

STABY
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Concerning the Keeping Quality
of Cut Flowers

A Translation from Dutch
(Tables and Graphs not Included)

of

Over De Houdbaarheid
Van Snijbloemen

door

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Summary

Literature

1.1 Literature

The desire to keep flowers fresh as long as possible is inherent to the idea of cut flowers. One endeavors to keep flowers fresh on the one hand by influencing the milieu during the storage, on the other hand by lengthening the keeping quality in the normal room climate. Palladius (85) in 350 A.D. in his publication "De Re Rustica" devoted a chapter "De rosis viridibus servandis" (On the storage of green roses) to this matter. It has been established in a large number of diverse experiments that the following factors influence the keeping quality of cut flowers: nutrition; temperature and light intensity before cutting (39, 52, 67, 109); the time of the day the flowers are cut (40, 52, 58, 76, 82, 83, 90); the development stage of the flower when cut (58, 72, 82, 85, 108); pollination (21, 22, 26, 41, 117); the method of cutting (52, 90, 109); temperature, composition and humidity of the air during transport and storage thereafter (14, 34, 66, 67, 68, 69, 70, 76, 77, 81, 85, 91, 99, 106, 108, 110, 119); mechanical (55, 58, 59, 72, 89, 104, 122) and chemical (4, 5, 13, 23, 33, 35, 36, 54, 55, 58, 59, 60, 65, 80, 86, 88, 122) methods to prevent the hindrance of water uptake, methods to limit water loss (2, 36, 48, 90, 100, 122); chemical methods to influence the metabolism of the flower (4, 5, 13, 19, 20, 21, 23, 31, 48, 53, 58, 59, 60, 72, 73, 77, 82, 109, 110, 122).

Summaries of these experiments have been published by Anon. (3), Arnold (5), Dickie (16), Post (90) and Tinker (109).

Only those results where chemical methods were used are discussed here in any detail. The research began with the arbitrary and separate testing of a large number of organic and inorganic salts, acids and bases and substances such as ethanol, chloral and sugar by Fowton and Ducomet (23), Knudson (54) and Hitchcock and Zimmerman (33). Thereafter critical observations were made on the influence of home remedies such as aspirin (acetylsalicylic acid) (4, 5, 13, 36, 58); kitchen salt (NaCl) (4, 5, 23), metallic copper (58, 93), etc. The majority of researchers have obtained negative results and only in isolated cases positive results. That the development of bacteria plays a role here is mentioned by Arnold (4,5), Laurie (59, 60) and Hatsehn (93).

As the first combination Arnold (5) tried the bactericide toluol with Knop's nutrient media and with sugar. Laurie (58, 59, 60) also tried experiments with mixtures of bactericides and other physiologically active substances. From these results he concluded that substances used to prolong the keeping quality of cut flowers must meet the following requirements:

- a) reduce bacterial activity;
- b) improve transpiration;
- c) limit the respiration;
- d) be at the most favourable pH;
- e) possess an optimal osmotic value.

These partial statements supported by experiments are the cause of the development of many commercial preparations, such as bloomlife, floral-life, and chrysol.

Laurie (59, 60) names floroglucinol, recorcinol and hydrazine-sulphate (also used in 13, 80, 122) as respiratory inhibitors. He does not, however, give results of respiration measurements. Potassium alum and Sodium hypochloride

were added as bactericides and he mentions thereafter a favourable influence of boric acid and manganese sulphate with carnation and of "Sodium amycol" with sweet-pea.

Fahrenkamp (19, 20), Mertens (73) and Otto and Kamrodt (82) found in certain cases a favourable influence of extracts of Digitalis, Convallaria and Scilla and of the purified glucosides from the extracts such as strophantine, digilanide, scillaren and folinerine. Mertens sought an explanation for the effect of these substances in their influence on the osmotic ratio. He presents no experimental data to support this theory.

Favourable results with growth substances are limited to occasional incidental observations such as those of Whiteman (121) with Paeonia, Otto and Kamrodt (82) with Euphorbia and Wester and Marth (120) with Prunus serrulata and Cornus florida.

Pastac and Drignet (26) observed that color changes with Dahlia are delayed by addition of $\text{Ca}(\text{HCO}_3)_2$ and AgNO_3 to the water. He explains these favourable results by suggesting that as a result of the Donnan equilibrium HCO_3 penetrates the cell and results in an acid environment, while $\text{Ca}(\text{OH})_2$ does not penetrate and results in an alkaline environment outside the protoplasm. He regards an increase in pH as one of the most important factors in the aging of the cells in the corolla but he gives no experimental evidence for this theory.

In all these investigations, results vary with different substances at different concentrations and with different plant species. Bactericides give favourable results in certain cases but not with all plants; the results with sugar become more regular, if combined with a bactericide, but here also the optimal concentrations vary with different authors (4, 5, 23, 55, 58, 59, 60, 77) and the results are irregular for different crops. Also with the use of commercial preparations varying results are obtained for each crop (2, 6, 33, 35, 53, 80, 90, 119).

1.2 Object of Investigation

To find a practical substance and method to lengthen the life of cut flowers one must find an answer to the following questions:

- a) What is the cause of early wilting?
- b) Are the causes the same for all plants?
- c) Can we remove these causes and with what substances?
- d) Can the normal cessation of blossoming be delayed in a normal room climate?

To be able to approach these problems more closely, a better insight into the physiological changes occurring in the cut flower, stem and leaf, and the influence of chemical substances on these processes is needed.

2. Organization of Investigation

2.1 Method and material

In order to obtain a rough survey into the possibilities a great number of substances were tested for their influences on the keeping quality of different crops.

As a measure of the keeping quality during each experimental period graded values were assigned for the condition of the flowers, while after specific periods the weight was obtained and expressed as a percentage of the original weight. In these experiments each treatment consisted of at least three flower stems and was repeated 2 to 3 times. Still, care was taken to see that the original material was as uniform as possible, and that it was distributed evenly in all the treatments. The differences in weights, of the replicates, expressed as a percentage of the original weight were as a result very small. According to whether the percentage was higher, equal or lower than that of the control it was concluded as to whether there was a favourable, no, or an injurious effect. In addition at the end of every experiment the amount of water taken up was measured and expressed on the original weight of the flowers. When necessary the experiment was repeated until a sufficient probability was established, or a concentration range between injury and "no effect" was determined and also a favourable range found. Control treatments were included in each experiment. Because the experiment extended over a period of two years, one could not always work under the same conditions and a large number of experimental crops had to be used. Therefore for the bactericide investigation use was made of Antirrhinum majus, Chrysanthemum morefolium, Cyclamen persicum, Dahlia variabilis, Dianthus caryophyllus, Iberis sambervivans, Lathyrus odoratus, Mathiola incana, Rosa hibrids, Sacchiosa atropurpurea, and Zinnia elegans. The results therefore give only a rough survey of the possibilities.

The influence of bactericides on the development of the bacteria was followed by taking, once or twice during the experiment, a drop of the vase water with a sterilized platinum needle and streaking it on a peptone-glucose-agar medium.

The nonbactericidal substances were also tested in combination with a bactericide whether or not the optimal sugar concentrations for the respective crops had been added.

2.2 Abbreviations of common basic mixtures

A basic mixture consists of one or more bactericides, a fungicide and sometimes sugar being added to the water, thus the following abbreviations are used:

| | |
|------|--|
| ACAC | AgNO_3 0.003% + $\text{Ca}(\text{NO}_3)_2$ 0.1% + Aaradon 0.001% + Cladox 0.025%; |
| Us | Uspulun 0.02% (org. Mercuric compound); |
| UsCi | Uspulan 0.02% + citric acid).02%; |
| S | Saccharose (S_6 = Saccharose 6%); |
| G | Glucose |

2.3 Results.

2.3.1 Bactericidal compounds.

According to their action the bactericides tested can be divided as follows:

- a. Phytocide concentration equal to or lower than the bactericide.
- b. During a short time a favourable effect is observed, thereafter no effect, because harmful side effects occur, such as the dying off of stems, or because the development of the bacteria is no longer suppressed.
- c. Bactericidal and unharmed until the moment at which wilting occurs due to other causes.

Table 1 Page 6 gives a survey of the compounds tested and divided according to these criteria.

The completely useless compounds belong to the first group. The slowly acting plant toxins were included in the second group, such as organic mercury preparations and compounds which are only harmful in high concentrations, such as acids and enzyme toxins. They first kill the living cells of the stem, so that this loses its rigidity. In the second group also many bacterial static compounds should be included, such as sulphur preparations and antibiotics. After some time the bacteria flora adapts itself to these compounds. Some of the compounds belonging to this group [such as sulphurous acids, hypochlorides, hydrogen peroxide and potassium permanganate] lose their properties due to oxidation or reduction [after some time]. The oxidative compounds lose their activity even faster if sugar is added. The compounds which under normal circumstances escape the disadvantages mentioned belong to the last group (C). Their effect is also lost under extreme circumstances, such as high temperature, the presence of high amounts of organic matter due to the placement of many plants in a little water, or due to the damage of stems as caused by the adding of compounds which combine themselves with the bactericides. Silver nitrate (0.002 to 0.006 percent) gave by far the longest protection and the least damaging effect. Silver nitrate also combines easily with proteins. This causes the rapid death of bacteria present in the water and on the bases of the stem, but silver nitrate penetrates the plant very little. Furthermore the silver slowly liberated from the compounds would suppress further development of bacteria in an oligo-dynamical way (27, 47). In the beginning after the addition of silver nitrate to the water a slight cloudiness forms, but after addition of calcium nitrate (0.1% calcium nitrate combined with four molecules of water) a precipitate is quickly formed. As reserve in general, the organic mercury compound "Aaradon" was added in a concentration which alone is not bactericidal but also not toxic.

Protargol had a favorable effect especially in combination with acid (to pH 4). Aluminum sulfate and lead acetate lower the pH.

2.3.2 Effect of Sugar

With a number of crops the effect of sucrose and glucose in different concentrations was studied. In this case silver nitrate 0.003% was always added as bactericide and in general also calcium nitrate 0.1% plus Aaradon

0.001% plus Cladox 0.025% (AGAC). In Table II the weight in percentage of the original value is given as combined measure for the development and keeping quality. Glucose and sucrose in equal weights give a difference in effect only in a few cases; the optimal sugar concentration varies very strongly however for different crops. In many cases the drop of turgid flowers' flow parts could be prevented by the addition of sugar. For instance with Laburnum anagyroides, Lupinus polyphyllus, Ribes sanguineum, and Tulipa (see 1).

2.3.3 Influence of Acidity

Lowering of the pH of the water in itself gives a strongly inhibiting effect on the development of the bacteria. In case one wants to study the physiological effect of the pH of the water on the flower, it is especially necessary here to suppress the growth of the bacteria also at a higher pH. Aluminum sulfate and lead acetate themselves are acidic so that only silver nitrate and organic mercury compounds can be used as bactericides. However, the pH of the water also affects the precipitation velocity of the insoluble silver and mercury compounds. Thereby the physiological effects of the acids and their direct effect on the blocking of the vascular bundles could not be quite separated. The development and keeping quality of Dahlia was for instance improved if the water was acidified to a pH of about 3.5 and in addition silver nitrate plus sugar were added as a basic mixture. However, in the case where calcium nitrate at 0.1% was also given the effect of the acid disappeared practically completely. With Rosa on the other hand the pH optimum was at 4 with and without calcium nitrate. Also with Convallaria the effect of calcium nitrates on acids was decreased but the pH remained at an optimum of 3.2. With many other crops such as Antirrhinum, Dianthus and Zinnia no effect of the pH was found.

The types of acid added were not very important. For instance good results were obtained with citric acid, maleic acid, malic acid, and tartaric acid, but also oxalic acid, phosphoric acid and even nitrate and sulphuric acid could be used as long as the pH range of 3 to 4.5 was not exceeded. The desirable pH range is easier to obtain with the weaker dissociated acids.

2.3.4 Fungus Development.

Especially at a low pH development of fungi on the water often occurred and if the stem was attacked this rapidly resulted in wilting and the development of bacteria. Therefore the following commercial preparations were tested for their fungicidal action on Chrysanthemum morifolium: AApirol (tetramethylthiuramdisulfide), cladox (2,4-dinitrorodanebenzene), copper oxi-chlorides, orthocides (M-trichloromethylthiotetrahydrothalimide), scabex (organic mercury preparation) and sulphur spray. As a basic mixture, silver nitrate at 0.003% plus citric acid 0.04% plus saccharose 2%, was used.

Copper oxi-chlorides, spray sulphur and AApirol in non-phyto-toxic concentration did not give protection. The best results were obtained with cladox 0.05 to 0.01% orthocides 0.025 to 0.005% and scabex 0.02 to 0.002%. In most experiments a filtrate of cladox (2.5% filtrate of a 1% suspension) was added to the basic mixture.

2.3.5 Growth compounds and inhibitors.

With the potassium salt of alpha NAA, the potassium salt IAA 2-methyl-5-chlorophenoxy acetic acids and 2:4-dichlorophenoxy acetic acid added to the water at low concentration favourable effect could be obtained with Antirrhinum majus, Cyclamen persicum, Chrysanthemum morifolium, Dahlia variabilis, Dianthus caryophyllus, Dianthus plumarius, Fraxinum parofakianum, Matthiola incana, Narcissus pseudonarcissus, Rosa "Perel van Aalsmeer", Scabiosa atropurpurea, Tagetes patula and Tulipa. Also of the addition of ascorbic acids or fumaric acid gave no favourable growth effect. Spraying Antirrhinum majus, Cyclamen persicum, Delphinium ajacis, Lathyrus odoratus, Matthiola incana and Prunus triloba with growth compounds also had no favourable effect. With the crops mentioned most compounds had no effect on the life-span of the flower and could not prevent flower drop. Flower drop prevention was possible with Alnus glutinosa, Corylus avellana, Lupinus polyphyllus. These are cases where the flower or the flower structure drops completely in a turgid condition (see 1). With Lupinus polyphyllus spraying with growth compounds had only an effect, if the spraying was followed by one day of sunny weather before the flower was cut, or if the sprayed flowers were placed directly in the 1 to 3% solution of saccharose. In 4 to 8% saccharose solution also without spraying, the flowers did not drop.

No lead to further investigation was obtained in experiments with the sodium salt 2:3:5-triiodobenzoic acid (0.0001 to 0.005%) with Antirrhinum majus, Lathyrus odoratus, and Matthiola incana, with B 542 (equals triethynol amine salt of α -cyno- β (2:4-dichlorophenyl) acrylic acid) (0.0001 - 0.02%) with Bellis perennis, Dianthus plumarius, Lilium henryi, Magnolia stellata and Tulipa stellata and with maleic hydrazide (0.0005 to 0.025%) with Dahlia variabilis, Dianthus caryophyllus, Freesia "Buttercup", Godetia grandiflora, Lathyrus odoratus, Rosa "Perel van Aalsmeer", Scabiosa atropurpurea, Tagetes patula. Only with Amelanchier spicata, Dianthus plumarius, Godetia grandiflora, Iberis sempervirens, Scabiosa atropurpurea and Tagetes patula were the toxic concentrations of IAA increased by addition of maleic hydrazide and maleic hydrazide reversedly was less detrimental in combination with IAA.

2.3.6 Enzyme toxins.

In most cases where enzyme toxins were added in different concentrations with and without sugar and intermittantly or continuously their effect on the keeping quality was absent or negative. DNP, hydrazine sulphate, malachite green, malonic acid, monoiodoacetic acid, sodium acid (NaO_2), sodium fluoride (NaF), sodium diethyl, -dithio-carbamate, (disca) phenyl urethan, fluoreglucinol, resorsinol and cycnolite sulphate (superol) with Chrysanthemum morifolium, Convallaria majalis, Dahlia variabilis, Dianthus plumarius and Lathyrus odoratus. DNP, (Sodium azide and superol were also tested with Antirrhinum majus, Dianthus caryophyllus, Rosa hibrids, Scabiosa atropurpurea and Tulipa. Only 2:4-dinitrophenol (0.0001 to 0.001%), malachite green (0.003 to 0.01%), sodium azide (0.002 to 0.0015%) and superol (0.005 to 0.002%) gave a favourable effect with Chrysanthemum morifolium, Convallaria majalis, Rosa hibrids and Scabiosa atropurpurea. Malachite green at 0.005% was favourable

with Chrysanthemum morifolium, Convallaria majalis, Dahlia variabilis and loose petals of Dianthus sp.

2.3.7 Glucosides.

Strophantine (0.0005% to 0.05%) and digoxin (0.0001 to 0.00025%) were tested on Dianthus caryophyllus, Freesia "Buttercup," Matthiola incana, Rosa "Kirsten Poulsen" and Tulipa. Both with and without bactericide or sugar, a clearly favourable effect was never observed. The favourable effects of Fahrenkamp (19, 20) and Mertens (73) are probably correlated with a weak bactericidal effect of these compounds.

2.3.8 Inorganic salts and micro-elements

Especially calcium nitrate, magnesium nitrate, magnesium sulphate and soluble phosphates give favourable effects in certain cases. Whether these results are based on a direct effect on the plant or an indirect one caused by a quicker precipitation of silver and mercury compounds could not be determined by the available bactericides. But with other bactericides active over a short period it could be determined that in any case nutritional salts never are a limiting factor originally. With the micro-elements molybdenum, iron and copper, a favourable effect was never obtained. In some cases (Dianthus plumarius) manganese sulphate 0.01% had a favourable effect. Boric acid (0.05 to 0.125%) prevented flower drop with Lupinus polyphyllus. Further results with boric acid are discussed on page 44.

2.4 Discussion of Preliminary Investigations.

Most of the so-called household remedies such as splitting and hammering of the stem, addition of aspirin and bleaching water are aimed to prevent the obstruction in the uptake of water. In most cases however detrimental side effects of these remedies are worse than the disease. Notwithstanding this, the favourable effect of many bactericidal compounds is confirmed by the opinion of Laurie (59, 60), the suppression of the development of bacteria in the water is a necessary requirement which can only be satisfied by a few compounds, however. Because of its bactericidal and bacterial static properties, silver nitrate was most suited in this respect. Bacterial static compounds in general are too specific in their action, and therefore can be only used if they in addition lower the pH, or if an acid is added. This possibility was not completely investigated, although it can be of practical importance. For the investigation such compounds were less suited because the effect of the pH varied strongly with different crops.

That the osmotic pressure of the vase water as such would play a role (59, 60) does not seem probable. In many cases sugar had a favourable effect. whereas inorganic salts had no effect. For the action of these salts another explanation is therefore sought (p. 18). One can limit oneself with the remark that the action of these salts was clearest with those crops where a lowering of the pH and the addition of an enzyme poison

also had a favourable effect. The idea that the same process in the plant were influenced was justified therefore.

Sugar on the one hand had an important effect on the development and the keeping quality, but on the other hand was also effective with nearly completely developed flowers. Therefore, for the effect of sugar a correlation was sought with the osmotic pressure of the cell sap and with the respiration.

As far as could be determined, the incidental favourable effects of growth compounds (82, 120, 121) and some glucosides (19, 20, 73, 82) could not be confirmed. From this it may be concluded that they have only a favourable effect under certain conditions and with certain crops.

3. Causes of blocking of vascular bundles and methods of prevention.

As a result of the fact that certain bactericides have an influence on the keeping quality, the following questions need to be answered:

a) Do bacteria exert a harmful effect and does the influence of bactericides rest exclusively on the suppression of the bacteria development in the water or in the bundles, or does the bactericide itself have a favourable effect?

b) If bacteria do exert a harmful influence, is the harm done directly by the accumulation in and blocking of the bundles or indirectly by the formation of toxic substances?

c) Does blocking of the vascular bundles never occur if the bacteria growth is suppressed?

d) Do different plant species all react in the same manner?

3.1 Influence of bacteria.

Material and Methods: If one wishes to investigate whether bacteria cause vascular bundle blocking or whether the plant itself plays an active part in bundle blocking, then one must vary the number of bacteria in the water. Here biological methods are considered exclusively, because physical (temperature and illumination) or chemical methods also influence the plant stem. One can add cultured bacteria to a harmless nutrient solution, or vary the amount of water per stem and thus vary the probability of infection. The influence of these treatments were examined by:

- a) viewing longitudinal sections of the stem base microscopically
- b) noting the time wilting took place
- c) determining the water utilization
- d) directly measuring the vascular bundle blocking.

Before the last determination could be made the methods, described by Gottlieb (29) and Warne (118), to determine the specific water permeability of stem pieces had to be adapted for use on a large scale in comparable experiments. Stem pieces of equal length were connected from the top surface by means of a rubber tube to an aspirator and the base was placed in a known amount of water. After a certain period (depending on the plant) the amount of water drawn thru was measured. By using 3 main

tubes each with 10 side tubes the water permeability of 30 stem pieces could be measured simultaneously (photo 1). By taking the average of at least 10 measurements before each determination any differences in stem diameter were eliminated.

To see whether bacteria had a direct or indirect harmful influence, flowers were placed in water in which flowers had previously stood. The water was sterilized by means of a Pasteur filter (P7), heating in an autoclave (125°C) by both, or by the addition of silver nitrate or uspulun.

For the majority of experiments concerning the influence of bacteria Dahlia variabilis "Gerrie Hoehn" without leaves was used. Although similar results were obtained with Chrysanthemum morifolium, Coreopsis lanceolata, Cosmos bipinatus and Matthiola incana these results are not mentioned in any detail.

Results. Under the microscope a shiny accumulation of bacteria and breakdown products are observed with many crops after only two days, especially at the surface or even in the wide vascular bundles (photo 2). Simultaneously a partial blocking of the base portion of the stem was measured with Alnus glutinosa, Amelanchier spicata, Chrysanthemum morifolium, Dahlia variabilis and Dianthus caryophyllus (Table 3).

Primarily the water uptake decreases and wilting begins (weight reduction) (graph 1). As a result of adding ACAC (p4) the downward trend later changes to an upward trend.

By adding of a 24-hour old bacteria culture in peptone 0.5% + glucose 1% (one part added to 10 parts of water) the development of Coreopsis lanceolata was stopped immediately (table 4). If the bacteria are killed with $AgNO_3$ the original harmful effect is removed. After 30 hours where the controls treatments (PG) became cloudy a loss in weight was observed.

From the above it appears that living bacteria in the water for a short time exert a harmful effect on the keeping quality.

Although no extensive investigation on the question whether specific bacteria have specific effects was done, it was observed that generally different bacteria species were isolated from the water.

If one begins with a pure culture it usually changes quickly to a mixed bacteria population when the flower stems are placed therein.

Two answers are found to the question: How do bacteria exert their harmful effects?

- a) A direct blocking action, this blocking remains even after the death of the bacteria;
- b) an indirect harmful effect by the formation of harmful substances.

Water which had had Dahlias standing in it for two days was harmful to fresh Dahlias. This harmful effect remains even if the bacteria have been killed by silver nitrate 0.003%. Where harmful substances had been formed they could be removed by filtering through Pasteur filter (p. 7).

If the flowers had stood in the water for a longer period, then the harmful effect of the used water could not be completely removed by filtering (table 5). If the filtrate is heated to 125°C. in an autoclave for one hour, there again develops a cloudiness and the harmful effect is still only small. By filtering and heating twice the water generally lost its harmful effect. Apparently the harmful substances are of a proteinaceous nature. In these experiments with used water, the bacteria development was still prevented by addition of silver- and calcium nitrate or uspulun and citric acid.

In water, wherein the bacteria development was suppressed by AgNO_3 , there developed no harmful effects in the same time, and with the same number of stems, as was the case with bacteria present. The harmful substances are therefore not formed by the plant itself. The likelihood that these substances are bound into salts by silver nitrate is not great because if silver nitrate is added later it cannot bind the harmful substances.

The harmful effects of the formed substances were never specific for the plant from which the substance was developed e.g. water used for Matthiola incana was harmful to Amelanchier canadensis and used Dahlia water harmful to Chrysanthemum morifolium.

The question as to how these harmful substances act still remains to be answered. Therefore the influence of used water on the vascular bundle blocking of Dahlia variabilis "Gerrie Hoehn" and Amelanchier spicata was investigated after the water had undergone the mentioned treatments. It appears from these experiments that as the mentioned treatments influence the harmful effects on the keeping quality they also influence the degree of vascular bundle blocking (table 6).

In summary one can conclude:

- a) Bacteria have a harmful action
- b) The harmful effect rests primarily on the formation of filterable particles. Later other wilting inducing substances are formed, which are not filterable, but coagulate with heating and can then be filtered off. Apparently these substances are proteinaceous.
- b) Both groups of substances cause the blocking of the vascular bundles.

3.2 Nonbactericidal blockage of vascular bundles.

Symptoms. With silver nitrate or uspulun the development of bacteria in the water is completely prevented, and no bacteria could be isolated from sterile cut stem pieces, but one still frequently notices a blocking of the bundles. These blockages usually moved up and were also measurable higher in the stem (Graph 1 on Page 13).

With Alnus glutinosa, Dahlia variabilis and to a lesser degree with Amelanchier spicata a gummy substance can be microscopically observed in the vascular bundles after any time. In the beginning the blockages are completely colorless, but after some time the bundles become brown. (Photo 3). This ties in with the observations of Bawley (11) and Ludwig (64) on the wilting disease of tomato. In many cases before the blockage could be microscopically observed, an almost complete stoppage was measurable with

the suction methods described on Page 11. Air in the bundles could not be the cause, because in resting branches of Alnus glutinosa there is a large amount of air in the bundles, but they still have a considerable ability to transport water.

Further investigation of the chemical nature of the blocking was not conducted, and also a literature search concerning the appearance of vascular bundle blockings with diverse wilting diseases [8, 11, 15, 17, 28, 29, 37, 50, 64, 96, 105, 123, 125] gave, for what it is worth, little concrete evidence. The most likely idea seems to be, that in wilting diseases, many breakdown products of pectin are formed [18, 28, 64, 123].

Materials and methods. With the further investigation of the causes and prevention of these nonbactericidal induced blockages, most of the work was done with one and two-year old branches of Alnus glutinosa and Amelanchier spicata. The branches of Alnus glutinosa were brought to bloom at 25°C in the dark during the experiment. These experiments with Amelanchier spicata were originally done with branches in forced winter rest, but later also leafy branches were used. This was done in the light and the temperature was not controlled, so that light experiments are not comparable due to the difference in developmental stages. The water permeability was always measured, using stem pieces eight centimeters long over a period of fifteen minutes and under a pressure of two centimeters of mercury. The water permeability of the lowest twenty-four centimeters of the stem was determined separately in three parts. As controls, the average water permeability of fresh branches was taken at the beginning of the experiment and that of twigs, which were measured at the same time as the branches but were freshly cut immediately before measurements were taken. For the main part, these values differ only slightly. Each reading gives the average water permeability of at least ten branches. The influence of varying thicknesses of the twigs has already been eliminated, since the material was divided evenly between the different treatments.

Because the measurements have been taken so that the worst treatment shows the first signs of wilting, the influence of the treatment on the amount of wilting could not be determined at the same time. This was done with one crop which is more susceptible to blockage of the vascular bundles, namely with Convallaria majalis, which was cut just before or during the opening of the first flowers. It also appears here that the results with the different stages of development cannot be compared. In general, the results are clearer the younger and earlier the flowers are cut. The addition of 6 to 8% sugar and a bactericide (silver nitrate 0.003% or uspulun 0.01%) is therefore necessary, but is not sufficient for complete development.

Results. Table 7 shows that by damaging the stem by boiling, no blocking occurs in the dead portion of the stem, but just above the dead part complete vascular blocking appears. It thus seems clear that before the occurrence of vascular blocking the presence of living cells is necessary, on the other hand a stimulus may go out of the damaged cells and stimulate the living cells to a blocking of the vascular bundles.

By applying a finely divided air stream into the water under the cut surface of the stem, blocking is increased. By subjecting the whole

plant or stem to vacuum injection with water (taking air out of all the intercellular spaces under water and thus replacing them with water) bundle blockage is prevented. In conclusion it appears that branches of Amelanchier spicata placed 6, 15 or 40 centimeters deep in an equal volume of water the vascular bundle blocking is less and the keeping quality greater in proportion to the depth of the stems are placed in the water.

This all points to the fact that active vascular bundle blockage is an aerobic process.

But of more practical importance are the chemical substances used to prevent vascular bundle blockage. Of the enzyme poisons tested, sodium azide 0.001% and 2:4-dinitrophenol 0.001 to 0.003% (DNP) resulted in a great decrease in bundle blocking. Malachitegreen 0.001% had a small effect; sodium diethyldithiocarbamate 0.01%, phenylurethan 0.01% and 8 hydroxyquinoline sulphate (superol) 0.001% had no effect.

The action of sodium azide and DNP respectively and the other enzyme poisons suggests, that the occurrence of bundle blocking is a phosphorolating process [44, 63, 103, 107].

Besides the above-mentioned enzyme poisons vascular bundle blocking can also be prevented by the addition of calcium nitrate (Graph 2). Although higher concentrations best prevented blockage of the bundles, 0.5% and higher was also injurious to the keeping quality of Amelanchier spicata; this was optimal at 0.1 to 0.2% calcium nitrate.

Decreasing the pH with citric acid 0.04% to \pm 3.5 (Table 7) had approximately the same effect on bundle blocking as calcium nitrate 0.1% and higher.

It is apparent from these data taken as a whole that before the occurrence of active bundle blocking the following factors must have taken place: a) damaging of the cells; b) the presence of air (oxygen); c) the release of a certain enzyme whose action is lost by enzyme poisons and possibly also by low pH and calcium ions.

The connection between bundle blockage and keeping quality is clear if one compares the effect of the discussed treatments on the blocking with Amelanchier spicata on the keeping qualities (as a percent of their original weight) with Convallaria majalis. All those treatments which were favourable to Amelanchier were also favourable to Convallaria (Graph 3), while sodium diethyldithiocarbamate (disca) had no effect and the action of malachitegreen was also slight.

It must be mentioned here that the concentrations used would be too high for other crops. Convallaria takes up relatively small amounts of water and thus also the chemicals mentioned.

Discussion. The plant itself can prevent the development of blockage, but no general rules are valid; only with Dahlia, Rosa and Convallaria was a favourable effect of low pH observed. Calcium nitrate can replace this effect of acid completely (Dahlia) or partly (Rosa), but has other favourable effects with a large number of other plants also. These differences can be explained by a difference in sensitivity to the toxic action of

acids and salts, by a difference in transpiration speed thus in water and salts or acid uptake, and above all the different influence silver compounds have on the precipitation of suspensions that occurs in the water. The nature of the precipitation rate of these suspensions depends above all on the plant, which is placed on the silver nitrate solution. It occurs for example more slowly in Dahlia than in Carnation.

Although the practice generally used by florists is to place the flowers as deep as possible in the water, Laurie [59, 60] finds generally no favourable effect of deep water and in many cases placing in shallow water is favourable. On the one hand there is less danger for fungus infection, because the bases of a stem are firmer, on the other the surface of the stem is under the water and the infection possibility and food availability for bacteria is less. Laurie demonstrates by smearing the stems with vaseline and paraffin that almost no water enters the stem via the bark, so that the absorbing surface does not become greater by placing of stems deeper in the water. Post [90] observes, that by placing stems in deep water the air is more easily driven out of the bundles, by the establishment of a system of communicating vascular bundles.

The old conception, that by cutting the stem the cohesion of the water in the vascular bundles is broken, that the resulting amount of air that enters into the vascular bundles and the resulting gas embolism hinders the water uptake [38, 116], is not in accord with the conception of Peirce [87] and Preston [92] and with the results of Scholandar et al [97, 98]. With the cutting of liane air in fact enters into the vascular bundles, but water uptake is not influenced hereby. It is understandable that, notwithstanding whether the flowers are cut or recut under water [3, 16, 59, 60, 90, 109], the placing in deep water has a favourable effect if the presence of oxygen is a requirement for the development of vascular bundle blocking.

The favourable influence of the immersion of the stem bases in boiling water can be explained by the fact that air is driven out of the vascular bundles. Boiling does not repair the continuity of water stream as Peirce suggests, but removes air as an accompanying cause to the appearance of vascular bundle blocking. Above all, the placing in boiling water [58, 90, 104, 122] or hydrochloric acid [82] or nitric acid [122] harmful enzymes are broken down or neutralized.

Tinga [110] suggested some influences when he placed flowers for one hour in a solution containing household detergent for an enzyme poison. The first influence of the detergent one considers is a breaking of pectin esterase [71] (compare page 16). Tinga suggests that the applied enzyme poison effects the respiration of the flower directly and thus enhances the keeping quality. His method of pre-treatment during a short time, gives special perspective to the case where the water uptake is so great that in all the previously discussed solutions would be harmful if flowers were placed there for a long time.

The favourable effect of gas absorbing substances, such as wood charcoal [58, 88] in the water is understandable if the vascular bundle blocking is an archic process.

With Cyperus Overton [83] observes that after steaming one portion of the stem leaves occur eight days later. He ascribes the gradual death to the formation to toxic substances from the damaged cells. In connection with the experiments described here where stem portions of Anemone

and Alnus were killed by boiling water, it seems possible that also with Cyperus a gradually increasing vascular bundle blocking occurs above the dead stem portion. Possibly this process also plays a role with many wilting sicknesses, the wilting could be ascribed to the formation of toxic substances which would have a direct, harmful effect on the plasma of the wilted tissue [17, 29, 125].

Although not looked at in any detail, it is possible that silver nitrate can prevent the vascular bundle blocking partly by binding the stimulant freed by the wounding or by binding directly with the blocking enzyme. Thus the influence of silver nitrate solution with vacuum infiltration was greater than that with water. It is also possible that other bactericides which on their own give poorer results than silver nitrate, after the addition of an acid or enzyme poison, in certain cases form a good basic mixture. Us-pulun, for example, is by itself completely unusable with roses, but in combination with an acid it is not improved upon by silver nitrate plus calcium nitrate.

4. Influence of sugar

4.1 Introduction

If one does not consider vascular bundle blockage, sugar was the only substance which had any general influence on the keeping quality of cut flowers. In order to get a better insight into the wilting and aging causes it seems that a closer analysis of the action of sugar is the most logical starting point.

Arnold [5] from his experiments concerning the influence of sugar on the keeping quality concluded that a limiting of the water uptake was favourable for the keeping quality; Hitchcock and Zimmerman [36] and Laurie [59, 60] were of a completely opposite opinion. As a result of this the influence of sugar on the water economy of leaf and flower and on the osmotic relationships was investigated.

As a result of the experiments of Odom [80] on the influence of light intensity on the keeping quality, the influence of light, leaf and sugar on one another were investigated. Above all the influence of sugar on the growth, respiration and keeping quality in their mutual positions were studied. In these experiments special attention was given to the developmental stage at the time of cutting. According to Geach and Dugger [24] boron influenced the transport of sugar and according to Laurie [58] and Odom [80] a favourable influence of boric acid on the keeping quality was noticed, therefore this compound was included in the investigations.

It would be of practical importance if the expensive sugar could be replaced by some other organic or inorganic compound; therefore some attention was paid to this point.

In conclusion the relationship between nitrogen and carbon with respect to the keeping quality was also discussed.

C/N ratios

4.2 Influence of light, leaf and sugar on keeping quality and water conservation.

Methods. Growing flowering plants of Matthiola incana in clay pots were illuminated in boxes with 0, 4, or 8 fluorescent tubes (TL 40) over a twelve-hour period. At leaf height the light intensity was 0, $\pm 2,000$ resp. $3,000 \mu W/cm^2 d$. Due to a good free ventilation the temperature at the highest light intensity during the illumination period was $\pm 1.5^\circ C$. and with four lamps $\pm 0.5^\circ C$. higher than in the dark room.

The flowering plants were placed in the boxes in toto [with clay pots] as well as when cut. This last group had five to seven leaves and were grown in jam pots with 0, 2, or 4% saccharose and as a basic mixture silver nitrate 0.003% plus citric acid 0.04% plus cladox 0.025%. The same experiments were done with cut flowers of Dianthus caryophyllus "Williamson" with four leaf pairs and Tulipa "Van Der Eerden" with two leaves.

The influence of the leaf was investigated in a box. Here the influence of the leaves was varied by removing them or by covering them with paper bags. The transpiration was limited by covering the leaves in poly-ethalene sacks or by smearing them on both sides with vasoline.

The water uptake was determined by periodic weighing of the vases without the flowers, and as controls the vases contained only solution.

The degree of opening of the stamata was only roughly determined at 11 a.m. by seeing how quickly and in how many places a drop of xylol, alcohol or petroleum ether placed on the under side of the leaf penetrated into the tissues (57). The results obtained agree in general with the microscopic pictures of portions of the epidermis fixed directly in absolute alcohol (62).

Influence of light. With Matthiola all the flowers wilted after 13 days in the dark, both with and without roots; above all the leaves were yellow and the development was completely stopped, unless sugar was added (Photo 4). With 2% saccharose the wilting began after 18 days in the dark and with 4% after 24 days. In the light the wilting began after 20 days, both with and without sugar, and the keeping quality of the flowers with roots was longer than that of cut flowers. A small favourable difference in keeping quality at $2,000 \mu W/cm^2 d$ as compared with $3,000 \mu W/cm^2 d$ must apparently be ascribed to the lower temperatures or to a lower uptake of water, and thus a damaging influence of the bacteriacide. If no sugar was added, light had a considerably favourable effect.

With Dianthus caryophyllus no influence of the light intensity was found, both with and without sugar (Grspñ 4).

With Tulipa the life span at $3,000 \mu W/cm^2 d$ was about two days shorter than in the dark, or at $2,000 \mu W/cm^2 d$. If 2% saccharose was added, the difference was shifted to a later interval. The flowers placed under four lamps or in the dark showed no difference in keeping quality, but the stems were weaker and more bent in the dark. The same also holds true for carnations.

Apart from the much higher light intensity which goes hand in hand with a higher temperature, a damaging influence of light was never found, so that the observation of Odom (80) could not be confirmed. With Matthiola incana light itself had a noticeably favourable effect which could be replaced by sugar.

Influence of leaf. That the favourable influence of light is indirectly active through the leaf can be demonstrated by investigating in the light the influence of the leaf on the keeping quality. Similar experiments were done with Chrysanthemum coccineum, Chrysanthemum morifolium, Dahlia variabilis and Matthiola incana.

In all cases the presence of the leaf was favorable for the keeping quality and the influence of the leaf could be replaced or even improved upon by sugar. With Dahlia and Chrysanthemum coccineum the presence of the leaf also in combination with sugar was favourable, with Matthiola the opposite was the case (Graph 5, page 23). The difference in reaction of Dahlia and Matthiola is connected with the difference in sugar requirement and the influence of sugar on the transpiration and water uptake.

In general the transpiration of the leaf is limited by sugar (Graph 5), but with Dahlia the presence of leaves as well as the addition of much sugar in the beginning causes appreciably more water and thus more sugar to be taken up, but with Matthiola with higher sugar concentration the water uptake is so strongly limited that the water and sugar uptake with and without leaves are almost the same.

The cause of the limit in transpiration must be sought in the influence of sugar on the stomata, the development of the degree of opening of the stomata with Matthiola (Graph 6) shows, that by the addition of sugar the stomata are quickly closed. Although with 3-4% saccharose (in the light) the chlorophyll diminishes and the leaves become yellow after 5-6 days, they still remain turgid and the opening mechanism of the stomata is not destroyed. These react to changes in weather conditions.

Also with Dahlia high sugar concentrations have a closing effect on the stomata, but much less so, and here with 8% saccharose especially in the beginning more sugar is taken up with leaves than without leaves. With these high sugar concentrations the influence of leaf was favourable for the development and keeping quality.

By preventing the transpiration of the leaf with plastic bags or vaseline, or by shading the leaves, the favourable influence of the leaf disappears, both with and without sugar (Table 8). With Dahlia the shaded leaves dried up completely in seven days if no sugar was supplied. With sugar the shaded leaf remained fresh, but had no influence on the keeping quality of the flower.

One may thus conclude that the favourable influence of the leaf on the flower is mainly or partly due to the formation of assimilation products.

Discussion

The observed influence of sugar on the stomatal transpiration gives an explanation for the conflicting opinions of Arnold (5) on the one hand and Hitchcock and Zimmerman (36) and Laurie (59, 60) on the other hand. On the basis of this fact, that the water uptake is limited by sugar, Arnold (5) concluded that the decrease in transpiration is favourable for the keeping quality of the flower. Hitchcock and Zimmerman and Laurie established on the other hand, that in general an increased water use goes hand in hand with an increased keeping quality. The observation of Arnold only holds for flowers with leaves, in the light, and with sugar. In all other cases an increased life span of the flower is accompanied by an increased water consumption. The yellowing of the leaves of Matthiola with high sugar concentrations in the light (also observed with Chrysanthemum coccineum and Chrysanthemum morifolium) as a result of the disappearance of chlorophyll, agrees with the results of Mudrack (75) with isolated chloroplasts in sugar solutions, where a too rapid increase in the osmotic pressure outside the chloroplasts breaks the membranes.

4.3 The osmotic pressure of the cell sap, the keeping quality and development.

Each wilting is a result of the loss of osmotic potential of the cell. According to the formula of Ursprung (114) $\text{cell} = \text{cell sap}$, the osmotic potential of the cell becomes smaller, if the osmotic potential (= osmotic pressure) of the cell sap (cell sap) becomes smaller with constant wall pressure (). The possibility thus exists that at a given moment the osmotic potential of the cell sap is so small, that with a decrease in the wall pressure due to transpiration, loss of turgor the increasing cell sap is not in a position to allow cell to increase sufficiently to supplement the water shortage of the specific cell. Especially if by obstruction of the water transport in the bundles a higher osmotic tension is required, can increase in the osmotic tension of the cell sap be of importance. In this connection it was, therefore, important to investigate the development of the osmotic pressure of the cell sap. In doing so one must not lose sight of the fact that the absence of substances, can on the one hand form the basis for the osmotic pressure of the cell sap, and on the other hand can influence the structure of the cell plasma and the chemical processes in the cell (respiration).

Materials and methods. For the determination of the osmotic pressure of the cell sap, the plasmolytic method is used. When the observations, as in this case, and also with Levitt and Scarth (61) are stretched out over a long period, calcium chloride, (purum siccum) is used as a plasmolite. For the experimental series, the same series of solutions are used. For all experiments, naturally colored epidermal cells are used, so that the concentration at which the cells began to plasmolyze, could be clearly determined. (Edge cells remained out of sight (95)). Directly after the cutting of the slices, they were transferred to the solution and after 30 minutes plasmolysis was controlled. As the numbers are only relative, the osmotic pressure is given in weight, percent calcium chloride. Will intrude plasmolysis had just begun to appear. Each figure gives an average of 6-10 determinations of different flowers, which had all been treated similarly.

Experiments with Dianthus caryophyllus. It appears that with Dianthus caryophyllus the further addition of sugar, after 6-8 days, had no influence

on the keeping quality. Therefore, the osmotic pressure of the cell sap of the inner epidermis of the outermost petals was investigated with various sugar concentrations applied for 0, 4 and 8 days and continually. Graph 7 shows that as soon as the sugar supply ceased, the osmotic pressure of the cell sap decreased quickly, and that the deviation from the normal weight change became apparent, so that the osmotic pressure decreased to about 80% of the original value. By adding more than 4 percent sugar for 4 days, the osmotic pressure increased above the original value, and continued longer before the osmotic pressure dropped to about 80%. Also, then, the keeping quality differed only from the control, which was constantly placed in sugar, when the 80% level was passed.

With carnation, there exists a critical value, below which the osmotic pressure (as far as these values are determined by sugar) may not fall. At the same time, it appears that by (pre-testing) with sugar, the osmotic pressure can be increased artificially, and thereby, also the keeping quality, to a certain level. Further, the keeping quality of carnations which had not received any sugar thus far, could be increased by additional sugar, as long as the osmotic pressure had not decreased below the critical level (about -4 in Graph 7, page 27).

That the osmotic pressure of the cell sap in each case is not the only factor which determines keeping quality, is apparent from the fact that also with high and very high osmotic pressures, wilting of the cell occurs. Increasing the osmotic pressure above the original level with 8 percent saccharose gave no better keeping quality than when the osmotic pressure was maintained with 4 percent saccharose at the original level.

Experiments with *Cosmos bipinnatus*. When *Cosmos bipinnatus* is cut at the completely closed bud stage, the development of the flowers is determined by the amount of sugar added. At the same time, it seems that the diameter of the capitulum is strongly correlated with the osmotic pressure of the cell sap of the inner epidermis (Graph 8). Here the osmotic pressure is correlated with the growth of the petals. With the lowest sugar concentration this correlation appears with the keeping quality but with 2 percent saccharose, wilting begins at approximately the same moment as at higher concentrations, although the osmotic pressure is not so high and the flower is not full grown.

Experiments with *Matthiola incana*. With *Matthiola incana* it is observed that without sugar the lowest (oldest) flowers wilt quickly, while at the top growth still takes place. If sugar is added, however, the lowest flowers live as long as the upper ones. Therefore, the flower weight decreases much later with sugar, but very often much quicker than without sugar (Graph 9). If one investigates the wilting pressure, it appears that the osmotic pressure of young flowers without sugar remained at their original level, while that of the mature flowers declines quickly (Graph 9). With sugar there is no such gradient. The osmotic pressure in this case was also correlated with the keeping quality.

One could suggest that the above-mentioned gradient could result in removal of water and nutrients. By removing the incompletely developed flowers, the keeping quality of the lowest flowers is hardly increased, but the removal of the open flowers (nutrient source) has no harmful effect on the unopened flowers.

The influence of substances other than sugar. Only a few substances are able to increase the osmotic pressure of the cell sap of mature flowers. Acids, salts and substances such as alcohol, glycol, glycerol, or urea are not usable on account of their great speed of permeability; before these enter the flower in sufficient quantity, they have been harmful to other parts of the plant. Mannitol and maltose appear to be more suitable; these were compared with saccharose, with Rosa, "Kirsten Poulsen". In low concentrations, maltose has a small favorable effect on the keeping quality of roses (see page 50), in higher concentrations it is not directly harmful, but also not favorable. The last point is also valid for mannitol, in that it has no favorable effect at any concentration, and up to 0.2 molar it is not harmful.

Graph 10 showed that both these substances are able to maintain or increase the osmotic pressure of the cell sap. They have, however, no influence on the keeping quality. (See above and page 50). The increase in osmotic pressure was even greater than with saccharose. This is also to be expected, since a portion of the saccharose is used for the further growth of the corolla.

Discussion. Though, in many cases, the influence of sugar on the keeping quality up to a definite concentration was correlated with the osmotic pressure (Chrysanthemum morifolium, Coreopsis lanceolata, Dianthus plumarius, Freesia "Buttercup", Tulipa "Van der Esden", and others), it appears unlikely that the osmotic pressure of the cell sap itself determines the keeping quality. Thus the maximum attainable osmotic pressure without any damage, is usually higher than the optimum sugar concentration. It could not be demonstrated that by an application of sugar, which increases the osmotic pressure of the cell sap, the resistance to blocking was increased (by the addition of a bacterial culture). An osmotic gradient in the flower cluster of Matthiola was correlated with, but was not the cause of, the difference in keeping quality. In conclusion, as the most important argument, the keeping quality could not be increased by increasing the osmotic pressure, by the addition of slowly permeating substances, if these substances were not able to partake in the metabolism.

In this connection, it is also of importance to mention the ideas of some of the investigators (46, 112, 113) on the question of winter hardiness. They do not connect the action of a high sugar concentration in the cell with the osmotic system of the plant, but would rather regard sugar as a stabilizer of plasma proteins. This idea deserves primary attention, since it can be demonstrated that sugar has a protecting action on the maintenance of the colloidal nature of plant proteins, at low temperatures in vitro (112, 113).

Even if the osmotic pressure is not a causal factor in the keeping quality, it still is, in many cases, a simple method to obtain an insight into the sugar level of the cell.

4.4 Correlation between respiration and keeping quality.

After Van Herk (115) and James and Beavers (45) demonstrated a definite relation between respiration and blossom development, with a spadix of Saurauatum and Arum, it was of importance to investigate whether a similar relationship existed with other crops, and how it was influenced by substances which increased the keeping quality of the flower.

4.4.1 Method.

With the help of the Warburg technique, oxygen uptake was periodically measured, at 25°C. over a one-hour period. Large flasks (30 CC.) with loose stoppers, and with 0.2 milliliters, potassium hydroxide (20 percent) in one side-arm were used. Although not all the carbon dioxide given off is bound, it appears that the method is useful to indicate relative differences in oxygen uptake. Firstly the plant part, of which the respiration is being measured, is placed in the same solution that the plant part will be placed in during the determination. It appears, however, that this procedure was not necessary for the smooth running of the experiment; in later experiments the plant part was placed in the vessels in a dry state. The same Warburg vessel was used for each successive determination for each specific plant part. Using this method the respiration course could be determined in percentage of the original value, namely, directly after cutting. By using large vessels, the error as a result of growth and thus change in gas volume is at a maximum one percent. This error is ignored in calculation of the respiration progress.

Between successive measurements the cut surface of the plant parts are placed in the different solutions at one temperature, namely 25°C. It is essential that a semi-sterile method is used. The solution wherein the plant parts are standing can be kept sterile with ACAC (see page 4); this prevents the hindrance of the water uptake by bacteria development without having to sterilize the whole plant.

4.4.2 Influence of sugar.

As Table 9 indicates, a decrease in the oxygen uptake occurs in all of the cases studied after cutting. If sugar is administered, then this decrease was less and in some cases even an increase in oxygen uptake occurred. This was a result usually of growth of a certain plant part. But then the respiration intensity on a per gram fresh weight still decreases. After wilting it is sometimes noticed that the plants have a higher oxygen uptake mainly as a result of the appearance of microorganisms.

It has been determined with Dianthus plumarius (Graph 11) and also with Lathyrus odoratus and Matthiola incana, that the influence of different sugar concentrations on the keeping quality is correlated with the influence on the respiration. A maximal respiration intensity goes hand in hand with the best keeping quality. This influence on the concentration was especially clear in the first period after cutting.

With Dianthus plumarius the end of the flowering period is initiated by a sudden collapse of the petals. This folding up (at 25 degrees C. three days after the flowers had been cut at the nearly open flower stage) is accompanied by sudden increased respiration (Graph 11) followed by a quick decrease during the subsequent death of the petals. The collapse and the respiration increase is delayed by the addition of sugar, this is dependent on the concentration and the development stage at the moment of cutting. With the addition of 6 percent or more of saccharose this petal collapse and respiration increase does not occur. The wilting then begins at the edge of the petals and proceeds gradually.

The sudden increase in respiration is limited to the petals. If the respiration development of loose petals is investigated, the increase in respiration and collapse of the petals occurs at the same time as with flowers which are not separated (compare Graph 22 on page 48).

Discussion. Siegelman (99) sought a connection between the respiration development of cut flowers (Rose and Gardenia) and fruit. As a result of these investigations he mentions the lack of a climacterium during the flowering process with flowers. As the flowers could not absorb any water during the measuring (12 days under bell jars) the conditions were almost abnormal. The petals of Rose and Gardenia do not wilt at the same time usually. So that the increase in the respiration of whole flowers could hardly be noticed.

In the experiments with Dianthus plumarius described here, a definite revival of the oxygen uptake was observed. Notwithstanding, it is unlikely that this revival can be compared with the climacteric rise (51) of fruit. Although not strictly shown, there is a strong indication that the moment of this respiration revival with fruit is not determined by the amount of carbohydrate or sugar (51). In the case of Dianthus plumarius the revival of respiration could be delayed or even prevented by the addition of sugar.

More supporting evidence is also given with respiration experiments with cut off leaves (44, 56, 124). Almost all researchers have found with detached leaves, that a correlation exists between the decrease of the quantity of carbohydrates, especially sugars, and respiration (44); the following revival of respiration is accompanied with a strong protein loss. This is opposite to what occurs in ripening fruits where during the climacterium protein synthesis occurs (42). Van Herk (115) and James and Beevers (45) found during the unfolding of the spadices of Saurumatum and Arum an increase in the respiration. This increase in the respiration continues longer than the increase in dry weight which shows the oxygen uptake during the beginning of the wilting was greatest. James and Beevers mention that the carbohydrate shortage is the primary cause for the later wilting. The cause of the higher respiration would be due to the appearance of certain "no-metallo enzymes" (only inhibited with monoiodoacetic acid or sodium fluoride), according to Van Herk a flavo-protein. The cause of the increased activity of these enzymes cannot be pointed out. Whether these enzymes occupy in other flowers also the role of end-oxidase is not known.

In any case the function of sugar with keeping quality in cut flowers can be regarded in part as supplementary to the reduced level of carbohydrates by oxidation. It is possible that by adding sugar: a) that in an unknown way the induced increase of respiration is caught up with so that the plasma proteins do not have to be called upon. b) the emergence of the inducing factor is prevented so that this is not formed and transported (influence of sugar on the plasma permeability, "organization resistance" (12). c) the colloidal structure of the plasma is directly protected by sugar so that this plasma is not concerned with the metabolism. d) a combination of the mentioned factors maintains the structure and semi-permeability of the plasma.

4.4.3 Influence of pH and enzyme toxins.

Lowry (59, 60) considered that one of the properties of a substance used for the increase of the life span is the ability to decrease the respiration. As usable respiration inhibitors, he mentions hydrazine sulfate, florigucinol, and resorcinol. He does not give data on these substances' influence on respiration. Tinga (110) also thought that there is a connection between the favorable action of a short treatment with enzyme poisons (sodium azide, sodium malonate, sodium iodo-acetate) on the keeping quality and the reduction of the respiration.

Asit undoubtedly would be cheaper to stop respiration, thus a breakdown of carbohydrates, than to supplement the substrate by sugar, inhibition by means of chemical substances would be of the utmost importance.

As described under 2.3.6, and 3.2, substances such as 2:4-dinitrophenol and sodium azide in certain cases had a favorable influence on the keeping quality. Therefore, the influence of these substances in non-damaging concentrations on respiration was studied.

As graphs 12 and 13 show, sodium azide (NaN_3) with Dahlia and Iberis sempervirens had a stimulating rather than an inhibiting effect on the oxygen uptake, while in both cases favorable influence on the development and keeping quality was observed.

The same results are found with Dahlia when floroglucinol 0.006, 0.03 percent (Table 10) is used. Pyrogallol had an inhibitory influence on the oxygen uptake in the same concentration range, but was also damaging and harmful to the keeping quality. With Dianthus plumarius sodium azide and 2:4-DNP had no influence on the oxygen uptake. The keeping quality of loose petals of Dianthus caryophyllus was strongly favored by adding Malachite green 0.005 percent. This results in a slight inhibition of the oxygen uptake during the collapse of the untreated petals (after two days), but not before wilting (after one day); after wilting the oxygen uptake with Malachite green was even higher. There can be no doubt that the saving of the respiration substrate is the cause of this favorable action.

The respiration development with Dahlia and the influence of low pH (by addition of tartaric acid, citric acid (Graph 12), malic acid, phosphoric acid (Table 10)) shows the same increase of oxygen uptake as occurs with sodium azide. In both cases a faster growth occurs so that the oxygen uptake is only influenced to a slight degree on a per gram fresh weight basis.

Discussion. If these results are combined with the data on page 18, on the influence of the discussed substances on the blocking on the stem vascular bundles, then it appears that enzyme inhibitors and acids exert no direct influence on the metabolism of the cells of flowers, but only enhance water and sugar absorption, whereby a shortage of water (18, 43) or sugar (10, 51, 124) as respiration limiting factors are excluded. Above all it must be mentioned, that before flowering usable concentrations are considerably lower than those concentrations of DNP and sodium azide as enzyme poisons which are used in biochemical and physiological research.

If one considers a slight increase in the respiration under the influence of DNP and NaN_3 to be an uncoupling of respiration and synthesis (63, 103, 107) it is difficult to see an explanation of this action on the favorable effect on the keeping quality. The available substrate is in any case oxidized.

Favorable action of hydrazinesulfate, floroglucinol and resorcinol (13, 59, 60, 80) never shows its effect clearly with mature flowers with stems when in combination with silver nitrate or uspulum. Possibly the substances react favorably with other bactericides through their reducing properties; also in this case the result depends on the result of the prevention of vascular bundle blocking.

4.4.4 Influence of gibberellic acid.

Only two cases have been found up to the present, where a substance has a favorable influence on the keeping quality as well as limiting the oxygen intake

of the flower, namely, boric acid with *Dianthus* (page 48) and gibberellic acid (GA_3) with *Matthiola incana*.

0.0001 percent gibberellic acid in the water of the vase with or without sugar had a favorable influence on the keeping quality of double stock gilly flowers (Graph 14). In both cases the oxygen uptake of the flower, but especially on a per gram fresh weight basis, is inhibited (Graph 15). This inhibition occurs before the first signs of wilting become apparent with the untreated flowers. During the wilting (weight decrease) of the control flowers the difference in respiration becomes greater.

The only case until now where a favorable influence of GA_3 (1-10ppm) on the keeping quality has been found was with *Ribes sanguineum*. In this case no respiration experiments were done. No influence of GA_3 added to the water in the vase were observed with *Aquilegia chrysantha*, *Convallaria majalis*, *Dianthus plumarius*, *Laburnum anagyroides*, *Lathyrus odoratus*, *Muscari armeniacum* and *Scabiosa caucasica*. It is possible in these cases that the amount of gibberellic acid taken up was too small.

With *Iberis sempervirens* GA_3 especially in combination with sucrose (0.5 to 2 percent), a strong influence on elongation of the flower spikes (Graph 16) and parthenocarpic fruit formation was induced; keeping quality of the flowers was, however, not influenced. The growth increasing effect of GA_3 with *Iberis*, with and without sugar, is accompanied with an increase in the oxygen uptake on a gram fresh weight basis of approximately 10 percent (Graph 16, page 40).

Discussion. The fact that gibberellic acid retains its influence on the keeping quality and oxygen uptake even after the addition of sugar suggests that the working of GA_3 is not due to a saving of respiration substrate. It is more likely that it prevents the evolution or the working of an age-inducing factor (enzyme?). The decrease in oxygen uptake by GA_3 with *Matthiola* suggests that these aging factors induce certain oxidative processes. If one brings this in connection with the action of sugar then the idea originates that after addition of sugar the aging induced and respiration increasing factors are capable of working but the damaging effect (increased respiration) are dealt with without the plasma being affected.

The connection between the decreased oxygen uptake with *Matthiola* and the increased oxygen uptake with *Iberis* and also with stem sections of peas (49) is not completely clear. If one considers that increased oxygen uptake is a result of increased energy use for growth, then one can conclude that gibberellic acid has an inhibitory effect on certain still unknown metabolic processes.

4.4.5 Connection between development stage, respiration and sugar requirement.

Carnations, chrysanthemum, dahlias, freesias, lathyrus and many other cut flowers develop only slightly or very badly if they are cut before they are completely opened. In different cases the keeping quality of a flower cut while still in bud is shorter than a flower completely opened which is physiologically an older blossom.

The fact that nearly all these crops could be cut considerably earlier if sufficient sugar were added was also studied here in an effort to obtain a connection between this and the respiration.

Materials and methods. The oxygen uptake was determined according to the method described on page 19 where the vessel constant is determined with the specific weight of the flowers set at 1. This gives rise to a maximum error of 0.1 percent. With *Freesia* and *Dahlia* the oxygen uptake of the successive flowers from one inflorescence was compared to each other; with *Dianthus plumarius* the

flowers of one plant in different stages of development were used; with Lathyrus odoratus both methods were used, no difference being found. Directly after each experiment the fresh and dry weight was determined. The sugar requirements of the different development stages were investigated on the one hand by determining the optimal sugar concentration for the development and keeping quality of the different flower stages, and on the other hand by following the influence of sugar during a short period just after the flowers had been cut. The single flowers out of a flower cluster of Freesia or out of the flower heads of Dahlia were placed in half petri dishes. These flowers were supported by glass tubes and rings and were kept separated from each other (Photo 5).

Results. The results with Freesia (Graph 17) show that the influence of sugar on the keeping quality as well as on the oxygen uptake calculated on a weight basis is greatest with the youngest flowers.

With individual flowers of Dahlia it has been determined that the addition of sugar is necessary during a certain specific period. But after three to four days the keeping quality is even better if no further sugar is added (Table 11). It is apparent that the younger the flowers are when cut the more sugar is needed and for a longer period. Also with Dahlia the respiration intensity of young flowers was considerably higher than that of full grown flowers (Graph 18A). This result was established with whole inflorescences of Dahlia, where the keeping quality was at an optimal, if in the beginning a lot of sugar was administered and later less sugar.

With Lathyrus the addition of sugar for longer than eight days was hardly necessary, unless the flower was cut at a young stage (Table 12). If the flowers are placed in a sugar solution twenty-four hours after cutting, then the sugar had no influence on the inflorescence (Photo 6), but the fruit developed better. Also here the oxygen uptake declines rapidly, as the development proceeds (Graph 18B).

With a plant such as Cosmos bipinnatus (cut while still a bud) or Dianthus caryophyllus the addition of sugar immediately after cutting had an effect, but here the sugar requirement lasted much longer (see page 16).

Dianthus plumarius acts differently to Lathyrus and Dahlia. The respiration decreases only very slightly during the development (Graph 18C), but the optimum sugar concentration was also independent of the stage of development (Table 13).

Young buds of Dianthus plumarius, without the addition of sugar, were able to adapt themselves to a lower carbohydrate level; this is in contrast to open flowers. Without sugar the development of the buds is stopped quickly; with 2 percent saccharose they still develop, but remain smaller and completely white (normal Rose) and the ovary does not grow out; the keeping quality of the crown is only a few days shorter than of flowers in 8 percent saccharose which have a normal development. As soon as the color has developed adaptation is more difficult.

Discussion and practical conclusion. As a general conclusion one can say that the respiration and sugar requirements run parallel. Although the number of investigations is limited, it seems here, that with crops where the practical solution is said to be "cut in completely open condition", such as Dahlia and Lathyrus, a strong decline in respiration is shown at the termination of the development.

At the same time it appears that flowers cut during the period of very high respiration intensity, develop good keeping quality if sugar is added.

On the basis of the above considerations one can classify cut flowers as follows: a) Flowers, which during the development cycle must be freely supplied with sugar. Example, Dianthus. b) Flowers, which due to the presence of carbohydrate reserves or of leaves plus light can supply their own sugar requirements. Example, Cyclamen and Pyrethrum. c) Flowers whose respiration decreases rapidly just after the opening, so that the sugar requirement becomes small. In this case one must decide whether the flower has decorative value before opening or if it is not better for the flower to be cut in an unopened condition due to handling techniques. If it is so, sugar must be added for a good development and keeping quality. All cut flowers where the flowers or florets are found in different stages on the same stem must be considered in this group except those described under paragraph b.

4.5. Influence of boric acid on the keeping quality and sugar requirement of certain crops.

Laurie (58, 59, 60) and Odom (80) mention the favourable influence of boric acid with Carnations. Gauch and Dugger (24) were of the opinion that sugar transport was favoured by the addition of boric acid. This gives a lead to study the influence of boric acid on the sugar requirement and sugar distribution. Thereafter the influence of boric acid on the metabolism of the flower could be sought.

Results. The influence of boric acid was investigated with a number of crops with and without sugar (Table 14). Only with Convallaria, Dianthus, Lathyrus and Syringa could a favourable effect of boric acid be found. The working concentrations of boric acid with these crops was so high, that they were harmful to other crops. In all experiments the water was kept free of bacteria with ACAC (p. 4). Boric acid also had a favourable effect with Dianthus and Lathyrus when used with 0.01 or 0.02 uspulum as a bactericide. The action of boric acid thus does not depend on the exclusion of bacteria and apparently also not on the neutralization of harmful substances in the basic mixture.

Also the pH does not play a role because the influence of boric acid on the acidity is small in the concentrations used, while at low pH's and with sodium baborate ($\text{Na}_2\text{B}_4\text{O}_7 \cdot 10\text{H}_2\text{O}$) with Lathyrus and Dianthus a favourable effect was observed (Table 15).

Graph 19 shows, that with Lathyrus, on the one hand the optimal sugar concentration under the influence of boric acid decreases and on the other hand under the influence of sugar the optimal boric acid concentration decreases. The same effect was observed with Dianthus species. It is postulated that a correlation exists between sugar transport and boric acid. The following observations show, that the transport, especially with Dianthus caryophyllus and Dianthus plumarius, is changed in a direction favourable to the keeping quality.

The dry weight of the petals, sepals and ovary of Dianthus caryophyllus "Rode Sim" decline gradually and evenly under the influence of boric acid. (Graph 20). This is also the case with the fresh weight. Without boric acid, however, the fruit grows very rapidly during the wilting of the corolla (photo 7) but the calyx remains constant in weight. With boric acid the calyx turns yellow and withers sooner than the corolla and much sooner than without boric acid.

Measurements of the osmotic pressure of the epidermal cells of the calyx and corolla (Graph 21) show that with Dianthus plumarius the osmotic pressure of the

cell sap (sugar level?) of the calyx under the influence of boric acid declines rapidly, while the osmotic pressure of the corolla decreases in the beginning at the same rate, with and without boric acid, until wilting when the decrease is slightly faster without boric acid.

Both these experiments suggest that under the influence of boric acid sugars are withdrawn from the calyx and not from the corolla. On the one hand no sugars are transported to the fruits, on the other hand these are not withdrawn from the corolla but from the calyx.

Boric acid also had a favourable effect on the keeping quality of isolated petals (photo 8) of Dianthus plumarius. This shows that the action of boric acid does not rest on the distribution of sugar reserves within the flower. Above all with Dianthus caryophyllus the removal of the ovary at different stages of development was never favourable and especially with young flowers was harmful to the keeping quality of the corolla. It is possible here that the wounding itself is the damaging influence.

Especially with whole florets, but even more so with isolated petals (Graph 22) the oxygen uptake before the wilting is reduced ten to twenty percent by the presence of boric acid 0.075 percent. Above all the respiration increase during the wilting does not appear.

Also with whole florets after the addition of boric acid a sudden increase in oxygen uptake is never observed.

Discussion. Following from the last discussed experiments, the favourable action of boric acid could be due to a reduced usage of the respiration substrate but this does not seem likely. The effect on the respiration is slight and above all no difference in the osmotic pressure of the cell sap of the flower was observed.

If one starts with the theory that the revival of the respiration with Dianthus plumarius is caused by oxidation of the plasma it appears that after the addition of boric acid there is no possibility or requirement to use the cell plasma as a respiration substrate. If one regards the wilting and the accompanying increase in the respiration exclusively as a result of structure loss of the plasma, thus not directly dependent on the respiration, then it is possible that boric acid alone or with the help of sugars prevents structural changes in the plasma. In this connection one can think of the concept of Torrrell (111), that "the complexes between boric acid and carbohydrates control the deposition of orientated cellulose micells." In vitro the aggregation of an amylose solution is prevented by boric acid (111). Baumeister (7) found a connection between boron on the one hand and protein synthesis colloidal condition of the plasma on the other.

If one thinks of the connection between keeping quality and winter hardiness (p. 19) then the favourable influence, found by Beltram (9), of boron on the frost resistance is of importance.

In connection with the observed different distribution of carbohydrates in the flower under the influence of boric acid the possibility exists, that with loose petals the inactivation of carbohydrates is prevented by the formation of molecule complexes, or that carbohydrates are liberated from the cell walls. The retarding influence of boric acid on abscission phenomena (see 2.3.8) makes it less likely.

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The concept of Gauch and Dugger (24) that boric acid eases the transport of sugar is established in a certain sense with experiments concerning the dry weight distribution in carnations. One must observe, however, that it is apparently not valid for all tissues and thus does not give an explanation of the favourable effect of boric acid.

4.6. Influence of various sugars and other carbon sources,

Most of the commercial preparations used for the preservation of keeping quality contain glucose; this gives rise to the question whether glucose is used for other reasons besides financial ones. Therefore, the possibility that other sugars, alcohols, and organic acids could also be used as carbon source with cut flowers as is the case with other tissue cultures, was studied.

Material. Single flowers from one composite flower in the case of Chrysanthemum morifolium and Dahlia variabilis were used with Dianthus caryophyllus, D. plumarius, Dahlia variabilis and Rosa "Kirsten Poulsen" whole flowers or inflorescences were used. As basic nutrient solution ACAC (see p. 4) was used.

Results. In Table 2 on page 7 it appears that glucose and saccharose in many cases gave similar results. In low concentrations saccharose was sometimes more favourable but with Rosa and Convallaria glucose was slightly better. From Table 16 it is seen that with Dahlia variabilis fructose had the same effect as glucose; lactose and maltose only had a favourable effect with this plant when in low concentration, but it was never as good as an equal quantity of saccharose or glucose; higher lactose and maltose concentrations retard the development and are harmful to the keeping quality.

Also with Rosa, maltose in low concentrations had a slight favourable effect (Table 17). With Dianthus plumarius, however, the effect of maltose was equal to that of saccharose, also in higher concentrations (Table 17). With Dianthus caryophyllus the influence of maltose on the development was comparable to that of saccharose, but the keeping quality with maltose was less (Table 17). Mannose appears to be harmful both with Dahlia (Table 16) and with Dianthus (and also Antirrhinum) in concentrations higher than one percent (0.055 M).

Notably a large secretion, especially from the edges and wound sites of tissues, of glucose, lactose, mannose, maltose and mannitol took place when these substances were used. With fructose and saccharose no sugar secretion was observed.

Since ethanol, glycol, glycerol, erythritol, mannitol, dextrine, sodium succinate, sodium citrate and sodium oxalate with Antirrhinum majus, Dianthus plumarius, Lathyrus odoratus and Matthiola incana could not replace the influence of sugar in any single concentration, these results will not be presented in detail.

Discussion. According to Said (94) and Harley and Smith (32) working with Peltigera oat leaves, saccharose is almost exclusively, after hydrolysis, taken up by the cell as reducing sugars. Similar effects of equal quantities of saccharose and glucose or fructose are therefore to be expected.

Although maltose and lactose are absorbed by the cell (see 4.3.), it is apparently taken up very slowly or only after a time, within which the necessary adaptive enzyme is formed, into the metabolism. If too much is administered, it cannot be consumed and a harmful accumulation occurs in the cell. For mannose

there is apparently no adaption possible. A difference in the permeability speed as a possible explanation for the damaging effect does not seem likely as the same amount of water and thus sugar is absorbed by the stem. Above all with Dianthus a favourable result with maltose has been found, also in high concentrations.

4.7. Influence of sugar and urea on Dahlia.

For growth, protein synthesis and thus nitrogen is necessary and according to some authors (30, 120) nitrogen is drawn from the older plant parts when plants grow. Therefore with plants which have flowers in different stages of growth such as Dahlia variabilis and Matthiola incana a study was made to see whether by supplying nitrogen the keeping quality, especially of the older flowers, could be lengthened. Because, by changing the amount of applied nitrate, the effect of the cations on the vascular bundle blocking is modified, and moreover, disregarding ammonium nitrate, only a small amount of nitrate as an inorganic salt can be supplied, use was made of urea.

Results. Graph 23 (p. 51) shows, with Dahlia, urea in concentrations of 0.2 percent and higher is harmful if no or only a slight amount of sugar is added, but that 0.8 percent urea after an initial inhibitory influence is favourable if a large amount of sugar is added.

Without urea the optimal sugar concentration during the development moves from 6 percent to 3 percent; if urea is added the optimal sugar concentration is increased.

Discussion. According to Paech (84) the protein level in the plant is determined by the ratio of the amount of carbohydrates in active form and the amount of soluble nitrogen compounds. If carbohydrates are used by respiration then the equilibrium change results in a protein hydrolysis which can be prevented by administering sugar. When carbohydrates are in excess protein synthesis can take place if sufficient soluble nitrogen compounds are present.

During the first phase of the growth of the Dahlia flower there is a great carbohydrate requirement and added nitrogen without an accompanying sugar supply is not utilized but apparently accumulates in the form of harmful ammonia (74). If much carbohydrate is supplied there develops a demand for nitrogen necessary for protein synthesis. Urea has, therefore, a favourable influence provided a surplus (6 percent or more) of sugar is available.

4.8. Conclusions concerning the action of sugar.

If the answers to the questions that have arisen in this chapter are brought together we determine:

1) The flower uses a large amount of sugar especially during development and, if no additional sugar is forthcoming from the leaf, stem or the water sugar deficiency can be one cause of early wilting.

2) The loss of osmotically active substances in the cell by sugar respiration is not the cause of early wilting. By addition of mannitol and in some cases

by maltose the osmotic pressure of the cell sap is maintained but not the keeping quality.

3) The respiration of the corolla of cut flowers decreases but by the addition of sugar this decrease is reduced and the keeping quality is enhanced. In some cases where the flowers have not been cut the respiration decreases after the flowers have opened and then the addition of sugar has no longer an effect. With Dianthus plumarius, during the beginning of the wilting, a sudden increase in respiration is observed.

4) Up until now only two cases have been found where, besides sugar and vascular bundle blocking, the metabolism of the flower has definitely been favourably influenced viz. by gibberellic acid with Matthiola incana and by boric acid with Dianthus species. This was not possible with various enzyme inhibitors.

The most likely explanation of this data is that sugar has an indirect action on the keeping quality by supplying the necessary respiration substrate. A disturbance of the plasma is also prevented by sugar. From the fact that maltose is absorbed into the cell, but in some cases has no influence on the keeping quality, it does not seem possible that sugars have a direct protecting influence on the structure of the plasma. Gibberellic acid and boric acid may well act in this way or possibly they may prevent the liberation or the action of substances that could induce such structural changes.

5. General Conclusions

It is possible in many cases to lengthen the keeping quality of cut flowers. The degree and the means by which the keeping quality can be changed is not the same for all flower species.

The first requirement is that water uptake should take place unhindered. For this it is necessary that the development of bacteria and sometimes also algae and fungi in the water be prevented. This, however, is not sufficient. The plant itself is in a state, as a reaction to the wounding and the changed constitution of the vascular sap (especially the oxygen level), to actively block its own vascular bundles. Chemical and physical methods that hinder the entrance of oxygen into the vascular bundles or slow the living processes in the stem without exerting any further harmful effects can have a favourable effect on the keeping quality of the flower. This is not always the case, for the degree to which vascular bundle blocking occurs is not always the same for every species and sometimes the flower wilts due to other causes before the vascular bundles have become blocked.

Possibly the life processes in the flower itself could be influenced. By the addition of sugar the appearance of age inducing factors is apparently not prevented, but rather their harmful action is expressed in a form of a sugar deficiency. Substances which are more likely to inhibit the metabolism directly were in certain cases gibberellic acid and boric acid. Although sugar is necessary for a good development of the flower it is possible to reduce the sugar requirement by means of these substances. It is in this direction that the most success is expected with further research.

With our present knowledge it is not possible to develop one mixture of chemicals that will have an optimal increase of the keeping quality in all cases and this is due especially to the differences in the optimal sugar concentrations. On the one hand the transpiration and therefore the water and sugar absorption is not the same

for all plants, on the other hand the sugar requirement varies depending on the species and the development stadium. As a practical solution to this difficulty it is suggested that a specific basic media should be supplied and then an amount of sugar added to each different plant according to its requirements.

The advantages of cutting flowers in an unopened condition can be realized in almost all cases by using chemicals. These mixtures must prevent the blocking caused by bacteria as well as active vascular blocking (e.g., ACAC, finally with an acid or enzyme poison), and must supply the sugar requirements. In certain cases the addition of urea (e.g., Dahlia) or boric acid (e.g., with Syringa [1]) can influence the result favourably. It is also often possible by a short pre-treatment with sugar to improve the keeping quality in later stages. Also occasionally silver nitrate and boric acid had a favourable after effect, but this possibility has not yet been completely investigated.