potential (Ψ_{osm}) of petals of cut flowers cv. 'Wageningen Rood' increased the first 6 days of vase life, followed by a decrease. Pressure potential (Ψ_{press}) decreased during the entire vase period. When flowers were left on the plant, Ψ_{osm} was steady during the first 6 days and increased thereafter, whereas Ψ_{press} was steady until day 6 and then decreased. This different behaviour of the various components of water potential was due to the increase of ion leakage of petal cells of ageing cut flowers, whereas ion leakage remained constant when flowers were ageing on the plant. An increase of ion leakage of petal cells will decrease the osmotic potential of the xylem fluid of the petals. This change in xylem osmotic potential will not influence the potential difference between vase water and petal cells and thus absorption rate of vase water. However, it will decrease the water potential of the petal cells and therefore water content, osmotic potential and pressure potential. The increase of ion concentration of the xylem fluid of the petals will cause a water shortage in the petal cells, even when these cells still act as good osmometers.

Comparison of the results with literature data are difficult because of different measuring techniques and experimental circumstances. Mayak et al. (1974) using an isopiestic method, found a decline of petal water potential after 6 days with roses. However, they demonstrated an increase in stem water flow resistance when the flowers aged. Osmotic values of ageing carnation petals as given by Mayak et al. (1978) are conflicting with that given by Acock and Nichols (1979).

Changes in ion leakage from the petal cells dominate the petal water relations of cut Gerbera flowers as discussed already previously. To obtain a better understanding of factors involved in keeping-quality of cut flower it will be important to know more about the triggering processes inducing the changes in ion leakage. Some experiments in this aspect are described in parts V and VI.

It is known for many plant species that root-synthesized cytokinins an transported to the shoots, while ageing of leaves is hastend by excising an retarded by exogenous cytokinins. Moreover, ageing of cut flowers can be retarded by application of cytokinins. Therefore, experiments were done to investigate if differences in ion leakage between Gerbera petals of flower ageing in a vase and on the plant could be ascribed to differences in cyto-kinin activities (part V). Cytokinin activities in petal-extracts of 3 cul-vars, differing in their keeping-quality, were also compared. Activities decreased when the flowers aged (except on day 8 of the experiment). Howeve there were no differences between flowers ageing in a vase or on the plant With the 3 cultivars used, there was no correlation between cytokinin content of petals at day of harvest and their keeping-quality. The results suggest strongly that no correlation exists between cytokinin activities of Gerbera petal cells and changes in their ion leakage.

From the data given in part VI, it is concluded that changes in pressure potential of Gerbera petal cells can induce changes in the leakag of ions from the cells. The positive results of "pulsing" flowers, either with sugar (Kohl and Rundle, 1972; Mayak et al., 1973; Nichols, 1974; Sacalis and Chin, 1976) or mineral salts (Halevy, 1976), could also be a result of enhancing the pressure potential of the petal cells. Carnation flowers grown under dry conditions kept longer than those grown under mois irrigation regime (Hanan and Jasper, 1969; Mayak and Kofranek, 1976). It i likely, that the "dry grown" flowers have a higher pressure potential at the same water potential, than the "moist grown" flowers, as was found wit leaves of plants grown in culture solutions with different osmotic potenti

(Jarvis and Jarvis, 1963).

For the 3 Gerbera cultivars used, there was a correlation between their keeping-quality and their pressure potential at day of harvest.

When a decrease of pressure potential initiates an increase of ion leakage, and subsequently causes a decrease of water content, the process of ageing will accelerate itself, once it has began.

There seems to be a discrepancy between the conclusion that pressure potential of petal cells influences ion leakage of the cells and the data in Fig. 4 of part III where induced changes of water content did not influence ion leakage. The changes in water content in part III, however, were induced within 24 h, while the results in part VI were obtained when pressure potential was influenced during some days.

The dominant influence of ion leakage on water relations, as demonstrated in parts III and IV, and the results of part VI suggest strongly that keeping pressure potential of flower petals above a certain level will be very important for a good keeping-quality of cut flowers. It might be possible that pressure potential at day of harvest, can be a selection criterion for potential keeping-quality of cut flowers.

References

Aarts, J.F.Th., 1957. Over de houdbaarheid van snijbloemen. Meded. Landbouwhogeschool, Wageningen, 57(9): 62 pp.

Acock, B. and Nichols, R., 1979. Effects of sucrose on water relations of cut, senescing, carnation flowers, Ann. Bot., 44: 221-230.

Carpenter, W.J. and Rasmussen, H.P., 1973. Water uptake rates by cut roses (Rosa hybrida) in light and dark. J. Amer. Soc. Hortic. Sci., 98(3): 309-313.

De Jong, J., 1978. Dry storage and subsequent recovery of cut gerbera flowers as an aid in selection for longevity. Scientia Hortic., 9: 389-397.

Halevy, A.H., 1976. Treatments to improve water balance of cut flowers. Acta Hortic., 64: 223-230.

Halevy, A.H. and Kofranek, A.M., 1977. Silver treatment of carnation flowers for reducing ethylene damage and extending longevity. J. Amer. Soc. Hortic. Sci., 102: 76-77.

Hanan, J.J. and Jasper, F.D., 1969. Consumptive water use in response of carnation to three irrigation regimes. J. Amer. Soc. Hortic. Sci., 94: 70-73.

Jarvis, P.G. and Jarvis, M.S., 1963. The water relations of tree seedling IV. Some aspects of the tissue water relations and drought resistanc Physiol. Plant., 16: 501-516.

Kohl, H.C. and Rundle, D.L., 1972. A producer-applied treatment to improv rose vase life (Abstract). HortScience, 7(3): 344.

Mayak, S. and Kofranek, A.M., 1976. Altering the sensitivity of carnation flowers (*Dianthus caryophyllus* L.) to ethylene. J. Amer. Soc. Hortic Sci., 101(5): 503-506.

Mayak, S., Bravdo, B., Gvilli, A. and Halevy, A.H., 1973. Improvement of opening of cut Gladioli flowers by pretreatment with high sugar concentrations. Scientia Hortic., 1: 357-365.

Mayak, S., Halevy, A.H., Sagie, S., Bor-Yoseph, A. and Bravde, B., 1974. The water balance of cut rose flowers. Physiol. Plant., 31: 15-22.

Mayak, S., Garibaldi, E.A. and Kofranek, A.M., 1977. Carnation flower longevity: Microbial populations as related to silver nitrate stem impregnation. J. Amer. Soc. Hortic. Sci., 102(5): 637-639.

Nichols, R., 1974. Developments in bud-opening and flower-preservative solutions for carnations *Dianthus caryophyllus* L. Annu. Rep. 1973 Glassh. Crops Res. Inst., Littlehampton: 136-142.

Nowak, J., 1979. Transport and distribution of silver ions in cut Gerbera inflorescences. Acta Hortic. (In press).

Sacalis, J.N. and Chin, C., 1976. Metabolism of sucrose in cut roses. I. Comparison of sucrose pulse and continous sucrose uptake. J. Amer. Soc. Hortic. Sci., 101(3): 254-257.

Veen, H. and Van de Geijn, S.C., 1978. Mobility and ionic form of silver as related to longevity of cut carnations. Planta, 140: 93-96.

Zieslin, N., Kohl, H.C.Jr., Kofranek, A.M. and Halevy, A.H., 1978. Changes in the water status of cut roses and its relationship to bent-neck phenomenon. J. Amer. Soc. Hortic. Sci., 103(2): 176-179.

SAMENVATTING

Zoals uiteengezet in de inleiding, hebben de proeven die in dit proef-
schrift worden beschreven, tot doel meer inzicht te verkrijgen in de water-
huishouding van afgesneden bloemen in een vaas. Voor het beoogde onderzoek
is de gerbera als proefplant gekozen.

Een groot probleem voor de houdbaarheid van gerbera bloemen is het
plotseling knikken van de stengels als de bloemen enige dagen in water staan.
Aangezien dit verschijnsel waarschijnlijk wordt beïnvloed door de water-
huishouding van de bloemen en bovendien zeer hinderlijk is bij het doen van
experimenten, werd het onderzoek begonnen met een bestudering van het knikken.
De resultaten hiervan zijn beschreven in deel I. Het versgewicht van afge-
sneden bloemen die knikten daalde scherp 3 dagen voor het knikken optrad.
Deze daling werd vergezeld door een daling van de wateropname door de
bloemen. De waterpotentiaal van de petalen van knikkende bloemen daalde,
terwijl deze constant bleef in bloemen die niet knikten. Het knikken van
de stengel kon worden voorkomen door een korte voorbehandeling van de
stengels met natriumhypochloride of zilvernitraat, door toevoeging van
zilvernitraat of dichlorophen aan het vaaswater, of door de stengels zo-
danig te behandelen dat wateropname via de mergholte mogelijk was. Bij 1
van de 4 gebruikte cultivars ('Wageningen Rood') varieerde het aantal
knikkende bloemen sterk met het seizoen. In de winter knikten er bij deze
cultivar bijna geen bloemen, terwijl in de zomer 90 tot 100% van de
bloemen dit verschijnsel vertoonden. Dit bleek gecorreleerd te zijn met
het volume van de mergholte in de bloemstengels.

Er is geconcludeerd dat er 2 verschillende mogelijkheden zijn waarop
afgesneden gerbera bloemen water kunnen opnemen: een directe mogelijkheid,
waarbij het water vanuit de vaas via het snijvlak de houtvaten bereikt,
en een indirecte mogelijkheid waarbij het water via de mergholte de hout-
vaten bereikt. Alleen de directe wateropname wordt sterk geremd door
bacteriegroei in het vaaswater. Het knikken van stengels treedt op als de
directe wateropname is geblokkeerd door activiteit van bacteriën en de
mogelijkheid voor indirecte wateropname afwezig is doordat de mergholte

gevuld is met merg of doordat de stengel niet door de mergholte is afgesn

In deel II wordt het verloop in de tijd weergegeven van versgewicht (F.W.), watergehalte als percentage van het drooggewicht van petalen (W.C maximaal watergehalte na verzadiging van petalen (W.C.$_{max}$), relatief wate gehalte van petalen (R.W.C.), wateropname snelheid (abs.), transpiratie s heid, waterpotentiaal van petalen (Ψ_{total}), de weerstand van de stengel v watertransport (R$_{stem}$) en bloemontwikkelingsstadium van afgesneden gerber bloemen, geplaatst in diverse oplossingen. In een oplossing van zilvernit was er een duidelijke stijging van R$_{stem}$ na 4 dagen ("fysiologische vat-verstopping"), resulterend in een daling van abs., F.W., W.C., R.W.C. en Ψ_{total}. Alhoewel de stengels van bloemen waarvan de wateropname geremd is door bacteriën in het vaaswater knikken (deel I), ging fysiologische vat-verstopping niet gepaard met zichtbare symptomen. Hiervoor zijn verschil-lende verklaringen mogelijk: (a) De gevoeligheid voor knikken daalt als d bloem ouder wordt. Daar in het geval van bacteriële vatverstopping Ψ_{total} begint te dalen na ongeveer 2 dagen, terwijl in het geval van fysiologisc verstopping Ψ_{total} begint te dalen na 4 dagen, is in dit laatste geval de bloem minder gevoelig voor knikken. (b) Bij bacteriële vatverstopping daa Ψ_{total} veel sneller dan bij fysiologische verstopping, te weten respectie velijk 3 bar/dag en 0.2 bar/dag. (c) Knikken treedt op als er een water-tekort is in de stengel. Bacteriële vatverstopping begint op het snijvlak van de stengel, terwijl fysiologische verstopping optreedt in een hoger gedeelte van de stengel. Aangezien Ψ_{total} de waterbalans weergeeft van de petalen is het niet bekend of er een watertekort is in het gevoelige stengelgedeelte.

Een constante pH van het vaaswater van 3.5 kon de fysiologische vat-verstopping voorkomen. De pH van het vaaswater werd door de bloem beïnvlo

Wanneer een stijging van R$_{stem}$ werd voorkomen, was de wateropname-snelheid gedurende de eerste 5 dagen na het afsnijden hoger dan de trans-piratie snelheid. Vanaf dat moment daalde F.W., W.C., W.C.$_{max}$ en R.W.C., terwijl Ψ_{total} constant bleef. Blijkbaar daalt het "water-vasthoudend vermogen" van petalen als deze ouder worden.

De stijgende ionen lekkage toonde aan dat de semi-permeabiliteit van petaal cellen van afgesneden gerbera bloemen verandert tijdens verouderin (deel III). Het moment waarop de ionen lekkage begon te stijgen werd mede bepaald door de gebruikte cultivar en viel samen met het moment waarop de daling van het watergehalte van de petalen begon. Temperatuur en cytokini behandelingen beïnvloedden het verloop van het watergehalte en de ionen

lekkage, maar niet de onderlinge samenhang. Petalen van bloemen die ver-
ouderden aan de plant vertoonden noch een stijging in ionen lekkage, noch
een daling in watergehalte.

Regressielijnen tussen watergehalte enerzijds en ionen lekkage en droog-
gewicht van petalen anderzijds worden eveneens in deel III weergegeven.

De relatie tussen R.W.C. en Ψ_{total} van verouderende, afgesneden gerbera
bloemen wordt besproken in deel IV. De regressie van osmotische potentiaal
(Ψ_{osm}), matrix potentiaal (Ψ_m) en turgor potentiaal (Ψ_{press}) ten opzichte
van R.W.C. bleek dezelfde te zijn voor jonge en oude bloemen.

Het berekenen van Ψ_{press} als het verschil tussen Ψ_{total} en $\Psi_{osm} + \Psi_m$
voor oude bloemen geeft foutieve resultaten als Ψ_{total} wordt gemeten met
een drukvat. Dit wordt veroorzaakt door een stijgende ionen concentratie
in het xyleem van de petalen, als gevolg van een toenemende ionen lekkage
van de petaal cellen. Doordat er een correlatie bleek te bestaan tussen
Ψ_{press} en het doorbuigen (B) van de petalen tengevolge van een klein
gewichtje, was het mogelijk het verloop van Ψ_{press} tijdens de veroudering
te bepalen door het meten van B.

Het verloop in de tijd van Ψ_{osm} en Ψ_{press} was volkomen verschillend
als bloemen verouderden aan de plant vergeleken met bloemen die verouderden
in een vaas. Van bloemen die verouderden in een vaas zonder dat er een
verandering van de stengelweerstand voor watertransport optrad, steeg Ψ_{osm}
gedurende de eerste 6 dagen, gevolgd door een daling, terwijl Ψ_{press} de
gehele vaasperiode daalde. Wanneer bloemen verouderden aan de plant was
Ψ_{osm} constant gedurende de eerste 6 dagen en steeg daarna, terwijl Ψ_{press}
constant was tot dag 6 en daarna daalde.

De experimenten beschreven in deel V werden gedaan om na te gaan
of de verschillen in ionen lekkage, resulterend in verschillen in water-
huishouding, tussen petalen afkomstig van bloemen die verouderden in een
vaas of aan de plant konden worden toegeschreven aan verschillen in cyto-
kinine activiteit. Bovendien werden de cytokinine activiteiten van petalen
van 3 cultivars, die verschilden in houdbaarheid, vergeleken. De cytokinine
activiteiten ("vrij" en "gebonden") in petalen daalden gedurende de eerste
6 dagen van het experiment, zowel in de vaas als aan de plant. Op dag 8
werden er zeer hoge activiteiten gevonden, verspreid over het gehele chroma-
togram. Na dag 8 daalden de activiteiten weer. Voor jonge bloemen die zich
aan de plant ontwikkelden werd er een top in de "vrije" cytokininen gevonden
in een zeer vroeg knopstadium. De "gebonden" cytokininen vertoonden een
hoge activiteit op het moment waarop de petalen juist geheel waren ontvouwd.

Er bestonden geen correlaties tussen cytokinine activiteiten op het moment
van oogsten van 3 gerbera cultivars en hun respectievelijke houdbaarheden.
Gezien deze resultaten lijkt het niet waarschijnlijk dat de veranderingen
in ionen lekkage van petalen, die optreden tijdens veroudering van gerbera
bloemen in een vaas, worden veroorzaakt door veranderingen in cytokinine
activiteiten.

De gegevens weergegeven in deel VI laten zien, dat het mogelijk is om
de ionen lekkage van cellen van gerbera petalen te beïnvloeden door de turgc
potentiaal te veranderen. De stijging van ionen lekkage tijdens veroudering
van afgesneden petalen werd versneld door de turgor potentiaal te verlagen.
Verhogen van de turgor potentiaal door de bloemstengels in KNO_3-oplossingen
te plaatsen, verminderde de stijging van de ionen lekkage. Het lijkt niet
onwaarschijnlijk dat verschillen in het verloop van de ionen lekkage tussen
bloemen die verouderen aan de plant en in de vaas kunnen worden veroorzaakt
door verschillen in het verloop van hun turgor potentialen.

De dominerende invloed van ionen lekkage op de waterhuishouding,
zoals aangetoond in de delen III en IV, en de resultaten weergegeven in
deel VI suggereren sterk dat het voor een goede houdbaarheid van afgesneden
bloemen van groot belang is dat de turgor potentiaal van de bloembladen
boven een bepaald niveau wordt gehandhaafd.

Tenslotte wordt bediscussieerd dat bepalingen van turgor potentiaal,
watergehalte per drooggewicht en drooggewicht per oppervlakte-eenheid van
petalen goede indicaties kunnen geven voor de potentiële houdbaarheid van
afgesneden bloemen.

CURRICULUM VITAE

U. van Meeteren werd geboren op 2 augustus 1950 te Hilversum.
Na het behalen van het einddiploma HBS-B aan de Gemeentelijke Hogere
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