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Bud necrosis, a storage disease of tulips
IV. The influence of ethylene concentration and storage temperature on bud development

W. J. DE MUNK

Bulb Research Centre, Lisse

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Abstract

Ethylene in concentrations as low as 0.05 ppm inhibited the elongation growth of the main generative bud within tulip bulbs during storage after lifting. The sooner the ethylene was administered after lifting and the higher the storage temperature, the higher the concentration of ethylene needed to obtain the same degree of inhibition. Fifty percent inhibition was found at concentrations between 0.05 and 10 ppm.

Stamens within the buds were inhibited to a degree which was generally lower compared with the leaves; the largest differences were found at 13°C, whereas at 23°C the degree of inhibition was nearly equal.

Open buds (which result from unequal growth of stamens and young leaves and are the prerequisite of bud necrosis) were induced by exposure to ethylene in concentrations as low as 0.1 ppm. This phenomenon occurred in bulbs exposed to ethylene for 6 weeks at 17°C shortly after lifting; at other temperatures and later exposure times, higher concentrations were needed to obtain the effect.

During storage after exposure to ethylene, growth resumed and the degree of bud deformation mostly decreased; in bulbs that had been treated later, an increase was found when the ethylene concentration had been higher than 1 ppm.

After planting, shoots emerging from ethylene-treated bulbs were shorter, basal internodes of the stem were shorter if the concentration was 1 ppm or higher, and the width of leaves was reduced after early exposure.

Introduction

Bud necrosis in tulip bulbs, a storage disease frequently occurring in stocks of bulbs stored under conditions resulting in poor ventilation, is caused in many cultivars by ethylene and mites. In storage rooms the source of ethylene is often bulbs infected with *Fusarium oxysporum* Schlecht *f. tulipae* Apt. This gas causes stronger inhibition of elongation growth of the young leaves of tulip buds than of the floral organs within these buds. As a consequence, the floral organs grow faster than the enveloping young leaves and the buds open, allowing mites to penetrate the bud and initiate decay starting at the stamens (De Munk, 1972).

In previous experiments (De Munk, 1972) tulip bulbs were exposed to ethylene at a concentration of 3 ppm and stored at 20°C. The results raised questions concerning the influence of other ethylene concentrations and storage temperatures on the development and deformation of the buds.

A question also to be answered is: to what degree the buds will recover from ethylene damage if bud necrosis does not occur? The effect of ethylene on growth was

studied only in bulbs exposed during the first ten weeks after lifting, because later exposure to ethylene causes flower-bud blasting (De Munk, 1972). The results concerning that disorder will be published separately (De Munk, in preparation).

Material and methods

Tulip bulbs from commercial stocks of the cultivar 'White Sail' (circumference 11–12 cm) were lifted mid July and stored at 13°, 17°, 20°, and 23°C until the end of November. Samples of 90 bulbs each were treated with ethylene for 6 weeks in closed 5-litre plastic pails through which an airstream containing 0, 0.05, 0.1, 0.5, 1, 10, or 100 ppm ethylene was conducted. Two series of treatments were carried out; the first was started on July 14th and the second on August 11th.

To prevent bud necrosis, mites were controlled as much as possible by dipping the bulbs in a suspension of 0.2% endosulfan before exposure to ethylene.

To examine the buds, bulbs from samples of ten bulbs each were dissected after 2 and 4 weeks of exposure, at the end of the exposure period, and at the end of the storage period in November. The length of buds and stamens was measured and the degree of inhibition calculated. Bud deformation was estimated according to a scale from 0 to 6 (De Munk, 1972), scores of 3 and higher indicating that the buds are open and can be invaded by mites.

In the middle of November the remaining bulbs of the samples were planted, cooled for 14 weeks, and brought to flowering in a greenhouse at 18° to 20°C. Several measurements were carried out during the final developmental period. Statistical calculations were performed according to Wijvekate (1960).

Results

Inhibition of elongation growth of the young leaves. The inhibition of elongation growth after 2 weeks' exposure to ethylene was of the same order as after 4 and 6 weeks (Fig. 1A, representing the data of 17°C-bulbs). Because of this similarity, mean percentages of growth inhibition were calculated from the values obtained after 2, 4, and 6 weeks (Table 1). These data show that the inhibition increases regularly with increasing concentrations of ethylene. Doses of 10 and 100 ppm gave complete inhibition, and even a concentration as low as 0.05 inhibited to some extent.

Fifty percent inhibition of growth was found at concentrations between 0.05 and 10 ppm, depending on time of exposure to ethylene (series I and II) and the storage temperature. At higher temperatures and with earlier ethylene administration, the high concentrations were needed to obtain this level of inhibition. The influence of the ethylene concentration is, however, much stronger than the influence of the storage temperature and the time of ethylene administration. This is shown by a comparison of the totals of the inhibition percentages (Table 1).

It is concluded that the inhibition, which increases with increasing ethylene concentrations, is strongest at lower temperatures and later exposure.

Inhibition of elongation growth of the stamens. At the beginning of the experiments the stamens had just been formed, and their length and growth during the first two weeks of the ethylene treatments were too small to permit exact measurement and calculation

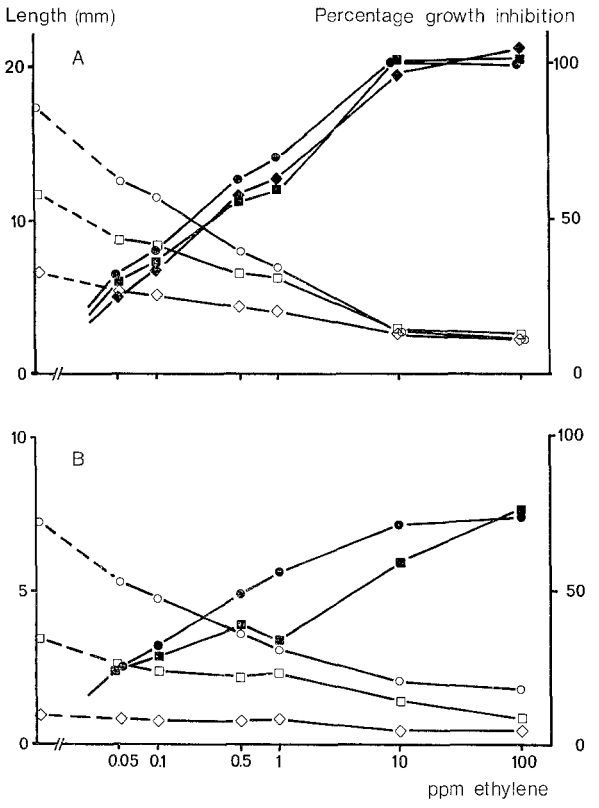

Fig 1. Length (open symbols) and inhibition of growth (solid symbols) of buds (A) and stamens (B) of bulbs 'White Sail', stored at 17 °C and exposed to ethylene in various concentrations for 2 weeks (◇ and ◆), 4 weeks (□ and ■), and 6 weeks (○ and ●). Ethylene treatments started on July 14th, immediately after lifting of the bulbs.

Fig 1. Lengte (open tekens) en groeiremming (gevulde tekens) van knoppen (A) en meeldraden (B) in bollen 'White Sail', bewaard bij 17 °C en blootgesteld aan verschillende concentraties ethyleen gedurende 2 (◇ en ◆), 4 (□ en ■) of 6 weken (○ en ●). De ethyleenbehandelingen begonnen 14 juli, direct na het rooien van de bollen.

Table 1. Mean percentages of growth inhibition of buds in bulbs 'White Sail', stored at various temperatures after exposure to ethylene at various concentrations (n = 30). Treatments of series I and II started on July 14 and August 11, respectively.

Ethylene concentrations (ppm)	Series I: storage temperature (°C)					Series II: storage temperature (°C)				
	13	17	20	23	total	13	17	20	23	total
0.05	29	30	16	5	80	47	38	32	40	157
0.1	43	37	26	13	119	58	56	47	38	199
0.5	68	60	43	30	201	80	79	68	58	285
1	76	65	57	38	236	74	83	79	61	297
10	107	100	96	87	390	88	88	91	88	355
100	103	102	97	95	397	95	86	90	90	361
Total	426	394	335	268		442	430	407	375	

Tabel 1. Groeiremming van knoppen (in %) in tulpebollen 'White Sail', bewaard bij verschillende temperaturen en blootgesteld aan verschillende concentraties ethyleen (n = 30). De ethyleen-behandelingen van de series I en II begonnen respectievelijk op 14 juli en 11 augustus.

of reliable inhibition percentages (Fig.1B). Mean percentages of growth inhibition were therefore calculated only from data obtained after 4 and 6 weeks of exposure to ethylene (Table 2). It is evident from the results that, as for young leaves, the inhibi-

Table 2. Mean percentages growth inhibition of stamens in bulbs 'White Sail', stored at various temperatures after exposure to ethylene at various concentrations (n = 20). Ethylene treatments of series I and II started on July 14 and August 11, respectively.

Ethylene concentrations (ppm)	Series I: storage temperature (°C)					Series II: storage temperature (°C)				
	13	17	20	23	total	13	17	20	23	total
0.05	23	25	16	11	75	13	15	19	30	77
0.1	31	31	18	11	91	20	25	27	35	107
0.5	49	44	28	26	147	35	45	53	71	204
1	47	44	29	26	146	37	55	59	70	221
10	60	66	64	78	268	52	66	78	92	288
100	67	76	76	85	304	52	66	83	93	294
Total	277	286	231	237		209	272	319	391	

Tabel 2. Groeiremming van meeldraden (in %) in tulpebollen 'White Sail', bewaard bij verschillende temperaturen, na blootstelling aan verschillende concentraties ethyleen (n = 20). De ethyleen-behandelingen van de series I en II begonnen respectievelijk op 14 juli en 11 augustus.

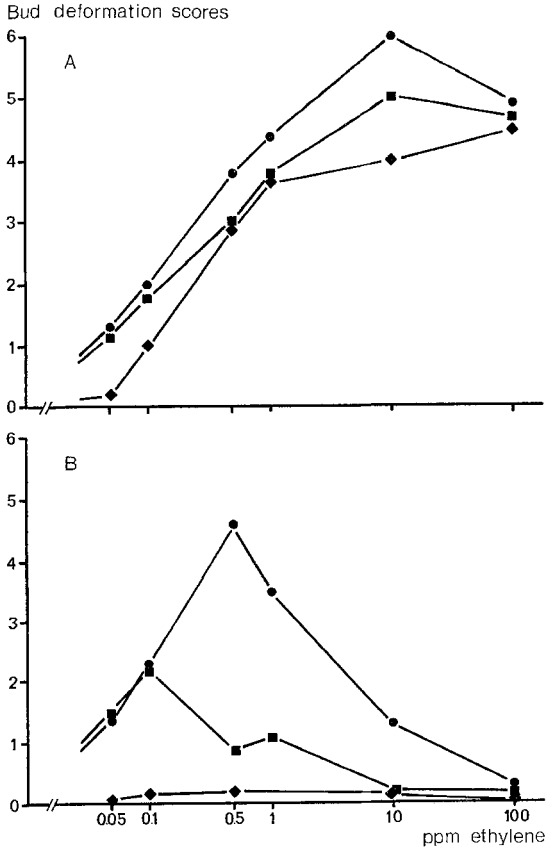

Fig. 2. Bud deformation expressed in scores (scale De Munk, 1972) of bulbs 'White Sail' stored at 20 °C and exposed to ethylene at various concentrations for 2 weeks (▲), 4 weeks (■), and 6 weeks (●) in different periods. The ethylene treatments started on July 14 (A) and August 11 (B).

Fig. 2. Knopafwijkingen (schaal volgens De Munk, 1972) in bollen 'White Sail', bewaard bij 20 °C en blootgesteld aan verschillende concentraties ethyleen gedurende 2 (▲), 4 (■) of 6 weken (●) van de bewaarperiode. A: de ethyleen-behandelingen begonnen op 14 juli; B: de ethyleen-behandelingen begonnen op 11 augustus.

tion increased with increasing ethylene concentrations. The degree of inhibition, however, is lower than that found for the leaves: inhibition was not complete at 100 ppm and very slight at 0.05 ppm. This was found for all treatments except after some applied to bulbs at 23 °C.

In the first series the inhibition tended to decrease as the storage temperature increased (except at 10 and 100 ppm ethylene) whereas in the second series the inhibition increased with increasing storage temperature. At 13 ° and 17 °C the inhibition in the first series was somewhat stronger than in the second series, whereas at 20 ° and 23 °C it was lower. As was observed for leaves, the influence of the phase of development and the storage temperature can be seen here, but is again of less importance than the concentration of ethylene.

Aberrant bud shape. In bulbs of the first series, scores of 3 or higher (open buds) were found after only two weeks of exposure to 0.5 ppm or more ethylene (Fig. 2A). The highest scores were found after 6 weeks of exposure to 10 ppm of the gas. In the second series scores of 3 or higher were found only after six weeks of exposure to 0.5 and 1 ppm ethylene (Fig. 2B).

Table 3. Mean scores of bud deformation (scale according to De Munk, 1972) for bulbs 'White Sail' stored at various temperatures and exposed to ethylene at various concentrations for 6 weeks. Ethylene treatments of series I and II started on July 14 and August 11, respectively. a: evaluation immediately after exposure to ethylene; b: evaluation in the middle of November after the total storage period (n = 10).

Ethylene concentration (ppm)	Storage temperatures (°C)							
	13		17		20		23	
	a	b	a	b	a	b	a	b
Series I								
0	0	0	0	0.6	0	0	0	0
0.05	2.0	2.0	1.9	1.8	1.3	1.2	0	0
0.1	2.4	2.5	3.2	1.9	2.0	2.1	1.5	0
0.5	4.0	3.6	4.6	3.0	3.8	2.5	1.5	0
1	4.5	3.9	5.3	4.1	4.4	3.3	3.2	3.1
10	5.8	4.1	6.0	4.6	6.0	4.2	4.8	3.1
100	5.3	4.2	5.7	4.2	4.9	3.5	4.4	3.0
Series II								
0	0	0	0	0.6	0	0	0	0
0.05	0	0.2	0.6	0	1.4	0.2	0	0
0.1	1.6	1.0	1.5	0.2	2.3	0.8	0.6	0.2
0.5	2.0	1.5	2.9	2.0	4.6	1.8	0.6	1.1
1	1.6	2.1	2.6	2.4	3.5	2.8	0	1.8
10	1.0	2.8	2.9	3.6	1.3	4.5	0	0.6
100	0.5	2.9	1.9	4.5	0.3	3.9	0	0

Tabel 3. Knopafwijkingen (volgens schaal De Munk, 1972) in tulpebollen 'White Sail', bewaard bij verschillende temperaturen na blootstelling aan verschillende concentraties ethyleen gedurende 6 weken. De ethyleen-behandelingen van de series I en II begonnen respectievelijk op 14 juli en 11 augustus. a: beoordeling direct na afloop van de ethyleen-behandeling; b: beoordeling na afloop van de gehele bewaarperiode (midden november).

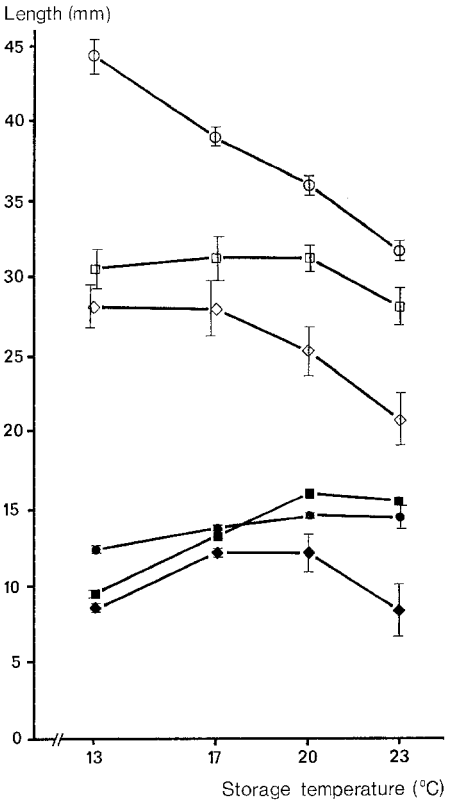

Fig. 3. Length of stamens (solid symbols) and buds (open symbols) of bulbs 'White Sail' determined at the end of the storage period (middle of November) after storage at different temperatures and exposure to ethylene for 6 weeks from July 14th until August 25th. Concentrations of ethylene: 0 (● and ○), 1 ppm: (■ and □) and 10 ppm (◆ and ◇).

Fig. 3. Lengte van meeldraden (gesloten tekens) en knoppen (open tekens) in bollen 'White Sail', gemeten aan het eind van de bewaarperiode (midden november) na bewaring bij verschillende temperaturen en blootstelling aan ethyleen van 14 juli tot 25 augustus. Ethyleen-concentraties: 0 (● en ○), 1 (■ en □) en 10 ppm (◆ en ◇).

With regard to the concentration, the reaction showed an optimum which occurred at a lower concentration in later exposed bulbs. Bulbs of the second series, which were in a later developmental phase, were also less susceptible with regard to the duration of the exposure but after longer exposure equally or more susceptible at low concentrations (0.5 ppm and lower).

An influence of the storage temperature is evident from Table 3, columns a. In the first series the highest scores at each concentration (except at 0.05 ppm) were found at 17 °C and the lowest at 23 °C. Score 3 was reached in 17 °-bulbs at a concentration of about 0.1 ppm, in 13 °- and 20 °-bulbs between 0.1 and 0.5 ppm, and in 23 °-bulbs at about 1 ppm. In the second series the highest scores were found at 20 °C and the lowest at 23 °C. Score 3 was exceeded only at 20 °C and was reached in many bulbs at 17 °C.

Finally, a delayed effect of ethylene was observed, changing the degree of bud deformation and occurring during the period of storage after exposure to the gas. This can be seen by comparing columns a and b in Table 3.

Almost all of the scores of the first series decreased with time. Those of the second series decreased only when the bulbs had been exposed to low concentrations of ethylene; after exposure to 10 and 100 ppm, the scores increased. This increase led to the opening during subsequent storage of a large number of buds belonging to bulbs stored at 13 °, 17 °, and 20 °C (score 3 and higher).

From these data it is concluded that the development and the degree of bud deformation depends on:

1. the ethylene concentration;
2. the developmental phase of the buds in which exposure occurs;
3. the duration of exposure to ethylene;
4. the storage temperature;
5. certain conditions after the exposure to ethylene.

Resumption of growth after ethylene treatment. In the middle of November the stamens of bulbs exposed to low concentrations of ethylene (up to 1 ppm) were usually (except at 13 °C) as long as or slightly longer than those of untreated bulbs. (Fig. 3, from data of the first series). Post-treatment growth of the stamens must therefore have been faster or lasted longer in treated bulbs than in untreated bulbs. The growth of the buds recovered also, but the arrears in length persisted (Fig. 1 and 3). The largest differences were found between buds of untreated bulbs and buds of bulbs exposed to 10 ppm (Fig. 3) or higher.

After the bulbs had been planted and cooled, the shoots emerging from ethylene-treated bulbs were shorter than the controls (Table 4). The higher the concentrations during exposure, the shorter the shoots.

When the treated bulbs reached the flowering stage it was found that the basal internodes of the stems were shorter after exposure to 10 and 100 ppm and the leaves narrower than normal (Table 4). The latter effect was found only for bulbs exposed to ethylene during the first weeks after lifting. The higher the ethylene concentration had

Table 4. Mean length of shoots and basal internodes and width of the basal leaves (in cm) of tulips 'White Sail' stored at various temperatures and exposed to ethylene in various concentrations for 6 weeks in the period shortly after lifting. Ethylene treatments of series I and II started on July 14 and August 11, respectively. The shoot length was determined after cooling, i.e. at the beginning of the period of growth in the greenhouse, the other determinations were made at the onset of flowering. (Standard error for length of shoots and internodes ranging from 0.20–0.50, and for width of the leaves from 0.04–0.21).

Ethylene concentrations (ppm)	Shoot length		Length of basal internode		Width of basal leaf	
	series I	series II	series I	series II	series I	series II
0	14.1	14.1	11.8	11.8	4.6	4.5
0.1	13.7	13.3	12.0	11.7	4.1	4.5
1	12.5	12.2	12.0	11.1	3.8	4.5
10	10.9	10.0	10.5	10.7	3.6	4.6
100	10.5	9.7	9.9	9.0	3.3	4.3

Tabel 4. Lengte (in cm) van spruiten en onderste internodiën en breedte van de onderste bladeren van tulpen 'White Sail', bewaard bij verschillende temperaturen en blootgesteld aan verschillende concentraties ethyleen gedurende 6 weken van de bewaarperiode. De ethyleen-behandelingen van de series I en II begonnen respectievelijk op 14 juli en 11 augustus. De spruitlengte is gemeten na de koeling, d.w.z. bij het begin van de groeiperiode in de kas; de andere metingen zijn gedaan bij het begin van de bloei. (Standaardfout voor lengte van spruiten en indernodiën van 0,20–0,50 en voor de bladbreedte van 0,04 tot 0,21).

been, the larger the differences. Differences in the total length of the stem and length of the leaves and petals showed no correlation with prior ethylene treatments.

Thus, it is concluded that bulbs exposed to ethylene in the period shortly after lifting, can resume their growth during subsequent storage and after planting. However, the influence of early exposure to ethylene can be seen in dissected buds at the end of the storage period and, to some degree, in mature plants in the greenhouse. Plants developing from exposed bulbs were generally more tenuous.

Discussion

The lowest concentration of ethylene tested, i.e. 0.05 ppm, caused inhibition of elongation growth of both young leaves and stamens, and even lower concentrations may have this effect. The lowest concentration leading to open buds was 0.1 ppm. These concentrations are similar to those responsible for such effects as growth inhibition of dark-grown seedlings and epinasty and abscission of leaves, acceleration of fruit ripening (Burg, 1962; Pratt and Goeschl, 1969), gummosis of tulip bulbs (Kamerbeek et al., 1971), and an increased respiration rate in iris bulbs (Kamerbeek and Verlind, 1972).

Inhibition of elongation growth by ethylene is also known for other monocotyledonous plants (Van der Laan, 1934; Michener, 1938; Roberts, 1951), although Ku et al. (1970) found that the growth of rice coleoptiles is stimulated by low concentrations of ethylene. Most of the investigations were performed with Gramineae, but Hitchcock et al. (1932) showed that the growth of lilies, daffodils, tulips, and hyacinths is inhibited by various dilutions of illuminating gas containing ethylene. Their experiments with tulips were, however, restricted to actively growing, planted bulbs, and the strongest dilution of illuminating gas tested contained about 3 ppm ethylene. The conclusion that monocotyledonous plants are rather insensitive to ethylene (Burg and Burg, 1968; Hall and Morgan, 1964) is not confirmed by the present results with tulips.

Small differences between the degree of inhibition of the elongation growth of stamens and leaves appeared to be sufficient to induce open buds. Large differences in growth inhibition between stamens and leaves were, however, not always correlated with high scores of bud deformation: viz. for 23 °C-bulbs of the first series small differences in growth inhibition coincide with high scores whereas for 13°-bulbs of the second series large differences correspond with relatively low scores. As for the inhibition itself, an additional temperature effect is present. The genesis of open buds must therefore be understood as the result of several differential processes of which the elongation growth of stamens and young leaves are two components. Not only the length of the organs of the bud but also the width increases during development. Open buds can therefore originate from a process involving a kind of intrusive growth of the stamens or from failure of the young leaves to encircle the floral organs. With respect to the first process it is important to note that a phase of rapid elongation growth of the stamens, coinciding with meiotic divisions in pollen mother cells, occurs during storage in the period from the end of August to the end of September (unpublished results). This phase is reached earlier at 13 ° and 17 °C than at 20 ° or 23 °C. Furthermore, it can be seen from Fig. 3 that at 23 °C without ethylene, the stamens become longer and the leaves shorter than at 13 ° and 17 °C. These growth patterns

determine the ratio between the stamen length and the length of the first leaf in a characteristic way during development (De Munk, 1971). Similar ratios have been found for lilies (Erickson, 1948). It will depend on this ratio at the beginning of exposure to ethylene and on the growth rate of the stamens and leaves during and after exposure, whether stamens will reach the ceiling of the buds and grow out, and if so, how long this will take. This complex type of development and the differences in susceptibility to ethylene between the two types of organs during divergent developmental phases also explain why 'optimal' concentrations were found and why they differed for the two series of treatments.

The habit of the mature plants was changed by a delayed effect of ethylene. The leaves were narrower and basal internodes of the stem shorter. These changes cannot be used in practice as indications that ethylene was present during storage, because the same effects can be caused by temperature. For example, the decrease in the width of the leaves caused by exposure to ethylene in a concentration of 100 ppm at 23 °C, (5.4 cm versus 4.1 cm), was equivalent to the decrease caused by storage at 13 °C without ethylene (5.4 cm versus 3.9 cm). In this respect low temperature has an additive effect.

Samenvatting

Kernrot, een bewaarziekte in tulpen. IV. De invloed van ethyleenconcentratie en bewaartemperatuur op de knopontwikkeling

Ethyleen veroorzaakte in een concentratie van 0,05 dpm nog een aanzienlijke remming van de lengtetoename van de generatieve hoofdknop in tulpebollen van de cultivar 'White Sail', wanneer het gas kort na het rooien werd toegediend tijdens bewaring (Tabel 1). Bij toedoening van 10 dpm ethyleen was de remming in de meeste gevallen maximaal (Fig.1).

De lengtetoename van de meeldraden in de knoppen was in vergelijkbare behandelingen meestal minder sterk geremd dan van de jonge bladen die de knoppen omsluiten (Tabellen 1 en 2). Hoe eerder de bollen na het rooien aan ethyleen werden blootgesteld en hoe hoger de bewaartemperatuur was, des te hoger was de concentratie nodig om even sterk te remmen; afhankelijk van temperatuur en tijdstip van toedienning (of van de ontwikkelingsfase van de bol) werd een remming van 50 % gevonden bij concentraties tussen 0,05 en 10 dpm.

De laagste concentratie ethyleen waarbij open knoppen ontstonden – als gevolg van ongelijke groei van meeldraden en jonge loofbladen, de voorwaarde voor het ontstaan van kernrot – was 0,1 dpm. Dit werd geconstateerd bij bollen die bij 17 °C werden bewaard en direct na het rooien gedurende 6 weken aan ethyleen werden blootgesteld (Fig.2A en Tabel 3). Bij vroeg behandelde bollen werden de grootste knopafwijkingen gevonden bij 10 dpm ethyleen; bij later behandelde bollen bij een concentratie van 0,5 dpm (Fig.2A en B).

Bij bollen die bij 23 °C werden bewaard, was de ontwikkeling van de knopvorm minder afwijkend dan bij bollen die bij lagere temperatuur werden bewaard; bij behandelingen in het begin van het bewaarseizoen was dit het geval bij lage concentraties ethyleen, later in het seizoen ook bij hoge concentraties.

Na beëindiging van de toediening van ethyleen verminderde de mate van afwijking

in de meeste gevallen tijdens de verdere bewaring. Bij laat behandelde bollen, die aan 10 en 100 dpm waren blootgesteld, nam de afwijking daarentegen toe, zodat nog in een groot aantal bollen het stadium van 'de open knop 'werd bereikt (Tabel 3).

Hoewel na beëindiging van de ethyleen-toediening de groei van de knoppen zich tijdens de verdere bewaring herstelde, waren aan het eind van de bewaarperiode (midden november) en aan het begin van de groeiperiode in de kas na beëindiging van de koeling, de knoppen van behandelde bollen kleiner dan die van onbehandelde (Fig. 3 en Tabel 4). Bij het begin van de bloei waren de onderste internodiën korter na blootstelling aan hoge concentraties. De bladeren waren smaller wanneer de ethyleen-behandeling vroeg was toegediend; hoe hoger de concentratie ethyleen, hoe groter de verschillen ten opzichte van planten van onbehandelde bollen (Tabel 4).

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Address

Laboratorium voor Bloembollenonderzoek, Heereweg 345a, Lisse, the Netherlands.