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Bud necrosis, a storage disease of tulips. III. The influence of ethylene and mites

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Abstract

Experiments demonstrated that bud necrosis in tulip bulbs is caused by mites that penetrate the flower bud during storage. This penetration is only possible if the buds, which are normally closed, are open at their tips. Such buds were found after administration of ethylene (3 ppm) during storage at 20 °C shortly after lifting and in 'Red Champion' also after storage at higher temperatures (20 to 23 °C) in ethylene-free atmospheres.

Open buds, caused by ethylene, resulted from unequal growth inhibition of the young leaves and stamens. The difference in sensitivity of both organs to ethylene decreased during storage. Later on, the growth inhibition of stamens and leaves became equal, and the buds remained closed. Then ethylene caused blasting of the flower buds.

Open buds in 'Red Champion', caused by higher storage temperatures, resulted from aberrant differentiation of the tips of the young leaves.

The production of ethylene by tulip bulbs infected with *Fusarium oxysporum* f. *tulipae* was measured and proved to be sufficiently high to cause open buds in non-infected bulbs stored in the same room if ventilation is not adequate. The highest production of ethylene, averaging 140 µl/24 h/bulb was found at a storage temperature of 20 °C.

Introduction

Analysing the disease-syndrome relationships were found which led to the hypothesis that bud necrosis in tulip bulbs is a multifactorial disorder, depending on at least two conditions (de Munk, 1971a). These are the existence of abnormal, unclosed buds during storage and the penetration of those buds by the mites *Rhizoglyphus echinopus* Fumouze & Robin and *Tyrophagus* spp. It was supposed that open buds were caused by ethylene, and in some cultivars e.g. 'Red Champion' also by higher storage temperatures. The source of ethylene was thought to be the *Fusarium*-infected bulbs often present between healthy bulbs.

This hypothesis remained to be tested experimentally and the following questions were raised. Can the formation of open buds be caused by administration of ethylene? Are the *Fusarium*-infected bulbs a source of ethylene, and are the quantities of ethylene produced high enough to cause open buds? Does bud necrosis originate only when bulbs with open buds are exposed to mites? Experiments were therefore performed with bulbs stored in atmospheres containing ethylene, or, in the case of 'Red Champion', at higher temperatures, and then exposed to mites.

Material and methods

Samples of bulbs of the cultivars 'White Sail', 'Red Champion', and 'Rose Copland' taken from storage at 20 °C were treated with ethylene at a temperature of 20 °C during periods of 2, 4, 6, and 8 weeks in closed plastic 5-litre pails through which an airstream (100 litre/h) was led, containing 3 microlitre ethylene per litre (3 ppm). This concentration was chosen as it was the average of the concentrations detected in boxes filled with bulbs of which some were affected by the disorder and others by *Fusarium oxysporum* (de Munk, 1971a). The first series of treatments started immediately after lifting in the middle of July; 9 series of successive treatments were started at intervals of two weeks until the beginning of November. The concentration of ethylene in the air was checked regularly by means of gas chromatography (de Munk, 1971a).

To detect morphological aberrations of the habit of the buds and to measure the length of the buds and stamens, samples of 10 bulbs each of ethylene-treated and untreated bulbs were dissected.

A portion of the bulbs were treated with endosulfan (0.2 % in suspension) to prevent accidental infestation with mites as long as possible; another portion were contaminated with the mites *Rhizoglyphus echinopus* Fumouze & Robin and *Tyrophagus* spp. For this purpose, populations of these mites were reared together on decaying tulip bulbs. To be certain that the mites could reach the buds within the bulbs, the tips of the bulb scales were cut such that the central cavity of the inner bulb scale was exposed. After contamination with mites and continued storage during 6 weeks at 20 °C, the occurrence of bud necrosis was determined. The tips of the bulb scales of control bulbs were cut also, and the bulbs were stored under the same conditions.

Bulbs of 'Red Champion' were stored also at 13° and 23 °C. At intervals of two weeks, samples comprising 30 bulbs of this material were contaminated with mites in the same way as the samples of ethylene-treated bulbs.

To measure the ethylene production of *Fusarium*-infected bulbs, specimens of 'White Sail' with unequivocal symptoms of the disease were selected and placed separately in closed 1100-ml vessels. After 24 hours in these vessels, the amount of ethylene produced was measured by gas chromatography.

Statistical calculations are performed according to Wijvekate (1960).

Results

The administration of ethylene caused a number of morphological changes. The most interesting effects were: inhibition of the elongation growth of the young leaves and flower parts and the occurrence of open buds.

1. *Inhibition of elongation growth*

In 'White Sail' in all series treated, the inhibition of the elongation growth of the young leaves was almost complete during the whole period of exposure to ethylene (Fig. 1A). The elongation growth of the flower parts was also inhibited. This is illustrated by the growth curves of the stamens (Fig. 1B). The degree of the growth inhibition of the stamens, however, is not equal in all series treated, in contrast to the inhibition of the growth of the young leaves. In the first series the inhibition of stamen growth amounted to about 65 %; in the second and third series to 84 and 76 % respect-

Fig. 1. Elongation growth of buds (A) and stamens (B) in bulbs of 'White Sail' stored at 20°C without ethylene (●) and with 3 ppm ethylene (○). The first series of treatments (I) was started on July 14, successive series at 2-week intervals (II to IX). The dotted lines in B indicate the blasting of the flowers.

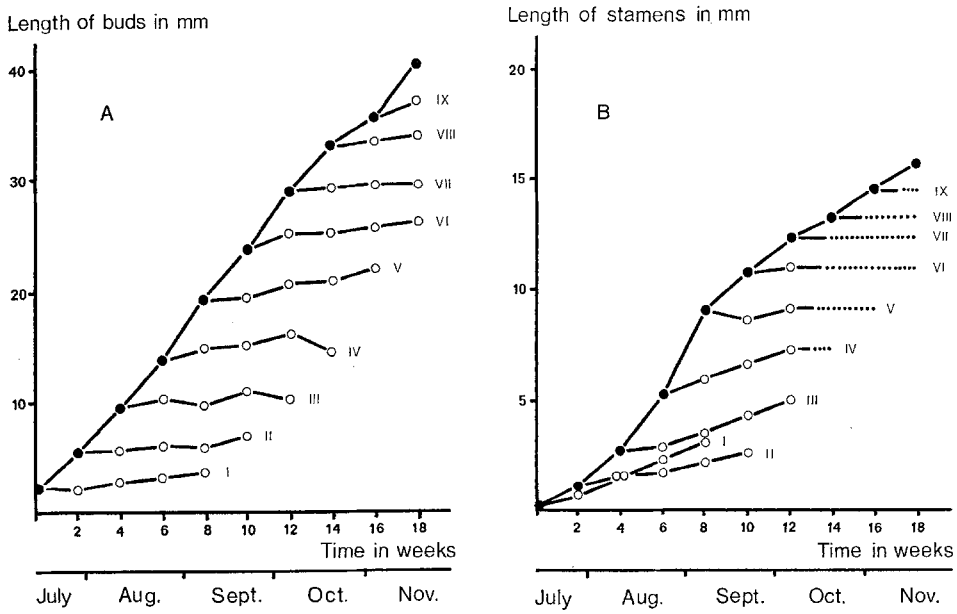

Fig. 1. De lengtegroei van knoppen (A) en meeldraden (B) in bollen van 'White Sail' die bij 20°C werden bewaard, resp. zonder ethyleen (●) en met 3 dpm ethyleen (○). De eerste serie behandelingen (I) begon op 14 juli, de volgende series (II tot IX) telkens 14 dagen later. De gestippelde lijnen in B geven aan dat de bloemdelen verdroogden.

ively. In the fourth series the inhibition was initially about 71 % and became complete after 6 weeks of exposure to ethylene. In the fifth and following series this inhibition was complete from the beginning to the end of the exposure to ethylene. It is clear that the inhibitory effect of ethylene on the growth of the stamens increases in the later phases of development.

Comparison of Fig. 1A with Fig. 1B shows that the difference between the degree of inhibition of young leaves and stamens is most evident in the first series and decreases gradually. The differences result in an abnormal development of the buds, because the growth of the stamens within the buds is relatively faster than the growth of the enveloping young leaves. This abnormal development did not occur in bulbs exposed to ethylene later in the storage period because in these series there was no difference between the degree of inhibition of young leaves and stamens.

To investigate the reversibility of the growth inhibition, bulbs previously exposed to ethylene were stored in an ethylene-free atmosphere until the end of November. At the end of this storage period the buds were shorter in bulbs previously exposed to ethylene than in the controls. The length of the stamens from early-treatment bulbs was equal to or even greater than those of the untreated controls. The growth of the stamens of late-treatment bulbs did not recover, because the stamens became blasted. This

blasting of stamens and later of all flower parts was observed when the ethylene treatment had been started at the end of August or later (series IV to IX) i.e. when growth inhibition was complete. In series IV, blasting was found after eight weeks of exposure to ethylene, in series VII and VIII after only two weeks of exposure. The occurrence of blasting is indicated in Fig. 1 B by dotted lines.

From these results it can be concluded that in bulbs given early treatment the abnormal development, which resulted from the unequal growth inhibition of stamens and young leaves, will become more pronounced due to the difference in reversibility of the inhibitory effect. The relatively faster growth of inner parts of the buds as compared with the growth of outer parts, does not occur after later exposure of bulbs to ethylene because the growth of the flower parts will not recover after blasting.

2. *Occurrence of open buds*

Seven stages were distinguished corresponding to the degree of aberration of the habit of the buds of 'White Sail' bulbs. Although each stage can be an endphase, the stages are arranged in a sequence terminating with open buds (Fig. 2). The stages are:

stage 0: a normal closed bud with overlapping leaf margins;
stage 1: buds showing an opening in the first leaf at the level of the basal conjunction of the leaf margins;
stage 2: buds showing a chink over the total length of the bud or at its top, caused by the disappearance of the overlap of the leaf margins:
stage 3: buds with an opening at the tip;
stage 4: buds with a wider opening than in stage 3, through which the stamens are visible;
stage 5: buds showing the outgrowth of stamens through the opening at the tip of the bud;
stage 6: buds showing a degree of outgrowth of the stamens such that these organs project above the tip of the bud.

On the basis of this scale it was possible to evaluate the degree of bud deformation in samples of bulbs from the nine series treated with ethylene. Score numbers for a given sample are determined as the mean of the sum of the number of stages observed in bulbs of that sample (Table 1).

Fig. 2. Scale of bud deformation (0–6) in 'White Sail' caused by ethylene. Left: normal bud shape; right: most severe aberration.

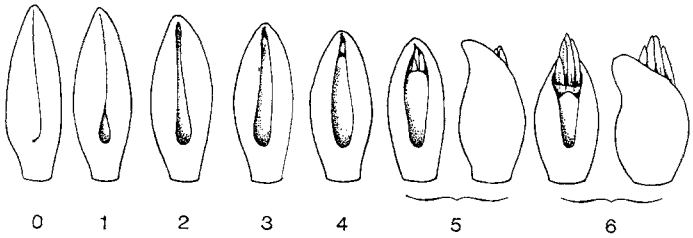

Fig. 2. Schaal voor knopafwijkingen (0–6) in bollen van 'White Sail', veroorzaakt door ethyleen. Links: normale knopvorm; rechts: meest afwijkende knopvorm.

Table 1. Mean score numbers of bud deformation, determined on the basis of the scale shown in Fig. 2, for bulbs 'White Sail' stored at 20°C and exposed to ethylene (3 ppm) for 2, 4, 6, and 8 weeks in different periods during storage.
a: evaluation immediately after exposure to ethylene;
b: evaluation at the end of November after the total storage periode (n = 10).

Starting of exposure to ethylene	Series number	2 weeks of exposure		4 weeks of exposure		6 weeks of exposure		8 weeks of exposure	
		a	b	a	b	a	b	a	b
July 14	I	4.5	2.0	5.8	3.3	5.9	4.4	5.8	4.7
July 28	II	0.2	0.8	1.7	2.2	3.4	3.8	3.1	4.5
August 11	III	0	1.0	0	3.0	0.6	4.2	2.8	3.5
August 25	IV	0	0.6	0.4	1.4	0.5	0.6	0.8	0.4
Sept. 8	V	0	0.6	0.5	0	0	0	0	0
Sept. 22	VI	0	0	0	0	0	0	0	0
Oct. 6	VII	0	0	0	0	0	0	–	–
Oct. 20	VIII	0	0	0	0	–	–	–	–
Nov. 3	IX	0	0	–	–	–	–	–	–

Tabel 1. Gemiddelde knopafwijkingen uitgedrukt in getallen volgens de schaal gegeven in Fig. 2, bij bollen van 'White Sail' na blootstelling aan ethyleen (3 dpm) gedurende 2, 4, 6 of 8 weken in verschillende perioden tijdens de bewaring bij 20°C.
a: beoordeling direct na afloop van de ethyleen-behandeling;
b: beoordeling eind november na afloop van de gehele bewaarperiode.

High scores were found in series treated with ethylene during the first few weeks after digging. Open buds i.e. scores of 3 and higher, were observed after a two-week exposure period in series I and after a 6-week exposure period in series II. In bulbs exposed to ethylene later in the season, the normal bud shape was deformed to a lower degree (series III and IV) or persisted even after an exposure period of 8 weeks (series V and VI).

When the score numbers determined directly after the ethylene treatment are compared with those determined at the end of November after the bulbs had been stored for an additional period in an ethylene-free environment, it can be seen that the values for the first series decreased, whereas those for series II, III, and IV increased. Since the changes in the first and third series are significant, according to Wilcoxon, it is concluded that for bulbs exposed to ethylene soon after lifting there is a slight tendency to recover after cessation of the ethylene treatment, whereas for bulbs exposed to ethylene some weeks later the degree of deformation will continue to increase.

In 'Red Champion' the same kind of deformation as that described for 'White Sail' can be induced by ethylene. Moreover, it was observed that in 'Red Champion' open buds can result from higher storage temperatures. The influence of temperature differs from the influence of ethylene, and has an effect on the shape of the leaf tips. At a temperature of 13°C the tips become pointed and at a temperature of 23°C they become obtuse and show inward bending. As a consequence of this unusual shape the buds remain unclosed when the leaves become folded during growth at 23°C, whereas at 13°C the buds gradually become closed (Fig. 3).

Fig. 3. Changes in the shape of bud and leaf tip in 'Red Champion' at storage temperatures of 13° and 23°C.

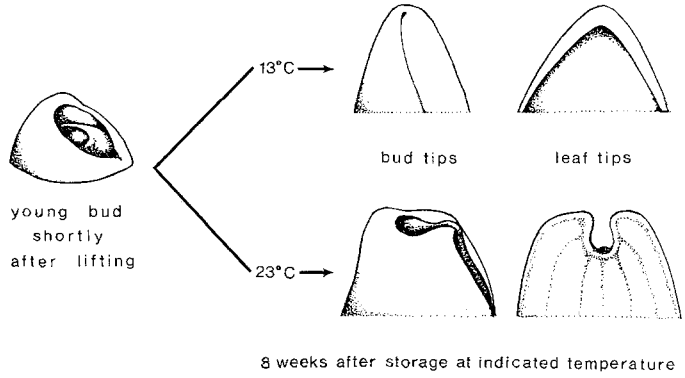

Fig. 3. Verandering in de vorm van de top van knoppen en jonge bladeren bij 'Red Champion' bij bewaartemperaturen van 13° en 23°C.

In 'Rose Copland' the formation of open buds could not be induced either by storage in atmospheres containing ethylene or at higher temperatures, although the growth of the buds was still inhibited.

From these findings it is concluded that ethylene, and in some cultivars also higher storage temperatures, can cause open buds. During the first few weeks after lifting the bulbs are most susceptable. Open buds caused by ethylene are the result of a relatively more rapid growth of the flower parts, as compared with the growth of the leaves as a consequence of unequal growth inhibition. The changes in the degree of bud opening occurring during successive storage after exposure to ethylene show a relationship with differences in the growth recovery of the stamens and young leaves. In the case of 'Red Champion' open buds also result from the morphogenetic effect of the temperature on the tips of the leaves.

3. *The influence of mites*

In 'White Sail' no bud necrosis was found when mites were applied to bulbs stored in the absence of ethylene (treatment 1 in Table 2). When mites were applied to bulbs exposed to ethylene during the first few weeks after lifting, high percentages of bud necrosis were found, whereas bulbs exposed to ethylene in the same period but not contaminated with mites, remained almost free of bud necrosis (treatments 2, 3, and 5 in Table 2). When mites were applied to bulbs exposed to ethylene later in the storage period, bud necrosis was negligible (treatment 4 in Table 2).

As shown in the preceding section, only early exposure to ethylene causes open buds. The results of the contamination experiments show that mites cause bud necrosis only in bulbs exposed to ethylene soon after lifting. Therefore, it is concluded that mites cause bud necrosis only in bulbs with open buds.

In 'Red Champion' the influence of mites on bulbs stored at 13° and 23°C is different. In bulbs stored at 13°C, bud necrosis was found only to some extent when the mites were applied in the middle of August. Later contamination gave hardly

Table 2. Percentage bud necrosis in tulip bulbs 'White Sail' stored at 20 °C with and without ethylene treatment (3 ppm) and with or without contamination with mites. After contamination, the bulbs were incubated for 6 weeks at air humidities (r.h.) of 50 or 90% (n = 60).

Exposure to ethylene before contamination	Contaminated with mites		Not contaminated with mites	
	r.h. 50%	r.h. 90%	r.h. 50%	r.h. 90%
1. none	0	0	0	0
2. from 15/7 to 26/8	92	–	15*	–
3. from 5/8 to 1/10	70	84	3	3
4. from 1/0 to 22/10	0	3**	0	0
5. from 5/8 to 1/10 and from 14/10 to 12/11	61	76**	0	3

* Mites present due to accidental contamination.
** All flowers became blasted during ethylene treatment.

Table 2. Percentage kernrot in bollen van 'White Sail', bewaard bij 20 °C, die al of niet behandeld waren met ethyleen (3 dpm) en al of niet werden besmet met mijten. Na de ontsmetting zijn de bollen gedurende 6 weken geïncubeerd bij een relatieve luchtvochtigheid van 50 of 90% (n = 60).

any bud necrosis. A decreasing effect of contamination with mites in later phases of bud development is distinctly observable as the storage period proceeds (Table 3). In bulbs stored at 23 °C and contaminated with mites, the percentages of bud necrosis were high in all experiments throughout the storage period. A decreasing effect of contamination with mites in the bulbs contaminated later, such as was observed in bulbs stored at 13 °C, was not obvious.

As in 'White Sail', the differences in the effect of mite contamination correspond consistently with differences in the occurrence of open buds, and it may be concluded that in 'Red Champion', too, bud necrosis is caused by mite contamination in bulbs with open buds.

Table 3. Percentage bud necrosis in bulbs 'Red Champion' stored at 13 ° or 23 °C and contaminated with mites at different times (n = 30).

Date of contamination	Storage temperature 23 °C			Storage temperature 13 °C		
	with mites	without mites	% open buds	with mites	without mites	% open buds
Aug. 17	78	10*	90	32	0	46
Aug. 31	89	23*	90	7	0	20
Sept. 14	73	0	87	3	0	7
Sept. 29	60	20*	83	0	3	4
Oct. 14	53	3*	92	–	–	0
Oct. 27	70	20*	87	–	–	0

* Mites present due to accidental contamination.

Tabel 3. Percentage kernrot in bollen van 'Red Champion', die bij 13 ° of 23 °C bewaard werden en op verschillende data met mijten werden besmet (n = 30).

Besides the dependence of bud necrosis on the presence of open buds and mites, it is clear that the relative air humidity (r.h.) also has an influence. It can be seen from Table 2 that at a r.h. of 50% in the storage room, the percentage of bud necrosis is lower than at 90% r.h. In uncontaminated bulbs an influence of the r.h. is not obvious.

From these data it is clear that higher air humidities enhance the influence of mite contamination. Although the present findings do not explain the influence of this factor, it can be suggested that it enhances the activity of mites and outgrowth of fungi and bacteria on infected flower parts. Enhancement of the growth of mite populations by higher air humidities was observed during the rearing of the mites.

4. *The ethylene production of Fusarium-infected tulip bulbs*

The production of ethylene by healthy tulip bulbs was too low to be detectable by gas chromatography in samples of the surrounding air. *Fusarium*-infected bulbs, to the contrary, produced relatively large amounts of ethylene. The production seemed to be temperature dependent and was highest at 20 °C (Fig. 4). Notwithstanding the large differences between the highest and lowest production rate at each temperature, which showed no correlation with a certain degree of decay, the mean values at 13°, 17°, and 20 °C were significantly divergent.

Calculations based on the production rates of ethylene by *Fusarium*-infected tulip bulbs and the amount of fresh air required in storage rooms, showed that the ethylene level in storage rooms under conditions of poor ventilation can rise to such a degree that biologically active concentrations capable of causing open buds will occur if *Fusarium*-infected bulbs are present. These calculations will be discussed elsewhere.

Fig. 4. Emanation of ethylene from Fusarium-infected tulip bulbs 'White Sail' at several storage temperatures. The standard deviation is indicated.

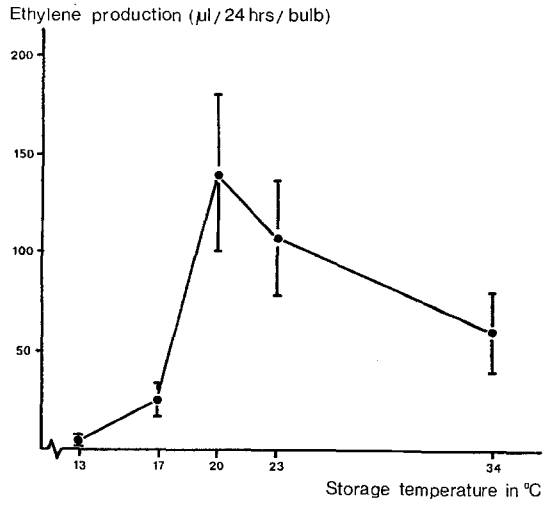

Fig. 4. De hoeveelheden ethyleen afgegeven bij verschillende bewaartemperaturen door bollen 'White Sail' die met Fusarium waren geïnfecteerd. De standaard-deviatie is aangegeven.

Discussion

The data presented here prove the validity of the hypothesis put forward in the introduction. In the first place, it was demonstrated experimentally that low concentrations of ethylene caused such abnormal growth that the buds opened and the stamens even protruded from the buds. In the case of 'Red Champion' open buds resulted from storage at temperatures of 20° to 23 °C. Secondly, the results show that bud necrosis only occurs when mites are present on these open buds. From this it may be concluded that the young leaves in normally closed buds prevent the penetration of mites and protect the weaker floral organs. This explains why the first symptoms are always found in the stamens (de Munk and Beijer, 1971).

Bud necrosis in tulips resembles certain disorders caused by mites in other crops, such as bud necrosis in carnations (Stewart and Hodgkiss, 1908; Heald, 1928; Cooper, 1940; Andreucci, 1962), phyllody of chrysanthemums (Breakey and Batchelor, 1950; French, et al., 1968), and flower bud necrosis in Michaelmas Daisies (Harris, 1968). Carter (1962) reports a number of disorders caused by mites of the eriophyid type which kill or injure young buds. The common feature in all these disorders is that mites penetrate young generative buds and cause an internal rot on flower parts, while the outer parts of the buds continue to appear healthy. In the case of bud necrosis in Michaelmas Daisies the disorder is found more frequently in glabrous varieties than in pilose varieties with buds better protected against penetration of mites. Here, as for bud necrosis in tulip bulbs, a morphological determined condition is the principal prerequisite for the occurrence of the disorder.

The results also show that the induction of open buds in tulip bulbs caused by ethylene depends on unequal growth inhibition of the young leaves and flower parts. In some cases differences in growth inhibition of different parts of the same plant are explained by differences in the action of ethylene on cell expansion, cell division, and auxin concentration (Burg, 1962; Burg et al., 1971). The growing points of tulips and, after flower formation, the developing young buds represent systems consisting in part of meristematic cells and in part of expanding cells. Too little is known about these systems to permit assessment of the contribution of the processes of cell division and expansion to the elongation growth of the different parts of tulip buds. Since the stamens are one of the most dominant organs within developing buds (Mulder and Luyten, 1928; Beijer, 1952) having an active synthetizing metabolism (Wiermann, 1970), and since they react in different degrees to ethylene during their development, these organs offer a good object for further investigation.

The stages of bud deformation described in this paper may suggest that they reflect the ontogeny of open buds. A more detailed investigation is needed, however, before the dynamic process of bud development can be described. The stages have served only as a scale to evaluate the degree of bud deformation.

The processes of decay in necrotic buds appear to be very complicated, involving the host plant, mites, bacteria, and fungi. It was suggested earlier that mites can consume healthy stamen tissue and are vectors of the micro-organisms (de Munk, 1971a), but it is not yet clear just how the metabolism of the host is involved in the process of decay. The influence of ethylene is approached as a morphogenetic factor. However, ethylene may also change the composition and metabolism of the stamens, in such a manner that they become more attractive to the mites and micro-organisms.

In preliminary experiments in our institute a breakdown of starch in stamens from ethylene-treated bulbs, exudation of stamens before flower blasting, an increase in the respiration rate of dissected stamens and intact bulbs, and gummosis of bulb scales and stem plate have been observed (Kamerbeek et al., 1971). The genesis of bud necrosis in 'Red Champion' stored in the absence of ethylene at higher storage temperatures can be considered to contradict this suggested influence of ethylene, but in this cultivar some of these metabolic changes can also be induced by higher storage temperatures. The analysis of factors influencing the processes of decay requires further investigation.

The growth inhibition described in this paper was caused by ethylene at a concentration of 3 µl/litre in bulbs stored at 20 °C. It is important, not only for practical purposes but also to collect relevant information, to know the influence of ethylene administered in other concentrations to bulbs stored at other temperatures. The results of investigations on this point will be published elsewhere.

To prevent bud necrosis during the storage and transportation of tulip bulbs, it is recommended that bulb stocks be carefully inspected to remove as many *Fusarium*-infected bulbs as possible; that storage of tulip bulbs in the neighbourhood of other sources of ethylene (fruit, flowers, apparatus producing oil combustion gases) be avoided; that storage rooms be ventilated with fresh air as much and as constantly as possible; that measures be taken against the spread of mites. These recommendations have been published in detail elsewhere (de Munk, 1971b and c).

Samenvatting

Kernrot, een bewaarziekte in tulpen. III. De invloed van ethyleen en mijten

Proeven toonden aan dat kernrot in tulpebollen wordt veroorzaakt door mijten (*Rhizoglyphus echinopus* Fumouze & Robin en *Tyrophagus* spp.) als deze tijdens de bewaring in de bloemknoppen binnendringen (Tabel 2 en 3). Dit konden mijten alleen bij knoppen die aan de top open waren; normaal zijn de knoppen gesloten. Open knoppen ontstonden door blootstelling van de bollen aan ethyleen (3 dpm) bij 20 °C vlak na het rooien (Tabel 1 en Fig. 2) en bij bollen van 'Red Champion' ook door bewaring bij hoge temperaturen (20 tot 23 °C) in een ethyleen-vrije atmosfeer. Dit laatste berustte op een afwijkende differentiatie in de top van de pas aangelegde bladeren (Fig. 3). Ethyleen kon open knoppen doen ontstaan, doordat de lengtegroei van de jonge bladeren sterker werd geremd dan die van de meeldraden (Fig. 1). De snellere groei van de binnenste delen van de knop resulteerde dan in open knoppen. Het verschil in gevoeligheid van beide organen voor ethyleen was het grootst vlak na het rooien en nam af gedurende de bewaring. Later in het seizoen (na augustus) was de remming van meeldraden en jonge bladeren gelijk (100 %) en ontstonden geen open knoppen meer. Ethyleen veroorzaakte toen verdroging van de bloemknoppen.

De door ethyleen geïnduceerde groeiremming was ten dele reversibel. De groei van de jonge bladeren herstelde gedeeltelijk; de groei van de meeldraden geheel, tenzij verdroging van deze organen had plaats gehad als gevolg van blootstelling aan ethyleen laat in het seizoen. Door het verschil in reversibiliteit van de groeiremming van meeldraden en loofbladen kan de toename van de mate van knopafwijking tijdens verdere bewaring na de toediening van ethyleen verklaard worden (Tabel 1).

De ethyleenafgifte van bollen die met *Fusarium oxysporum* f. *tulipae* waren geïnfecteerd, is gemeten. De geproduceerde hoeveelheden ethyleen bleken afhankelijk te zijn van de bewaartemperatuur. Gemiddeld werd de grootste hoeveelheid gevonden bij 20 °C, namelijk: 140 µl per dag per bol (Fig. 4). Deze hoeveelheid blijkt voldoende te zijn om in slecht geventileerde ruimten bij bollen die niet door *Fusarium* zijn aangetast, bovengenoemde abnormale groei te veroorzaken.

References

Andreucci, E., 1962. Osservazioni sul marciume centrale dei fiori di Garafano. Riv. Ortoflorofruttic. ital. 46: 171–179.

Beijer, J. J., 1952. De ontwikkelingsstadia van de tulp. Laboratorium voor Bloembollenonderzoek, Lisse, Publ. No. 92, pp. 7.

Breakey, E. P. & Batchelor, G. S., 1950. Phyllody of *Chrysanthemum* and the eriophyid mite *Paraphytoptus chrysanthemi* Keifer. Ann. ent. Soc. Am. 43: 492–494.

Burg. S. P., 1962. The physiology of ethylene formation. A. Rev. Pl. Physiol. 13: 265–302.

Burg, S. P., Apelbaum, A., Eisinger, W. & Kang, B. G., 1971. Physiology and mode of action of ethylene. Hort. Sci 6: 359–364.

Carter, W., 1962. Insects in relation to plant disease. Interscience Publishers, New York.

Cooper, K. W., 1940. Relations of *Pediculopsis graminum* and *Fusarium poae* to central bud rot of carnations. Phytopathology 30: 853–859.

French, N., Vernon, J. D. R. & Woodville, H. C., 1968. Cyclamen mite (*Steneotarsonemus pallidus* Banks) on chrysanthemums. Pl. Path. 17: 143.

Harris, K. M., 1968. Cyclamen mite: a pest of Michaelmas Daisies. Pl. Path. 17: 71–75.

Heald, F. D., 1926. Manual of plant diseases. McGraw-Hill, New York.

Kamerbeek, G. A., Verlind, A. L. & Schipper, J. A., 1971. Gummosis of tulip bulbs caused by ethylene. In: First int. Symp. Flowerbulbs, Noordwijk/Lisse 30 March–4 April, 1970. Vol. I: 167–172. Int. Soc. hort. Sci., Den Haag.

Mulder, R. & Luyten, I., 1928. De periodieke ontwikkeling van de Darwin tulp. Verh. K. ned. Akad. Wet. Afdeeling Natuurkunde, Sectie 2, 26 (3).

Munk, W. J. de, 1971a. Bud necrosis, a storage disease of tulips. II. Analysis of disease-promoting storage conditions. Neth. J. Pl. Path. 77: 177–186.

Munk, W. J. de, 1971b. Kernrot in tulpen; een kwalijk gevolg van het zuur. BloembollCult. 81: 1030–1031.

Munk, W. J. de, 1971c. Die Kernfäule der Tulpen. Gartenwelt 71: 399–400.

Munk, W. J. de & Beijer, J. J., 1971. Bud necrosis, a storage disease of tulips. I. Symptoms and the influence of storage conditions. Neth. J. Pl. Path. 77: 97–105.

Stewart, F. C. & Hodgkiss, H. E., 1908. The *Sporotrichum* bud rot of carnations and the silver top of June grass. Techn. Bull. N.Y. St. agric. Exp. Stn. 7: 83–119.

Wiermann, R., 1970. Die Synthese von Phenylpropanen während der Pollenentwicklung. Planta 95: 133–145.

Wijvekate, M. L., 1960. Verklarende statistiek, Utrecht.

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