

Effect of Exogenous Hormones (NAA, BA, GA₃, and Ethephon), Chemical Inhibitors (MH and CIP) and Low Temperature on Sprouting of Onion Bulbs, *Allium cepa* L.

N. Benkeblia

Department of Food and Nutrition Sciences, Graduate School of Dairy
Science Research, Rakuno Gakuen University, 582 Bunkyo-dai
Midorimachi, Ebetsu, Hokkaido 069-8501, Japan

تأثير الهرمونات الدخيلة والمثبطات الكيميائية وانخفاض درجة الحرارة على نمو
البصل

نور الدين بنكيبلية

خلاصة: تم دراسة تأثير الهرمونات الدخيلة (ABA, NAA, BA, GA₃ وأنيثون) والمثبطات الكيميائية (MH, CIP) وعلاقتهم مع درجات الحرارة المنخفضة على نمو براعم البصل الخامل (المحصد حديثاً) وغير الخامل (محفوظة لفترة 6 أشهر على درجة حرارة 6-5 درجة مئوية). أظهرت الدراسة بأن تأثير هرمون NAA مع التبريد على نمو الأصيل مشابه لتأثير هرمون BA مع التبريد. إن معاملة الأصيل الخاملة في درجات حرارة منخفضة مع هرمون NAA و BA أدى في كلا الحالتين إلى الإنبات بعد 10 أسابيع بينما أدت معاملة الهرمونات بدون التبريد إلى الإنبات بعد 10 و 12 أسبوعاً، على التوالي. لوحظ عدم وجود تأثير للمثبطات الكيميائية MH و CIP و STS على نمو الأصيل التي لم تكن خاملة وكذلك لم يكن هناك تأثير معنوي لجيرالين و أنيلين على نمو الأصيل الخاملة. بالرغم من ذلك وجدت فروقاً معنوية بين GA₃ أو أنيلين على الأصيل المبردة والأصيل الأخرى التي تمت معاملة الأصيل الغير خاملة لوحظ وجود فروقاً معنوية بين الأصيل المعاملة ب GA₃ و ethephon و MH-CIP. كما بينت الدراسة تأثير نمو الأصيل بمعاملة ABA بينما أدت درجات الحرارة المنخفضة إلى انخفاض معنوي على تأثير تثبيط ABA.

ABSTRACT: The effects of exogenous hormones (ABA, NAA, BA, GA₃ and ethephon) and chemical inhibitors (MH and CIP), associated with cooling, on sprouting of dormant (freshly harvested) and non dormant (kept six months at 5-6 °C) onion bulbs were investigated. Effects of NAA and BA on the sprouting of the bulbs were similar, particularly when associated with cooling. Cooled + NAA and BA treated dormant bulbs, both sprouted after 10 weeks, while non-cooled bulbs sprouted after 10 and 12 weeks, respectively. Non-dormant bulbs sprouted after 3 and 4 weeks, respectively. No significant effect of MH, CIP and STS on sprouting of non dormant bulbs was observed. Gibberellin and ethylene were less effective on sprouting of dormant onion bulbs. Nevertheless significant differences were observed between GA₃ or ethylene treated and cooled bulbs, and others treated bulbs. For non dormant bulbs, significant differences were noted among GA₃-ethephon-control, and MH-CIP treated bulbs. Sprouting of bulbs was also affected by ABA treatment, while cooling slowed down significantly this inhibitory effect of ABA.

Keywords: *Allium cepa*, cooling, ethylene, sprouting.

Abbreviations: ABA: abscissic acid, BA: 6-benzylaminopurine, CIP: carbamate isopropyl N-phenyl, ethephon: 2-chloroethylphosphonic acid, MH: maleic hydrazide (1,2-dihydro-3,6-pyridazinedione), NAA: 1-naphthylacetic acid, STS: silver thiosulfate; GA₃: Gibberellic Acid.

Onion bulbs (*Allium cepa* L.), the most widely cultivated vegetables in the world, are extensively used for culinary purposes. During their storage, bulbs are exposed to changes in environmental conditions, such as atmospheric composition and temperatures, which can affect their quality attributes (Benkeblia,

2003a). Dormancy of onion bulb, defined as a temporary suspension of visible growth of the meristematic tissues of the sprouts, has a major impact on the storage of bulbs. The popular approach in the study of dormancy, has been to study the physiological basis of dormancy in sprouts during exposure to low

temperature (Dennis, 1987; Benkeblia and Selselet-Attou, 1999a, Benkeblia, 2003b) and exogenous hormones (Thomas, 1981).

The roles of hormones in the various growth and development processes of plants are extensively documented (Hartmann, 1992; Mohr and Schopfer, 1995; Weyers *et al.*, 1995). The involvement of these active molecules in dormancy and sprouting of onion bulbs has been little investigated (Abdel-Rahman and Isenberg, 1974; Thomas, 1981), and their cellular metabolism remains still unclear (Mohr and Schopfer, 1995), although it was demonstrated that specific aspects of growth and differentiation depend on quantitative and qualitative balances among the contents of the different endogenous hormones in the bulb tissues (Mohr and Schopfer, 1995; Sobeih and Wright, 1988).

Auxins are involved in bulb development during growing (Lercari and Ceccarelli, 1975). The high concentrations of auxins induce ethylene biosynthesis (Mathooko *et al.*, 1993), act on phenylalanine ammonia lyase (PAL) and peroxidase (POD) and affect phenolic concentrations, particularly flavonoides (Given *et al.*, 1988; Ke and Saltveit, 1988).

Isenberg *et al.* (1974) reported that gibberellins are associated with vernalization and floral induction of flower bulbs. Aung and Paterson (1974) reported that gibberellic acid (GA) concentration seems dependent on onion type, and high concentration was observed in dormant onions, while in non-dormant bulbs, the concentration was lower.

Cytokinins stimulate cellular division, and are present in all the parts of the plant (Kaminek *et al.*, 1997). However, their content is higher in root tissues where they are synthesized (Heller, 1982). During growing, Lercari and Micheli (1981) reported that cytokinins increase with the photoperiod, and during the last stage of bulbing.

Ethylene is an essential hormonal factor of onion bulbing (Lercari, 1983). However its role in sprouting is not clearly understood, although Benkeblia and Selselet-Attou (1999b) reported a significant but indirect effect of ethylene in the termination of dormancy of onions. According to Ke and Saltveit (1988), ethylene induces the activities of peroxidase (POD), phenylalanine ammonia-lyase (PAL) and oxidation of phenolic compounds in lettuce tissues. On the other hand, PAL and POD activities and phenolics seem to be linked to the dormancy and sprouting stages of onions, as previously reported (Benkeblia, 2000; Benkeblia and Selselet-Attou, 1999a).

Abscissic acid (ABA), an antagonist of indol acetic acid (IAA), increases in tissues during bulb maturity (Kato, 1966; Yamazaki *et al.*, 1995). Optimal maturity stage is characterized by an increase in ABA synthesis induced by drought stress, and dormancy is ABA dose-dependent (Matsubara and Kimura, 1991). Isenberg *et al.* (1974) reported that sprout inhibitors of onions are exported from leaves to bulb scales during maturity, and

their concentrations are high in sprout and basal plate of the bulbs during this period. Unfortunately, the exact nature of these inhibitors is not elucidated, although previous investigations suggest ABA as a principal inhibitor (Stow, 1976).

Maleic hydrazide (1,2-dihydro-3,6-pyridazinedione) is used as a systemic plant growth regulator or inhibitor and herbicide, and has enjoyed extensive use as a commercial onion sprout inhibitor since its introduction within the last 40 years (Isenberg and Ferguson, 1981). CIP (carbamate isopropyl N-phenyl or its chlorinated form: CIPC) is a selective systemic herbicide and plant growth regulator belonging to the N-phenylcarbamate group of pesticides. In agricultural practice, CIP (Propham) is used for pre-emergence control of grass weeds, woody nursery stock and the control of annual grasses. It is also used for the control of sprouting in potato tubers during storage (Meister, 1992).

However, in spite of the large literature available on hormonal factors and their involvement in different metabolism processes, little is known about the effect of exogenous hormones on the sprouting of onion bulbs, as well as other bulbous plants, particularly ornamentals bulbs.

The objective of this investigation was to study the effect of exogenous hormones (promoters and inhibitors), associated with cooling, on dormancy release and sprouting of onion bulbs. Common commercial chemical inhibitors of sprouting were also tested simultaneously.

Materials and Methods

ONION BULBS: Onion bulbs var. Rouge Amposta harvested in August and dried in the field for 2 weeks, were obtained from the local farm of the university. They were then sorted for uniformity and absence of defects, and divided into 2 groups: group 1: dormant bulbs (freshly harvested and dried bulbs), and group 2: non-dormant bulbs (kept at 5- 6°C for six months and without any visible sprouts). Experiment 1 was conducted on group 1, and experiment 2 conducted on group 2.

CHEMICAL TREATMENTS: Chemical treatments were applied immediately after harvesting and drying for experiment 1 and after six months for experiment 2.

STS TREATMENT: Prior to hormonal application, onion bulbs were placed on their base in a 0.2 mM of STS solution for 24 hours, and dried at 35°C for 30 min.

MH AND CIP TREATMENTS: Prior to hormonal application, onion bulbs were dipped into 2.2 mg mL⁻¹ MH and 60 µg mL⁻¹ CIP solutions (Sigma, St Louis, MO, USA) for 30 min. Then, they were dried in a ventilated oven at 35 °C for 30 min.

COOLING: Prior to ethephon and hormonal applications, onion bulbs of experiment 1 (group 1) were cooled for three weeks at 9°C and 90% relative humidity.

EFFECT OF EXOGENOUS HORMONES (NAA, BA, GA₃, AND ETHEPHON), CHEMICAL INHIBITORS (MH AND CIP) AND LOW TEMPERATURE ON SPROUTING OF ONION BULBS, *ALLIUM CEPA* L.

HORMONAL TREATMENTS: Immediately after chemical treatment and/or cooling, onion bulbs were injected in the central region with 1 ml of aqueous solution of 0.54 $\mu\text{mol mL}^{-1}$ NAA (1-naphthylacetic acid), 0.44 $\mu\text{mol mL}^{-1}$ BA (6-benzylaminopurine), 0.29 $\mu\text{mol mL}^{-1}$ GA₃ (gibberellic acid), 0.69 $\mu\text{mol mL}^{-1}$ ethephon (2-chloroethyl-phosphonic acid) and 0.38 $\mu\text{mol mL}^{-1}$ ABA (abscisic acid) (Sigma[®].Co, USA) using a sterile syringe for each solution. These concentrations are equivalent to 100 $\mu\text{g mL}^{-1}$, thus each bulb received 100 μg of active compound. The needle was introduced from the neck of the bulb and solution was injected slowly to avoid liquid leakage. The bulbs of experiment 1 were treated immediately after chemical treatments and cooling, while the bulbs for experiment 2 were treated after six months.

STORAGE CONDITIONS: Following treatments and hormonal applications, onions of each experiment were transferred to commercial plastic (PVC) trays of 12 kg, and kept in the dark at 20 °C and 70 % RH.

STATISTICAL ANALYSIS: Each experiment was performed in triplicate, and conducted during two successive years (2001 and 2002). Statistical analysis of the data was conducted using GraphPad Prism 4 statistical software (San Diego, CA, USA). Differences among means were determined by the Least Significant Difference (LSD) test with significance defined at $P < 0.05$.

Results

Effect of NAA on sprouting was effective as shown in Table 1. In experiment 1, cooled + NAA treated bulbs sprouted after 10 weeks, while non-cooled bulbs sprouted after 12 weeks. On the other hand, in bulbs treated with MH, CIP and STS, total sprouting was observed after 19, 19 and 16 weeks respectively, whereas control bulbs sprouted after 22 weeks. On the other hand, in experiment 2, the effect of NAA on sprouting was more visible, and total sprouting was observed after three weeks, while no significant difference was observed among HM, CIP, STS treated and control bulbs.

BA showed similar effects as NAA, particularly when BA was associated with cooling (Table 2). In experiment 1, total sprouting of BA treated bulbs was observed after 10 weeks, while non-cooled bulbs sprouted after 12 weeks. On the other hand, bulbs treated with MH, CIP, STS and control bulbs sprouted after approximately 22 weeks. In experiment 2, BA treatment was also effective, and total sprouting was observed after four weeks. However, the differences observed among HM, CIP, STS treated and control bulbs were not statistically significant.

GA₃ appeared less effective on the sprouting of the bulbs than NAA and BA (Table 3). In experiment 1, GA₃ + cooled bulbs sprouted after 17 weeks, and non cooled bulbs sprouted after 21 weeks. On the other hand, MH, CIP, STS and control bulbs sprouted after 23, 22, 24 and 22 weeks respectively, without significant differences. In experiment 2, GA₃ treated bulbs sprouted after five weeks, whereas MH, CIP, STS treated and control bulbs sprouted after 8, 8, 7 and 6 weeks respectively, without significant differences noted among the MH, CIP and STS treated bulbs.

The effect of ethephon on the sprouting of the bulbs was not significant as shown in Table 4. In experiment 1, a non significant difference was observed between ethephon + cooled and non-cooled bulbs which sprouted after 16 and 19 weeks respectively. Similar and non significant difference was noted on MH, CIP treated and control bulbs, which sprouted after 22, 23 and 22 weeks, respectively.

In experiment 2 also, no significant difference was noted, between ethephon treated and control bulbs which sprouted after 7 and 6 weeks respectively, and, between MH and CIP treated bulbs which both sprouted after 12 weeks.

TABLE 1

Effect of exogenous NAA, cooling and chemical inhibitors (MH and CIP) on sprouting of onion bulbs (weeks).

| % Sprouting | Experiment 1 | | Experiment 2 | |
|---------------|-----------------|-----------------|----------------|----------------|
| | 50% | 100% | 50% | 100% |
| NAA + Cooling | 7 ^a | 10 ^a | | |
| NAA | 9 ^{ab} | 12 ^a | 2 ^a | 3 ^a |
| NAA + HM | 10 ^b | 19 ^b | 3 ^a | 7 ^b |
| NAA + CIP | 10 ^b | 19 ^b | 4 ^a | 7 ^b |
| NAA + STS | 10 ^b | 16 ^c | 4 ^a | 6 ^b |
| Control | 17 ^c | 22 ^d | 3 ^a | 6 ^b |

Means followed by different letters in each column are significantly different at $P < 0.05$.

TABLE 2

Effect of exogenous BA, cooling and chemical inhibitors (MH and CIP) on sprouting of onion bulbs (weeks).

| % Sprouting | Experiment 1 | | Experiment 2 | |
|--------------|-----------------|-----------------|-----------------|----------------|
| | 50% | 100% | 50% | 100% |
| BA + Cooling | 8 ^a | 10 ^a | | |
| BA | 10 ^a | 12 ^a | 1 ^a | 4 ^a |
| BA + HM | 10 ^a | 19 ^b | 3 ^{ab} | 7 ^b |
| BA + CIP | 10 ^a | 19 ^b | 4 ^b | 7 ^b |
| BA + STS | 10 ^a | 17 ^b | 4 ^b | 6 ^b |
| Control | 17 ^b | 22 ^c | 3 ^b | 6 ^b |

Means followed by different letters in each column are significantly different at $P < 0.05$.

TABLE 3

Effect of exogenous GA₃, cooling and chemical inhibitors (MH and CIP) on sprouting of onion bulbs (weeks).

| % Sprouting | Experiment 1 | | Experiment 2 | |
|---------------------------|------------------|------------------|----------------|-----------------|
| | 50% | 100% | 50% | 100% |
| GA ₃ + Cooling | 11 ^a | 17 ^a | | |
| GA ₃ | 12 ^{ab} | 21 ^b | 2 ^a | 5 ^a |
| GA ₃ + HM | 14 ^{bc} | 23 ^{bc} | 4 ^a | 8 ^b |
| GA ₃ + CIP | 15 ^c | 22 ^{bc} | 4 ^a | 8 ^b |
| GA ₃ + STS | 14 ^c | 24 ^c | 4 ^a | 7 ^{ab} |
| Control | 17 ^d | 22 ^{bc} | 3 ^a | 6 ^a |

Means followed by different letters in each column are significantly different at $P < 0.05$.

TABLE 4

Effect of exogenous ethephon, cooling and chemical inhibitors (MH and CIP) on sprouting of onion bulbs (weeks).

| % Sprouting | Experiment 1 | | Experiment 2 | |
|---------------|-----------------|-----------------|----------------|-----------------|
| | 50% | 100% | 50% | 100% |
| Eth + Cooling | 12 ^a | 16 ^a | | |
| Eth | 13 ^a | 19 ^b | 4 ^a | 7 ^a |
| Eth + HM | 17 ^b | 22 ^c | 7 ^b | 12 ^b |
| Eth + CIP | 16 ^b | 23 ^c | 8 ^b | 12 ^b |
| Control | 17 ^b | 22 ^c | 3 ^a | 6 ^a |

Means followed by different letters in each column are significantly different at $P < 0.05$.

TABLE 5

Effect of exogenous ABA, and cooling on sprouting onion bulbs (weeks).

| % Sprouting | Experiment 1 | | Experiment 2 | |
|-----------------|------------------|------------------|----------------|-----------------|
| | 50% | 100% | 50% | 100% |
| ABA + Cooling | 14 ^a | 20 ^a | | |
| Chilled control | 7 ^b | 12 ^b | | |
| ABA | 16 ^{ab} | 23 ^c | 6 ^a | 11 ^a |
| Control | 17 ^b | 22 ^{ac} | 3 ^b | 6 ^b |

Means followed by different letters in each column are significantly different at $P < 0.05$.

As shown in Table 5, ABA significantly delayed the sprouting of the bulbs. In experiment 1, significant effects of cooling were noted on ABA untreated bulbs and treated bulbs which sprouted after 12 and 20 weeks, respectively. On the other hand, without cooling, no significant difference was observed between control and ABA treated bulbs. In experiment 2, the difference was significant between control and ABA treated bulbs which sprouted after 6 and 11 weeks, respectively. It seems that sensitivity of bulbs to exogenous ABA disappeared during storage at low temperature, and cooling decreased this sensitivity of onion bulbs to ABA.

Discussion

Auxins, the most important promoter, have an effectively break dormancy and sprouting, and Isenberg *et al.* (1974), and Thomas (1969) noted a peak of auxin levels preceding the onset of sprouting of onion bulbs. However, Thomas (1969) noted that this optimum peak of auxins occurred immediately after the peak of cytokinins. On the other hand, Mohr and Schopfer (1995) suggest that organ developments are regulated by the ratio of auxins/cytokinins. Gaspar *et al.* (1990) also noted that endogenous IAA induced formation of adventitious roots which could probably contribute in sprouting induction by cytokinins production. Auxins also have other metabolic effects such as induction of ethylene biosynthesis (Mathooko *et al.*, 1993), which is indirectly involved in the ending of dormancy and induction of sprouting (Benkeblia and Selselet-Attou, 1999b).

The role of cytokinins in onion bulb development during growing was reported by Keller (1993), and Lercari and Micheli (1981). BA also seems to induce sprouting of onion bulbs (Miedema and Kamminga, 1994; Miedema, 1994). According to Miedema and Kamminga (1994), temperature could have a notable effect on the activity of cytokinins, and maximum activity was observed at 5 and 15 °C while minimum activity was observed at 30 °C.

The involvement of gibberellins in the break of dormancy has not been established yet; however, after Aung and Paterson (1974), total GA content is higher in dormant onion bulbs than in sprouted bulbs. On the other hand, their content in onion is irregular and varies considerably during the dormancy and the onset of sprouting (Kielak and Bielinska-Czarnecka, 1991).

The role of ethylene in the break of dormancy remains uncertain, although investigation showed its indirect involvement in dormancy release (Benkeblia and Selselet-Attou, 1999b). Abeles *et al.* (1992), and Woltering and Sterling (1986) suggested that ethylene had a role regulating the hormonal balance in tissues. Indeed, ethylene synthesis is induced by auxins (Yang, 1980) and gibberellins (Mohr and Schopfer, 1995). Nevertheless, the mechanisms of this induction remain still unclear.

The involvement of ABA in prolonging dormancy of onion bulbs was reported by some authors. It was noted that immediately after harvesting, ABA concentration was high, but decreased during storage (Matsubara and Kimura, 1991; Yamazaki *et al.*, 1995). This hormone acts by inhibiting nucleic acids activity and blocking the cellular cycle (Bouvier-Durand *et al.*, 1989).

Conclusions

It seems that dormancy is highly temperature-dependent; however, hormonal factors play a central role in regulating and triggering the sprouting process,

EFFECT OF EXOGENOUS HORMONES (NAA, BA, GA₃, AND ETHEPHON), CHEMICAL INHIBITORS (MH AND CIP) AND LOW TEMPERATURE ON SPROUTING OF ONION BULBS, *ALLIUM CEPA* L.

particularly under favorable environmental conditions. It also seems that auxins and cytokinins are fundamentally involved in the break of dormancy and probably a balance between these two hormones could be the "key" to ending dormancy in onion bulbs. However, the nature and the period of dormancy are not exactly determined, and numerous terminologies and periods have been suggested. Thus, further investigations are needed to evaluate the exact nature of bulb dormancy and the balance and relation among the different hormonal factors.

Acknowledgements

The author expresses his gratitude to D. Fekir and H. Fekir (Fekir's farm) for providing organic onions, and Mr. D.E. Benmiloud (MAGMOS) for cooling facilities and technical assistance.

References

- Abdel-Rahman, M.A. and F.M. Isenberg. 1974. The role of exogenous plant regulators in the dormancy of onion bulbs. *Journal of Agricultural Science* 82:113-116.
- Abeles, F.B., P.W. Morgan, and M.E. Saltveit. 1992. *Ethylene in Plant Biology*. Academic Press, San Diego, U.S.A.
- Aung, L.H. and C.E. Paterson. 1974. Gibberellin-like substances of dormant and non-dormant bulbs of *Allium cepa* L. *Journal of the American Society of Horticultural Science* 99:279-281.
- Benkeblia, N. and G. Selselet-Attou. 1999a. Changes in oligosaccharides, phenolics and peroxidase activity in inner bud of onion bulbs during break of dormancy by low temperatures. *Acta Agriculturae Scandinavica* 49:98-102.
- Benkeblia, N. 2003a. Postharvest technology of onions. In: *Crop Management and Postharvest Handling of Horticultural Products*, R. Dris, R. Niskanen, and S.Mohan Jain (Editors), 107-137. Science Publishers, Enfield.
- Benkeblia, N. 2003b. Low temperature and braking of dormancy effects on respiration rate, sugars, phenolics and peroxidase activity changes in inner buds of onion *Allium cepa* L. *Acta Agriculturae Scandinavica* 53:16-20.
- Benkeblia, N. and G. Selselet-Attou. 1999b. The role of ethylene in sprouting of onion bulbs. *Acta Agriculturae Scandinavica* 49:122-124.
- Benkeblia, N. 2000. Phenylalanine ammonia-lyase, peroxidase, pyruvic acid and total phenolics variation in onion tissues during storage. *Lebensmittel Wissenschaft und Technologie* 33:112-116.
- Bouvier-Durand, M., M. Real, and D. Côme. 1989. Changes in nuclear activity upon secondary dormancy induction by abscisic acid in apple embryo. *Plant Physiology and Biochemistry* 27:511-518.
- Dennis, F.J. 1987. Two methods of studying rest: temperature alternation and genetic analysis. *HortScience* 22:820-824.
- Gaspar, T., C. Moncoussin, and H. Greppin. 1990. The place and role of exogenous and endogenous auxins in adventitious formation. In: *Intra and Intercellular Communication in Plants. Reception, Transmission, Storage and Expression of Messages*, B. Millet, and H. Greppin (Editors.), 125-139. INRA Press, Paris.
- Given, N.K., M.A. Venis, and D. Grierson. 1988. PAL activity and anthocyanin synthesis in ripening strawberry fruit. *Journal of Plant Physiology* 133:25-30.
- Hartmann, C. 1992. *La Sénescence des Végétaux*. Editions Herman, Paris, France.
- Heller, R. 1982. *Physiologie Végétale. 2: Développement*. Editions Masson, Paris, France.
- Isenberg, F.M., T.H. Thomas, M. Abdel-Rahman, A. Pendergrass, J.C. Carrol, and L. Howell. 1974. The role of natural growth regulators in rest, dormancy and regrowth of vegetables during winter storage. *Proceedings of the XIXth International Horticultural Congress*, 129-138. Warszawa University, Warszawa, Poland.
- Isenberg, F.M. and W.L. Ferguson. 1981. Maleic hydrazide for use on storage onions. *Search Agricultural Cornell University of Ithaca Bulletin* 15:1-21.
- Kaminek, M., V. Motyka, and R. Vankiva. 1997. Regulation of cytokinin content in plant cells. *Physiologia Plantarum* 101:689-700.
- Kato, T. 1966. Physiological studies on the bulbing and dormancy of onion plants. VII: Effects of some environmental factors and chemicals on the dormant process of bulbs. *Journal of the Japanese Society for Horticultural Science* 3:49-56.
- Ke, D. and M.E. Saltveit. 1988. Plant hormone interaction and phenolic metabolism in the regulation of russet spotting in Iceberg lettuce. *Plant Physiology* 88:1136-1140.
- Keller, E.R.J. 1993. Sucrose, cytokinin and ethylene influence formation of *in vitro* bulblets in onion and leek. *Genetic Resources and Crop Evolution* 40:113-120.
- Kielak, E. and M. Bielinska-Czarnecka. 1991. Changes in endogenous gibberellin-like substances in onion bulbs (*Allium cepa* L.) during storage. *Acta Agrobotanica* 44:65-71.
- Lercari, B. and N. Ceccarelli. 1975. Azione di alcuni fitoregolatori sull'induzione a bulbo in *Allium cepa* L. *Rivista Ortoflorofruitticoltura Italiana* 59:262-272.
- Lercari, B. and P. Michelli. 1981. Photoperiodic regulation of cytokinin levels in leaf blades of *Allium cepa* L. *Plant and Cell Physiology* 22:501-505.
- Lercari, B. 1983. The role of ethylene in photoperiodic control of bulbing in *Allium cepa*. *Physiologia Plantarum* 59:647-650.
- Mathooko, F.M., Y. Kubo, A. Inaba, and R. Nakamura. 1993. Inhibition of auxin-induced ethylene production in cucumber fruit discs by carbon dioxide. *Postharvest Biology and Technology* 3:313-325.
- Matsubara, S. and I. Kimura. 1991. Changes in ABA content during bulbing and dormancy and *in vitro* bulbing in onion plant. *Journal of the Japanese Society for Horticultural Science* 59:757-762.
- Meister, R.T. 1992. *Farm Chemicals Handbook*. Meister Publishing, Willoughby, Ohio, U.S.A.
- Miedema, P. and G.C. Kamminga. 1994. Bulb dormancy in onion. II: The role of cytokinins in high-temperature imposed sprout inhibition. *Journal of Horticultural Science* 69:41-45.
- Miedema, P. 1994. Bulb dormancy in onion. III: The influence of the root system, cytokinin and wounding on sprout emergence. *Journal of Horticultural Science* 69:47-52.
- Mohr, H. and P. Schopfer. 1995. *Plant physiology*. Springer Verlag, Berlin, Germany.
- Sobeih, W.Y. and C.J. Wright. 1988. Effects of ethephon, gibberellins and benzyladenine combination on bulb development and flowering in spring-sown bulb onions (*Allium cepa* L.). *Proceedings of the 4th Allium Symposium*, 6-9. EUCARPIA, Vienna.
- Stow, J.R. 1976. The effect of defoliation on storage potential of bulbs of the onion (*Allium cepa*). *Annals of Applied Biology* 84:71-79.
- Thomas, T.H. 1969. The role of growth substances in the regulation of onion bulb dormancy. *Journal of Experimental Botany* 20:124-137.
- Thomas, T.H. 1981. Hormonal control of dormancy in relation to postharvest horticulture. *Annals of Applied Biology* 98:531-538.
- Weyers, J.D.B., N.W. Paterson, R. A'Brook, and Z.Y. Peng. 1995. Quantitative analysis of the control of physiological phenomena by plant hormones. *Physiologia Plantarum* 95:486-494.
- Woltering, E.J. and E.P. Sterling. 1986. Design for studies on ethylene sensitivity and ethylene production of ornamental products. *Acta Horticulturae* 181:483-488.
- Yamazaki, H., T. Nishijima, and M. Koshioka. 1995. Changes in ABA content and water status in bulbs of *Allium wakegi* Araki throughout the year. *Journal of the Japanese Society for Horticultural Science* 64:589-598.
- Yang, S.F. 1980. Regulation of ethylene biosynthesis. *HortScience* 15:238-243.

Received April 2004.

Accepted December 2004.