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Regulation of Cell Division in the Subapical Shoot Meristem of Dwarf Watermelon Seedlings by Gibberellic Acid and Polyethylene Glycol 4000

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Abstract. The stimulatory effects of gibberellic acid (GA_3) and the inhibitory effects of polyethylene glycol 4000 (PEG) on hypocotyl elongation and cell cycle kinetics in subapical pith cells of dwarf watermelon seedlings (*Citrullus lanatus* [Thunb.] Matsu and Nakai) were investigated. Mitotic indices (MI) were determined from direct counts of pith cells stained by a modified Feulgen technique. Labeling indices (LI) were determined from direct counts of labeled pith cells sampled 1.5 h after apical applications of ^{3}H-thymidine. Root application of 0.32 mM GA_3 at 96, 120, or 144 h after sowing resulted in significant increases in both mitotic and labeling indices within 4.5 to 7.5 h following treatment. A single mitotic peak at 13.5 h occurred in all three treatment periods. Labeling peaks were often less defined than mitotic peaks; however, a relatively high proportion of labeled nuclei were usually observed between 7.5 and 9 h after GA_3 treatment and at 16.5 h, the latter period coinciding with progression of cells into S phase from the peak period of mitosis. The results suggest that GA_3 increases the proportion of rapidly dividing cells in the subapical meristem by increasing the probability that slowly cycling or nonproliferative cells in both 2C and 4C DNA states will enter the proliferative pool. The addition of PEG (200 g/l, ψ = 1.5 mPA) to the rooting medium of dwarf watermelon seedlings inhibited hypocotyl elongation and reduced both mitotic and labeling indices simultaneously within 4.5 h after treatment. Within 24–28 h after PEG treatment, mitotic and labeling indices approached 0. Seedlings transferred from PEG to either water or GA_3 exhibited rapid recovery of

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cell division and hypocotyl elongation. Mitotic and labeling indices increased within 4.5–7.5 h into the recovery period in either water or GA_3 and reached control values within 10.5 h. GA_3 hastened the recovery from PEG-induced stress. It is concluded that water stress imposed by PEG 4000 causes arrest of cell division in meristematic cells of watermelon seedlings in both G_1 and G_2 periods. PEG and GA treatments resulted in only a partial and transitory synchronization of the cell cycle.

Gibberellic acid (GA_3) stimulates both cell elongation and cell proliferation in the subapical meristem of many dwarf and rosette plants (Greulach and Haeslip 1958, Jacqmard 1968, Okuda 1964, Sachs et al. 1959a,b). In the subapical meristem of dwarf watermelon seedlings, GA_3 increases cell proliferation both by shortening the cell cycle (Liu and Loy 1976) and by increasing the growth fraction of cells (Loy 1977). The time course of cell cycle response to GA_3 has not been studied in dwarf watermelon, nor has it been well documented in other plants. Studies to date suggest that GA_3 promotes cell division by inducing cells in G_1 phase to enter the DNA synthesis phase of the cell division cycle (Jacqmard 1968, Okuda 1964, Sachs et al. 1959a), thereby producing a partial synchrony of cell division.

Polyethylene glycol (PEG) has frequently been used as an osmoticum for studying the effects of water stress on meristematic activity (Burstom 1976, Husain and Aspinall 1970, Terry et al. 1971, Yee and Rost 1982). PEG molecules with molecular weights of 1000 or greater are not readily absorbed by plant tissues (Janes 1974, Lawlor 1970), and PEG-induced water stress can be reversed by transferring tissue out of the osmoticum (Yee and Rost 1982).

Because of the reversibility of PEG-induced stress and evidence that PEG-induced water stress inhibits DNA synthesis in meristematic tissue (Gardner and Nieman 1964, Meyer and Boyer 1972), we speculated that PEG in combination with GA_3 might be an effective tool for synchronizing cell division. The objectives of present study were to perform kinetic analyses of cell division following either GA_3 treatment or PEG-imposed water stress and to examine subsequent recovery from PEG-induced stress in a medium containing either water alone or GA_3. Cell cycle kinetics were followed by examining both mitotic and labeling indices of subapical pith cells of dwarf watermelon seedlings at 3- or 4-h intervals following treatments.

Materials and Methods

Plant Materials and Growing Conditions

Seedlings of an inbred *dw*-2 dwarf strain of watermelon (*Citrullus lanatus* [Thunb.] Matsu and Nakai), designated WB-2, were used for all experiments. Mechanically scarified seeds were germinated at 29 ± 1°C in black plastic germinating trays on a layer of absorbent wadding saturated with distilled water. After 72 h of dark germination, uniformly germinating seedlings were selected, their seed coats removed, and 10 seedlings each were transferred to 9-cm Petri dishes containing a layer of absorbent wadding saturated with 10 ml

of distilled water. The dishes were placed in transparent germinating trays layered with water-saturated wadding to maintain high humidity and then placed in a growth chamber maintained at 29 ± 1°C under continuous cool white fluorescent lights (5 Wm^{-2}).

GA_3 and PEG Treatments

Gibberellic acid (0.32 mM) or polyethylene glycol 4000 (200 g/l, ψ = 1.5 mPA) was administered by saturating the rooting medium (absorbent wadding) at the different treatment times. GA_3 treatments began at 96, 120, or 144 h of incubation by transferring five seedlings each to 5-cm Petri dishes and anchoring roots in the absorbent wadding. Mitotic and labeling indices were determined every 3 h for 30 h following the start of GA_3 treatments. Seedlings were transferred to PEG at 96 h of development, and mitotic and labeling indices were determined every 3 h over a 30-h stress period. For analyzing the recovery from PEG-induced stress, seedlings were transferred to either water or GA_3 at 120 h, following a 24-h PEG treatment. Mitotic and labeling indices were determined every 3 h over a 30-h recovery period.

Determination of Mitotic and Labeling Indices

At each 3-h interval of a treatment period, five seedlings were labeled with 5 μCi of ^{3}H-thymidine (sp. act. 20 Ci/mmole; New England Nuclear). The labeled thymidine was applied with a microsyringe in 5-μl droplets to the apex (between the cotyledons) of each seedling. After a 45-min labeling period, the apices were rinsed with distilled water, and the seedlings were incubated for 1 h to allow for additional incorporation of the label into DNA. Subsequently, 1-cm apical segments were excised and fixed in ethanol:acetic acid (3:1) for 24 h and then transferred to 70% ethanol for storage. Medial longitudinal sections 200 μm thick were cut from the apical segments with a hand microtome. The sections were hydrolyzed in 1 N HCl for 10 min at 60°C and then stained by the Feulgen reaction for 60 min, using 3% pararosaniline in place of basic fuchsin for the Schiff's reagent (Gude 1968). Following staining, the upper 1 mm of the subapical pith meristem was removed and squashed in 45% acetic acid on slides pretreated with Haupt's adhesive. Cover glasses were removed by the dry-ice method (Conger and Fairchild 1953). The slides were stored in 95% ethanol and transferred to a darkroom with a Kodak No. 1 safelight, where they were coated with Ilford L-4 autoradiographic emulsion. Slides were dried and then stored in the dark with desiccant in a refrigerator for an exposure period of 14 days. Following exposure, the slides were developed for 5 min in Kodak D-19 developer, rinsed for 10 s in a stop bath, fixed for 5 min in Kodak fixer, and washed for 10 min with running distilled water. The slides were then dehydrated through an ethanol series and made permanent by affixing a cover glass with Euparol. The mitotic and labeling indices were determined by examining autoradiographs for stained mitotic figures and nuclei displaying silver grains appreciably (~20 times) above background, which was negligible in all

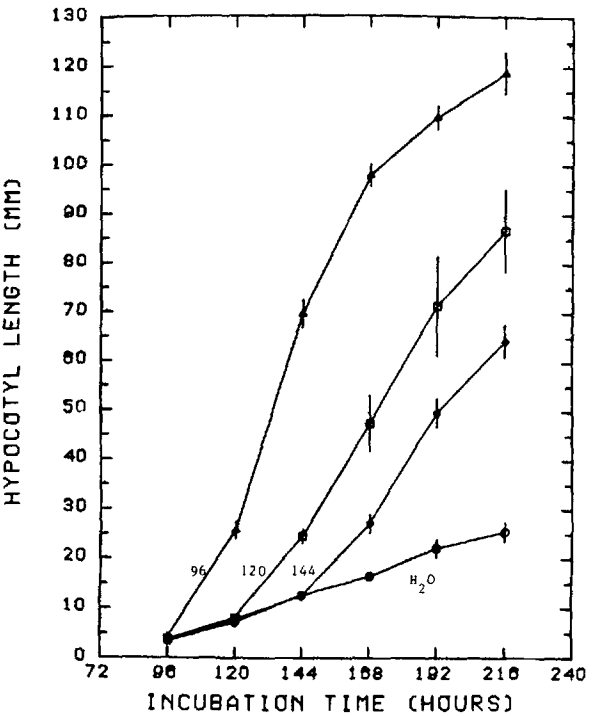

Fig. 1. The effect of 0.32 mM GA_3 on hypocotyl length when applied through the root medium at 96, 120, or 144 h after sowing seeds. Vertical bars indicate SE for five replications.

experiments. Four meristems were examined for each time interval, and at least 2000 cells were scored for each data point. A Zeiss phase-contrast microscope was used for all observations. The mean mitotic and labeling indices and their standard errors were calculated and plotted at points 1.5 h after application of the label to account for the approximate labeling and incubation time prior to sampling and fixing the meristems.

Results

Stimulation of Hypocotyl Elongation by GA_3

Figure 1 shows hypocotyl elongation following GA_3 treatments at 96, 120, and 144 h. Growth was markedly enhanced by GA_3 at all treatment times; however, with delayed time of hormone application, both the rate of growth and final hypocotyl length declined. Some hypocotyl growth continued after the last measurement at 215 h, but hypocotyl length of seedlings treated at 120 or 144 h remained well below those treated at 96 h.

Inhibition of Hypocotyl Elongation by PEG

When dwarf watermelon seedlings were transferred at 96 h from a water-saturated medium to a medium containing 200 g/l PEG, there was an immediate

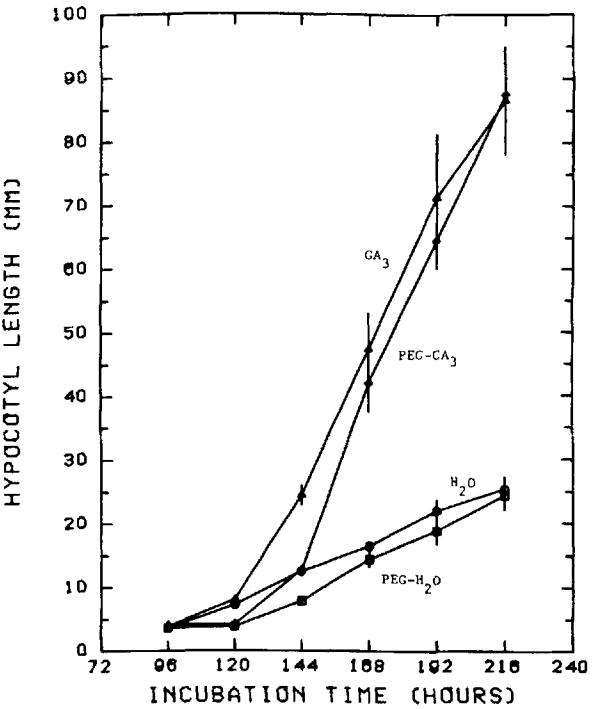

Fig. 2. Hypocotyl elongation of dwarf watermelon seedlings in water or 0.32 mM GA_3 following transfer from a 24-h treatment (96–120 h of incubation) in PEG. H_2O, control seedlings maintained in water; GA_3, seedlings transferred from water to GA_3 at 120 h; PEG-H_2O, seedlings transferred from water to PEG at 96 h and from PEG 4000 to water at 120 h; PEG–GA_3 seedlings transferred from water to PEG at 96 h and from PEG to GA_3 at 120 h. Vertical bars indicate SE for five replications.

cessation of hypocotyl elongation (Fig. 2). In seedlings exposed to PEG-induced water stress for 24 h, hypocotyl length increased an average of only 5%, compared to a 113% (or 3.6 mm) increase in hypocotyl length in untreated seedlings during the same period. Roots of stressed plants were thin, fragile, sparsely branched, and more elongated than in control seedlings. The normal formation of chlorophyll in expanding cotyledons was suppressed during PEG treatment.

Recovery from PEG-Inhibited Growth in Water or GA_3

Inhibition of growth due to 24 h of osmotic stress was rapidly alleviated after transfer of seedlings from PEG to water or GA_3 (Fig. 2). Hypocotyls of seedlings recovering in water or GA_3 attained growth rates between 24 and 48 h of recovery (144–168 h of incubation), which exceeded that of the respective unstressed control seedlings. By 48 h after transfer from PEG (i.e., 168 h of incubation), this "extra" growth produced hypocotyl lengths in recovering plants that were not significantly different from that of unstressed plants.

Effect of GA_3 on Mitotic and Labeling Indices

GA_3 markedly increased mitotic indices (MIs) of seedlings during all treatment periods; however, the response to GA_3 decreased with increasing seedling age

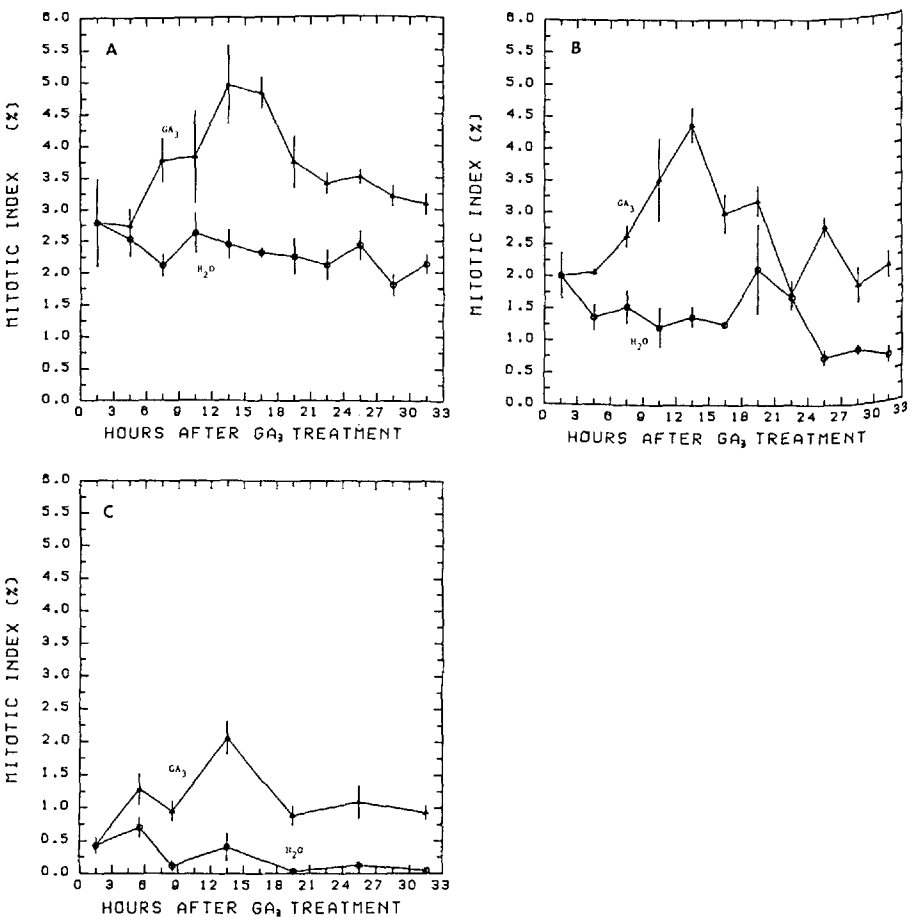

Fig. 3. The effect of GA_3 treatment at 96 h (A), 120 h (B), and 144 h (C) of seedling incubation on mitotic indices between 1.5 and 31.5 h following treatment. Vertical bars indicate SE for four replications of 400–600 cells per meristem.

(Fig. 3). The response to GA_3 was evident within 4.5–7.5 h after treatments, and MIs rose progressively to a peak at 13.5 h in all three treatment periods. Mitotic indices subsequently declined but remained well above control values even 31.4 h after treatment. Mitotic figures were nearly absent in control seedlings after 163.5 h of incubation (i.e., 19.5 h of the 145.5- to 175.5-h sampling period), whereas some GA_3-treated cells continued to divide after 175 h of seedling growth.

Labeling indices (LIs) increased significantly between 4.5 and 7.5 h after GA_3 application at the three treatment times (Fig. 4). There was variation in the pattern of labeling peaks among the treatments. GA_3 treatments beginning at both 96 and 120 h produced peak LIs at 16.5 h, corresponding to transition

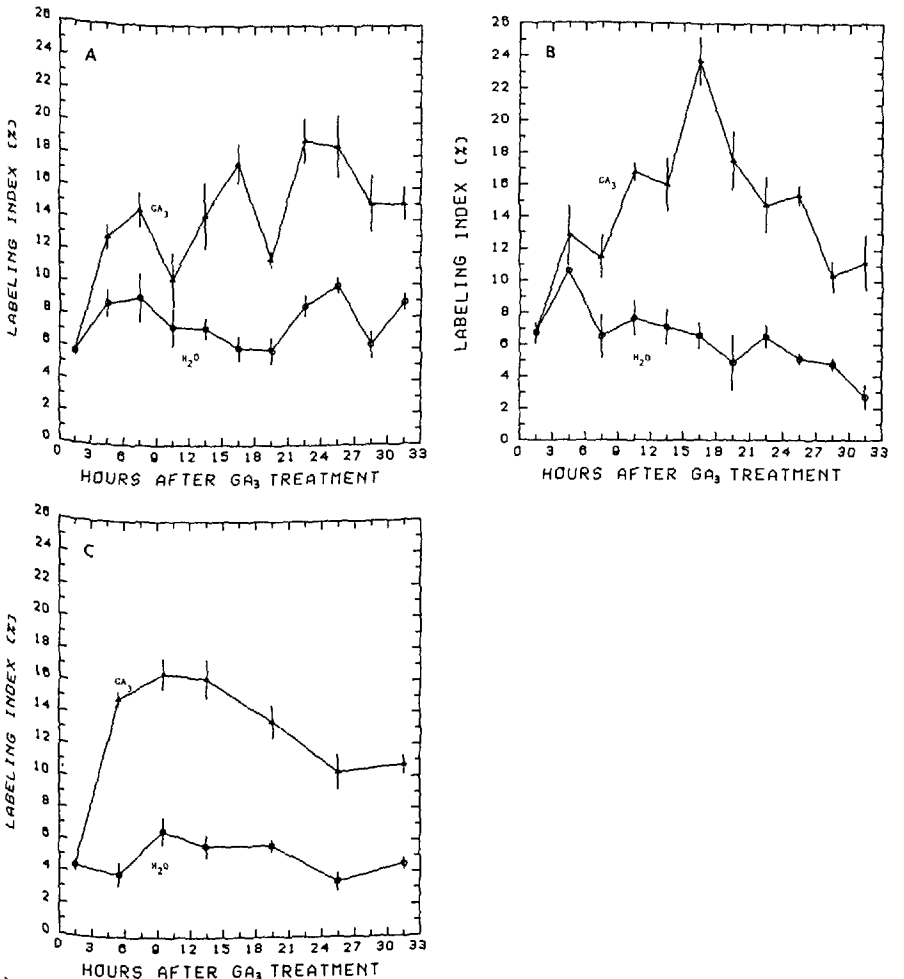

Fig. 4. The effect of GA_3 treatment at 96 h (A), 120 h (B), and 144 h (C) of seedling incubation on labeling indices between 1.5 and 31.5 h following treatment. Vertical bars indicate SE for four replications of 400–600 cells per meristem.

of cells from the mitotic peaks at 13.5 h through G_1 to the DNA synthesis phase. However, the 96-h GA_3 treatment resulted in two additional peaks, at 7.5 h and at 22.5–25.5 h. The interval between these two peaks approximates the cell cycle time estimated for subapical meristematic cells of GA_3-treated seedlings of dwarf watermelon (Loy 1977), suggesting partial synchronization of a subpopulation of cells.

GA_3 treatment beginning at 144 h produced a more rapid initial increase in L_1 and a single, broad peak between 5.5 and 13.5 h. Labeling indices of GA_3-treated seedlings remained well above those of untreated seedlings in all three treatment periods.

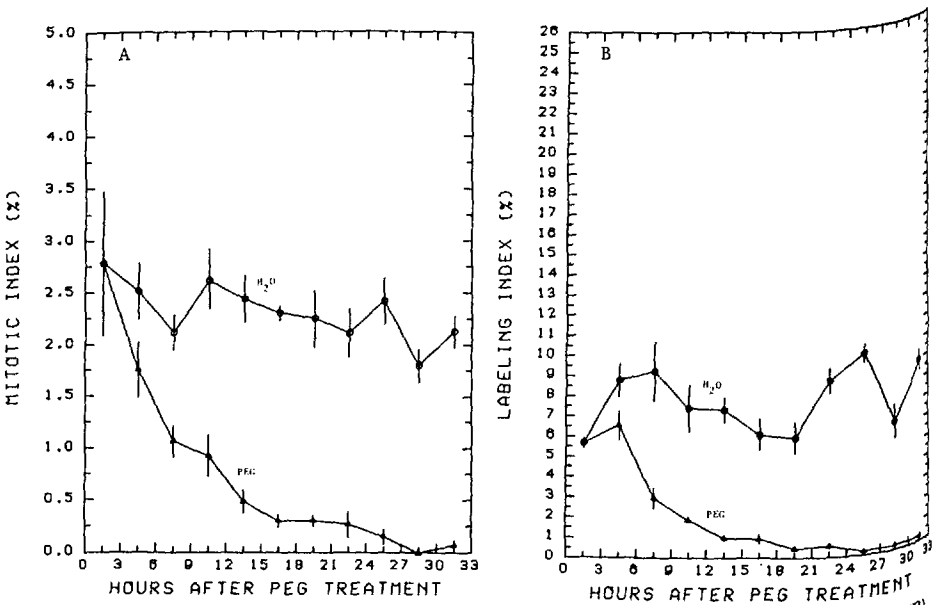

Fig. 5. The effect of PEG 4000 treatment on time course changes in the mitotic (A) and labeling (B) indices of subapical meristematic pith cells in dwarf watermelon seedlings between 97.5 and 127.5 h of incubation. Vertical bars indicate SE for four replications of 400–600 cells per meristem.

PEG Inhibition of Mitosis and DNA Synthesis

The MI declined rapidly after exposure of seedlings to PEG (Fig. 5A). Within 7.5 h, the MI was reduced more than 50%, and it approached zero by 28.5 h, with only a few leaky cells continuing to enter mitosis during exposure of seedlings to PEG.

PEG treatment also resulted in a rapid reduction in the proportion of labeled nuclei (Fig. 5B). By 7.5 h, the LI for PEG-treated seedlings dropped to 30% that of untreated seedlings. LIs of stressed seedlings continued to decrease over time and approached 0 after 25.5 h of PEG treatment.

Recovery from PEG Inhibition of Cell Division

Figure 6 shows the mitotic recovery for PEG-stressed seedlings in comparison to untreated seedlings following their transfer to either water or GA_3. In both instances there was a 4.5- to 7.5-h lag preceding a sharp increase in the MI. In seedlings transferred out of PEG and into water (Fig. 6A), the MI reached a near maximum value of 2.3 at 13.5 h and remained at or near that plateau, markedly above control values, for the next 18 h. In seedlings transferred from water to GA_3 (Fig. 6B), the MI reached a maximum value of 4.4 at 13.5 h and then declined to 2.1 after 31.5 h. In seedlings transferred from PEG to GA_3, a maximum MI of 4.7 occurred 3 h later at 16.5 h, and MI's remained relatively high throughout the observation period.

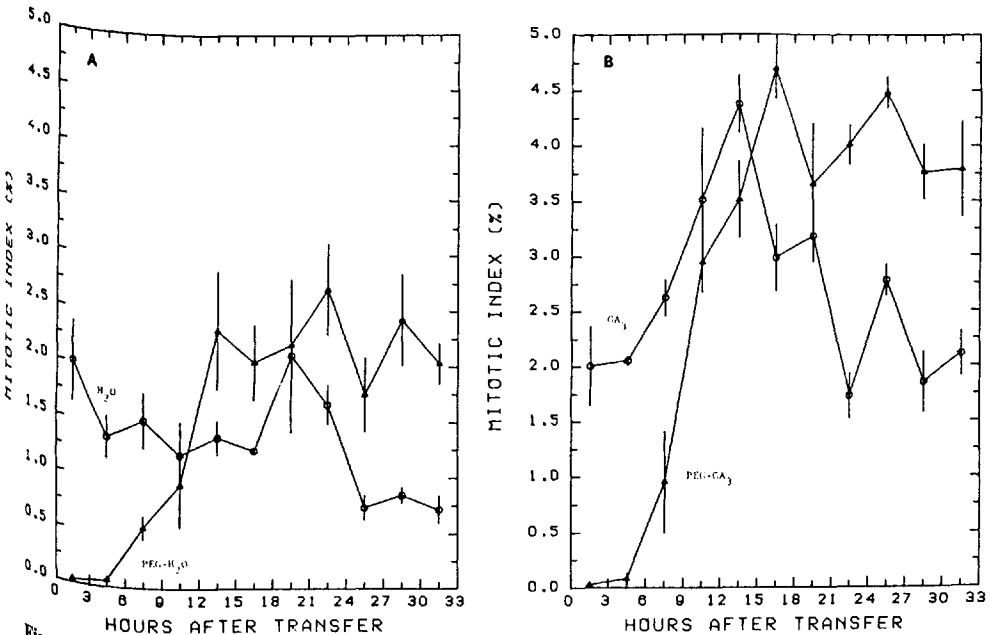

Fig. 6. Time course changes in mitotic index between 121.5 and 151.5 h of incubation following transfer of seedlings from a 24-h PEG 4000 treatment. (A) Seedlings receiving continuous water are compared to those transferred from PEG to water at 120 h. (B) Seedlings transferred from water to 0.32 mM GA_3 are compared to those transferred from PEG to GA_3 at 120 h. Vertical bars indicate SE for four replications of 400–600 cells per meristem.

Following a transfer out of PEG and into water, the LI rose slowly during the initial 4.5–7.5 h and then increased sharply to a peak value at 13.5 h, which was nearly double that of controls (Fig. 7A). The LI decreased to near control levels at 19.5 and 22.5 h, but then it rose progressively over time while the proportion of labeled nuclei in control meristems was declining.

Compared to seedlings transferred from water to GA_3, subapical pith cells from seedlings transferred from PEG to GA_3 exhibited a 3-h delay prior to the initial rise in LI (7.5 h) and peak LI (19.5 h) (Fig. 7B). Otherwise, the labeling patterns for the two treatments (water to GA_3 and PEG to GA_3) were similar.

A comparison of the two recovery treatments (PEG to water and PEG to GA_3) shows that GA_3 promoted a relatively rapid initial increase to a peak LI at 10.5 h (Fig. 7B) as compared to a first peak at 13.5 h for recovery in water (Fig. 7A). The PEG-to-water treatment resulted in a partial synchronization of cell division as indicated by the sharp LI peak at 13.5 h. This effect appeared to be transient, as indicated by a lack of a definitive corresponding MI peak (Fig. 6A) following the LI peak.

Discussion

GA_3 enhancement of stem elongation in dwarf watermelon decreased with increased seedling age at the time of hormone application. These results were

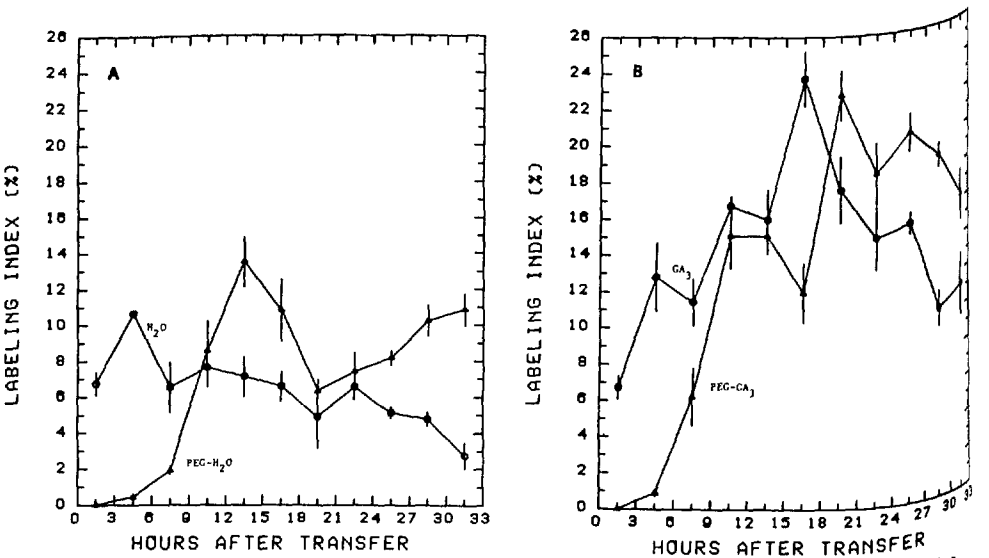

Fig. 7. Time course changes in labeling index between 121.5 and 151.5 h of incubation following transfer of seedlings from a 24-h PEG 4000 treatment. (A) Seedlings receiving continuous water are compared to those transferred from PEG to water at 120 h. (B) Seedlings transferred from water to 0.32 mM GA_3 are compared to those transferred from PEG to 0.32 mM GA_3 at 120 h. Vertical bars indicate SE for four replications of 400–600 cells per meristem.

not unexpected and are consistent with those of previous studies (Katsumi and Kawamura 1980, Kazama and Katsumi 1973, Wright 1961). The capacity of GA_3 to promote mitotic activity likewise decreased with seedling age, such that peak mitotic indices in GA_3-treated seedlings decreased from 5.0 in the 97.5- to 127.5-h sampling period (Fig. 3A) to 2.0 in the 145.5- to 175.5-h sampling period (Fig. 3C). Nonetheless, GA_3 prolonged the duration of mitotic activity in the subapical meristem. The MI was near zero in 163-h-old untreated seedlings, compared to 1% in GA_3-treated seedlings (Fig. 3C).

Labeling indices also decreased with seedling age in both untreated and GA_3-treated seedlings, but to a much lesser extent than mitotic indices (Fig. 4). In untreated seedlings, an LI close to 4% was maintained through the 145.5- to 175.5-h observation period, whereas the MI approached zero by 163 h. During the same treatment period, GA_3 elicited a rapid increase in LI by 5.5 h, and yet no corresponding increase in MI appeared between 18 and 24 h, as would be expected if cells in S phase continued through to mitosis. The above observations suggest that some endoreduplication may be occurring as seedlings age and cell division declines. The phenomenon of endoreduplication is common in the plant kingdom (Dyer 1976), and varying ploidy levels have been observed in different organs at different developmental stages in plant species (Evans and Van't Hof 1975b).

The effect of GA_3 on the cell cycle in watermelon was rapid, as indicated by the rise in labeling and mitotic indices within 4.5–7.5 h after treatment. This short lag period suggests that some cells responding to GA_3 must have been

near the G_1/S and G_2/M boundaries. On the other hand, LI peaks occurred at various times after GA_3 treatment, depending on seedling age, and in seedlings treated with GA_3 at 120 h, the single major peak did not occur until 16.5 h after treatment. Mitotic peaks did not occur until 13.5 h after GA_3 treatment. These results indicate that cells entered the growth fraction or proliferative pool from both 2C and 4C states. Furthermore, cells entered the proliferative pool either gradually following GA_3 treatment or from different points in G_1 and G_2 phases.

In other higher plants meristematic cells have been shown to arrest in G_1 (2C state) or G_2 (4C state), the relative proportions being specific for species (Evans and Van't Hof 1975a, Sans et al. 1980) and tissues (Evans and Van't Hof 1975b). Evans and Van't Hof (1975a) studied the age distribution of cell cycle populations in root meristems and classified cells into three types: (1) rapidly proliferating cells, (2) slowly proliferating cells that were temporarily arrested in G_1 and/or G_2, and (3) nondividing cells arrested in G_1 and/or G_2. The results with dwarf watermelon conform with the above model for complex meristems. Although we could not identify a nonproliferative population with our analysis, the existence of such a population can be at least inferred for cells in basipetal regions of the subapical meristem and in older meristems where mitotic indices approached zero.

GA_3 treatment produced some synchronization of cell division, as indicated by the mitotic and labeling peaks following GA_3 treatment (Figs. 3, 4). MI peaks were usually followed by LI peaks about 3 h later, suggesting a shorter G_1 period than that of 4.2 h estimated from labeled mitotic curves of GA_3-treated dwarf watermelon seedlings (Loy 1977). There were no corresponding MI peaks following LI peaks. This could be due to the longer duration and greater heterogeneity in duration of S and G_2 periods, coupled with the presumed exit of a proportion of cells from S phase into a nonproliferative 4C state. Considerable variation in cell cycle time has been observed within a cell population, so that the degree of synchrony diminishes over time even in well-synchronized cell populations (Webster 1979).

The use of the osmoticum, PEG 4000, in the rooting medium provided a convenient system for studying the effects of water stress on stem growth and meristematic activity. Treatment of dwarf watermelon seedlings with PEG immediately suppressed hypocotyl elongation and reduced mitosis and nuclear DNA synthesis to nearly zero within 25–30 h after treatment. Hypocotyl growth and cell division resumed immediately following transfer of seedlings from PEG to water. Hypocotyls of seedlings recovering from PEG treatment displayed a compensatory growth period between 24 and 48 h into the recovery period, during which their growth exceeded that of untreated seedlings (Fig. 2). An analogous "stored" growth phenomenon was reported for elongation of maize leaves following a mild and short (1-h) exposure to water stress (Acevedo et al. 1971). Mitotic and labeling indices were also maintained above control levels during the PEG recovery period (Figs. 6A, 7A). It appears that in suppressing hypocotyl development for short periods of time, PEG suppresses the aging process as well, so that in seedlings recovering from short periods of PEG-imposed stress, the full extent of hypocotyl length is eventually attained.

During recovery of seedlings from PEG-induced stress in either water or

GA_3, the observed increases in MI and LI were simultaneous and of a similar order of magnitude. This suggests that cells were arrested in both G_1 and G_2 periods. Moreover, the entry of cells into S and M phases was gradual during recovery from water stress, suggesting that PEG arrested cells at different points in G_1 and G_2 and not just as G_1/S and G_2/M boundaries. PEG alone produced some cell cycle synchronization, as indicated by mitotic and labeling peaks following recovery of seedlings in water (Figs. 6A, 7A). The degree of synchrony was enhanced by GA_3 treatment during the recovery period. In these GA_3-treated seedlings, a steep mitotic peak occurred at 13.5 h (Fig. 6B), and a corresponding peak of labeled nuclei appeared 3 h later (Fig. 7B).

Our analysis does not provide an unequivocal answer as to whether osmotic stress is inhibiting concurrent DNA replication in S phase or the entry of cells from G_1 into S phase. The gradual decrease in LI over time following PEG treatment and the sharp rise to a peak LI following recovery from PEG favor the hypothesis that the PEG-induced decrease in LI is due to failure of G_1 cells to enter S. Likewise, data on mitosis indicate that PEG does not block the ability of cells to complete mitosis but decreases movement of cells through G_2 and into M phase. These results agree with the hypothesis that principal control points exist in G_1 and G_2 for regulation of mitosis and DNA replication (Van't Hof and Kovacs 1972) and are consistent with the general observation that numerous types of environmental stress imposed on plant tissues increase the proportion of cells in G_1 and G_2 (Rost 1977).

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