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Thermo- and Photoperiodicity and Involvement of Gibberellins during Day and Night Cycle on Elongation Growth of *Begonia x hiemalis* Fotsch

J. Myster,[1,*] A. Ernstsen,[2] O. Junttila,[2] and R. Moe[1]

[1]Department of Horticulture and Crop Sciences, Agricultural University of Norway, Ås NLH; and the [2]Institute of Biology, University of Tromsø, N-9037 Tromsø, Norway

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Abstract. The effects of thermo- and photoperiodicity on elongation growth and on endogenous level of gibberellins (GAs) in *Begonia x hiemalis* during various phases of the day-night cycle have been studied. Plant tissue was harvested during the day and night cycle after temperature and photoperiodic treatments and analyzed for endogenous GAs using combined gas chromatography and mass spectrometry. Elongation growth increased when the difference between day and night temperature (DIF = DT − NT) increased from a negative value (−9.0 and −4.5°C) to zero and with increasing photoperiod from 8 to 16 h. When applied to the youngest apical leaf, gibberellins A_1, A_4, and A_9 increased the elongation of internodes and petioles. GA_4 had a stronger effect on elongation growth than GA_1 and GA_9. In relative values, the effect of these GAs decreased when DIF increased from −9 to 0°C. The time of applying the GAs during a day and night cycle had no effect on the growth responses. In general, endogenous levels of GA_{19} and GA_{20} were higher under negative DIF compared with zero DIF. The level of endogenous GA_1 in short day (SD)-grown plants was higher under zero DIF than under negative DIF, but this relationship did not appear in long day (LD)-grown plants. The main effects of photoperiod seem to be a higher level of GA_{19} and GA_1 at SD compared with LD, whereas GA_{20} and GA_9 show the opposite response to photoperiod. No significant differences in endogenous level of GA_1, GA_9, GA_{19}, and GA_{20} were found for various time points during the diurnal day and night cycle. Endogenous GA_{20} was higher in petiole and leaf compared with stem, whereas there were no differences of GA_1, GA_9, and GA_{19} between plant parts. No clear relationship was found between elongation of internodes and petioles and levels of endogenous GAs.

Key Words. *Begonia*—Endogenous GAs—GA application—Photoperiod—Stem elongation—Thermoperiod

High day temperature (DT) and low night temperature (NT) increase stem elongation in tomato compared with high NT and low DT (Kristofferson 1963, Went 1953). Recently, it has been shown that internode elongation is closely related to DT − NT (DIF) in many plant species (Erwin 1991, Erwin et al. 1989, Moe 1990, Moe and Heins 1990). For strong growing cultivars of the short day (SD) plant *Begonia x hiemalis* negative (DT < NT) or zero DIF (DT = NT) results in compact plants of good quality (Myster and Moe 1995, Myster et al. 1997, Willumsen et al. 1995). Also, a temperature drop during the last 2 h of the night or in the beginning of the day decreases stem elongation in *B. x hiemalis* (Grindal and Moe 1994, Myster and Moe 1995, Willumsen et al. 1993). Another factor affecting elongation growth is the photoperiod (Heide and Rünger 1985, Sandved 1969, 1971) (Myster, unpublished data). SDs decrease elongation growth and sometimes induce dormancy. Stem elongation is shown to fluctuate during the photophile and the skotophile phases in several plants (Bertram 1992, Bertram and Karlsen 1995, Erwin et al. 1992, Torre 1995) and also in *B. x hiemalis* (Myster, unpublished data). Environmental factors affecting elongation growth in higher plants are shown to involve gibberellins (GAs) (Gilmour et al. 1986, Jensen et al. 1996, Jones and Zeevaart 1980, Junttila and Jensen 1988, Talon and Zee-

Abbreviations: DT, day temperature; NT, night temperature; DIF, DT − NT; GAs, gibberellins; GC-MS, gas chromatography-mass spectrometry; LD, long day; PPFD, photosynthetic photon flux density; SD, short day; PVPP, polyvinyl polypyrrolidone; SPE, solid phase extraction; HPLC, high performance liquid chromatography; MSTFA, *N*-methyl-*N*-trimethylsilyltrifluoroacetamide; SIM, selected ion monitoring.

*Author for correspondence: Ullensvang Research Center, N-5774 Lofthus, Norway.

vaart 1990, Zeevaart et al. 1991, Zeevaart and Gage 1993). It is also reported that endogenous levels of GAs fluctuate during the day and night cycle (Foster and Morgan 1995, Talon et al. 1991).

Here we have examined the effects of thermo- and photoperiodicity and of applied GAs during the photophile and scotophile phases on elongation growth in *B. x hiemalis*. Furthermore, we have studied the effects of thermo- and photoperiodicity and time of harvesting plant parts during day and night phases on endogenous GAs, which may mediate elongation growth.

Materials and Methods

Plant Material and Growing Conditions

All experiments were carried out with *B. x hiemalis* ''Aphrodite Pink.'' Rooted top cuttings were obtained from Ljones Gartneri (Hardanger, Norway). Plants were potted in fertilized and limed Norwegian peat (Floralux) in 12-cm black plastic pots and raised at 20°C, first in an 18-h photoperiod and then in a 10-h photoperiod for flower induction (Heide and Rünger 1985).

In a phytotron, daylight was supplemented by irradiance from high pressure sodium lamps giving 63 ± 7 μmol m^{-2} s^{-1} photosynthetic photo flux density (PPFD) under long day (LD) in both experiments and under SD in the application experiment. Under SD (8 h) in the second experiment, irradiation was 90 ± 5 μmol m^{-2} s^{-1} PPFD with fluorescent tubes (TLD 33) in growth chambers. In both experiments, the irradiation level was 95 ± 5 μmol m^{-2} s^{-1} PPFD for 8 h with fluorescent tubes. For the 16-h photoperiod, the 8-h basic light period was extended with irradiation from incandescent bulbs (2 ± 0.5 μmol m^{-2} s^{-1}). Irradiation was measured by a Lambda LI-185B instrument with quantum (400–700 nm) sensor. The average relative humidity ranged from 66.7 to 95.4% in both experiments.

Plants were fertilized with a complete nutrient solution. The pH and content of soluble salts in the growth medium were monitored during the experiments. Plants were selected for uniformity and randomized before they were taken into the experiments.

GA Application, Temperature, and Photoperiod

In the first experiment, GA_1, GA_4, or GA_9 was dissolved in 10% ethanol containing 0.2% Tween 20 and applied (20 μg $plant^{-1}$) to the youngest apical leaf after a 3-day temperature treatment. The plants were grown under 16/25 and 19/19°C (16-h DT/8-h NT). The mean temperature was 19.0 ± 0.2°C. The experiment lasted for 26 days and was repeated once. Each treatment consisted of four plants.

In the second experiment, the temperature treatments under a 16-h photoperiod were 16/25 and 19/19°C (DT/NT) and under an 8-h photoperiod 16/20.5 and 19/19°C. The mean temperature was 19.0 ± 0.1°C. The number of plants varied from 32 to 40 in each treatment.

Analyses of Endogenous Plant Hormones

Stem and leaf (17–120 g fresh weight) were collected in the second experiment after growth periods of 26 and 27 days. These two harvests were used as replicates. Under LD, time of harvests were 8 h after the start of day and 0.5, 4.0, and 7.5 h after the start of night. Under SD, plants were sampled 4 h after the start of day and 0.5, 8.5, and 15.5 h after the start of night. Samples were frozen in liquid nitrogen and stored at −80°C until homogenization in 250–500 mL of cold 80% ethanol. Internal standards of 500 ng (leaf samples; for stem samples 200 ng was used) of $[^2H_2]GA_{19}$ and 250 ng (leaf samples; for stem samples 100 ng was used) each of $[^2H_2]GA_1$, $[^2H_2]GA_9$, and $[^2H_2]GA_{20}$ were added, and the samples were extracted overnight at −20°C. [Deuterated GAs were obtained from Professor L. Mander (Australian National University, Canberra, Australia)]. The extracts were filtered and after the addition of 6–30 mL of 0.5 M sodium phosphate buffer, pH 8, reduced to the aqueous phase in vacuo at 40°C. Samples were stirred for 15 min with 1.5–2 g of insoluble polyvinyl polypyrrolidone (PVPP) and left overnight at −20°C. The PVPP was removed by filtering. Filtrates were adjusted to pH 2.8 with 1 N hydrochloric acid and partitioned three times against equal volumes of ethyl acetate. The ethyl acetate fractions were combined, washed four times with water (5% volume of ethyl acetate) at pH 2.5 to remove residual orthophosphoric acid, and reduced to dryness in vacuo at 40°C. Samples were dissolved in 5 mL of water at pH 8 (adjusted with KOH) and applied to a 5-mL bead volume QAE-Sephadex A-25 column (Pharmacia AB, Uppsala, Sweden). Columns were prepared and stored in sodium formate and conditioned with water at pH 8. After application, columns were washed with 20 mL of water at pH 8 and eluted with 25 mL of 2 M formic acid on to a 1-g C_{18} solid phase extraction (SPE) column (Bond-Elute, Supelco Inc., Bellefonte, PA) conditioned successively with methanol and 0.2 M formic acid. Samples were eluted from the C_{18} columns with 5 mL of methanol, reduced to dryness in vacuo (Speed-Vac, Savant Instruments, Farmingdale, NY), and methylated using ethereal diazomethane. Aminopropylsilyl SPE columns (100 mg, Varian, Harbor City, CA) were conditioned with methanol. Samples dissolved in 0.5 mL of methanol were applied and eluted with 3 mL of methanol. The elute (3.5 mL) was reduced to dryness (SpeedVac), redissolved in 100 μl of 50% methanol, and subjected to HPLC using standard commercially available instruments from Waters (Milford, MA). A 100- × 8-mm (inner diameter) C_{18} Waters Novapak column (4-μm particle size) was operated at 25°C. The mobile phase was a 25-min linear gradient of 20–80% methanol in water, followed by isocratic elution at 80% methanol. The flow rate was 2 mL min^{-1}, and 30 fractions (2 mL) were collected. Fractions of interest were pooled, reduced to dryness (SpeedVac), silylated with 15 μL of *N*-methyl-*N*-trimethylsilyltrifluoroacetamide (MSTFA; Pierce, Rockford, IL), and analyzed by capillary GC-MS. One-μL samples in MSTFA were introduced by splitless injection into an HP-1 column [25 m × 0.31 mm i.d. (inner diameter), 0.17 μm film thickness] installed in a Hewlett Packard 5890 GC and connected via a direct inlet interface to a Hewlett Packard 5970B mass selective detector. The column temperature was maintained at 50°C for 2 min, then increased by 10°C min^{-1} to 170°C, followed by 3°C min^{-1} to 280°C. The injector temperature was 240°C, the detector interface temperature was 270°C, and the ionizing voltage was 70 eV. Quantitative analysis was performed using the selected ion monitoring (SIM) technique. For each hormone and its ^2H analog, two characteristic ions were recorded. GA data are means of two independently analyzed extracts.

Data Collection and Statistics

At the start of the experiments the length of the internodes was recorded. During the experimental period in the second experiment, cumulative growth of the first internode was measured three times/week. At the end of the experiments, the length of internodes, petioles, and plant height was measured and the number of visible internodes counted. Plant tissue from the second experiment was analyzed for endogenous GAs.

Analysis of variance was performed with the GLM procedure in SAS

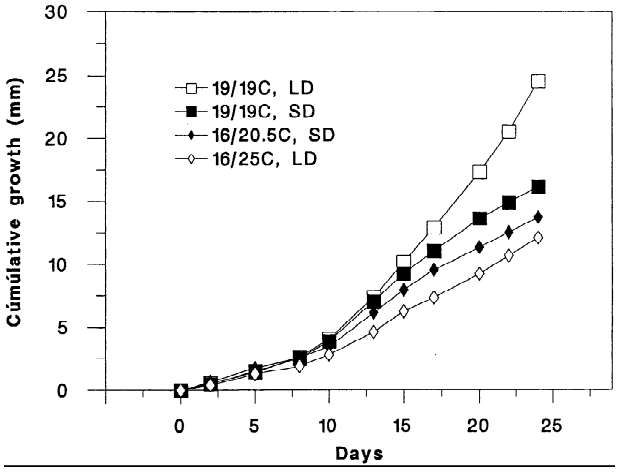

Fig. 1. Effect of day/night temperature alternations and day length (DL) on cumulative growth in the first internode developed after the treatments were applied in generative *B. x hiemalis.* Data were subjected to an analysis of variance at day 24. Negative and zero DIF values were used as the two levels of temperature in analysis of variance. Significance level was: DIF, $p < 0.001$; DL, $p < 0.001$; DIF × DL, $p < 0.001$ (experiment 2).

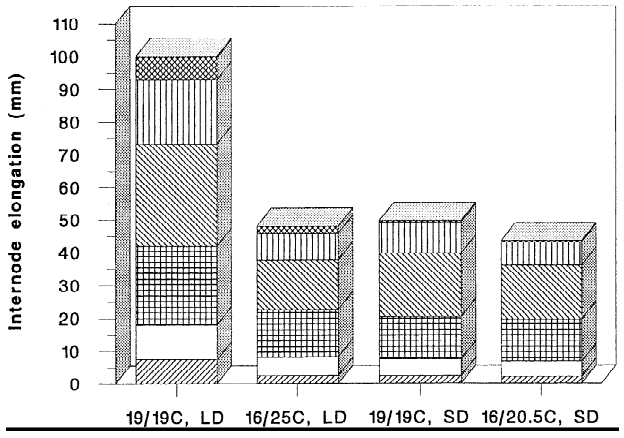

Fig. 2. Effect of day/night temperature alternations and day length (DL) on elongation of internodes in generative *B. x hiemalis.* Negative and zero DIF values were used as the two levels of temperature in analysis of variance. The individual internodes are shown by different patterns. Significance level on the sum of internode elongation at each treatment: DIF, $p < 0.001$; DL, $p < 0.001$; DIF × DL, $p < 0.001$ (experiment 2).

(PCSAS Release 610, SAS Institute Inc.). In the first experiment, a factorial model was used in analysis of variance of the means of each treatment. In the statistical analysis of endogenous GAs, the 2 days of harvest were used as replicates. All data in the second experiment were subjected to an analysis of variance with 32 individual plants as replicates. In this analysis, the factor DIF was separated in two levels, i.e. zero and negative DIF.

Results

Cumulative growth of the first internode developed in the experiment period (Fig. 1) and internode elongation (Fig. 2) were greater under zero DIF than under negative DIF and under LD compared with SD. However, there was also an interaction between the factors affecting the growth responses. Both the main effects and the interactions were statistically significant at $p < 0.001$ for the growth responses (Figs. 1 and 2). Plant height was also strongly affected by DIF ($p < 0.001$) and GAs ($p < 0.001$; Table 1). More detailed studies of DIF and applied GAs responses show that the two factors have a greater effect on elongation of internodes developed in the experiment period compared with internodes that were visible when the experiment started (Table 1). The three internodes in the bottom of the columns in Figs. 2 and 3, were visible when the experiment started, and the internodes above developed during the experimental period. GAs also had a strong effect on the elongation of petioles ($p < 0.001$), although there was no statistically significant effect of DIF (Table 1). However, the elongation of petioles on control plants (not applied with GAs) increased when DIF increased from −9 to 0°C (Fig. 4). Of the GAs applied, GA_4 had a stronger effect on elongation growth than GA_1 and GA_9. The number of visible internodes developed during the study increased by applying GAs ($p < 0.05$), whereas DIF was close to having a statistically significant effect ($p = 0.06$) on the same response (Table 1). The time of applying the GAs during day and night cycle had no effect on the growth responses (Table 1 and Fig. 5).

The main effects of DIF were a higher endogenous level of GA_{19} ($p < 0.05$) and GA_{20} ($p < 0.001$) under negative DIF compared with zero DIF (Fig. 6). Furthermore, the level of GA_{20} was also affected by an interaction between DIF and plant part ($p < 0.05$). The ratio of the endogenous level of GA_{20} in negative DIF-treated plants compared with zero DIF was 1.57 in leaf and petiole and 1.38 in stem. Furthermore, the leaf and petiole:stem ratio of endogenous level of GA_{20} was 1.89 and 1.66 under negative and zero DIF, respectively. An interaction among DIF, photoperiod, and plant part affected the endogenous level of GA_1 ($p < 0.01$; see Fig. 6). The endogenous GA_1 level in SD-grown plants was higher under zero DIF than under negative DIF, but this relationship did not appear in LD-grown plants (interaction DIF × photoperiod, $p = 0.07$). Under zero DIF, LD, and during the night phase, a strong increase of endogenous GA_9 in petiole and leaf occurred. However, the variation among the replicates was too great to get a statistically significant response.

The main effects of photoperiod were higher levels of GA_{19} ($p < 0.05$) and GA_1 ($p < 0.001$) under SD compared with LD, whereas GA_{20} ($p < 0.001$) and GA_9 (N.S.) showed the opposite response to photoperiod. The

Table 1. Effects of the difference between day and night temperature (DT − NT), applied GAs (20 μg plant^{-1}), and time of applying GAs during the day and night phase on growth responses under a 16-h photoperiod. The temperature at negative and zero DIF was 16/25 and 19/19°C, respectively. The significance of terms was determined in an analysis of variance ($\alpha = 0.05$), where * = 0.05 and *** = 0.001 significance of *F* parameter and N.S. = not significant. The main effects were separated by Duncan's multiple range test. Lack of a common letter indicates significant ($p < 0.05$) difference between treatments. None of the interactions was statistically significant (experiment 1).

	Internode elongation below applied meristem (mm)	Internode elongation above applied meristem (mm)	Petiole elongation above applied meristem (mm)	Plant height (mm)	No. of visible internodes developed in the experiment period
DIF	N.S.	***	N.S.	***	N.S.
Negative (−9°C)	28.6	38.6 b	37.6	360.2 b	4.0
Zero (0°C)	30.1	46.1 a	37.3	392.3 a	4.2
GAs	*	***	***	***	*
GA_1	26.7 b	45.3 b	40.6 b	382.2 b	4.2 a
GA_4	32.3 a	49.3 a	45.6 a	421.1 a	4.2 a
GA_9	30.9 ab	45.9 ab	40.9 b	398.6 b	4.1 a
Control	27.5 b	28.9 c	22.8 c	303.1 c	3.8 b
Time for applying GAs during day and night cycle	N.S.	N.S.	N.S.	N.S.	N.S.
Middle of the day	29.2	42.6	37.0	374.7	4.1
−0.5 h before start of the day	29.5	42.2	37.9	377.8	4.1

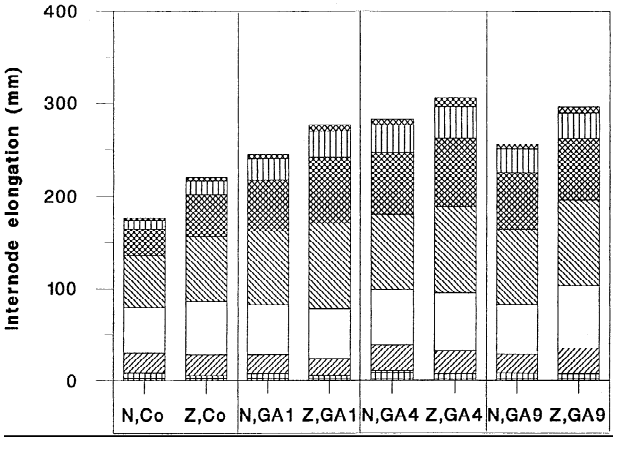

Fig. 3. Effect of day/night temperature alternations and applied GAs on elongation of internodes in generative *B. x hiemalis*, from data shown in Table 1 pooled across the time of applying GAs. *N*, negative, and *Z*, zero DIF. The individual internodes are shown by different patterns (experiment 1).

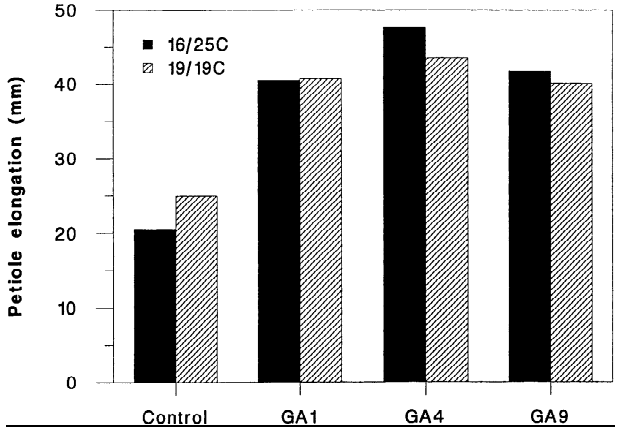

Fig. 4. Effect of day/night temperature alternations and applied GAs on elongation of petioles developed in the experimental period of generative *B. x hiemalis*, from data shown in Table 1 pooled across time of applying GAs (experiment 1).

endogenous level of GA_{20} showed an interaction between photoperiod and plant part ($p < 0.01$). The endogenous level of GA_{20}, pooled across time of harvesting plant tissue and DIF, was 10% higher in stem and 61% higher in leaf and petiole at LD compared with SD.

Under SD, the endogenous level of GA_{19} and GA_1 pooled across the other treatments was highest in the middle of the day and decreased toward the end of the night. GA_9 levels generally increased from the beginning to the end of the night. However, all effects of harvesting time during the day and night cycle and interactions with the other factors were not statistically significant.

Endogenous levels of GA_{20} ($p < 0.001$) were higher in petiole and leaf than in stem, but there were no differences in the levels of GA_1, GA_9, and GA_{19} among plant parts.

Discussion

Internode elongation and plant height increased as DIF increased from a negative value to zero in *B. x hiemalis* (Figs. 1–3 and Table 1). This was also reported by

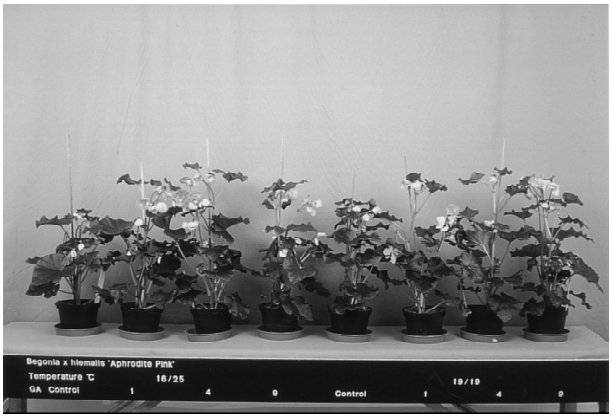

Fig. 5. Effects of temperature alternations (16-h day/8-h night) and GAs (20 μg plant^{-1}) on plant morphology of generative *B. x hiemalis.* From *left* to *right*, 16/25°C, control, GA_1, GA_4, and GA_9; 19/19°C, control GA_1, GA_4, and GA_9 (experiment 1).

Cuijpers and Vogelezang (1992), Moe and Mortensen (1992), Mortensen and Moe (1992), Myster et al. (1997), and Willumsen et al. (1995). Petiole elongation increased with increasing DIF (Moe and Heins 1990), and a similar response occurred in control plants (not applied with GAs) when DIF increased from −9 to 0°C under LD conditions (Fig. 4). Photoperiod affects internode elongation in *B. x hiemalis* (Sandved 1969, 1971). This is also observed under zero DIF conditions in the present study, where cumulative growth of the first internode developed during the experimental period (Fig. 1) and internode elongation (Fig. 2) were much greater under LD than under SD. These growth responses were similar under negative DIF conditions, probably because the negative DIF value was −4.5°C under SD and −9°C under LD.

Exogenously applied GAs can eliminate the negative DIF inhibition of stem elongation (Erwin 1991, Ihlebekk et al. 1995, Moe 1990, Myster et al. 1997, Tangerås 1979, Zieslin and Tsujita 1988), shown here with GA_1, GA_4, and GA_9. In relative values, the effect of applying e.g. GA_1 is shown to decrease with increased DIF (Ihlebekk et al. 1995, Myster et al. 1997). A similar response is shown in the present study with GA_1, GA_4, and GA_9 (calculated from the data in Fig. 3).

When DIF increased from a negative value to zero, and when applying GA_1 compared with untreated plants, the number of visible internodes increased (Myster, unpublished data). A similar response is shown for the DIF and the GA treatments in these studies (Table 1), and this may indicate that this effect of DIF is mediated by endogenous GAs.

GA_{19}, GA_{20}, GA_1, and GA_9 were identified as endogenous compounds in *B. x hiemalis* (Myster et al. 1997; Fig. 6). The endogenous level of GA_{19} increased when DIF increased from a negative value to zero DIF in plants grown under sunny days during the summer (Myster et al. 1997), whereas the relationship was opposite for plants grown under lower irradiance and a different quality of artificial light. As in the previous investigation, endogenous levels of GA_{20} were higher at negative DIF compared with zero DIF (Myster et al. 1997). This suggests that the conversion from GA_{20} to the bioactive GA_1 could be inhibited under negative DIF compared with zero DIF. In *Campanula,* endogenous GA_1 increased when DIF increased from a negative to zero value (Jensen et al. 1996). A similar increase was observed in *B. x hiemalis* under SD but not under LD. The lack of increased endogenous GA_1 in LD-grown *B. x hiemalis* may be explained by great variation in plant morphology (stem length) between negative and zero DIF-treated plants. Our analyses were based on the whole plant extracts. In the woody plant *Salix pentandra* L., the level of GA_1 was substantially higher in stem segments 5–20 mm below the apex than in other segments (Olsen et al. 1995). Our studies also show that applied GAs had a greater effect on stem elongation on the applied internode (leaf) and internodes above compared with internodes below. This can indicate that analyzing only the tissue just below the shoot tip could have shown other relationships of endogenous levels of GA_1 between zero and negative DIF-treated plants under LD conditions. Another interesting observation is that endogenous GA_1 in plants with a similar morphology (stem length) increased from 87 to 111 and further to 140 pg g^{-1} fresh weight pooled across plant part and time of harvest when DIF increased from −9.0 (LD) to −4.5 (SD) and further to 0°C (SD) DIF, respectively.

GA_{19} levels were higher in SD than in LD-grown plants, but the relationship for GA_{20} was the opposite. Similar observations are reported in *B. x cheimantha* (Odén and Heide 1989) and in *Spinacia oleracea* L. (Talon et al. 1991). Myster et al. (1997) could not find any correlation between GAs of the 13-hydroxylated pathway and stem elongation of *B. x hiemalis.* This could indicate that other biosynthetic pathways, e.g. through GA_9 and GA_4 and further to GA_1, might be involved (Graebe 1987, Pharis and King 1985, Wang 1996). Odén and Heide (1989) reported that levels of GA_9 and GA_4 were higher in *Begonia* under LD compared with SD conditions, as for GA_9 in our study. The level of GA_1 was significantly higher under SD than under LD. In addition, our application experiments showed that GA_4 had a stronger effect than GA_1 on internode and petiole elongation. This may suggest that in *B. x hiemalis* GA_4 is more important in elongation growth than GA_1. However, higher endogenous levels of GA_1 under SD compared with LD could also reflect that the sensitivity to GAs in the tissue is influenced by photoperiod or a higher consumption of GA_1 under LD.

The rate of stem elongation fluctuates during the diurnal day and night cycle under zero and positive DIF

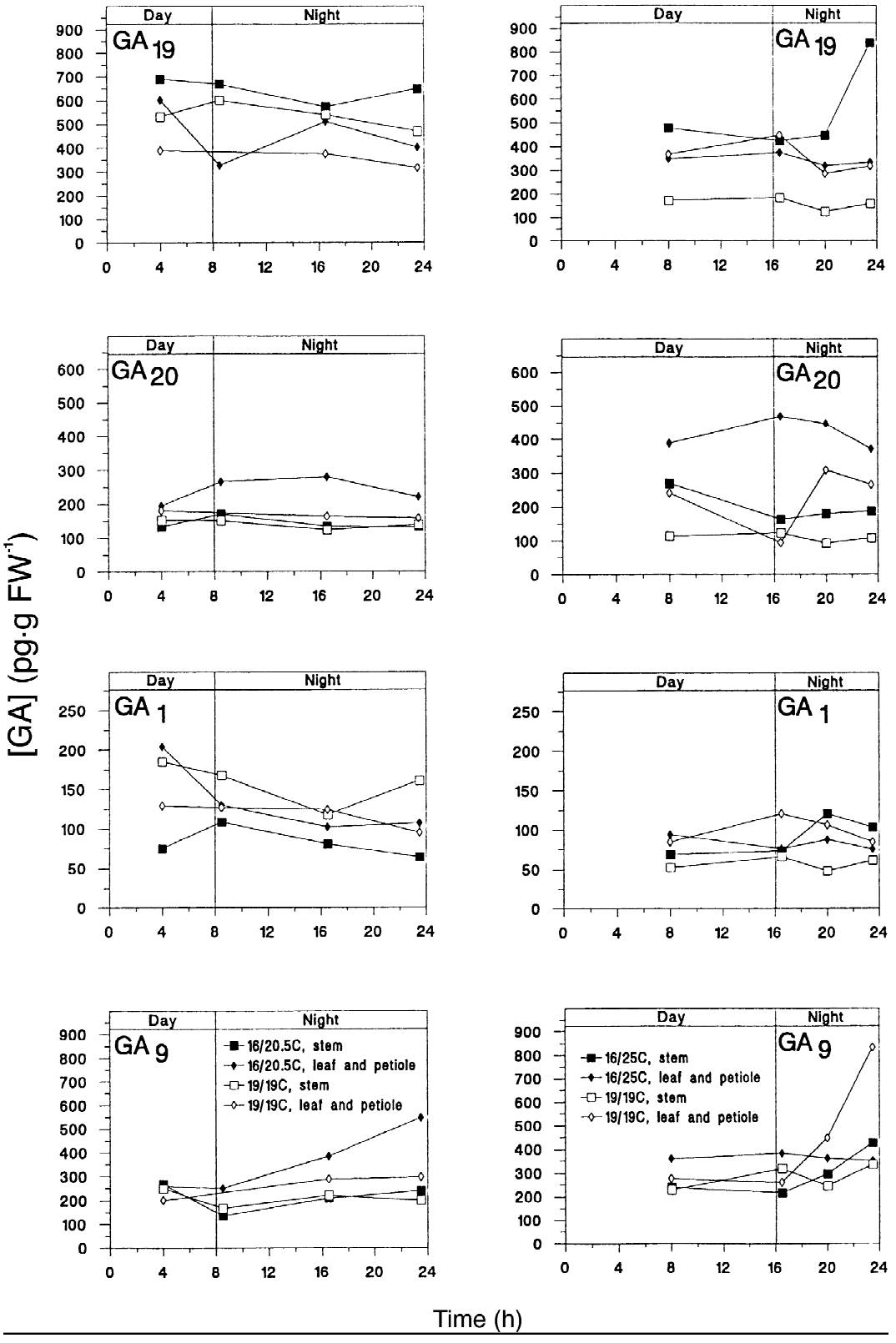

Fig. 6. Effect of day/night temperature alternations and photoperiod on endogenous GAs during the day and night cycle in plant segments of generative *B. x hiemalis*. The difference between DT and NT was −4.5 and 0°C under SD and −9 and 0°C under LD (experiment 2).

conditions in *B. x hiemalis* (Myster, unpublished data). However, there was no significant effect of harvest time on endogenous level of GAs which could be related to fluctuating stem elongation during the photophile and the skotophile phase.

A temperature drop at the end of the night or the beginning of the day decreased stem elongation in *B. x hiemalis* (Grindal and Moe 1994, Willumsen et al. 1993), and levels of endogenous GAs are reported to vary diurnally (Childs et al. 1995, Foster and Morgan 1995, Talon et al. 1991). In leaf and petioles under zero DIF and LD, the level of GA_9 increased (Fig. 6; not statistically significant) during the night phase, possibly accounting for the great elongation growth in this treatment (Figs. 1 and 2) and also relating to the effect of temperature drop.

Changes in the level of irradiance could explain the reduced levels of GA_{19} and GA_{20} in this study compared with our previous report (Myster et al. 1997). In the present investigation, plants were grown under 95 μmol m^{-2} s^{-1} PPFD with fluorescent tubes, whereas plants in the study by Myster et al. (1997) were grown under mostly sunny days in June and July in a phytotron. Levels of endogenous GA_{20} and GA_1 in plant tissue harvested in the middle of the day at LD show a similar pattern in these studies as in the previous studies with a higher level in leaf and petioles compared with stem. However, the level of GA_{19} in leaf and petioles compared with stem was enhanced in this experiment under low irradiance compared with plants grown under high irradiance by Myster et al. (1997).

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