METHYL JASMONATE-INDUCED STIMULATION OF CHLOROPHYLL FORMATION IN THE BASAL PART OF TULIP BULBS KEPT UNDER NATURAL LIGHT CONDITIONS

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ABSTRACT

Chlorophyll (a) and chlorophyll (b) were successfully identified in the scale tissues localized at root primordia, near the basal plate of tulip bulbs (*Tulipa gesneriana* L. cv. 'Apeldoorn') kept in a greenhouse under natural lighting conditions. The analyses were done using a reversed-phase high-performance liquid chromatography system, equipped with a multi-channel spectrophotometric detector and a column temperature controller. No chlorophyll formation was observed in the scale tissues localized at root primordia of tulip bulbs kept under dark conditions. Methyl jasmonate was applied as a lanolin paste to the basal part of tulip bulbs as a result of which significantly stimulated chlorophyll formation. The effect of methyl jasmonate, on chlorophyll formation in tulip bulbs, was greatly increased by the simultaneous application of ethephon, an ethylene-releasing compound. Methyl jasmonate also induced gummosis, in tulip bulbs kept under both natural lighting and in darkness, suggesting that chlorophyll formation in tulip bulbs is not connected to gummosis. The possible mechanism of methyl jasmonate effect on chlorophyll formation in tulip bulbs, applied with or without ethephon, is discussed.

Key words: methyl jasmonate, chlorophyll (a) and (b) formation, tulip bulbs, light, ethylene

INTRODUCTION

Scale tissues localized at root primordia, near the basal plate of tulip bulbs, had a tendency to form green pigments, during their storage under natural lighting conditions. These pigments seemed to be chloro-

phylls and/or their derivatives, but there is little information regarding this phenomenon. Factors affecting the mechanism regulating the formation of chlorophylls is also unclear. Although the formation of these pigments seems to be hormone-controlled, it is not known what kind of plant hormones regulate this in tulip bulbs. Among these, cytokinin has not only been known to inhibit degradation of chlorophyll but also to stimulate its biosynthesis in plant tissues. There have been a number of publications dealing with cytokinin-induced chlorophyll formation in some plant tissues, particularly in etiolated plants grown under dark conditions (Mcglassson et al., 1978). Cytokinins have also been reported to enhance 5-aminolevulinic acid (ALA) synthesis due to increase of 5-aminolevulinic acid dehydratase activity (Kaul and Sabharwal, 1974; Naito et al., 1979; Dei, 1985), which catalyzes the formation of porphobilinogen from two molecules of ALA, resulting in the increase of chlorophylls level.

Jasmonic acid and its related compounds have recently been discovered to be new types of plant hormones with some important physiological properties, and the ability to induce gummosis in some plants (Murofushi et al., 1999). Among them is methyl jasmonate, which has been shown to induce gum formation in tulip bulbs when it is applied as a lanolin paste (Saniewski and Puchalski, 1988; Saniewski et al., 1998ab; 2000; 2003; Ueda et al., 2003; Skrzypek et al., 2005). This effect was greatly stimulated by the simultaneous application of ethylene or ethephon, an ethylene-releasing compound. In addition, jasmonic acid, and its related compounds, have been reported to promote the degradation of chlorophylls or carotenoids, followed by senescence, in detached green or etiolated plant tissues, respectively (Ueda and Kato, 1980; 1987; Ueda et al., 1981). However, the effects of these compounds on the chlorophyll levels of intact plants have been debatable. In this paper we show that the green pigments found in the scale tissues localized at root primordia, near the basal plate of tulip bulbs, were identified as chlorophyll *a* and chlorophyll *b*; and that methyl jasmonate is strongly connected to the stimulation of chlorophyll formation in tulip bulbs, with or without the use of ethylene. A possible reason for the stimulating action of methyl jasmonate on chlorophyll formation, is shown in the discussion section.

MATERIAL AND METHODS

Tulip bulbs and application of chemicals

The experiments were conducted with tulip (*Tulipa gesneriana* L.) cv. 'Apeldoorn' from commercial stock. Methyl jasmonate and ethephon were applied to the basal part of the tulip bulbs as a lanolin paste, in accordance with usual practice (Saniewski and Puchalski, 1988; Saniewski et al.; 1998b; 2000). The treatment was administered on August 25, September 16, October 6 and October 15. Between 10 and 20 treated bulbs were

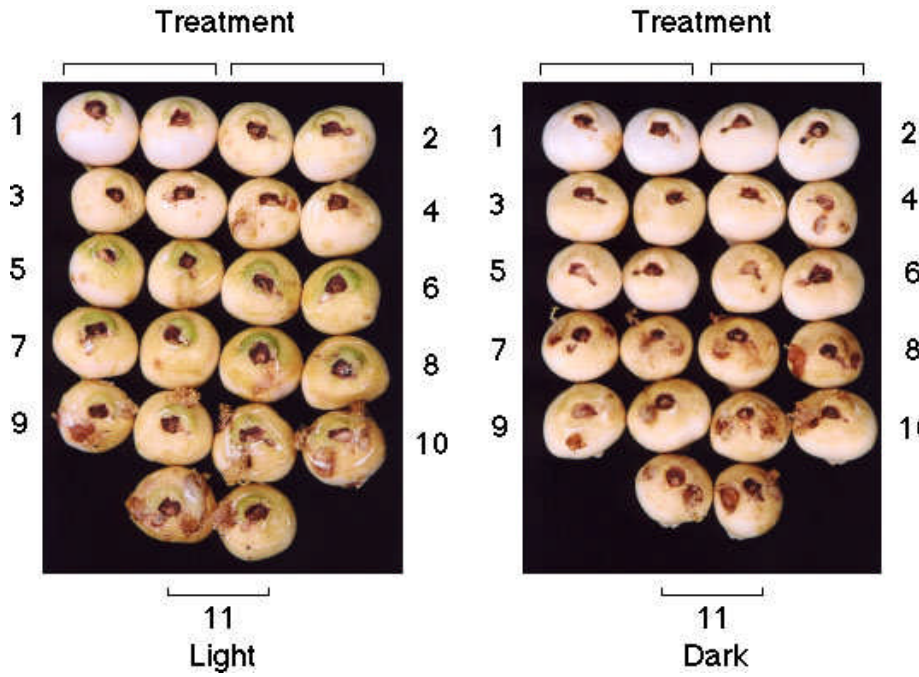
kept in greenhouses under natural lighting and in darkness for the same period.

Identification of chlorophyll (a) and chlorophyll (b)

The identification of green pigments in the tulip bulbs was made using a high-performance liquid chromatograph (HPLC), according to the method described by Iriyama et al. (1978) and Suzuki and Shioi (2003), with some modifications. All the procedures for the isolation and identification of green pigments were carried out under dim green light. Tissues containing green pigments were removed from the bulbs using a sterilized razor blade. They were weighed and then homogenized with sea sand in cold methanol. This procedure was repeated three times. The tissues and sea sand were sufficiently washed with acetone. Methanol and acetone extracts were combined and filtered. The organic solvent was then dried *in vacuo* and the residue was dissolved in a small volume of methanol. It was then analyzed using a JASCO reversed phase HPLC system, equipped with a DPL910/915 multi-channel spectrophotometric detector (at 350 to 800 nm), and a Chemcosorb 5-ODS-H column (4.6 x 150 mm). The column temperature was kept at a constant 30°C during the analysis. The solvent system was methanol-isopropanol (92:8, v/v) at a flow rate of 1 ml per min. For the purposes of the detection of pheophytin and other non-polar chlorophyll derivatives as well as for washing the column, acetone was introduced after 20 min of running, at a flow rate of 1 ml per min. Authentic samples of chlorophyll *a* and chlorophyll *a'*, chlorophyll *b* and chlorophyll *b'* were prepared from the fresh green leaves of spinach (*Spinacia oleracea* L.). The total amount of chlorophylls in the tulip bulbs were determined according to the method reported previously (Ueda and Kato, 1980; Ueda et al., 1981), with minor modifications. The tissue samples were homogenized and the green pigments were extracted by boiling for 30 min in 80% aqueous ethanol. The optical density of the alcoholic extract was measured at 662 nm, using a Hitachi U-3200 spectrophotometer.

RESULTS AND DISCUSSION

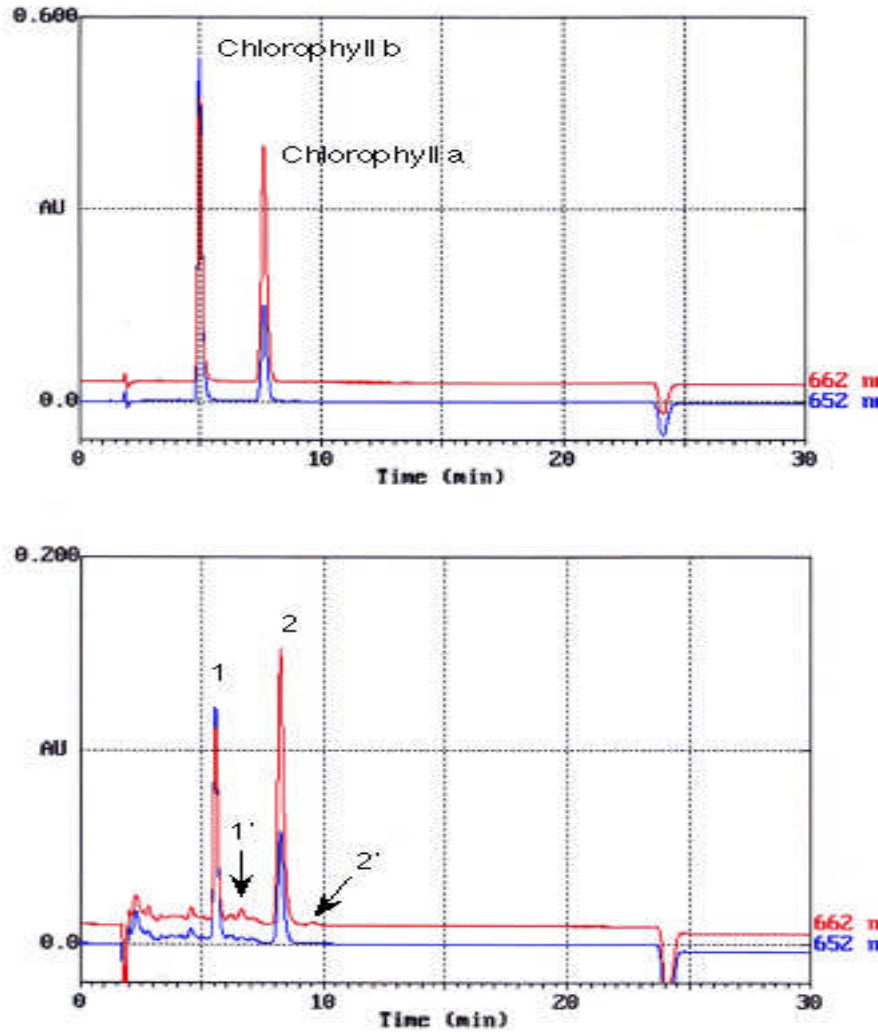
When tulip bulbs were kept under dark conditions, no green-colored tissues were observed in the bulbs after each treatment. However, the formation of green pigments was found to be present on those treated under natural lighting conditions, particularly in the scale tissues localized at root primordia near the basal plate (Fig. 1). These results indicate that light is an essential factor in the formation of green pigments in bulbs. As shown in Fig. 1, gum formation was also observed in those bulbs treated with methyl jasmonate, in the presence or absence of ethephon, under both dark and light conditions. Judging from the results, together with the facts described above, the formation of green pigments is considered not to be connected with gum formation in tulip bulbs.



1. control
2. lanolin only
3. ethephon 1.0 %
4. ethephon 2.0 %
5. methyl jasmonate 0.1%
6. methyl jasmonate 0.5%
7. methyl jasmonate 1.0%
8. methyl jasmonate 2.0%
9. methyl jasmonate 0.1% + ethephon 1.0%
10. methyl jasmonate 0.5% + ethephon 1.0%
11. methyl jasmonate 1.0% + ethephon 1.0%

Figure 1. Tulip bulbs stored in light conditions in phytotron from the beginning of July until the end of October (upper): and tulip bulbs treated with or without methyl jasmonate and/or ethephon (lower). The bulbs were kept for about 2 months in a greenhouse under both natural lighting conditions and in darkness. Each treatment was administered on August 25, 2002 and photographs were taken on October 31, 2002

On the dates during August, September and October, green-colored tissues were extracted and analysed, following the procedures described in "Materials and methods", in order to identify the pigments found in the experimental tulip bulbs. The HPLC system has been reported to be a useful and adequate method for qualitative and quantitative analyses



Figutre 2. HPLC profile of authentic samples of chlorophyll *a* and chlorophyll *b* (upper), and of extracts from the green-colored basal part of tulip bulbs treated with or without methyl jasmonate and/or ethylene (lower, 1: Chlorophyll *b*, 1': Chlorophyll *b'*, 2: Chlorophyll *a*, 2': Chlorophyll *a'*). The optical densities at 662 nm and 652 nm were monitored in each sample

of photosynthetic pigments (Iriyama et al., 1978; Suzuki and Shioi, 2003). To improve separation and sensitivity we introduced a reversed phase HPLC system in this study. This resulted in the clear detection of two major and some minor peaks. The HPLC profile showed two prominent peaks at retention times of 5 min and 49 sec and 8 min and 17 sec, corresponding to those of chlorophyll *b* and chlorophyll *a*, respectively (Fig. 2).

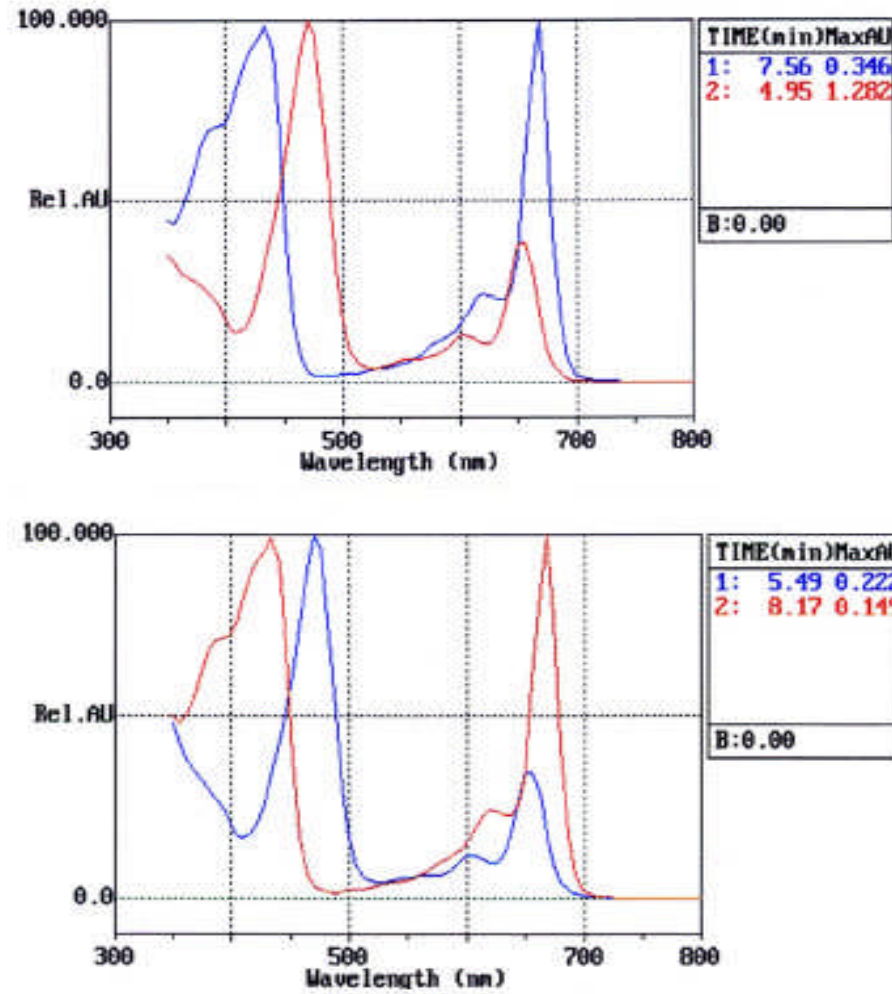


Figure 3. Spectroscopic analyses of authentic samples of chlorophyll (a) and chlorophyll (b) (upper), and extracts from the green-colored basal part of tulip bulbs treated with or without methyl jasmonate and/or ethylene (lower). Each sample was analysed immediately after elution from HPLC, described in Fig. 1. Each data value indicates the respective retention time in HPLC (Fig. 2)

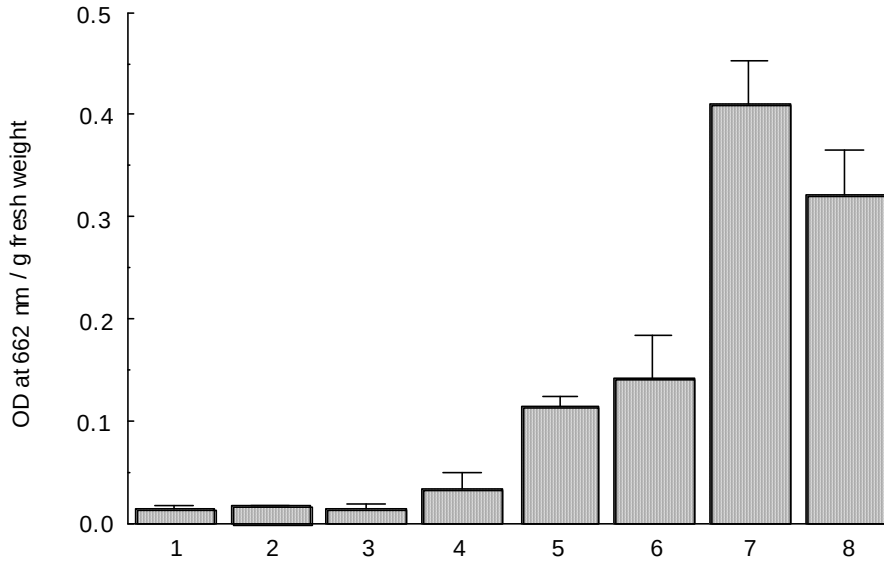
Chlorophyll *a'* and chlorophyll *b'* were also found to show noticeable minor peaks in the chromatogram. These results confirmed that a reversed phase HPLC system is of great use in the detection of chlorophylls and their derivatives. The spectroscopic data of compounds eluted at these prominent peaks corresponded with those of the authentic samples of chlorophyll *a* and chlorophyll *b*, as shown in Figure 3. Although plant tissues grown under natural lighting conditions have been known to contain some major chloro-

phyll metabolites such as pheophytin, chlorophyllide, pheophorbide and others (Simpson et al., 1976), almost none of them were found in the chromatogram during this experiment. As a result of the HPLC analyses, together with their spectroscopic data, major green pigments which had formed in tulip bulbs were successfully identified as chlorophyll *a* and chlorophyll *b*.

The formation of chlorophyll *a* and chlorophyll *b*, in tulip bulbs kept under natural lighting conditions, was stimulated by the application of methyl jasmonate. Although ethephon, an ethylene releasing compound, was almost non effective on chlorophyll formation in tulip bulbs, simultaneous application of methyl jasmonate and ethephon resulted in extreme stimulation of chlorophyll formation (Fig. 4). Chlorophyll accumulation, stimulated by methyl jasmonate, was found no earlier than at the beginning of August (data not shown), suggesting that the formation of root primordia is essential for chlorophyll formation in both intact bulbs and those treated with methyl jasmonate.

It should be mentioned that in all of the results from the treatments which commenced on August 25, and independently from the stage of root primordia formation, the parallel effects of the stimulation of both methyl jasmonate, and methyl jasmonate with ethephon were observed on chlorophyll formation, as shown in Fig. 4.

There are a number of papers which have reported the effects of natural and synthetic chemical compounds on higher plants. These include plant hormones, herbicides, antibiotics and others (Wolf, 1977). Almost all of them substantially inhibited chlorophyll biosynthesis, except cytokinins (Kaul and Sabharwal, 1974; Wolf, 1977; Naito et al., 1979; Dei, 1985). Jasmonic acid and its related compounds have been shown to stimulate the accumulation of plant pigments. Jasmonates, inducing chlorophyll accumulation, have already been reported to be effective in greening cucumber cotyledons (Fletcher et al., 1983) and *Chlorella vulgaris* (Czerpak et al., 2006), although they have generally been found to regulate plant growth and development, as potent inhibitors (Murofushi et al., 1999). Methyl jasmonate has also been reported to induce the formation and/or the accumulation of anthocyanin in peach shoots (Saniewski et al., 1998a), tulip stems (Saniewski et al., 1998b) and *Kalanchoe blossfeldiana* (Saniewski et al., 2003). The contents of chlorophyll *a* and chlorophyll *b*, as well as cell numbers and mono-saccharide content in *Chlorella vulgaris*, were substantially increased by the application of low concentrations of jasmonic acid (10^{-8}-10^{-6} M), although these were decreased in higher concentrations (10^{-5}-10^{-4} M). These results suggest that jasmonic acid and its related compounds have differing effects depending on dosage. Similar observations have already been found with regards to anthocyanin formation in *Kalanchoe blossfeldiana* (Saniewski et al., 2003). The application of higher concentrations of methyl



1. control
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5. methyl jasmonate 0.5%
6. methyl jasmonate 1.0%
7. methyl jasmonate 0.5% + ethephon 0.5%
8. methyl jasmonate 1.0% + ethephon 1.0%

Figure 4. Chlorophyll formation in the basal part of tulip bulbs. Chlorophyll contents were expressed as the value of the optical densities at 662 nm per g fresh weight. The determination of chlorophyll levels was made one and a half months after treatment. The results were expressed as the average values of three experiments with standard errors

jasmonates resulted in less accumulation of anthocyanin, compared to that administered in lower concentrations, which resulted in higher accumulation.

The mechanism by which jasmonates affect the accumulation of plant pigments is not yet clear. Chlorophyll accumulation, induced by methyl jasmonate under natural lighting conditions, was totally inhibited by the simultaneous application of fluridone (data not shown), which is a potent inhibitor of phytoene desaturate, resulting in the inhibition of carotenoids, chlorophyll and abscisic acid biosynthesis (Klicova et al., 2002; Arias et al., 2004; Michel et al., 2004). Low concentrations of jasmonates have been shown to induce the gene expression of enzymes involved in flavonoid biosynthesis: phenylalanine ammonia-lyase (PAL), chalcone synthase, 4-coumarate CoA ligase and dihydroflavonol-4-reductase

(Creelman et al., 1992; Gundlach et al., 2002; Tamari et al., 1995; Dittrich et al., 1992). A similar mechanism might explain methyl jasmonate's stimulation of chlorophyll formation in tulip bulbs. Methyl jasmonate may induce the gene expression of some key enzymes involved in chlorophyll biosynthesis through the formation of 5-aminolevulinic acid.

As described above, chlorophyll and gum formation in tulip bulbs was greatly stimulated by the promoting effects of methyl jasmonate, together with the simultaneous application of the ethylene-releasing compound, ethephon. Gum formation, induced by methyl jasmonate, was greatly stimulated by the simultaneous application of ethylene. The mechanism by which ethylene stimulates the promoting effect of methyl jasmonate, on gum formation in tulip bulbs, is not yet clear. As described in the "Introduction" above, the combination of methyl jasmonate and ethylene, on gum formation in tulips, has been studied intensively. Based on the results of these studies, it is probable that there is an interaction and/or a cross-talk in the signal transduction pathways between jasmonates and ethylene.

Our previous studies, showing the stimulating effect of ethylene on gum formation induced by methyl jasmonate, have suggested that methyl jasmonate changes sugar metabolism followed by upregulation of ethylene (Skrzypek et al., 2005). A similar explanation might be used regarding chlorophyll accumulation on tulip bulbs with a changed sugar metabolism, resulting from the application of methyl jasmonate. They have further suggested that the presence of leaves has been shown to be essential for methyl jasmonate's stimulating effect on anthocyanin formation in *Kalanchoe blossfeldiana* (Saniewski et al., 2003), showing that photosynthetic products, such as sugar molecules, are very important for anthocyanin formation. According to this hypothesis, methyl jasmonate might affect sugar metabolism in tulip bulbs and, as a result, the released sugar molecules could contribute to promoting chlorophyll formation in bulbs kept under natural lighting conditions. In this case sugars might be a signal molecule for the formation of chlorophylls in tulip bulbs. Further investigation linking sugar metabolism and chlorophyll formation will be required.

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JASMONIAN METYLU STYMULUJE AKUMULACJĘ CHLOROFILU W ŁUSKACH W POBLIŻU PIĘTKI CEBUL TULIPANA PRZECHOWYWANYCH NA ŚWIETLE

Junichi Ueda i Marian Saniewski

S T R E S Z C Z E N I E

Chlorofil a i chlorofil b zostały zidentyfikowane w tkankach łusek zlokalizowanych w pobliżu primordii korzeniowych przy piętce cebul tulipana (*Tulipa gesneriana* L.) przechowywanych w szklarni (naturalne warunki świetlne) stosując chromatograf wysokociśnieniowy w fazie odwróconej (HPLC) wyposażony w detektor wielokanałowy z pomiarem długości światła i z kontrolowaną temperaturą kolumny. Nie wykazano występowania chlorofilu w tych samych częściach cebul przechowywanych w ciemności. Jasmonian metylu zastosowany w paście lanolinowej na łuski u podstawy cebul tulipana stymulował tworzenie się chlorofilu. Stymulujący wpływ jasmonianu metylu na tworzenie się chlorofilu w cebulach tulipana był silnie wzmożony przez jednoczesne podanie etefonu, związku z którego uwalnia się etylen. Jasmonian metylu podany osobno lub łącznie z etefonem także indukował gumozę w cebulach tulipana przechowywanych na świetle i w ciemności, co sugeruje, że tworzenie się chlorofilu w cebulach tulipana nie jest związane z gumozą. Możliwy sposób działania samego jasmonianu metylu i w obecności etefonu w stymulacji tworzenia się chlorofilu w cebulach tulipana jest także dyskutowany.

Słowa kluczowe: jasmonian metylu, tworzenie się chlorofilu a i b, cebule tulipana, światło, etylen