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# Photoperiodic Floral Induction in *Pharbitis* Cotyledons Affected by Polyamines and Ethylene

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**Exogenous putrescine of 0.5 mM or higher concentrations applied during a 16 h inductive dark period could elevate putrescine content in cotyledons of *Pharbitis nil* Choisy cv. Violet, a short-day plant, resulting in complete blocking of photoperiodic floral induction. Titers of putrescine, spermidine and spermine in the cotyledons were traced throughout a 16 h dark period. While non-induced cotyledons under continuous light slightly increased levels of polyamines, induced tissue maintained its putrescine, spermidine and spermine levels as low as 66.4%, 60.9% and 84.9% of non-induced levels respectively. Endogenous polyamines kept at lower levels in the inductive dark period were found to upsurge by a night break treatment of 10 min light in the middle of the dark and consequently the inductive dark effect was canceled. Elevation of polyamine titers could also be induced by 100 μL/L ethylene treatment which completely suppressed floral induction. Compared to untreated cotyledons, ethylene-treated tissues increased putrescine content by as much as 136.5% in 12 h and spermidine level by up to 130.1% in 8 h. Ethylene-treated cotyledons not only increased endogenous polyamine content but also liberate ethylene in the second half of the inductive dark period accumulating up to three to fourfold level supporting a hypothesis that ethylene-treated tissues are stimulated to produce ethylene which in turn accelerates polyamine biosynthesis in the tissues. It is postulated that substantially low polyamine titers in the inductive dark period would be one of the necessary factors controlling photoperiodic induction of flowering in *Pharbitis nil* and the inhibitory effects of night break and exogenous ethylene treatment may be attributed to their action to stimulate endogenous polyamine production.**

*Keywords* : *Pharbitis nil*, flowering, floral induction, polyamine, ethylene

Polyamines, ubiquitous in eukaryotic cells, are known to have a regulatory role in plant growth and development (Tabor and Tabor, 1984; Smith, 1985; Galston and Kaur-Sawhney, 1987; Evans and Malmberg, 1989; Galston and Kaur-Sawhney, 1990). Recently considerable envidence has been accumulated on their possible involvement in floral induction, initiation and development. Putrescine titer in cotyledons of *Pharbitis nil* was found to decline during floral induction (Dai and Wang, 1987), while exogenously applied putrescine could induce flower buds (Wada *et al.*, 1994). In thin-layer tissue cultures of *Nicotiana tabacum*, floral bud initiation was closely related to high levels of spermidine (Kaur-Sawhney *et al.*, 1988), exogenous spermidine application with its dependency on the time and duration (Kaur-Sawhney *et al.*, 1990), and also to the binding of spermidine to a unique protein (Apelbaum *et al.*, 1988). Transfer of vegetative *Xanthium strumarium* to inductive cycles caused rapid and marked changes in putrescine titer of the leaves (Hamasaki and Galston, 1990). In duckweed system, floral formation of *Lemna pausicostata* 6746 grown under inductive photoperiods was inhibited by spermine, putrescine and spermidine added to the culture medium, and methylglyoxal-bis(guanylhydrazone)(MGBG), a blocker of spermidine and spermine biosynthesis, induced

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flowering under non-induced photoperiods (Tsao and Yin, 1985). MGBG and cyclohexylamine, another potent blocker of polyamine synthesis, however, were found to depress the flowering in *Spirodela punctata* strain O 5, a quantitative long-day duckweed, grown under continuous light (Bendeck de Cantú and Kandeler, 1989). Kim and Maeng (1992) reported that the flowering in *Lemna gibba* G3, a long-day duckweed, was promoted under continuous light by exogenous polyamines, and was depressed by inhibitors of their biosynthesis, postulating that endogenous polyamine status might play an important role in the very early stage of floral induction in *L. gibba* G3.

Ethylene, a gaseous plant hormone, has been extensively studied in conjunction with polyamine metabolism, since polyamines, which share a common intermediate, S-adenosylmethionine (SAM), with ethylene, exhibit marked anti-senescence properties, directly antagonizing many ethylene-mediated responses (Slocum *et al.*, 1984). It has been hypothesized that both may regulate each other's synthesis, either directly or by metabolic competition for SAM (Evans and Malmberg, 1989). Early studies on the action of ethylene and ethephon (2-chloroethylphosphonic acid), an ethylene releasing compound, in photoperiodic flowering showed its promotive effect in pineapple, mango and *Plumbago indica* L (Cooper and Reece, 1942; Nitsch and Nitsch, 1969; Chacko *et al.*, 1974a; Chacko *et al.*, 1974b). In contrast, in *Xanthium, Chrysanthemum, Lemna* and *Pharbitis* systems, ethylene was found to have inhibitory action (Abeles, 1967; Tjia *et al.*, 1969; Suge, 1972; Suge, 1974; Maeng, 1977; Cockshull and Horridge, 1978).

The present study aims to reveal possible involvement of polyamines in photoperiodic flower induction process by tracking polyamine titer changes in induced cotyledons of *Pharbitis nil* Choisy cv. Violet, a short-day plant.

## MATERIALS AND METHODS

### Culture of plant material

Seeds of *Pharbitis nil* Choisy cv. Violet, a short-day plant, were soaked in concentrated sulfuric acid for 40 min with occasional stirring and were rinsed with running water for 20 h. The seeds thus imbibed were sown in prewashed vermiculite in 12 cm diameter pots and the plants were grown with Hoagland nutrient solution under continuous light unless otherwise described. The irradiance from mixture of fluorescence lamps and incandescent bulbs was adjusted at 15 $W \cdot m^{-2}$. Temperature was kept 25± 1℃. When a pair of cotyledons were fully expanded in 6 d under continuous light, a 16 h dark treatment was imposed for floral induction. Night breaks, if needed, were given by interrupting the dark period with 10 min illumination.

### Application of polyamine and ethylene

Imbibed seeds sown in vermiculite were irrigated with 0.1, 0.5 or 1.0 mM putrescine solutions in place of the nutrient medium twice a day for 6 d under continuous light. For ethylene application, the imbibed seeds were surface-sterilized with 1-1.5% NaOCl solution for 10 min and rinsed three times with sterilized deionized water. The seeds were sown aseptically on autoclaved Murashige and Skoog (MS) medium supplemented with 3% sucrose and 0.8% bactoagar (Difco, U.S.A.) in 500 mL Erlenmeyer flasks. The plants were then grown under continuous light for 7 d. Culture conditions were as described above. At the onset of a 16 h dark period, each flask was plugged with a silicon stopper and appropriate amount of 99.5% ethylene was injected with a gas tight syringe to establish final concentrations of ethylene in the gas phase at 10, 50, 100, 200 and 500 μL/L respectively. At the end of the dark period, ethylene inside the flask was completely removed by thorough ventilation and the plants were kept under continuous light.

### Evaluation of floral response

Floral response was quantified in terms of numbers of floral buds per plant kept under continuous light for 20 d following a 16 h inductive dark period. Five plants were treated in each experiment repeated three times and means with errors were calculated from the results.

### Polyamine extraction and determination

Polyamines were extracted and quantified accor-

ding to a modified method of Smith and Davies (1987). Excised cotyledons were homogenized in chilled 0.2 N perchloric acid (100 mg fresh wt/mL of acid). The homogenates were kept at 4℃ for 1 h and then centrifuged at 15,000 *g* for 30 min at 4℃. To each mL of the supernatant was added 1 nmol of 1,6-diaminohexane as internal standard and 1 mL of 2 N sodium chloride followed by 10 μL of benzoyl chloride. The mixture was shaken using a vortex mixer for 10 s and incubated at room temperature for 20 min. Benzoylation was terminated by adding 2 mL of saturated sodium chloride and benzoylated polyamines were then extracted with 2 mL of chilled diethyl ether. After centrifugation at 1,500 *g* for 10 min, 1 mL of ether fraction was collected and evaporated in a stream of nitrogen. The residue was redissolved in 100 μL of methanol and kept at −20℃ until assayed by HPLC. Sample was injected into LKB HPLC system (LKB 2150 HPLC pump, LKB 2158 UVICORD SD, LKB 2220 recording integrator) with Lichrosorb RP-18 column (pore size 10 μm, 4×250 mm) and a UV detector at 254 nm. Sixty % (v/v) methanol was used as the mobile phase with flow rate adjusted at 1 mL/min.

### Ethylene determination

Ethylene evolved from the seedlings was analyzed by a Pye Unicam gas chromatography (Model 304) with a flame ionization detector using Pye Unicam SE 30 (silica gel) stainless column (bore 4 mm, o.d. 6 mm, length 1.5 m). Column temperature was adjusted at 150℃ and flow rate of carrier gas, nitrogen, at 40 mL/min.

## RESULTS AND DISCUSSION

To reveal the effects of exogenous polyamines on the photoperiodic induction of flowering in cotyledons of *Pharbitis nil*, a 16 h dark period was given to the plants after the seedlings had been irrigated with various concentrations of putrescine for 6 d of continuous light (Fig. 1). Putrescine level in the cotyledons at the beginning of the inductive dark treatment was analyzed and floral response was evaluated after 20 d of continuous light following the dark period. Endogenous putrescine level was found to be linearly proportional to the amount of exogenous

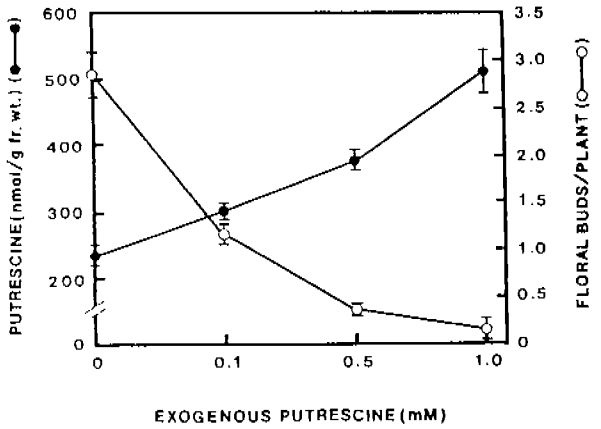


**Fig. 1.** Floral response and putrescine titer changes in *Pharbitis nil* supplied with exogenous putrescine. The plants were irrigated with various concentrations of putrescine for 6 d of continuous light at the end of which endogenous putrescine titer was analyzed and a 16 h dark period was given for floral induction. Floral response was evaluated 20 d of continuous light thereafter.

putrescine added to the plants. Compared to the control group, receiving no putrescine treatment, 0.1 and 0.5 mM putrescine declined flowering by 59% and 87.5% respectively. The flowering was further depressed at higher concentrations of putrescine. Virtually no flowering was detected by 1.0 mM putrescine treatment. It was assumed that high level of putrescine in cotyledons at the beginning of inductive dark period would act as an inhibitory factor in flowering.

The preliminary information on inhibitory effect of polyamines on flowering was further confirmed by tracing change of polyamine levels throughout the inductive dark period (Fig. 2). Putrescine, spermidine and spermine levels in florally induced cotyledons were detected at 4 h intervals during a 16 h dark period. The levels began to decline immediately after the start of the dark to reach their minimal levels in the middle or in the second half of the dark followed by the recovery at the end of the dark period. Putrescine titer was gradually increased under continuous light to reach 239.8 nmol/g fr. wt. at the end of light and the level was dropped to 148.0 in 12 h in the dark. The depression by 38.3% was partially recovered at the end of the dark period. Spermidine titer change was observed to be similar to that of putrescine. In the middle of the induction the level in the induced tissue was dropped to 39.1%

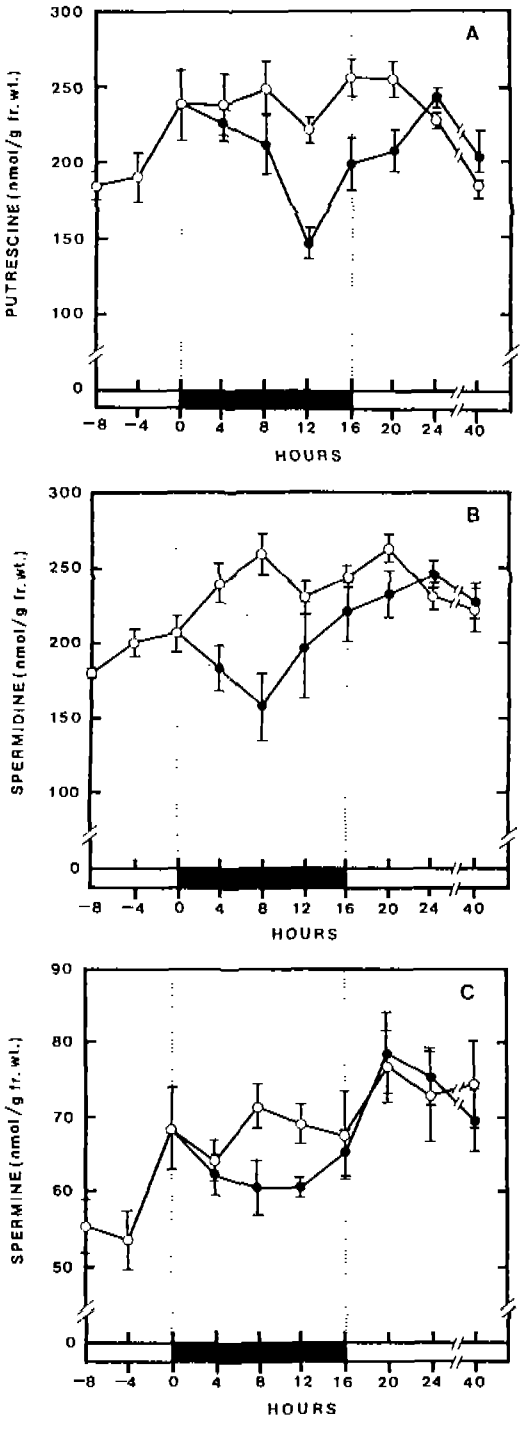


**Fig. 2.** Polyamine titer changes in the cotyledons of *Pharbitis nil*. ○, non-induced cotyledons kept under continuous light; ●, induced cotyledons exposed to a 16 h dark period. Duration of dark (■) and light periods (□) are depicted on the abscissa. Vertical bars represent standard errors.

level of the non-induced cotyledons. Spermine showed less steep and more gradual decreasing tendency than the former polyamines. Toward the end of the inductive dark period the polyamines steadily increased their titers to reach the levels comparable to those in the non-induced tissue in 20-24 h under continuous light following the dark.

To see if the difference in polyamine titers between induced and non-induced tissue was attributed to radiant energy *per se*, endogenous polyamines were analyzed after a night break by 10 min white light had been given to the plants 8 h after the onset of 16 h inductive dark which was known to be the most sensitive time to night break treatment (Fig. 3). Dark interruption by 10 min light at 8 h after beginning of the dark had an effect of canceling the inductive action of the dark period bringing flowering down to 25.9% level of the control. Concomitantly, the night break could drastically elevate putrescine, spermidine and spermine titers by 26.6, 43.9 and 23.6% respectively in 4 h. Night break-induced high level of putrescine titer during the second half of the dark was observed to be maintained at least for 24 h after the end of the inductive dark period and slowly decreasing to reach the control level in 40 h under continuous light. Spermidine titer was further increased even after the dark period had ended. It took 40 h for spermidine to bring its level to that in untreated tissue. Thus the results could lead to postulation that the elevated levels of polyamines in the cotyledons would closely correlated to abolishment of floral induction in *Pharbitis nil*.

Studies on possible involvement of polyamines in flowering are very limited and the results thus reported are not only diverse but also inconsistent and contradictory to each other depending on stages of flowering and plant systems. Discussing the inhibitory effects of polyamines on floral formation in *Lemna paucicostata* 6746, a short-day plant, Tsao and Yin (1985) observed decreasing level of endogenous spermidine and increasing titer of putrescine during 4 d dark induction. In contrast, Kim and Maeng (1992) found rapidly increasing level of spermidine in florally induced *Lemna gibba* G3, a long-day plant, postulating endogenous polyamine status might play an important role in the very early stage of floral induction in the plant. Hamasaki and Galston (1990) detected gradual decline of free putrescine when *Xanthium strumarium*, one of the most sensitive short-day plant, was induced by a 16 h dark period. Reports on *Pharbitis* system are further confusing. Dai and Wang (1987) observed that in induced cot-

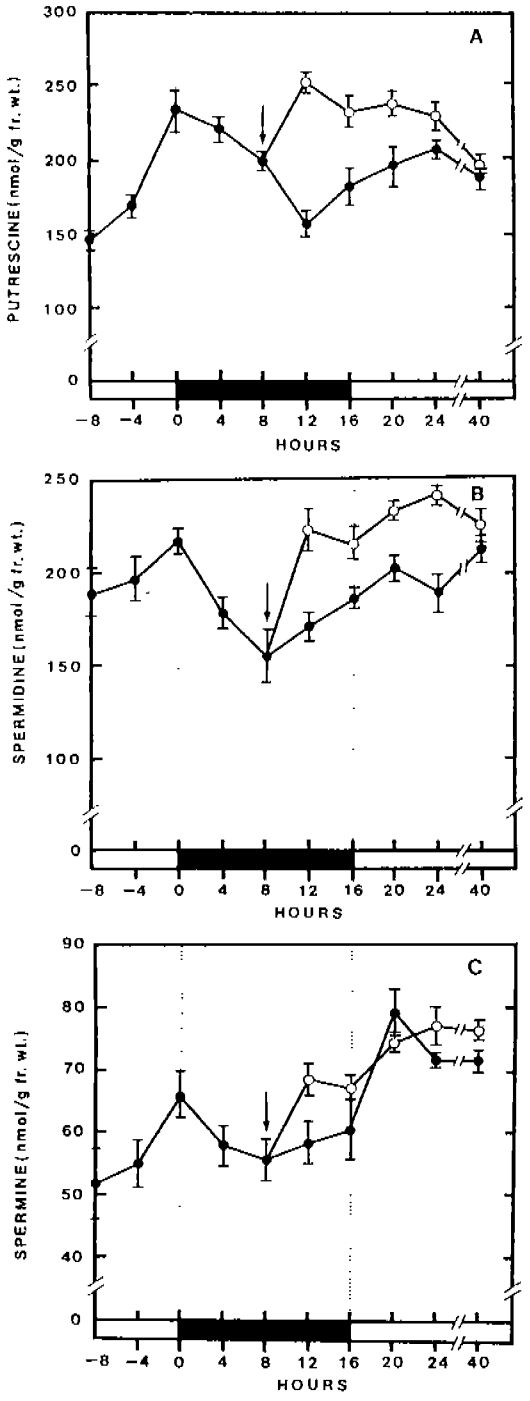


**Fig. 3.** Effect of night break during dark period on polyamine titers in the cotyledons of *Pharbitis nil*. ○, cotyledons exposed to 10 min light at 8th h in a 16 h dark period as indicated as an arrow; ●, cotyledons taking no night break. Duration of dark (■) and light periods (□) are depicted on the abscissa. Vertical bars represent standard errors.

yledons of *P. nil* cv. Violet putrescine maintained its level lower than non-induced one throughout a

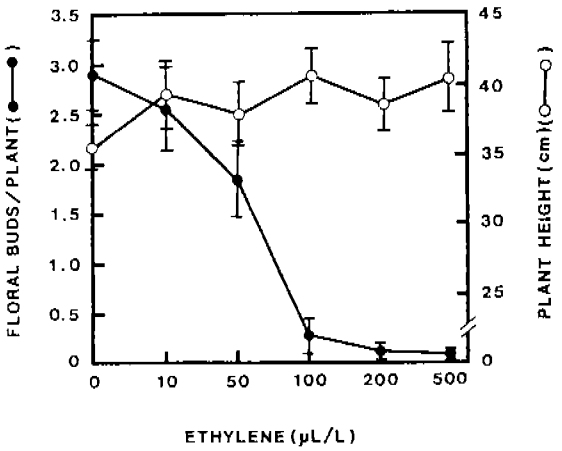


**Fig. 4.** Dose-response curve of ethylene action on the flowering in *Pharbitis nil*. The plants were exposed to ethylene throughout a 16 h dark period. Vertical bars represent standard errors.

16 h dark −8 h light period, while spermidine and spermine fluctuated during the short-day treatment. Using *P. nil* cv. Kidachi grown hydroponically, Wada *et al.* (1994) reported the first evidence that polyamines could induce flowering in intact plants under a non-inductive condition. They also found that putrescine content in the treated plants was increased concordantly with flower induction while spermidine titer was not significantly changed. Our result on inhibitory action of exogenous putrescine on flowering is completely contractory to that of Wada *et al.* (1994), although each used different strain of the short-day species.

To provide more evidence to further support the postulation that polyamine titers may be causally related to photoperiodic floral induction in *Pharbitis*, polyamine titer changes were traced as the plants were being exposed to ethylene, which has flower-inhibitory action (Suge, 1974; Amagasa and Suge, 1987; Lay-Yee *et al.*, 1987) and shares a common intermediate with polyamines in their biosynthetic pathways. Ethylene of 100 μL/L or higher concentrations was found to almost completely inhibit flowering without affecting vegetative growth (Fig. 4). As shown in Fig. 5, cotyledons exposed to 100 μL/L ethylene during the inductive dark period steeply increased their polyamine levels. Compared to the data depicted in Fig. 1, putrescine and spermidine content in ethylene-treated cotyledons was increased by 57.7 and 70.9% in 4 h, by 103.8 and 130.1% in 8 h, by 136.5 and 48.4% in 12 h, and by 131.7 and 21.6%

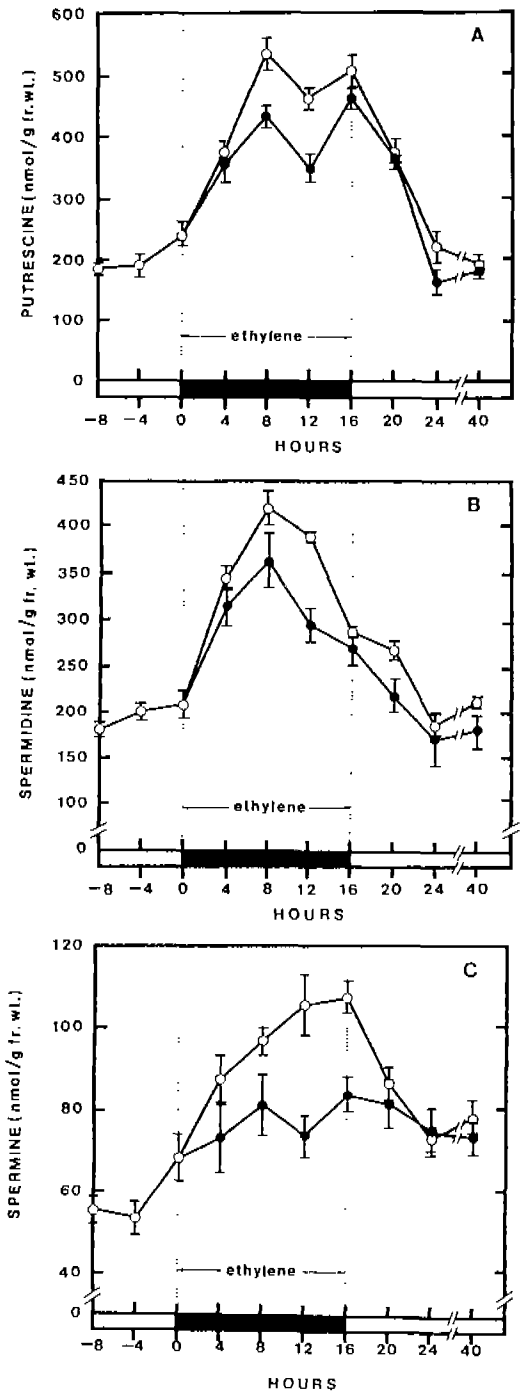


**Fig. 5.** Polyamine titers in the cotyledons of *Pharbitis nil* affected by exogenous ethylene. ○, non-induced cotyledons exposed to 100 μL/L ethylene for 16 h continuous light; ●, induced cotyledons by a 16 h dark period during which 100 μL/L ethylene was applied. Duration of dark (■) and light periods (□) are depicted on the abscissa. Vertical bars represent standard errors.

at the end of the dark, respectively. Spermidine surge by ethylene was found to be in smaller scale.

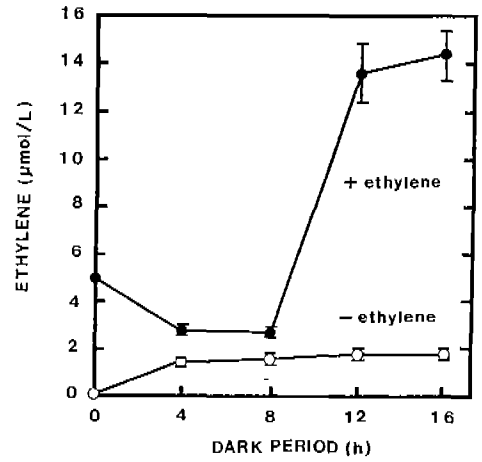


**Fig. 6.** Ethylene production by *Pharbitis nil* induced by exogenous ethylene. A single 5 d-old seedling was exposed to 100 μL/L ethylene at the beginning of the inductive dark period and levels of ethylene thus accumulated in the closed container were analyzed at 4 h-intervals in the dark. Vertical bars represent standard errors.

The information on the mechanism of inhibitory action of ethylene to floral induction and the mode of ethylene action on polyamine biosynthesis is so much limited that it is virtually impossible at present to explain the ethylene-induced polyamine titer elevation in *Pharbitis* cotyledons. Moreover, previous reports showed that ethylene exerted its inhibitory or promotive action depending on plant systems. A few reports revealed the inhibitory action of ethylene to the activities of enzymes involved in polyamine biosynthesis (Apelbaum *et al.*, 1985; Icekson *et al.*, 1985; Icekson *et al.*, 1986). On the other hand, some could observe that exogenous application of ethylene could induce polyamine accumulation, mainly putrescine, in deepwater rice system (Cohen and Kende, 1986) as well as in rice coleoptiles (Lee and Chu, 1992). Cotyledons with high levels of polyamines by exposing to ethylene during the inductive dark period are observed to liberate ethylene (Fig. 6). Seedlings exposed to 100 μL/L ethylene throughout a 16 h inductive dark period showed three or four fold upsurge of ethylene release in the second half of the dark period. Exposure to ethylene is assumed to increase ethylene production by changing permeability of tonoplast to methionine to increase availability of cytosol methionine, a precursor of ethylene biosynthesis (Kende and Baumgartner, 19 74) or by activating enzymes involved in ethylene synthesis (Fernández-Maculet and Yang, 1992). It

is assumed that ethylene-treated cotyledon tissues were stimulated to generate endogenous ethylene which in turn accelerated polyamine synthesis in the tissues. It is also noticeable that both the greatest difference in polyamine content between induced and non-induced tissues and sudden elevation of ethylene liberation by ethylene-treated tissues reside in the second half of the inductive dark period.

Summarizing the present study, a single inductive dark treatment significantly lowered putrescine, spermidine and spermine content in cotyledons where photoperiodic floral induction proceeded, which otherwise was completely blocked either by exogenous application of putrescine, by imposing a night break, or by ethylene treatment in the inductive dark period. Each of these inhibitory treatments significantly elevated polyamine content in the cotyledons. It is postulated that maintanance of low polyamine levels in cotyledons throughout the inductive dark period is one of the necessary factors for photoperiodic induction of flowering in *Pharbitis nil*.

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## Polyamine과 Ethylene 影響하에서의 나팔꽃 子葉內 光週期性 開花誘導

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### 적 요

단일식물인 나팔꽃 (*Pharbitis nil* Choisy cv. Violet)의 광주기성 개화유도 과정이 진행되는 자엽조직내 polyamine 함량 변화를 추적하였다. 개화유도 16시간 암기에 가한 0.5 mM 이상 농도의 putrescine은 자엽조직내 putrescine 함량을 증가시키면서 결과적으로 개화유도를 완전히 억제하였다. 비유도 광주기인 연속광하에서 자엽조직내 putrescine, spermidine 및 spermine 함량은 서서히 증가되는 반면, 16시간의 개화유도 암기에서는 putrescine, spermidine 및 spermine 함량은 각각 비유도 자엽조직의 함량의 66.4%, 60.9% 및 84.9% 수준까지 감소되었다. 이렇듯 개화유도 암기중 낮은 수준으로 유지된 3종류의 polyamine 함량은 암기중간인 암기시작 후 8시간째에 10분간의 백색광에 의한 암기차단처리로 급격히 증가되었고, 이에 따라 개화유도 암기의 효과도 소멸되었다. 식물을 유도암기중에 개화유도 과정을 완전히 억제하는 효과를 지닌 100 μL/L ethylene에 노출시킴으로서도 자엽조직내 polyamine 함량을 증가시킬 수 있었는데, 이렇게 ethylene으로 처리된 자엽조직은 비처리 조직에 비하여 putrescine을 처리 12시간만에 136.5%만큼 그리고 spermidine 함량을 처리 8시간만에 130.1%만큼이나 증가시켰다. Ethylene 처리 자엽은 내생 polyamine 수준을 증가시킬 뿐만 아니라 유도암기 후반부에 3내지 4배 수준으로 ethylene을 방출하는 것이 관찰되었는데 이는 자엽내로 흡수된 ethylene에 의하여 생산이 증가된 내생 ethylene이 내생 polyamine 생성을 촉진시키는 것이라는 가정을 뒷받침하여 준다. 나팔꽃의 광주기성 개화유도 과정에서 putrescine, spermidine 및 spermine의 자엽조직내 함량이 개화유도 암기중에 상당히 낮은 수준으로 유지되는 것이 개화유도의 필수적 조건의 하나이며, 암기차단이나 ethylene의 개화유도 억제효과는 이들 polyamine의 수준을 급격히 증가시킴에 기인된다고 추정된다.

주요어: 나팔꽃, 개화, 개화유도, polyamine, ethylene

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