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Flower-bud blasting in tulips caused by ethylene

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Abstract

Several symptoms are described that characterize the extent of flower-bud blasting in tulips. The disorder could be induced by ethylene applied in concentrations of 0.3 ppm and higher during storage of the bulbs. When ethylene was applied late, the symptoms could be observed in most of the buds immediately after exposure. During subsequent storage in an ethylene-free environment, the injury often increased. When ethylene was applied early, symptoms of blasting appeared only after subsequent treatment for early flowering.

The injury was worse the longer the storage period before exposure, the higher the storage temperature, the higher the concentration of ethylene, the longer the exposure period. Large differences in susceptibility between a number of tested cultivars were observed.

Introduction

Improper temperature treatment applied to tulip bulbs during pre-planting storage, transport, or after planting, can lead to flower-bud blasting (Van Slogteren, 1937; Le Nard and Cohat, 1968; Hoogeterp, 1969; Rees, 1967 and 1969). Exposure of tulip plants to illuminating gas containing ethylene (Hitchcock et al., 1932) or the presence in the soil of tulip bulbs infected by *Fusarium oxysporum* f. *tulipae*, which produce ethylene (De Munk and De Rooy, 1971), can cause the disorder after planting. Earlier experiments on bud necrosis (De Munk, 1972a) indicated that ethylene can cause flower-bud blasting also when applied to bulbs during dry storage before planting. Because it is known that *Fusarium*-infected bulbs are often present in stocks of bulbs (Kamerbeek and De Munk, 1968; Kamerbeek et al., 1971; De Munk, 1972a), more detailed information on the influence of ethylene on flower-bud blasting was considered important.

This report describes the results of experiments with tulip bulbs stored at different temperatures and exposed to various concentrations of ethylene during different phases of development. The effects of ethylene on bud development with regard to bud necrosis were published elsewhere (De Munk, 1972a and 1973) and are not mentioned in this paper.

Materials and methods

Treatment of bulbs

In the 1970–1971 season tulip bulbs of the cultivar 'White Sail' from commercial stocks, 11 to 12 cm in circumference, were stored at 13°, 17°, 20°, and 23°C after harvesting. Separate lots were exposed to ethylene in concentrations of 0, 0.05, 0.1, 0.5, 1, 3, 10, and 100 ppm for 2, 4, 6, or 8 weeks, according to the method described elsewhere (De Munk, 1972a). The ethylene treatments were given in different periods during storage from mid-July until mid-November, starting at 2-weeks intervals.

In the 1971–1972 season bulbs of other cultivars with a circumference of 11 to 12 cm and stored at 20 °C were exposed to ethylene in concentrations of 0, 0.3, and 3 ppm for 2, 4, or 6 weeks. The treatments were started at the end of July and in the middle of October.

Immediately after the exposure and at the end of storage (late November), 10 bulbs of each lot were dissected to evaluate the effects of the treatments. On the basis of the scale of symptoms described in the next section, the amount of injury was expressed in scores, calculated as average of the stages observed.

The remaining bulbs of each lot were planted in boxes at the end of November, cooled at 5 °C for 15 weeks, and brought to flowering in a greenhouse at 18 ° to 20 °C. In the experiments of the 1971–1972 season samples of 50 bulbs each were also planted at 5 °C directly after the ethylene treatment and forced (treatment for early flowering)

Symptoms during dry storage

In the symptoms of flower-bud blasting, which can be observed in dissected bulbs during storage, seven stages were distinguished, expressing the extent of damage.

In stage 1 the tips of one or more stamens are less rigid and their surface is lustreless. Sometimes these stamens are also water-logged and sap is exudated.

In stage 2 all stamens are flabby.

In stage 3 all stamens, filaments and perianth leaves shrivel.

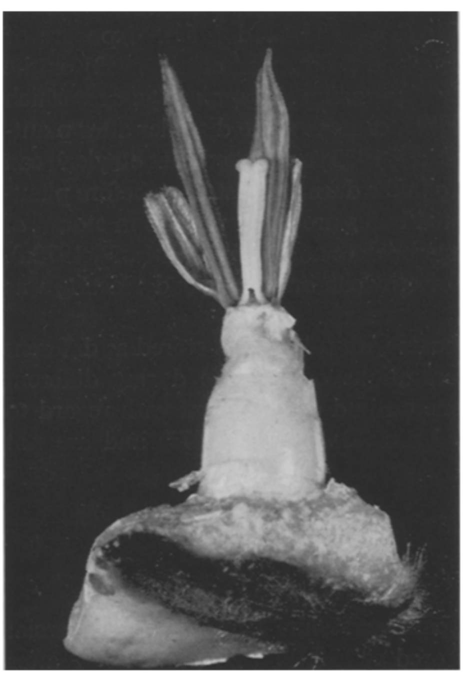

Fig. 1. Excised floral bud of tulip 'White Sail', showing blasted stamens and perianth. The tip of the pistil is still intact, unlike the base which has started to collapse.

Fig. 1. Uitgeprepareerde bloemknop van een tulpebol, 'White Sail', waarvan meeldraden en bloemdekbladen zijn verdroogd. De top van het vruchtbeginsel is nog intact in tegenstelling tot de basis die begint te verschrompelen.

Stage 4 is characterized by a withering of the pistil, starting at the base (Fig. 1) and a yellowing of all floral organs.
In stage 5, all floral organs are wilted, papery, and yellowish brown.
In stage 6, the innermost leaf of the bud is wilted in addition to the flower parts.
In stage 7, all leaves are wilted, papery, and discoloured. The process of leaf deterioration starts near the pistil.

Symptoms after planting
Symptoms in mature plants can be partly traced to damage already present before planting (direct effects) and partly to a desiccation occurring during the last few weeks before flowering (delayed effects). In the first case the affected organs are found as tiny and papery remnants. The symptoms reflect the stages of damage described for bulbs during storage. When damage is severe (stages 4 to 7), the last internode will not elongate and the upper leaf will not unfold. Then axillary buds, normally remaining vegetative, often become generative. The shoots from these buds differ from the main shoot by the tubular base of the first leaf and more leaves (Fig. 2).

In the lowest degree of damage, which originates during the growth in the greenhouse, only the stamens are blasted. More advanced are additional green streaks in or white tips on the perianth. Small flowers with green and twisted perianth leaves and blasted stamens represent more severe cases; then the pistil is intact (Fig. 3). Blasting was most severe when bud development and stem elongation ceased in the last few weeks before the expected flowering date. Under these conditions the buds become white and the top leaf does not unfold (Fig. 4).

Fig. 2. Two flowering shoots from the tulip 'Prominence'. Right: shoot originating from axillary bud showing a tubularly closed basal leaf. Left: shoot originating from the central meristem, showing normal amplexicaul leaf.

Fig. 2. Bloeiende spruiten van de tulp 'Prominence'. Rechts: spruit ontstaan uit okselknop: kokervormig gesloten basaal blad; links: spruit ontstaan uit de eindknop; normaal stengelomvattend blad.

Fig. 3. Flowers of tulip 'White Sail' showing varying degrees of blasting. From left to right: increasing 'greening' and decreasing size of perianth.

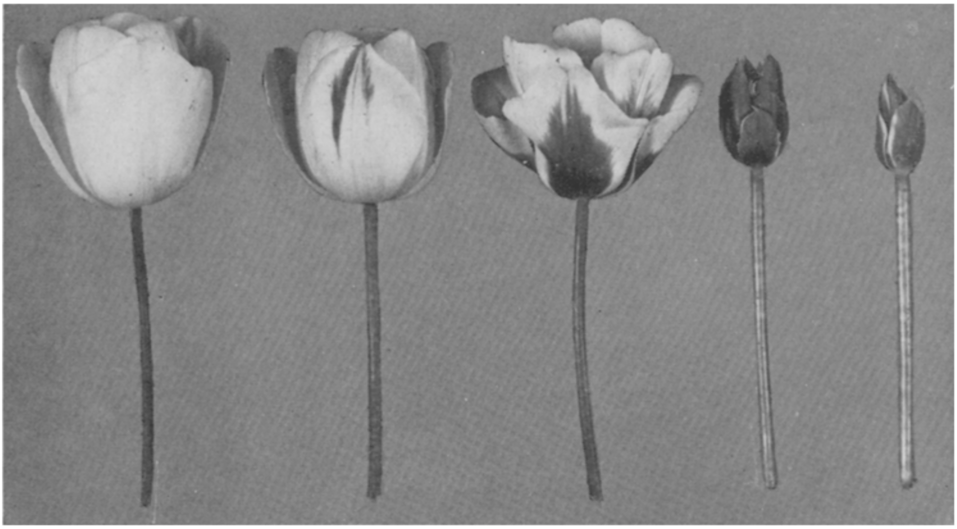

Fig. 3. Bloemen van tulp 'White Sail' in verschillende stadia van verdroging. Van links naar rechts: toenemende mate van vergroening en afnemende grootte van het bloemdek.

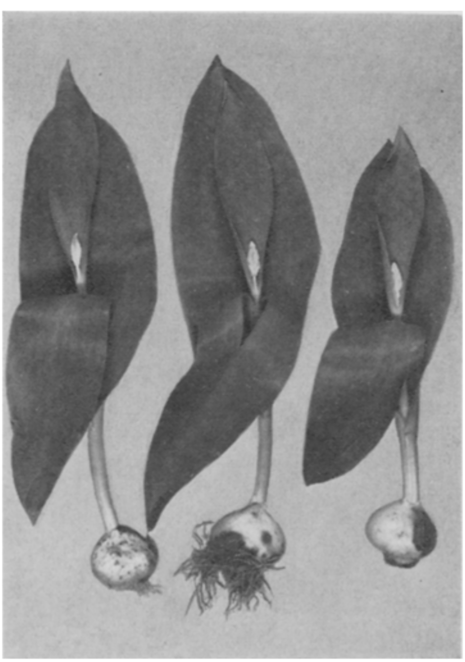

Fig. 4. Flower buds of tulip 'Apeldoorn' which became blasted during forcing.
The perianth is white and papery and the internodes are not fully elongated.

Fig. 4. Bloemknoppen van tulp 'Apeldoorn' welke verdroogden tijdens de groeiperiode in de kas. De bloemdekbladen zijn wit en vliezig; de stengelleden zijn niet ten volle uitgegroeid.

Results

Direct effects of ethylene

The amount of injury could be related to the following factors:

1. *Developmental state of the floral buds prior to exposure to ethylene.* Comparison of the data from 8 successive treatments with 3 ppm ethylene for 2, 4, 6, or 8 weeks at 20 °C, which were started at 2-week intervals, shows an increase in susceptibility during storage (Table 1). Blasting was not found in excised buds when the ethylene treatment had been started before the end of August. Later treatment led to increasing amounts of injury the longer the storage period before exposure lasted. The onset of the susceptible phase coincided with meiosis in the anthers, i.e. after the stamens had reached a length of 6 to 7 mm. From Table 1 it can also be seen that the scores increased with increasing duration of exposure to ethylene.

Table 1. Degree of blasting (0 = no symptoms to 7 = whole sprout blasted), for 10-bulb samples of 'White Sail' stored at 20 °C and exposed to ethylene (3 ppm). The ethylene treatments were started at 2-week intervals, and scoring was done immediately after treatment.

Starting date of ethylene treatment	Duration of ethylene treatment			
	2 weeks	4 weeks	6 weeks	8 weeks
July 14	0	0	0	0.3
July 28	0	0	0	0
August 11	0	0	0	0
August 25	0	0.1	2.2	2.4
September 8	0	0.9	5.3	6.0
September 22	0.3	2.3	5.8	6.0
October 6	0.5	4.3	6.0	6.0

Tabel 1. Mate van bloemknopverdroging (0 = geen symptomen; 7 = spruit geheel verdroogd) in tulpebollen 'White Sail' (n = 10), bewaard bij 20 °C en blootgesteld aan ethyleen (3 dpm). De ethyleenbehandelingen vingen aan met tussenpozen van 2 weken. De beoordeling vond plaats direct na behandeling.

2. *Storage temperature.* The influence of the storage temperature was demonstrated by experiments in which bulbs held at different storage temperatures were exposed to 10 ppm ethylene for 6 weeks. These experiments were started at the end of September when the bulbs were in a highly susceptible state. Bulbs kept at 23 °C showed the strongest damage (Fig. 5), and those held at 13 °C showed no symptoms of blasting. It may be concluded that the degree of blasting, due to the presence of ethylene, increases strongly with increasing storage temperature.

3. *Concentration of ethylene.* The influence of the ethylene concentration was investigated at several storage temperatures. The bulbs were exposed for 6 weeks, from late September until early November, to ethylene in the following concentrations: 0, 0.05, 0.1, 0.5, 1, 10, and 100 ppm. The lowest concentration that promoted blasting was 0.5 ppm, but only at 23 °C, where the predisposition for blasting must have been high

Fig. 5. Influence of storage temperatures on amount of injury (0 = no symptoms to 7 = whole sprout blasted), in tulip 'White Sail' exposed to ethylene (10 ppm) for 6 weeks starting on September 23th.

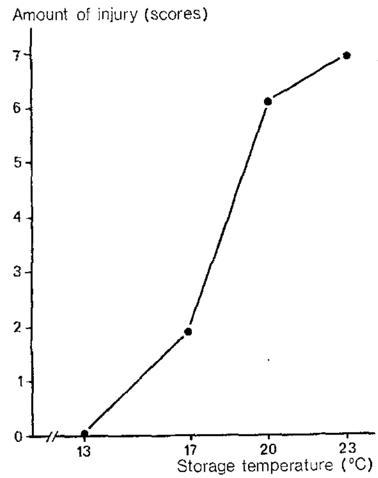

Fig. 5. Invloed van de bewaartemperatuur op de mate van bloemknopverdroging (0 = geen symptomen; 7 = spruit geheel verdroogd) bij tulp 'White Sail'; de bollen werden blootgesteld aan ethyleen (10 dpm) gedurende 6 weken vanaf 23 september.

Fig. 6. Influence of concentration of ethylene (exposure period 6 weeks) on amount of injury in bulbs of tulip 'White Sail' at storage temperatures of 23 °C (●), 20 °C (○), 17 °C (■), and 13 °C (□).

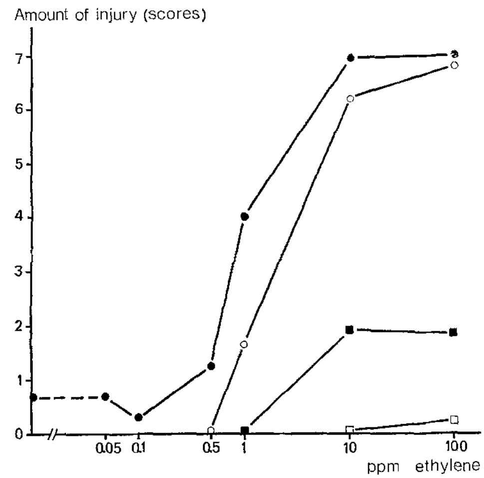

Fig. 6. Invloed van verschillende concentraties ethyleen (duur van de behandeling 6 weken) op de mate van bloemknopverdroging in bollen van tulp 'White Sail', respectievelijk bewaard bij 23°C (●), 20°C (○), 17°C (■) of 13°C (□).

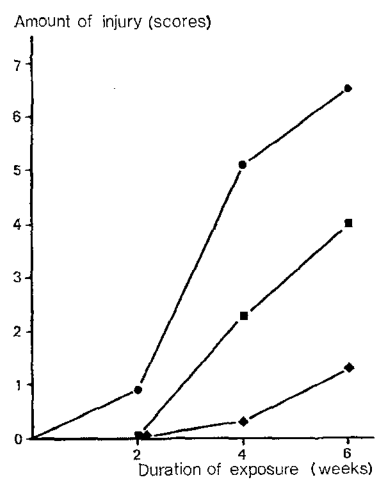

Fig. 7. Influence of duration of exposure to ethylene on amount of injury in bulbs of tulip 'White Sail', stored at 23 °C. Ethylene concentrations applied: 0.5 ppm (◆), 1 ppm (■), and 10 ppm (●).

Fig. 7. Invloed van de duur van de behandeling met ethyleen op de mate van bloemknopverdroging in tulpebollen 'White Sail', bewaard bij 23°C. Ethyleen-concentraties: 0,5 dpm (◆), 1 dpm (■) en 10 dpm (●).

because the first symptoms were even found in the controls (Fig. 6). At 20 °C, at least 1 ppm of ethylene was necessary to cause damage, and at 17 °C blasting was found only at concentrations of 10 ppm and 100 ppm. At 13 °C the bulbs showed hardly any damage even at a concentration of 100 ppm. Blasting increases with increasing concentrations of ethylene. The threshold concentration and the amount of injury at each concentration are, however, highly dependent on the storage temperature.

4. *Duration of exposure to ethylene.* The data in Table 1 as well as the results of experiments with bulbs stored at 23 °C and exposed to various ethylene concentrations for 2, 4, or 6 weeks (Fig. 7), clearly demonstrated the influence of the duration of the exposure period. After 2 weeks exposure at 23 °C (Fig. 7) low scores were found, at a concentration of 10 ppm ethylene only. After 4 weeks at that concentration all flowers were totally blasted, whereas after 4 weeks at 1 ppm blasting was restricted to the stamens and perianth. After an exposure period of 6 weeks, damage was also found at 0.5 ppm. Thus the amount of injury increases with increasing time of exposure, but strongly depends on storage temperature and ethylene concentration.

5. *Differences in varietal susceptibility.* The scores for the amount of injury found in bulbs of different cultivars after treatment with 3 ppm show clear differences (Table 2). After treatment with 0.3 ppm the scores are too low to permit conclusions about the susceptibility of the cultivar, but they are not contradictory with those found after treatment with 3 ppm. 'White Sail', which was mainly used in preceding seasons, seems to be moderately susceptible (score 2.3) compared with the high scores obtained for 'Thule' (6.9) and 'Apeldoorn' (5.5) and the low scores for 'Topscore' (0), 'Prominence' (0), and 'Queen of Sheba' (0).

Table 2. Degree of blasting (0 = no symptoms to 7 = whole sprout blasted) for 10-bulb samples of different cultivars stored at 20 °C and exposed to ethylene for 4 weeks (from the middle of October until the middle of November).

Cultivar	Ethylene concentration (ppm)		
	0	0.3	3
Thule	0	2.3	6.9
Kees Nelis	0	0.7	0.6
Mirjoran	0	0	1.9
Topscore	0	0	0
Apeldoorn	0	0	5.5
Prominence	0	0	0
Bellona	0	0	0.2
White Sail	0	0.2	2.3
Rose Copland	0.1	0.9	4.7
Queen of Sheba	0	0	0
Gander	0	0	1.0

Tabel 2. Mate van bloemknopverdroging (0 = geen symptomen; 7 = spruit geheel verdroogd) in tulpebollen (n = 10) van verschillende cultivars, bewaard bij 20 °C en blootgesteld aan ethyleen gedurende 4 weken (van midden oktober tot midden november).

Fig. 8. Percentage of bulbs with symptoms of blasting (8A) and amount of injury (8B) for tulip 'White Sail' exposed to ethylene (3 ppm) at 20 °C for 4 weeks in successive periods during storage. Determinations were made immediately after the exposure to the gas (□) and at the end of the storage period (late November) (*dotted*).

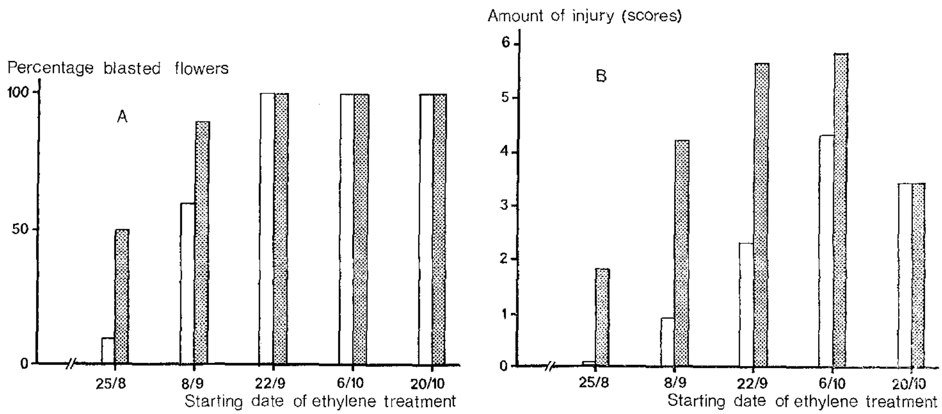

Fig. 8. Percentage bollen met verdrogingssymptomen (8A) en de mate van verdroging (8B) in tulp 'White Sail', bewaard bij 20 °C en gedurende 4 weken blootgesteld aan ethyleen (3 dpm) in opeenvolgende perioden tijdens de bewaring. De bepalingen zijn gedaan direct na de behandeling met ethyleen (□) en aan het einde van de bewaarperiode (eind november) (gestippeld).

Table 3. Percentage of flowers with symptoms of blasting in plants from tulip bulbs of different cultivars stored at 20 °C, exposed to ethylene for 6 weeks immediately after harvesting and treated for early flowering. No visible symptoms were observed in samples of the treated lots at the time of planting (early September) or after continued storage until late November.

Cultivar	Ethylene concentration (ppm)		
	0	0.3	3
Thule	0	91	94
Kees Nelis	13	13	63
Mirjoran	2	22	56
Topscore	4	33	100
Apeldoorn	69	81	98
Prominence	0	13	72
Bellona	0	8	31
White Sail	19	66	100
Rose Copland	56	88	100
Queen of Sheba	0	17	29
Gander	0	0	0

Tabel 3. Percentage tulpebloemen met verdrogingsverschijnselen in planten van verschillende cultivars, waarvan de bollen werden bewaard bij 20 °C, blootgesteld aan ethyleen gedurende de eerste 6 weken na het rooien en behandeld voor vroege bloei. Op het tijdstip van planten (begin september) en na voortgezette bewaring tot eind november waren in monsters bollen van deze partijen geen symptomen waarneembaar.

Fig. 9. Retarded outgrowth of roots after planting of tulip bulbs, 'Topscore', stored at 20 °C and exposed to ethylene (0.3 ppm) for 6 weeks before planting. Photograph taken 3 weeks after planting. Left: untreated bulb; right: ethylene-treated bulb.

Fig. 9. Vertraagde uitgroei van wortels bij tulp 'Topscore', waarvan de bollen werden bewaard bij 20 °C en gedurende 6 weken voor het planten (vanaf 8 september) werden behandeld met ethyleen (0,3 dpm). De opname is gemaakt 3 weken na het planten; de grondtemperatuur was 5 °C. Links: onbehandelde bol; rechts: behandelde bol.

Delayed effects of ethylene

During further storage after ethylene treatment, both the extent and the percentage of blasting increased in 'White Sail' bulbs (Fig. 8A and B). This increase was such that, for instance, in bulbs of the series treated from September 8th and 22nd only symptoms on stamens (scores 0.9 and 2.3) were found immediately after the ethylene treatment, whereas all floral organs were deteriorated (scores 4.2 and 5.6) at the end of the storage period. This effect is considered to be a delayed effect of ethylene, not only because the deterioration of affected organs increased, but also because previously unaffected organs, such as pistil and perianth, became blasted.

Another delayed effect became evident when early exposed bulbs were treated for early flowering (Table 3). In these plants blasting was found during growth in the glasshouse, whereas no symptoms had been observed in either samples of these bulbs before planting or samples which had been stored until mid-November at 20 °C. Because blasting was also found in plants from untreated bulbs (cultivars 'Kees Nelis', 'Apeldoorn', 'White Sail', and 'Rose Copland'), it cannot be concluded that ethylene is the only inductive factor, but it is clear that exogenous ethylene strongly stimulates blasting.

Table 3 also illustrates the differences in susceptibility of the tested cultivars, but not all scores in Table 2, found after exposure to 3 ppm ethylene, are correlated with the comparable percentages of Table 3: viz., the cultivars 'Kees Nelis', 'Topscore', and 'Prominence' show low scores (0.6, 0, and 0, respectively) but high percentages (63, 100, and 72, respectively). This indicates that additional effects occurred during treatment for early flowering. One of them might be the influence of ethylene on rooting. It was observed that in some cultivars the outgrowth of roots of ethylene treated bulbs was strongly delayed (Fig. 9).

Discussion

The results indicate that blasting of flower-buds of tulips can be induced by exogenous ethylene during storage. Early exposure of bulbs resulted in blasting occurring as a delayed effect after treatment for early flowering; later exposure resulted in a direct effect visible during storage when the bulbs were dissected.

Symptoms identical to those described for the direct ethylene effect are known as 'heating in transit' (Van Slogteren, 1937). This disorder can be caused by high temperatures during the storage period after August. Not only are the symptoms exactly the same, but both forms of blasting can be evoked during the same period of storage. The bulbs show an increasing susceptibility to both forms of blasting as the storage period proceeds. This raises the question of whether the autoproduction of ethylene by tulip bulbs will be stimulated by a higher storage temperature to such a level that in cases of 'heating in transit' a certain threshold value will be reached without supply of exogenous ethylene. Preliminary experimental results indicated, that the ethylene content of air extracted under vacuum from tulip bulbs stored at 30 °C, in which 'heating' occurred, was higher than that from bulbs stored at 20 °C, which remained unaffected. The differences were small, however, and the results do not permit conclusions about the level and activity of ethylene at the sites of action, i.e. the tissue of the floral organs. Besides this enhancement of the autoproduction of ethylene at higher temperature, it can be concluded from the different reactions on exposure of bulbs stored at high and low temperature, that an activated response mechanism must be present at higher temperature.

Blasting resulting from early exposure followed by treatment for early flowering and from ethylene treatments after planting (De Munk and De Rooy, 1971), closely resembles the symptoms evoked by a complex of conditions during storage, cooling and greenhouse cultivation in which the temperature is the most important factor (Hoogeterp, 1969; Rees, 1969). When this type of blasting is observed in mature plants, therefore, it cannot be concluded without detailed information about the history, whether this is caused by ethylene or unfavourable temperatures before or after planting.

Direct and delayed effects were also found in the experiments on the influence of ethylene on bud development and deformation with regard to bud necrosis (De Munk, 1973). Borriss (1943) distinguished a direct and an indirect effect of ethylene on the growth of etiolated seedlings of *Agrostemma*. The indirect effect proved to be localized in the cotyledons. One may ask whether the delayed effects on tulip bulbs can be localized in the bulb scales. It is known that ethylene has an effect on scales of tulip bulbs in connection with the disorder gummosis (Kamerbeek et al., 1971). Mastalerz (1965) showed a correlation between bud-blasting in *Lilium longiflorum* and deficiencies in the carbohydrate metabolism and an active carbohydrate metabolism is present in the scales of the tulip bulb (Algera, 1947; Beijersbergen and Lemmers, 1971). Further investigations are required to elucidate the effect of ethylene on flower-bud blasting in connection with changes in the chemical composition of bulb scales and the transport of metabolites.

The coincidence of meiosis in the anthers and the onset of the phase of susceptibility to 'heating in transit' and blasting during storage also deserves further attention. A similar phenomenon was observed by Kamerbeek and Durieux (1971) during the investigation of bud abscission in *Lilium* 'Enchantment'. Erickson (1948) found increasing permeability in stamens of *Lilium longiflorum* during meiosis. Long ago, Harvey (1915) found increasing osmotic pressures in pea seedlings exposed to ethylene as a consequence of increasing amounts of soluble components. The occurrence of exudation and infiltration processes in stamens observed at the onset of blasting could possibly be related to a combination of increasing permeability and osmotic pressure.

The onset of the susceptible period for the direct effect of ethylene is rather sudden, but this period continues up to some days before flowering (Hitchcock et al., 1932; De Munk and De Rooy, 1971). In recent experiments in our institute it was observed that exposure of tulips to 0.5 ppm of ethylene for three and a half and seven days at 18 °C to 20 °C in the greenhouse after natural cooling in the open, led to 64% and 100% blasting, respectively (De Munk, 1972b). This flower-bud blasting resembles ethylene-induced wilting in orchid flowers (Davidson, 1949) and sleepiness in carnations (Uota, 1970).

The most important sources of exogenous ethylene in stocks of tulips are bulbs infected with *Fusarium oxysporum* f. *tulipae* (Kamerbeek and De Munk, 1968; De Munk, 1972a). Similar conditions are encountered in lemons when specimens infected with *Penicillium digitatum* are present during storage (Biale and Shepherd, 1941). Because it is often very difficult to remove infected specimens during storage and transportation, adequate ventilation is recommended.

Samenvatting

Bloemknopverdroging bij tulpen veroorzaakt door ethyleen

De mate van beschadiging bij bloemknopverdroging is gekarakteriseerd in een aantal stadia variërend van 0 (geen symptomen) tot 7 (spruit geheel verdroogd). De afwijking kon worden opgewekt door tijdens de bewaarperiode ethyleen toe te dienen in concentraties van 0,3 dpm en hoger. Wanneer ethyleen laat (vanaf eind augustus) werd toegediend, konden de symptomen meestal direct na de behandeling worden waargenomen (Fig. 1). De mate van beschadiging was dan groter naarmate:

1. de bewaring voorafgaande aan de ethyleenbehandeling langer had geduurd (Tabel 1),
2. de bewaartemperatuur hoger was (Fig. 5),
3. de ethyleenconcentratie hoger was (Fig. 6),

4. de blootstelling aan het gas langer duurde (Fig. 7).
Er bleken grote verschillen in gevoeligheid te bestaan tussen een aantal onderzochte cultivars (Tabel 2).
Wanneer met-ethyleen-behandelde bollen werden geplant, ontwikkelde zich in een aantal gevallen uit okselknoppen – waaruit onder normale omstandigheden een nieuwe bol groeit – een spruit met bloem (Fig. 2). De verschijnselen werden directe effecten van ethyleen genoemd.

Na blootstelling aan het gas nam de mate van beschadiging tijdens voortgezette bewaring in ethyleenvrije omgeving in de meeste gevallen toe (Fig. 8A en B). Deze toename werd een uitgesteld ethyleen-effect genoemd.

Een ander uitgesteld ethyleeneffect trad op wanneer ethyleen vroeg in de bewaarperiode werd toegediend en de bollen daarna werden geplant en behandeld voor vroege bloei (koeling bij 5 °C en in bloei trekken in een kas bij 18 tot 20 °C). De verdrogingsverschijnselen ontstonden nu tijdens de groeifase in de kas (Fig. 3 en 4). Ook bij dit effect bleken verschillen in gevoeligheid tussen de onderzochte cultivars (Tabel 3). Bij deze behandeling bleek bovendien, dat de uitgroei van de wortels in een aantal gevallen werd geremd als gevolg van de voorafgaande ethyleenbehandeling (Fig. 9).

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