

VASCULAR OCCLUSION IN CUT FLOWERS. I. GENERAL PRINCIPLES AND RECENT ADVANCES

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Abstract

The vase life of many flowers is limited by an occlusion in the stem, leading to premature symptoms of water stress. The occlusion can be due to numerous factors inherent in the stem, such as the outflow - upon cutting - of latex, gum, mucilage, and resin, the deposition of mucilage into xylem vessels by adjacent living cells, or the formation of tyloses. The latter are outgrowths of living cells into the lumen of xylem conduits. These forms of occlusion are highly dependent on the species. Two other types of vascular occlusion occur in all cut flowers: blockage due to bacterial growth and the one due to the formation of gas bubbles (emboli). The latter is due to cavitation in the stems. Although bacterial occlusion occurs in all flowers, various species and cultivars respond differently. Although cavitation may occur in all flowers, there is a difference between species and cultivars in the time until the number of cavitations is high enough to hinder water flow. The literature on vascular occlusion has recently been summarised (van Doorn, 1997). In order to avoid repetition, a few recent developments are discussed in some detail: a) the effects of water temperature, b) cavitation as a result of bacterial blockage, and c) the importance of cavitation repair.

1. Introduction

The vase life of the majority of cut flowers depends on two main factors: hormonal control and water relations. In flowers in which vase life is limited by hormonal changes, the level of ethylene production suddenly increases dramatically, which leads to changes in petal color, in petal wilting, or in abscission of the petals. Flowers which have a short vase life due to the autocatalytic surge in ethylene production tend to be found in certain families.

In many other flowers, the length of vase life is limited by a drastic decrease in water uptake, which is accompanied by a decrease in transpiration rate. The latter is due to closure of the stomata, which react to the lowered water potential in the flowering stem. However, the decrease in transpiration does not equal the decrease in water uptake, and the water deficit thus still increases with time.

The decrease in water uptake can, depending on the species, be due to a range of factors. These factors can be categorized as those inherent in the stem (this has also been called the physiological blockage), the effects of microbial growth, and the formation of air bubbles (emboli). The mechanism of the formation of an occlusion in each of these categories will be briefly discussed.

More details can be found in two recent papers (van Doorn, 1997, and, for roses in particular, van Doorn, 1995). Both papers were finalised in 1995. In order to avoid too much repetition, a few results that were obtained or published after finishing of these manuscripts will now be discussed. These results pertain to a) the effects of water temperature, b) cavitation as a result of bacterial blockage, and c) the importance of cavitation repair.

2. Physiological blockage

The stems of many species contain specialized reservoirs containing substances that, depending on their composition, are called latex, gum, mucilage, or resin. Upon cutting of the stem, these substances cover the cut surface and may enter the xylem conduits. (The word conduit is used to indicate both xylem vessels and tracheids). Although the cells that have formed the ducts that contain these substances may be dead by the time the stem is full-grown, the ducts and their contents do owe their presence to living cells. Another mechanism whereby blockage depends on the activity of living cells is the deposition of mucilage into xylem vessels by cells adjacent to the xylem conduits. A third type of physiological occlusion is that due to tyloses, which are balloon-like outgrowths that protrude into the lumen of xylem conduits. These balloons may not occur in adequate numbers to explain the blockage, but their formation seems to be accompanied by the production of large molecular weight substances, that may account for the lack of water flow in stems with tyloses.

These physiological forms of occlusion are highly dependent on the species. In contrast, two other types of vascular occlusion occur in all cut flowers: the one due to bacteria or to air bubbles in the stems.

3. Blockage due to bacterial growth

Water always contains bacteria, and the cut surface of stems contains food for bacteria. Sugary substances will flow, for some time, out of the opened phloem cells. Bacteria are observed to grow first on the phloem of the cut surface of rose stems. All other cells at cut surface are also opened, thereby similarly providing a rich source of food. Bacteria grow on the cut surface, but are also growing in the vase solution, and these will be taken up with the water that flows in to the stem. Our experiments suggest that the occlusion is due not alone to living bacteria, but also to the extracellular polysaccharides produced by these living bacteria, and to dead bacteria and the macromolecular products that are formed upon the degradation of dead bacteria.

Although bacterial occlusion occurs in all flowers, various species and cultivars respond differently. The reasons for these differences in response are not wholly clear, but may relate, for example, to the rate of transpiration, hence to the leaf surface and stomatal opening.

4. Occlusion by emboli

Air will flow up into the xylem conduits as soon as these are opened by cutting. When placed in water after cutting, the water will compress the air in the opened conduits, which then forms a bubble. Usually these air bubbles are not hindering water uptake. The unopened conduits can also become filled by gas bubbles, in a process called cavitation. Two types of cavitation can be distinguished: a) those in which air is pulled into a conduit, from an adjacent one that already contains an embolus, and b) a spontaneous cavitation in which no such transfer takes place.

Although cavitation may occur in all flowers, there is a difference between species and cultivars in the time until the number of cavitations is high enough to hinder water flow.

5. Some recent developments

5.1. Effects of water temperature

Both low (Durkin, 1979) and high (de Vries, 1873) water temperatures are known to promote water uptake into flowers that have been stored dry. In a detailed study, including several cut flowers and cultivars, Slootweg (1995) compared the effects of placing flowers in either water of 0°C, 20°C, or 40°C. The results were dependent on the time the

flowers had been held dry prior to placement in water. In Sonia roses that were held dry for 1 hour, the water uptake rate was higher when the water temperature was lower. This would have been expected if the effect of water temperature would mainly be due to the dissolution of air into the bypassing water. Water at lower temperature can absorb more air. That this interpretation seems correct is borne out by an experiment which showed that the difference between the water temperatures completely disappeared when the water was degassed. Degassed water obviously can absorb more air than water that is not degassed, and the difference in temperature becomes irrelevant.

When the stems of Sonia roses had been held dry for 4 days, there was a similar positive effect of low (0°C) and high (40°C) water temperature on the rate of water uptake, compared with water at room temperature. The difference between this result and those obtained after a shorter period of dehydration, also in Sonia roses, is not obvious. After the longer period of dehydration, the effect of water at 40°C was relatively more positive than after a short duration of dehydration. Water is less viscous at higher temperatures. The factor of air absorption, important after a short time of dehydration, may become less important relative to the effect of water viscosity, when the stems are held dry for a longer period. It is not immediately clear, if this is true, why this would be so.

Similar results (water of room temperature was not as good as either cold water or warm water) were obtained with Mercedes roses, *Eustoma sp.*, chrysanthemum (cultivars Reagan and Cassa), Alstroemeria (cultivar Jubilee), Bouvardia, Astilbe, and field-grown Helianthus. All these tests occurred following 4 days of dehydration.

Interestingly, in a number of flowers, water temperature did not matter at all, even after 4 days of dehydration. These flowers included Osiana roses, Delphiniums, Lilies (cultivar Sun Ray), tulips (Monte Carlo), and greenhouse grown sunflowers.

5.2. Cavitation as a result of bacterial blockage

Our experiments with Cara Mia roses showed that cavitations in stems, detected with an ultrasonic microphone, were numerous when the stems were placed in water with a high bacterial count. Recutting more than 25 cm under water, which removes all the conduits that have been opened by cutting, had no effect on the number of cavitations. This indicates that the cavitations occurred irrespective of the presence of air in the stems. Two types of cavitations were distinguished above (in paragraph 4): those in which air is pulled into a conduit, from an adjacent one that already contains an embolus, and those that occur spontaneously, without air being pulled into the conduit. The experiments were so carried out that spontaneous cavitations prior to harvest were avoided. Assuming that no such spontaneous cavitations were present, the results indicate that in Cara Mia roses the second type of cavitation occurs, following a blockage due to bacteria. The cavitations following the bacterial blockage do, therefore, apparently not depend on the presence of aspired air in the conduits opened by cutting, as our previous experiments with *Thryptomene* flowers (van Doorn and Jones, 1994) had suggested.

The presence of a high number of cavitated conduits may exacerbate the blockage, hence further reduce water uptake. A high rate of cavitation events also occurred when the stems were placed in a dilute solution of India ink. The ink consists of colloidal particles that are bigger than the pores in the pit membranes between the xylem conduits. They will, just as bacteria, become trapped at the first membrane they come across during their passage - with the transpiration stream - up the stem. The result indicate that any blockage in the basal end of the stem, be it by bacteria or particulate matter, is able to induce cavitations.

5.3. Cavitation repair

The number of cavitated conduits in a stem may exceed a level whereby water uptake becomes impaired. However, when the conduits that are filled with gas would somehow

become rapidly refilled with water, not the number of cavitations but the rate of their repair would become limiting for the rate of water uptake. A surfactant solution is known to rapidly restore the rate of water uptake in stems that have been dehydrated for a prolonged period, hence contain a large number of cavitated conduits. The effect of this solution might be to aid in refilling of the cavitated conduits with aqueous solution. This hypothesis was tested by measuring the conductivity to air, at low pressure, in 2.5 cm stem segments. Air will flow freely in conduits that contain gas. At the pressure used, the air was unable to displace water, even in conduits that are open at both the upper and the lower end of the segment.

Sonia and Madelon roses were held dry at 20°C for various periods of time, and then placed in water or in a diluted aqueous surfactant solution. The results showed that the lowermost 2.5 cm segment became rapidly refilled with water, irrespective of the duration of dry storage. This is the segment which contains the highest number of conduits that are opened by cutting the flowers. These open conduits can therefore be rapidly refilled. However, all segments distal from the basal 2.5 cm took much longer to become refilled. These segments became evenly refilled: all were half refilled at a certain point in time, all were later on filled for three quarters, and eventually completely. The refilling thus did not slowly move up the stem, completely refilling the base, then the subsequent more distal segments. When the roses had been stored dry for a longer duration, the refilling process is to longer to complete. The flowers also took longer to regain turgidity. Following more than 36 h of dry storage the cavitations in stems of Sonia roses did not completely get refilled. These stems did not regain turgidity. The rate of water uptake was correlated with the degree of repair, and became only high when most cavitations had disappeared.

Compared to Sonia roses, the stems of Madelon roses show a high number of cavitations after a shorter period of dry storage. Madelon roses showed a similar repair of cavitations, but repair became very slow and water uptake remained low after 19 h of dry storage. Some Madelon roses did not recover turgidity after such a period of dehydration. The repair process, therefore, was slower when the stems contained a higher number of cavitations. Interestingly, placement of the stems in an aqueous surfactant solution resulted in very rapid repair of all cavitations, concomitant with a very rapid increase in water uptake rates.

It is concluded from these experiments that the repair of cavitations is slowed down when the number of cavitations is higher, and that cavitation repair is the factor that is limiting the rate of water uptake following a period of dry storage.

6. Conclusions

Vascular occlusion is one of the main factors that limit the vase life of flowers. Many flowers have one or several mechanisms to occlude any cut that is made in its tissues, apparently as a mechanism to prevent attack by micro-organisms. In cut flowers these physiological mechanisms can lead to severe obstruction of water uptake. Additionally, the water uptake in all flowers becomes impaired by bacterial growth and by the presence of air bubbles in the stems. The latter is mainly due to cavitation, which occurs as a response to a water deficit, either when the stems are stored dry or when the water uptake is blocked by bacteria.

Water at low temperature can aid in restoring the rates of water uptake following a period of dry storage, apparently by absorbing some of the air in the stems. Following an extended period of dry storage water at 40°C also helps in restoring the rate of water uptake.

The rate by which the cavitations are repaired seems to limiting the rate of water uptake, following a period of dry storage. Cavitation repair is faster when the period of dry storage is shorter, and very fast when a surfactant is added to the vase water.

References

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