pends on translocated material for metabolic substrate, a relatively high rate of photorespiration for the crops in question, added to normal dark respiration, may deprive non-photosynthetic tissue of substrate during growth and thus make white tissue more susceptible than green to deleterious effects of low O_2 or high CO_2 during storage. This presumed disadvantage would be enhanced when the proportion of white tissue is relatively large, as in cauliflower or head lettuce, or would be diminished when the proportion is small, or when the white and green tissues are in direct contact, as in the leaves of romaine lettuce or in the wrapper leaves of head lettuce.

This hypothesis also would be consistent with the finding that the midrib of head lettuce is very susceptible to various disorders not connected to CA storage, such as russet spotting, pink rib, rib discoloration, and internal rib necrosis (9).

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Effects of Applied Growth Substances on Growth of Shoot Apices Excised from Onions in Rest[1]

Sauveur Mahotiere[2], Robert C. Herner, and Frank G. Dennis
Department of Horticulture, Michigan State University, East Lansing, MI 48824

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Abstract. **Both 6-furfurylaminopurine (kinetin) and sucrose substituted for exposure to 10°C in promoting growth of excised shoots of onion (*Allium Cepa* L.), but no additive effect of these substances and exposure to 10°C was observed. Ammonium (5-hydroxycarvacryl) trimethyl chloride piperidine carboxylate (ACPC) nullified the promotive effect of 10°C treatment when applied prior to temperature treatment but was without effect when applied after temperature treatment. Sucrose and kinetin partially overcame the effect of ACPC. Abscisic acid (ABA) inhibited growth of onion shoots and nullified growth promoted by exposure to 10°C regardless of time of application of ABA. Kinetin reduced the effect of ABA but sucrose did not.**

Chemicals have been tested as a means of controlling rest in onion bulbs. The use of chemicals for prolonging rest has been more successful than for shortening it. For example, maleic hydrazide applied before harvest retards sprouting of onion bulbs very effectively (12) and ABA injected into onion bulbs has been reported to delay sprouting (2). Other chemicals such as ether and ethylene chlorhydrin (15) or applications of gibberellic acid (GA_3), a mixture of gibberellins 4 and 7 ($GA_{4/7}$), and napthaleneacetic acid (NAA) have not been successful in breaking rest in onions (22). However, the application of exogenous GA_3 induced bud break in various woody species (23) and its effectiveness in shortening rest in potato tubers is well documented (14, 18). The possible role of hormones in onion rest deserves more study if the phenomenon is to be understood and eventually controlled.

Excised shoot apices can be used as tools to study onion rest (17). Our object was to obtain information on the effects of temperature and growth substance treatments on growth of onion shoots excised from onion bulbs still in rest.

Materials and Methods

Bulbs of 'Spartan Banner', a good storage onion, were grown at the M.S.U. Muck Farm. After harvesting and curing, the scales were removed from the dormant bulbs to expose the shoot apices which were then washed with distilled water. For some experiments 'Abundance' and 'Downing Yellow Globe' were obtained from commercial growers after they were harvested and cured. All bulbs were held at 20°C until used and all experiments were begun within one month of harvest.

To test the effects of chemicals on growth of the excised shoots, the following substances were used either alone or in combination with a 10°C temperature treatment: sucrose (10%), (2 chloroethyl)phosphonic acid (ethephon) (100 ppm), kinetin (100 ppm), GA_3 or $GA_{4/7}$ (100 ppm), ABA (1 ppm),

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[2]Present address: Fort Valley State College, Division of Agriculture, Fort Valley, GA 31030.

Table 1. Effect of growth regulators on growth of excised 'Spartan Banner' onion shoots. Shoots were not exposed to 10°C.

Treatment	Growth[z] (% of initial length)
Water control	18.64a
Kinetin, (100 ppm)	37.13b
IAA (10 ppm)	17.19a
GA_3 (1000 ppm)	18.83a
$GA_{4/7}$ (1000 ppm)	18.67a
Ethephon (100 ppm)	14.83a

[z]Mean separation by Duncan's multiple range text, 5% level.

ACPC (100 ppm) and indoleacetic acid (IAA) (1 or 10 ppm). Distilled water was used as a control. The excised shoots were soaked in the test solution for 10 hr. Either before or after chemical treatment the excised shoots were exposed to 10°C, for 96 hr. After chemical treatment and/or exposure to 10°C, the excised shoots were planted in Petri dishes containing moist sand and held in the dark at 20°C.

The initial length and length after 96 hr at 20°C were measured in mm and the results expressed as percentage increase over initial length.

Four replicates of 5 shoots each were used and the Petri dishes containing the 5 shoots were arranged in a randomized complete block. The data were evaluated by analysis of variance and Duncan's multiple range test (9).

Results

When either IAA, GA_3, $GA_{4/7}$, ethephon, or kinetin was added to excised shoots which had not been exposed to 10°C, only kinetin was effective in promoting growth (Table 1). Kinetin treatment was as effective as exposure for 96 hr at 10°C in promoting growth of excised onion shoots (Table 2). There was no additive effect of kinetin and exposure to 10°C.

Sucrose (10%) was also as effective as exposure to 10°C for 96 hr in promoting growth of excised shoots (Table 3). There was no additive effect in promoting growth when sucrose (10%) was added to shoots exposed to 10°C.

ACPC, an inhibitor of gibberellin biosynthesis (2, 6), applied before exposure to 10°C was effective in inhibiting growth but was ineffective when applied afterwards (Table 4). When sucrose was added with ACPC, followed by exposure to 10°C there was no inhibition of ACPC on growth, in fact, there was some stimulation of growth (Table 3). Kinetin applied with ACPC partially overcame the inhibition of growth caused by ACPC in excised shoots which were and were not exposed to 10°C (Table 2).

ABA, in contrast with ACPC, was effective in inhibiting growth even when applied after exposure to 10°C (Table 5). Sucrose was without effect on ABA action, and kinetin was only partially effective in overcoming the ABA effect.

Discussion

Kinetin breaks the dormancy of buds and seeds of some species (10, 24), however, its injection into bulbs of onion had no effect on the rest period (2). Abdalla and Mann (1) have shown that derooting onion bulbs planted in moist sphagnum greatly retarded sprouting. A preliminary study on whole bulbs indicated that derooted onion bulbs planted in moist peat moss and injected with kinetin, sprouted nearly as fast as controls in which the roots were intact (16). There is evidence for roots being the source of cytokinins of several plant species (20, 21). The effect of kinetin on growth of excised onion shoots and the apparent ability of kinetin to substitute for exposure to 10°C suggested that both kinetin application and 10° treatment caused the production of some compound(s) which promoted growth. Our results suggest that cytokinins may be involved in the early stages of the breaking of rest in onions, and that the developing roots may produce cytokinins which promote sprouting. This is supported by work of Isenberg et al. (13).

The finding that sucrose substituted for exposure to 10°C in promoting growth suggested that carbohydrate metabolism may play a very important role in the early stages of termination of rest in onions. Cytokinins have been shown to affect carbohydrate metabolism (4). Cytokinin treatment or exposure to 10° may increase levels of readily metabolized carbohydrates which could then be available for growth.

Gibberellic acid breaks dormancy in buds and seeds (8, 10), but fails to do so in onion (2, 11, 22). It is also ineffective in promoting growth of excised onion shoots (Table 1). However, this failure does not necessarily exclude the participation of gibberellins in the dormancy-breaking process of onions, for they may act synergistically with other hormones. Furthermore, many different gibberellins are now known (7) and each may have a specific physiological role. Thus, gibberellins other than GA_3 and $GA_{4/7}$ may be involved in breaking dormancy of onion bulbs.

Both of the growth retardants, (2-chloroethyl)trimethylammonium chloride (chlormequat) and ACPC, are effective inhibitors of GA biosynthesis and most of their effects are attributed to this property (3, 5). If ACPC acted in a similar manner in our work, the fact that ACPC nullified the effect of exposure to 10°C when applied before but not after this treatment suggested that a gibberellin was synthesized during the 10°C exposure and exerted its effect when the tissue was trans-

Table 2. Effect of kinetin and ACPC, with and without exposure to 10°C, on subsequent growth of 'Spartan Banner' onion shoots at 20°C. Kinetin and ACPC were applied before the 10°C exposure.

Treatment	Growth (% of initial length)[z]	
	Not exposed to 10°C	Exposed to 10°C for 96 hr
None	21.9bc	45.0d
(100 ppm) ACPC	8.9a	17.1b
Kinetin (100 ppm)	42.6d	40.1d
ACPC (100 ppm) + kinetin (100 ppm)	24.9bc	29.7c

[z]Mean separation by Duncan's multiple range test, 5% level.

Table 3. Effect of sucrose, ACPC, and exposure to 10°C on subsequent growth of excised 'Downing Yellow Globe' onion shoots at 20°C.

Treatment	Growth[z] (% of initial length)
Water control	20.35a
10% sucrose	38.99b
96 hr at 10°C	39.18b
10% sucrose then 96 hr at 10°C	44.55b
100 ppm ACPC then 96 hr at 10°C	19.75a
100 ppm ACPC + 10% sucrose then 96 hr at 10°C	54.77c

[z]Mean separation by Duncan's multiple range test, 5% level.

Table 4. Effect of ACPC and exposure to 10°C on subsequent growth of excised 'Abundance' onion shoots at 20°C.

Treatment	Growth[z] (% of initial length)
Water control (no temp or chemical trt.)	14.40a
96 hr at 10°C	42.54c
100 ppm ACPC then 96 hr at 10°C	26.50b
96 hr at 10°C then 100 ppm ACPC	44.34c

[z]Mean separation by Duncan's multiple range test, 5% level.

Table 5. Effect of ABA, with or without kinetin or sucrose, on subsequent growth of excised 'Spartan Banner' onion shoots at 20°C.

Treatment	Growth (% of initial length)[z]	
	Not exposed to 10°C	Exposed to 10°C for 96 hr
None	16.0ab	37.6c
1 ppm ABA then temp trt.	9.0a	7.7a
Temp trt. then 1 ppm ABA	–	11.2ab
100 ppm kinetin	40.2c	–
1 ppm ABA + 100 ppm kinetin then temp trt.	14.0ab	18.4b
1 ppm ABA + 10% sucrose then temp trt.	7.1a	7.3a

[z]Mean separation by Duncan's multiple range test, 5% level.

ferred to conditions suitable for growth. This hypothesis is supported by Thomas' finding that chlormequat had no effect on sprouting of onions previously subjected to low temperature (22). Chilling sometimes predisposes a tissue to synthesize gibberellins but actual synthesis occurs after transfer to a higher temperature (19).

The fact that sucrose was effective in overcoming the inhibition of ACPC suggested that ACPC inhibited the production of carbohydrates available for growth either directly or indirectly by inhibiting gibberellin synthesis. Gibberellins have been shown to promote synthesis and/or release of hydrolytic enzymes which act on stored carbohydrates (6).

Finally, the actions of ABA and ACPC appear to differ when applied to excised onion shoots. ABA inhibited shoot growth when applied both before or after exposure to 10°C while ACPC was only effective when applied prior to 10°C exposure. Also, kinetin partially overcame shoot growth inhibition by ACPC.

In summary, we obtained evidence that the termination of dormancy of onions might be promoted by cytokinins, sucrose, and perhaps some other growth substance such as an unidentified gibberellin. We suggest that using the excised shoot system, the factors controlling dormancy can be investigated in relation to hormone levels and possibly to carbohydrate metabolism.

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