Effects of Daffodil Flowers on the Water Relations and Vase Life of Roses and Tulips

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ABSTRACT. Placing a daffodil (*Narcissus pseudonarcissus* L. ‘Carlton’) flower in a vase with a rose (*Rosa hybrida* L. Sonia) flower reduced water uptake by the rose and resulted in precocious wilting of its leaves and flower and in pedicel bending. These symptoms were also observed when mucilage from daffodil stems was placed in the vase water. The effects of the mucilage and the daffodil stem were overcome by adding 8-hydroxyquinoline (HQC) to the vase solution. HQC inhibits ethylene production and is an antimicrobial compound. Aminoethoxyvinylglycine (AVG) or silver thiosulfate (STS), inhibitors of ethylene synthesis and action, respectively, did not alleviate the mucilage effects, but sodium hypochlorite, an antimicrobial compound, did. Bacterial counts in the basal 5-cm segment of rose stems increased after placing mucilage or a daffodil stem in the vase water, and counts were reduced by adding HQC or sodium hypochlorite. One daffodil stem also reduced the vase life of tulips (*Tulipa gesneriana* L. ‘Frappant’ and ‘Apeldoorn’), which showed precocious leaf yellowing. This was not alleviated by HQC and was also found when mucilage was placed on the leaf surface. Placing mucilage on the leaf produced no effect in roses. Separating the mucilage indicated that the effect in roses is mainly due to the sugar and polysaccharide fraction and the effect in tulips is due to a fraction containing several alkaloids. The results indicate that the decreased vase life of rose flowers, after one daffodil is placed in their vase water, is due to daffodil mucilage, which, in the rose cultivar tested, blocks water uptake, mainly as a result of increased bacterial growth. In the tulip cultivars tested, the negative effect on vase life is primarily due to mucilage toxicity.

Daffodil flowers are known to adversely affect the vase life of other cut flowers (Barendse, 1974). Placing 10 ‘Carlton’ daffodil flowers in a vase with 10 cut ‘Baccara’ roses for only 4 h at 2 °C resulted in desiccation and leaf abscission in the roses. Furthermore, the rose petals changed from red to bluish red following this short incubation with daffodils. Parade tulips similarly exposed to daffodil flowers showed stem bending, leaf shrivelling, and precocious tepal blueing. In Iris (‘Ideal’), freesia (‘Golden Melody’) and anemones, flower opening was inhibited after the short exposure to ‘Carlton’ daffodil flowers. These negative effects on flower quality were also noted, and the symptoms were similar, when mucilage from the daffodil stem was placed in the vase solution, even though the mucilage was 100 times diluted in the final vase solution. There is some evidence that the mucilage effect is cultivar dependent, as mucilage of ‘Geranium’ daffodils was considerably less harmful than that of ‘Carlton’ daffodils (Barendse, 1974).

In our preliminary experiments, one ‘Carlton’ daffodil flower was continuously held in a vase together with one rose or tulip flower. This resulted in early symptoms of water stress in cut roses and precocious leaf yellowing in tulips. Interestingly, the effect of the daffodil on roses was completely overcome by including 8-hydroxyquinoline (HQC) in the vase water. HQC is known to inhibit ethylene synthesis (Parups and Peterson, 1973; van Doorn et al., 1989) and to reduce microbial growth in vase water (Marousky, 1968; 1969) and in rose stems (van Doorn and Perik, 1990). Although little evidence has been found for a role of ethylene in blocking water uptake in cut rose flowers (van Doorn et al., 1989), it cannot be excluded that ethylene plays a role in a blockage induced by daffodil mucilage. In rose flowers, we previously showed that bacteria result in a blockage of water uptake, mainly

by blocking the passage of water in the small pores of the pit membranes between the xylem vessels. An occlusion was also obtained when bacterial exopolysaccharides or lysed bacteria were placed in the vase solution. In these experiments, it was difficult to distinguish between exopolysaccharides and live bacteria, as bacterial growth was stimulated by placing exopolysaccharides in the vase solution (de Witte and van Doorn, 1992).

Based on our preliminary observations, we tested two hypotheses: the mucilage of daffodil stems produces a short vase life a) in Sonia roses mainly by inhibiting water uptake and b) in tulips by having a toxic effect. The experiments also attempted to distinguish, in rose flowers, between an ethylene-mediated effect and a bacterial-growth-inducing effect, and aimed at a preliminary separation of the various compounds in daffodil mucilage.

Materials and Methods

PLANTS. Cut flowering stems of ‘Carlton’ and ‘Cheerfulness’ daffodil (*Narcissus pseudonarcissus*), ‘Apeldoorn’ and ‘Frappant’ tulips (*Tulipa gesneriana*) and ‘Sweet Promise’ (trade name Sonia) rose (*Rosa hybrida*) were obtained from commercial growers. The flowers were commercially mature, i.e., in narcissus the tepals were about to emerge from the sheath leaves, in tulips the tepal tips had not yet separated, and in roses the petal tips had just separated. Immediately after harvest the flowers were placed in water and stored in a 4 °C room until transport to the laboratory, which occurred the same morning. Transport occurred with the stem ends in water and took <2 h. In the laboratory the rose and tulip stems were recut in air, removing ≈5 cm, to a final length of 50 and 40 cm, respectively. Flowers were placed in glass vials in a climate-controlled room at 20 °C, 60% relative humidity, and a photosynthetically active photon flux of 15 μmol·m⁻²·s⁻¹ (Philips TDL 36W/84 cool-white fluorescent tubes) from 7 AM to 7 PM. Rose and tulip flowers stood individually in vials with 200 mL of deionized water, with or without one, two, or three daffodil stems. Controls included two rose and two tulip stems per vase and vases with one to three daffodil stems. Stems were not recut during vase life.

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Mucilage from daffodil stems was obtained by recutting the flower stems and placing them in 1-L beaker glasses. The amount of mucilage that dripped out of the stems varied per experiment, from 5 to 200 mL/1000 daffodil stems. As this amount was sometimes inadequate, additional mucilage was isolated by pushing on the stems, from the flower head to the basal stem end. No clear difference was found between these two types of mucilage extraction when the mucilage was placed in vase water of roses or tulips. Mucilage was included in the vase water at a final dilution of 1 mL/100 mL. Undiluted mucilage was also placed on 1 cm² of the leaves of cut flowers, testing one leaf per flower and five flowers per experiment.

CHEMICALS. Treatments with chemicals started at the onset of vase life and were continuous. Ten replicate flowers, individually placed in vials, were used. Antimicrobial compounds were HQC (La Quinoléine, Oissel, France), at 100, 200, and 300 mg·L⁻¹, sodium hypochlorite (Merck, Darmstadt, Germany) at 20, 40 and 60 mg·L⁻¹, and aluminium sulfate (Merck) at 200, 400, and 800 mg·L⁻¹. Ethylene antagonists were aminoethoxyvinylglycine (AVG; Sigma, St. Louis) at 10, 20, and 40 mg·L⁻¹ and silver thiosulfate (STS) at 650, 1300, and 2600 mg·L⁻¹. STS was prepared by adding an aqueous solution of sodium nitrate (Merck) to an 8-fold more-concentrated solution of sodium thiosulfate (Merck).

WATER UPTAKE RATES AND HYDRAULIC CONDUCTIVITY. The rate of water uptake into cut flowers was assessed by daily weighing the pots and the flowers, using 10 replications. Evaporation was determined by weighing three vases that contained no flower.

Hydraulic conductivity was determined at intervals during vase life, in the basal 5 cm of the stems, using a method described previously (van Doorn et al., 1989). Briefly, stem segments 5 cm long are connected to 130 cm head pressure (13 kPa) of water, and the amount of water passing through these segments is weighed at 30-min intervals.

SEPARATION OF MUCILAGE. Freshly collected mucilage (50 mL) was centrifuged at 10,000 g_n and the supernatant was vigorously shaken in a mixture of 25 mL of millipore-filtered water and 25 mL n-butanol (100%). Two milliliters of the purified fractions was brought on silicagel-coated thin-layer chromatography (TLC) plates using 3 methanol : 1 chloroform as eluent. Following drying, TLC plates were sprayed with Dragendorff solution, which identifies alkaloids. Dragendorff solution is prepared by boiling 2.6 mg bismuth carbonate and 7.0 g sodium iodide in 25 mL acetic acid for 5 min. After 12 h, the deposited sodium acetate crystals are filtered off, and 20 mL of the filtrate is mixed with 80 mL ethylacetate and 0.5 mL water.

The aqueous fraction was hydrolyzed by placement in 1 M sulphuric acid at 100 °C for 2 h. The n-butanol fraction was similarly hydrolyzed after evaporation of butanol and replacement with equal amount of millipore-filtered water. The amount of reducing sugars in each fraction was determined before and after hydrolysis using the dinitrosalicylic acid assay (Chaplin, 1986). Hydrolysis releases all reducing sugars contained in polysaccharides. The sucrose content in the aqueous and butanol fractions was determined spectrophotometrically using a test kit (Boehringer, Mannheim, Germany), which is based on enzymatic (invertase) hydrolysis of sucrose. Glucose is converted to glucose-6-phosphate with hexokinase, then to gluconate-6-phosphate and NADPH. The latter is determined at 340 nm.

BACTERIAL COUNTS. Bacterial numbers were determined in the basal 5 cm of rose stems after removing the bark of the stem, using a previously described method (van Doorn et al., 1989) and three replications. Briefly, stems are surface sterilized and cut into 0.5 cm using standard sterile equipment. The parts are placed in sterile

aqueous 0.85% NaCl solution, and bacteria were removed by shaking. Solution samples were then placed on plate count agar and incubated at 30 °C for 48 h before the number of colonies were enumerated.

STATISTICS. Results were compared by analysis of variance using the GENSTAT V program (Rothamsted, U.K.) and F test at $P < 0.05$. All treatments included 10 replicate flowers. The experiments were repeated at least once.

Results

VASE LIFE. The vase life of 'Apeldoorn' tulips and Sonia roses was considerably reduced by placing one stem of 'Carlton' daffodils in the vase (Table 1). Vase life of control flowers was limited, in roses, by leaf and flower wilting, lack of flower opening, and bending of the pedicel (the stem segment between the flower and the uppermost node), and in tulips by flower wilting and tepal abscission. Placing a daffodil flower resulted, in roses, in advancement of the symptoms found in controls, whereas, in tulips, it mainly reduced vase life by precocious leaf yellowing. Additionally, the daffodil inhibited tulip stem elongation. Little additional effect on the length of vase life was found by increasing the number of daffodil flowers (Table 1). Mucilage from the stem of 'Carlton' daffodils had a similar effect on vase life as one daffodil flower (Table 1). Results with 'Frappant' tulips were essentially the same as those with 'Apeldoorn' tulips (data not shown). The vase life of daffodil flowers was not reduced by placing one or two additional daffodil flowers in the same vase (results not shown).

'Cheerfulness' daffodils had much less effect on vase life of tulips and roses than 'Carlton' daffodils. The volume of mucilage obtained from 'Cheerfulness' stems was about one-fourth of that obtained from 'Carlton' stems (results not shown).

Mucilage of 'Carlton' daffodils, placed on the leaf surface, produced no visible symptoms in Sonia roses but caused extensive leaf yellowing in tulips. The tulip leaves showed small holes in the leaf surface, which subsequently turned brown. Between these spots the leaf area became yellow, an effect that eventually extended several centimeters distal from the area where the mucilage had been applied. Experiments with 'Cheerfulness' mucilage, placing the same volume on tulip leaves as with 'Carlton' mucilage, resulted in slight leaf yellowing only.

Preliminary experiments were carried out with one 'Carlton'

Table 1. Effect of 'Carlton' daffodil (*Narcissus pseudonarcissus*) flowers and mucilage from stems (final concentration 1% v/v) on the vase life and the rate of water uptake² (during the first 3 d of vase life) of roses (*Rosa hybrida* Sonia) and tulips (*Tulipa gesneriana* 'Apeldoorn').

Treatment	Vase life (d)	Water uptake (mL/stem/h)
One rose per vase	10.9 ± 2.3 a ²	8.9 ± 1.8 a
Two roses per vase	10.2 ± 3.5 a	9.3 ± 2.0 a
One rose, one daffodil	3.3 ± 2.8 b	3.7 ± 1.4 b
One rose, three daffodils	3.0 ± 1.7 b	3.4 ± 1.6 b
One rose, daffodil mucilage	3.2 ± 2.3 b	3.3 ± 1.5 b
One tulip per vase	6.5 ± 1.9 a	5.1 ± 1.1 a
Two tulips per vase	7.3 ± 1.4 a	4.8 ± 1.0 a
One tulip, one daffodil	3.9 ± 2.0 b	4.2 ± 0.9 ab
One tulip, three daffodils	4.0 ± 1.7 b	4.0 ± 0.6 b
One tulip, daffodil mucilage	4.0 ± 1.9 b	4.0 ± 0.7 b

²Results are means of 10 replications ± SD.

³Statistically significant differences ($P > 0.05$) per flower species are shown with a different letter.

Fig. 1. Interaction between the effect of mucilage (muc) from 'Carlton' daffodil stems and chemicals included in the vase water on the vase life of cut Sonia roses. Chemicals are antimicrobial compounds [8-hydroxyquinoline citrate (HQC), sodium hypochlorite (chlor), and aluminium sulfate (alu)] and anti-ethylene compounds [aminoethoxyvinylglycine (AVG) and silver thiosulfate (STS)]. Results are means of ten replications $\pm$ sd.

daffodil stem placed in the vase of 'Enchantment' lilies (*Lilium multiflorum*) or 'Cassa' chrysanthemum (*Dendranthema grandiflora*) flowers, which tend to show, in control flowers, early leaf yellowing and early leaf wilting, respectively. In lily, the presence of one daffodil flower resulted in precocious leaf yellowing and browning of the leaf tips, followed by early tepal wilting. In chrysanthemum, it produced precocious leaf wilting and severe leaf necrosis. Placing undiluted 'Carlton' daffodil mucilage on the leaves of flowering stems that stood in water produced severe leaf necrosis in chrysanthemum but had no effect in lily.

WATER UPTAKE AND HYDRAULIC CONDUCTIVITY. The rate of water uptake of cut rose flowers was much reduced when a 'Carlton' daffodil or its stem mucilage was placed in the same vase, much more so than when another rose was placed in the vase. A 'Carlton' daffodil or its mucilage also tended to reduce the rate of water uptake in tulips, but the effect was smaller than in roses (Table 1). Hydraulic conductivity in the basal 5 cm of rose stems was reduced by placing a 'Carlton' daffodil flower in the vase from day 2 of treatment (data not shown).

EFFECTS OF ANTIMICROBIAL AND ANTI-ETHYLENE COMPOUNDS. The negative effect of mucilage from 'Carlton' daffodils on the vase life of cut roses was alleviated by including HQC at 300 mg·L⁻¹ or sodium hypochlorite at 40 or 60 mg·L⁻¹ in the vase water. Aluminium sulfate exacerbated the effect, and neither AVG nor STS modified it (Fig. 1). The rate of water uptake during the first 4 d of vase life and hydraulic conductance in the basal 5 cm of the stems (determined on day 3 of vase life) was restored by HQC and chlorine, was reduced by aluminium sulfate, and remained unaffected by AVG or STS (data not shown).

BACTERIAL COUNTS. Bacterial numbers in the basal 5 cm of Sonia rose stems increased when mucilage of 'Carlton' daffodils was added to the vase water (Fig. 2). HQC counteracted the effect of the daffodil mucilage on bacterial counts (Fig. 2), and chlorine had a similar effect. Aluminium sulfate, in contrast, had little effect on the number of bacteria (data not shown).

SEPARATION OF MUCILAGE FRACTIONS. 'Carlton' narcissus mucilage was separated into an aqueous and n-butanol fraction. The latter contained six alkaloids and the aqueous fraction none (Table

2). The aqueous fraction contained some sucrose, considerable amounts of reducing sugars, and some polysaccharides. These compounds were found in low amounts (sucrose and free reducing sugars) or not at all (polysaccharides) in the n-butanol fraction (Table 2). If these low amounts in the n-butanol fraction are neglected, 1 mL of mucilage contained about 4.5, 55, and 6.5 μ g of sucrose, reducing sugars, and polysaccharides, respectively.

Placing roses in the aqueous fraction produced the same visible symptoms of water stress as placing roses in narcissus mucilage. In contrast, the effects of mucilage on tulips were mimicked by placing the n-butanol fraction in tulip vase water.

Discussion

The present results corroborate the findings of Barendse (1974), showing that 'Carlton' daffodils have a negative effect on the vase life of roses and tulips. In 'Baccara' roses, Barendse (1974) found some effects not observed in Sonia roses, such as precocious leaf abscission and petal blueing. Leaf abscission may, hypothetically, relate to a toxic effect of the daffodil and to ethylene production due to water stress. Petal blueing is usually observed during the vase life of red roses such as 'Baccara', and is less evident in pink cultivars such as Sonia. He also observed tepal blueing in 'Parade' tulips, which have red tepals, an effect not observed in the present experiments with 'Apeldoorn' (yellow tepals) and 'Frappant' (pink tepals). These results indicate that the effect of daffodil stems on other flowers depend on the cultivar of the latter.

The effects obtained with daffodil flowers could be mimicked with mucilage from daffodil flowers in the experiments of Barendse (1974) and in the present tests. Mucilage often drips out of daffodil stems, immediately after cutting or recutting of the stems, and probably also leaks out into the vase solution.

Mucilage apparently can have two effects: it increases bacterial growth and it is toxic. Depending on the species and cultivar of other flowers, one or both of these effects may produce symptoms that limit vase life. In Sonia roses, where mucilage had no effect when placed on the leaf surface, its main effect is apparently blockage of water uptake due to bacterial growth, as no symptoms were observed other than those produced by other agents that block

Fig. 2. Bacterial counts in the lowermost 5 cm of the stems of Sonia roses after placing 'Carlton' daffodil mucilage in the vase water, and the effect of combining this with 300 mg·L⁻¹ of 8-hydroxyquinoline citrate (HQC) in the vase water. Results are means of three replications; cfu = colony-forming units.

Table 2. Sucrose, reducing sugars, polysaccharides, and alkaloids in the aqueous and n-butanol fractions of mucilage from stems of 'Carlton' daffodil (*Narcissus pseudonarcissus*). Mucilage (50 mL) was sampled from freshly cut flowers, placed in a mixture of 25 mL water and 25 mL n-butanol, and vigorously shaken.² The two fractions were analyzed quantitatively for sucrose and reducing sugars, the latter before and after acid hydrolysis, and, qualitatively, for the presence of alkaloids.

Class of compounds	Water fraction ($\mu\text{g}\cdot\text{mL}^{-1}$)	n-Butanol fraction ($\mu\text{g}\cdot\text{mL}^{-1}$)
Sucrose	8 $\pm$ 2	0.2 $\pm$ 0.1
Free reducing sugars	89 $\pm$ 3	0.9 $\pm$ 0.2
Reducing sugars contained in polysaccharides ³	10 $\pm$ 4	0.0
Alkaloids (spots on TLC)	None	Six

²Results (in $\mu\text{g}\cdot\text{mL}^{-1}$ of the fraction) refer to all data except alkaloids and are means of two replications $\pm$ sd.

³Determined after acid hydrolysis.

water uptake, such as a high bacterial titre (van Doorn and de Witte, 1991) or India ink. In tulips, the effect of daffodils and of daffodil mucilage on the rate of water uptake was small, but a clear toxic effect was observed. Compared to rose flowers, tulip flowers have been found to be much less sensitive to bacteria in the vase solution (O.L. Staden, unpublished observations). The mucilage may therefore have allowed bacterial growth, but this did not negatively affect tulip vase life. Rapid and extensive leaf yellowing was found when stems were placed in water with mucilage or when mucilage was placed on the leaf surface. In tulips, 'Cheerfulness' mucilage had less effect than 'Carlton' mucilage when a similar amount was placed on the leaves, indicating that the toxic effect is not only related to the amount of mucilage but also to the concentration of the toxic compounds.

In roses, the mucilage effect was counteracted by adding HQC or sodium hypochlorite to the vase solution. Mucilage increased bacterial counts in the stems, whereas the effect of HQC on vase life coincided with a reduction of the bacterial counts. These data indicate that mucilage stimulates bacterial growth; high bacterial numbers then block water uptake. The mucilage, similar to bacterial exopolysaccharides (de Witte and van Doorn, 1992), may by itself block the pores in pit membranes. This apparently was not important, as HQC or chlorine fully overcame the mucilage effect. The positive effect of HQC was apparently not related to inhibition of ethylene synthesis (as outlined in the Introduction), as AVG, a more efficient inhibitor of ethylene synthesis than HQC, and STS, which blocks ethylene action, did not overcome the mucilage effect. Aluminium sulfate also inhibits bacterial growth in rose stems, although not always effectively (van Doorn et al., 1990). Instead of alleviating the effect of mucilage, aluminium sulfate exacerbated it. When added to vase water under sterile vase water conditions, aluminium sulfate results in partial blockage of water flow in rose stems (unpublished results). This may be explained by the low solubility of aluminium hydroxides, of which a deposit is usually observed following addition of aluminium sulfate to vase water. Although it initially reduces water uptake, aluminium sulfate may become positive, relative to controls, after a few days of vase life, when the rate of water uptake in controls becomes very low. This effect is found when aluminium sulfate is able to adequately inhibit bacterial growth. In the present tests, aluminium was unable to reduce mucilage-induced bacterial growth. The exacerbation of the mucilage effect is probably due to the blockage by the aluminium hydroxide precipitate.

The effect of daffodil mucilage on cut roses was apparently mainly due to its sugars and polysaccharides, as the negative

effects on vase life were also produced by the aqueous fraction after separation into an aqueous and n-butanol fraction. The former contained no alkaloids, but did contain sucrose, reducing sugars, and polysaccharides. These may well be the main cause of increased bacterial growth. Although bacteria also grow well on bacterial exopolysaccharides (unpublished observations), the polysaccharide concentration of the mucilage was low compared to the concentration of sucrose plus reducing sugars. The effect of mucilage on tulip flowers is apparently mainly due to the mucilage alkaloids, as it could be reproduced by placing the n-butanol fraction, which contained the alkaloids, and only low amounts of sucrose and reducing sugars in tulip vase water. It is unclear which of the six alkaloids detected in mucilage produced the effect in tulips. At least 50 alkaloids from daffodils have been identified, mainly in bulb extracts (Kreh and Matusch, 1995; Kreh et al., 1995b; Wildman, 1960), the number of identified alkaloids in bulbs of 'Carlton' daffodils being ≈ 20 (Kreh et al., 1995a). The identity of alkaloids in daffodil mucilage has apparently not been reported.

It is concluded that daffodil flowers, depending on the cultivar, can negatively affect the vase life of cut rose and tulip flowers. Daffodils have two effects, which were apparently separated in the rose and tulip cultivars presently studied: a) stimulation of bacterial growth (as their mucilage contained some sucrose, considerable amounts of reducing sugars, and some polysaccharides), which, in roses, resulted in early water stress symptoms, and b) a toxic effect, expressed in tulips as precocious leaf yellowing, which is apparently mainly due to alkaloids in the mucilage.

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