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# The Response to Gibberellin in *Pisum sativum* Grown under Alternating Day and Night Temperature

G. Grindal,[1,*] O. Junttila,[2] J. B. Reid,[3] and R. Moe[1]

[1]Department of Horticulture and Crop Sciences, Agricultural University of Norway, P.O. Box 5022, N-1432 Ås, and [2]Department of Biology, University of Tromsø, Dramsv. 201, N-9037 Tromsø, Norway; [3]Department of Plant Science, University of Tasmania, G.P.O. Box 252-55 Hobart, Tasmania, Australia

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**Abstract.** The application of gibberellins (GA) reduces the difference in stem elongation observed under a low day (DT) and high night temperature (NT) combination (negative DIF) compared with the opposite regime, a high DT/low NT (positive DIF). The aim of this work was to investigate possible thermoperiodic effects on GA metabolism and tissue sensitivity to GA by comparing the response to exogenously applied GA (in particular, $GA_1$ and $GA_3$) in pea plants (*Pisum sativum* cv. Torsdag) grown under contrasting DIF. Control plants not treated with growth inhibitors or additional GA were 38% shorter under negative (DT/NT 13/21°C) than positive DIF (DT/NT 21/13°C) because of shorter internodes. Additional $GA_1$ or $GA_3$ decreased the difference between positive and negative DIF. In pea plants dwarfed with paclobutrazol, which inhibits GA biosynthesis at an early step, the response to $GA_1$ was reduced more strongly by negative compared with positive DIF than the response to $GA_3$. The induced stem elongation by $GA_{19}$ and $GA_{20}$ did not deviate significantly from the response to $GA_1$. Plants treated with prohexadione-calcium, an inhibitor of both the production and the inactivation of $GA_1$, grew equally tall under the two temperature regimes in response to both $GA_1$ and $GA_3$. We hypothesize that the reduced response to $GA_1$ compared with $GA_3$ in paclobutrazol-treated plants grown under negative DIF is caused by a higher rate of 2β-hydroxylation of $GA_1$ into $GA_8$ under negative than positive DIF. This contributes to lower levels of $GA_1$ and consequently shorter stems and internodes in pea plants grown under negative than positive DIF. Differences in tissue sensitivity to GA alone cannot account for this specific thermoperiodic effect on stem elongation.

**Key Words.** DIF—Gibberellin—Inactivation—Pea—Response—Stem elongation—Temperature—Thermoperiodism

Daily alterations in day (DT) and night temperature (NT) affect stem and internode elongation in long day plants as well as in short day plants (Erwin and Heins 1995, Myster and Moe 1995). In general, plants grow tall with long internodes when the DT is higher than the NT, whereas a short phenotype with short internodes is developed under a DT lower than the NT. These thermoperiodic responses have been utilized for control of plant height in commercial plant production in climate-controlled conditions (Bakken and Fløne 1995, Erwin et al. 1989, Moe 1994). The two opposite temperature combinations have been referred to as temperature regimes with a positive (positive DIF, high DT/low NT) and negative difference between DT and NT (negative DIF, low DT/high NT), respectively.

Many reports (Ihlebekk et al. 1995, Moe 1990, Pinthus and Meiri 1979, Tangerås 1979, Zieslin and Tsujita 1988) have suggested that the effects of daily temperature alternations on stem elongation are related to the metabolism and sensitivity to gibberellin (GA), a plant hormone required for stem elongation in plants (Graebe 1987). These studies have examined mainly the responses to external applications of GAs in plants grown under different temperature regimes. The experiments have been done in tall, GA-producing genotypes without any chemical or genetic inhibition of GA synthesis. As a

**Abbreviations:** DT, day temperature; NT, night temperature; DIF, difference between day and night temperature; GA, gibberellin.

*Author for correspondence.

consequence, altered stem elongation may theoretically have been a response to the combination of a change in the internal temperature-regulated GA content and the external application of GA.

Recent reports support the hypothesis that daily temperature alterations may control stem elongation through an altered level of bioactive $GA_1$ (Grindal et al. 1998, Jensen et al. 1996, Langton et al. 1997, Nishijima et al. 1997). The findings of a higher ratio of $GA_8$ to $GA_1$ in the stem tissue in pea grown under negative compared with positive DIF (Grindal et al. 1998) could indicate that temperature alterations may regulate the levels of endogenous $GA_1$ by affecting inactivation of $GA_1$ by 2β-hydroxylation.

In the present work we have compared the response to $GA_1$ and $GA_3$, GAs that differ in the ability to be inactivated through 2β-hydroxylation, in pea plants depleted for endogenously produced $GA_1$. The plants have been pretreated with either paclobutrazol or prohexadione-calcium, both potent inhibitors of GA biosynthesis. The former inhibits an early step in the GA biosynthesis, the oxidation of *ent*-kaurene (Hedden and Graebe 1985), whereas the latter inhibits both 3β- and 2β-hydroxylases converting $GA_{20}$ to $GA_1$ and $GA_1$ to $GA_8$, respectively (Nakayama et al. 1990a, 1990b). With these experiments, we wanted to investigate whether the inhibition of stem elongation by negative compared with positive DIF is related to enhanced inactivation of $GA_1$ and to evaluate the tissue sensitivity to GA in thermoperiodic stem elongation.

## Materials and Methods

Three different application experiments with GA were carried out in seedlings of *Pisum sativum* cv. Torsdag, without any addition of growth inhibitors and either with paclobutrazol or prohexadione-calcium. Seeds were germinated at 18–20°C in 11-cm pots and standard fertilized peat (Floralux, Nittedal Torvindustrier, Nittedal, Norway) before testing the differences in response to GA under two different temperature regimes.

When no growth inhibitor was added, the plants were grown for 7 days before the start of the temperature treatment and an application of $GA_1$ and $GA_3$ to a leaflet of the second foliage leaf. In the case of a combination of a paclobutrazol and GA treatment, the plants were grown 6 days before 1 mL of Bonzi (Zeneco Inc., UK, 4 g/liter paclobutrazol) in 50 mL of water was added, a dose of 4 mg of paclobutrazol/pot. By this time the cotyledenary hook was fully straightened. The temperature treatments were started, and $GA_1$, $GA_{20}$, $GA_{19}$, and $GA_3$ were applied to the second foliage leaf 12–14 days after sowing. For inhibition of the GA metabolism with prohexadione-calcium (BAS 125 10 W, BASF, Germany), nicked seeds were placed on filter paper soaked in 400 ppm of water suspension of prohexadione-calcium (10% granules dissolved in NaOH) for 2–4 h until the seeds were fully imbibed. The seedlings were then grown for 14 days before the application of $GA_1$ and $GA_3$ to the second or third foliage leaf. The plants were further sprayed daily with 250 ppm of prohexadione-calcium from the day before the GA application until the end of the experiment. GAs were applied in 10 μL of 96% ethanol. Control plants were treated with ethanol only. The dose (μg) of $GA_1$ and $GA_3$ applied to the plants was compared by combined gas chromatography-mass spectrometry and found to be equal.

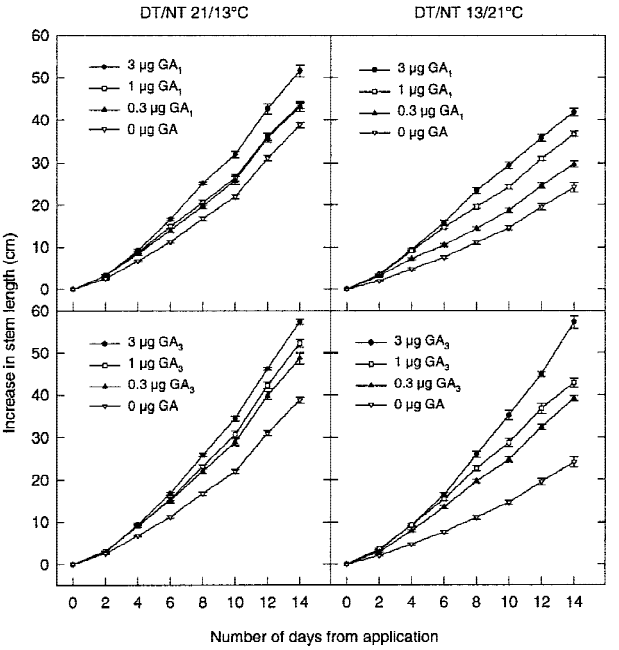


**Fig. 1.** Increase in stem length in response to $GA_1$ and $GA_3$ in *P. sativum* grown for 14 days under DT/NT 21/13°C (positive DIF) or 13/21°C (negative DIF). *Bars* indicate S.E. ($n \geq 8$, normally 10).

At the time of GA applications, the plants were moved to two different DT and NT combinations: a high DT and low NT (positive DIF, DT/NT 21/13°C) and a low DT and high NT combination (negative DIF, DT/NT 13/21°C). The length of both the day and night was 12 h, providing an average temperature of 17°C in both treatments. The actual average DT and NT throughout the experimental period did not vary more than 0.4°C from the set point, and the water vapor deficit was kept equal at 13 and 21°C (either at 0.3 or 0.5 kPa).

The plants were grown in air-conditioned greenhouse compartments during the summer in Norway, and no additional artificial light was supplied during the day period, which was defined by the temperature switches 6 h before and after noon. The stem extensions were recorded 14 days after the GA applications. The variations in the responses among plants in each treatment are indicated by the standard error, and an analysis of variance (ANOVA) based on average values was applied when appropriate.

## Results

### *Responses in Untreated Plants*

Pea plants expressing endogenously controlled levels of bioactive $GA_1$ responded to alternations in DT and NT by growing 38% shorter under a low DT/high NT, negative DIF, than under a high DT/low NT combination, positive DIF (Fig. 1). An increased stem elongation in response to exogenously applied $GA_1$ or $GA_3$ could be seen already 2–4 days after the GA application under both growing conditions (Fig. 1). The relative increase in

**Table 1.** Relative increase in stem length and the number of leaves developed in response to $GA_1$ and $GA_3$ in *P. sativum* grown for 14 days under DT/NT 21/13°C (positive DIF) or 13/21°C (negative DIF). S.E. was at the most ±0.2 for the number of leaves/plant ($n \geqslant 8$, normally 10).

| $GA_n$ | DT/NT (°C) | Dose of GA applied (μg) 0 | 0.3 | 1 | 3 |
|---|---|---|---|---|---|
| Relative increase in stem length | | | | | |
| $GA_1$ | 21/13 | 100 | 112 | 113 | 134 |
| | 13/21 | 100 | 124 | 153 | 175 |
| $GA_3$ | 21/13 | 100 | 126 | 136 | 149 |
| | 13/21 | 100 | 164 | 177 | 238 |
| No. of leaves | | | | | |
| $GA_1$ | 21/13 | 5.7 | 5.8 | 5.7 | 6.0 |
| | 13/21 | 5.7 | 5.1 | 5.5 | 5.8 |
| $GA_3$ | 21/13 | | 6.2 | 5.8 | 6.2 |
| | 13/21 | | 5.7 | 5.7 | 6.2 |

stem length in response to $GA_1$ or $GA_3$ was stronger under negative than positive DIF (Table 1), and consequently the difference in response decreased with increasing doses of GA. However, even at doses up to 3 μg, plants treated with $GA_1$ never became as tall under negative as positive DIF, whereas 3 μg of $GA_3$ leveled out the response to the two opposite temperature conditions. At the maximal dose applied (3 μg), $GA_3$ increased stem length 15% more than $GA_1$ under positive DIF, whereas under negative DIF the enhancement was 63% higher in response to $GA_3$ than to $GA_1$ (Table 1).

### *Responses in Plants Treated with Paclobutrazol*

In plants dwarfed with the growth inhibitor paclobutrazol, doses of exogenous $GA_1$ up to 3 μg induced 20–32% less stem extension under negative than positive DIF (Table 2). However, 10 μg of $GA_1$ increased stem length almost as much under negative as positive DIF (Table 2). An application of $GA_3$ resulted in a much smaller difference between plants grown under the two temperature regimes. The experiment was replicated twice, and a similar interaction between DIF and type of GA was found (Table 3). $GA_{20}$ and $GA_{19}$ were only applied in doses of 1 and 3 μg. Like $GA_1$, $GA_{20}$ and $GA_{19}$ resulted in a stronger increment in stem length under positive than negative DIF (Table 2).

The number of foliage leaves in the paclobutrazol-treated plants was only slightly lower, 0–8%, under negative compared with positive DIF. Therefore, again the internode lengths reflected the effect of the temperature regimes on the stem length. $GA_1$, $GA_{20}$, and $GA_{19}$ stimulated internode elongation to a greater extent under positive than negative DIF as shown for $GA_1$ in Fig. 2*A*, whereas the difference was much less between the two temperature regimes with a $GA_3$ application (Fig. 2*B*). The number of leaves and internodes produced during the experiment increased with increasing doses of GA, as can be seen from Fig. 2, *A* and *B*.

### *Responses in Plants Treated with Prohexadione-Calcium*

The stems of plants treated with prohexadione-calcium and no GA grew 5.3 and 4.5 cm under positive and negative DIF, respectively, during the 14-day experimental period. At the same dose of applied GA, plants grew equally tall under negative and positive DIF, when either $GA_1$ or $GA_3$ was used (Table 4, Fig. 3). Also, in plants treated with prohexadione-calcium the number of

**Table 2.** Increase in stem length (cm) in response to $GA_1$, $GA_3$, $GA_{20}$, and $GA_{19}$ in *P. sativum* dwarfed with paclobutrazol and grown for 14 days under DT/NT 21/13°C (positive DIF) or 13/21°C (negative DIF). RI, response index; response under negative/positive DIF × 100. S.E. are indicated as ± values ($n \geqslant 9$, normally 11).

| $GA_n$ and DT/NT (°C) | Dose of GA applied (μg) 0 | 0.1 | 0.3 | 1 | 3 | 10 |
|---|---|---|---|---|---|---|
| $GA_1$ | | | | | | |
| 21/13 | 2.3 ± 0.2 | 5.2 ± 0.4 | 9.9 ± 0.6 | 23.3 ± 1.5 | 39.2 ± 1.8 | 56.8 ± 2.1 |
| 13/21 | 2.5 ± 0.2 | 3.9 ± 0.3 | 7.5 ± 0.5 | 15.9 ± 0.7 | 31.5 ± 2.3 | 53.9 ± 2.3 |
| RI | 110 | 75 | 76 | 68 | 80 | 95 |
| $GA_3$ | | | | | | |
| 21/13 | | 8.9 ± 0.6 | 12.5 ± 0.9 | 25.3 ± 1.7 | 42.8 ± 1.1 | 52.5 ± 1.7 |
| 13/21 | | 7.7 ± 0.2 | 12.3 ± 0.6 | 27.7 ± 0.8 | 38.1 ± 1.5 | 47.8 ± 0.8 |
| RI | | 87 | 98 | 95 | 89 | 91 |
| $GA_{20}$ | | | | | | |
| 21/13 | | | | 15.0 ± 0.7 | 29.5 ± 1.1 | |
| 13/21 | | | | 12.3 ± 0.5 | 22.4 ± 0.8 | |
| RI | | | | 82 | 76 | |
| $GA_{19}$ | | | | | | |
| 21/13 | | | | 13.9 ± 1.1 | 26.8 ± 1.1 | |
| 13/21 | | | | 10.5 ± 0.5 | 24.4 ± 1.4 | |
| RI | | | | 76 | 91 | |

**Table 3.** Results from two additional experiments with $GA_1$ and $GA_3$ as described in Table 2 and analysis of variance (ANOVA) based on all three replications of the experiment and a split-plot design with temperature as whole plot and type of GA as subplot. N.S., not significant. RI, response index; response under negative/positive DIF × 100.

| DT/NT (°C) | 1 μg of GA applied | | 3 μg of GA applied | |
|---|---|---|---|---|
| | $GA_1$ | $GA_3$ | $GA_1$ | $GA_3$ |
| Replication 2 | | | | |
| 21/13 | 14.1 | 19.0 | 25.3 | 34.9 |
| 13/21 | 9.5 | 15.5 | 16.6 | 27.7 |
| RI | 67 | 82 | 66 | 79 |
| Replication 3 | | | | |
| 21/13 | 18.8 | 24.2 | 30.8 | 31.4 |
| 13/21 | 15.3 | 24.6 | 22.7 | 28.6 |
| RI | 69 | 102 | 74 | 91 |
| Statistical differences | | | | |
| Temperature | 0.067 | | 0.013 | |
| GA | 0.003 | | 0.016 | |
| Temperature × GA | 0.067 | | N.S. | |

nodes increased with increasing doses of GA but was not affected significantly by the DIF treatment (Table 4). For comparison, a new test with paclobutrazol was done simultaneously with the prohexadione-calcium experiment, and the results completely confirmed the described interaction between DIF and the growth-promoting effect of $GA_1$ and $GA_3$ (Table 3, replication 3).

## Discussion

Wild type plants of a broad range of species grow shorter under negative than positive DIF (Erwin and Heins 1995, Myster and Moe 1995). This is also found to be the case in pea (Fig. 1, Grindal et al. 1998). In *Fuchsia x hybrida* (Tangerås 1979), *Campanula isophylla* (Moe 1990), and *Lilium longiflorum* (Zieslin and Tsujita 1988), expressing normal endogenous levels of GA, the response to $GA_3$ or $GA_{4+7}$ was stronger in plants with reduced elongation because of negative DIF than in those where positive DIF had stimulated elongation. The same response pattern was observed when $GA_1$, $GA_{20}$, and $GA_{19}$ were applied to *Campanula* grown under the inverted temperature regimes (Ihlebekk et al. 1995), all GAs that are found to be native in *Campanula* (Jensen et al. 1996). Our findings in the pea plants grown without any growth inhibitors (Table 1, Fig. 1) correspond to and confirm these earlier reports. Correspondingly, growth inhibitors like B-9 (Moe 1990) and ancymidole (Erwin et al. 1989) inhibit stem elongation more under positive than negative DIF. Recently, a reduced content of endogenous GAs in plants grown under negative compared with positive DIF has been reported for several species (Grindal et al. 1998, Jensen et al. 1996, Langton et al. 1997, Nishijima et al. 1997).

In the application studies described above, it is difficult to distinguish between the possible effects of the specific temperature regimes on the tissue sensitivity to GA from those on the biosynthesis and the concentration of bioactive GA. In the present study we attempted to exclude the effect of temperature on the biosynthesis of $GA_1$, the bioactive GA for stem elongation in pea (Ingram et al. 1984), by blocking the biosynthesis at an early step by using paclobutrazol. We found that dwarfed pea plants always grew shortest in response to a GA application under negative DIF except when high doses of exogenous GAs were used (Tables 2 and 3, Fig. 2). Compared with $GA_1$, differences between the two temperature regimes were decreased significantly when $GA_3$ was applied (Tables 2 and 3). This means that differences in tissue sensitivity alone cannot account for the strong effect of temperature alternations on stem length in pea. It should be noted that the temperature alternations did not have the same strong effect on the leaf unfolding rate as an application of GAs. This appears contradictory because DIF affects the endogenous content of $GA_1$ in pea. However, applying 3–10 μg of GAs may simply represent a much stronger change in the GA status than what was established by DIF.

The present data give some indications on how the level of $GA_1$ is controlled by temperature alternations. The bioactive $GA_1$ is inactivated to form $GA_8$ through an addition of a hydroxyl group in the 2β-position (Graebe 1987). Because of the extra double bond in $GA_3$ between carbon 1 and 2, this molecule cannot follow the same enzymatic inactivation pathway as $GA_1$. In the fungus *Gibberella fujikuroi*, $GA_3$ is found to lose biological activity through an isomerization to iso-$GA_3$ and be decomposed further to gibberellenic acid (Pérez 1996). Because there was a higher difference for $GA_1$ than $GA_3$ in elongation response between the two temperature treatments (Tables 2 and 3, Fig. 2), we hypothesize that the reduced response to $GA_1$ under negative DIF could be the result of an enhanced inactivation of $GA_1$ by 2β-hydroxylation under this specific DT and NT combination.

To explain further the difference in response to $GA_1$ and $GA_3$ in plants grown under the two temperature regimes, we compared responses in pea plants dwarfed with either paclobutrazol or prohexadione-calcium. Prohexadione is found to inhibit 3β-hydroxylations such as the conversion of $GA_{20}$ to $GA_1$ as well as 2β-hydroxylations and thereby the inactivation of $GA_1$ into $GA_8$ (Nakayama et al. 1990a, 1990b). If temperature alternations affected the 2β-hydroxylation of $GA_1$, we would expect the same response to $GA_1$ in prohexadione-treated plants under both temperature regimes and the same relative response to $GA_1$ as to $GA_3$. Prohexadione-calcium is found to be a better inhibitor of 3β-hydroxylases than 2β-hydroxylases (Zeevaart et al. 1993), and therefore we maximized the dose of the

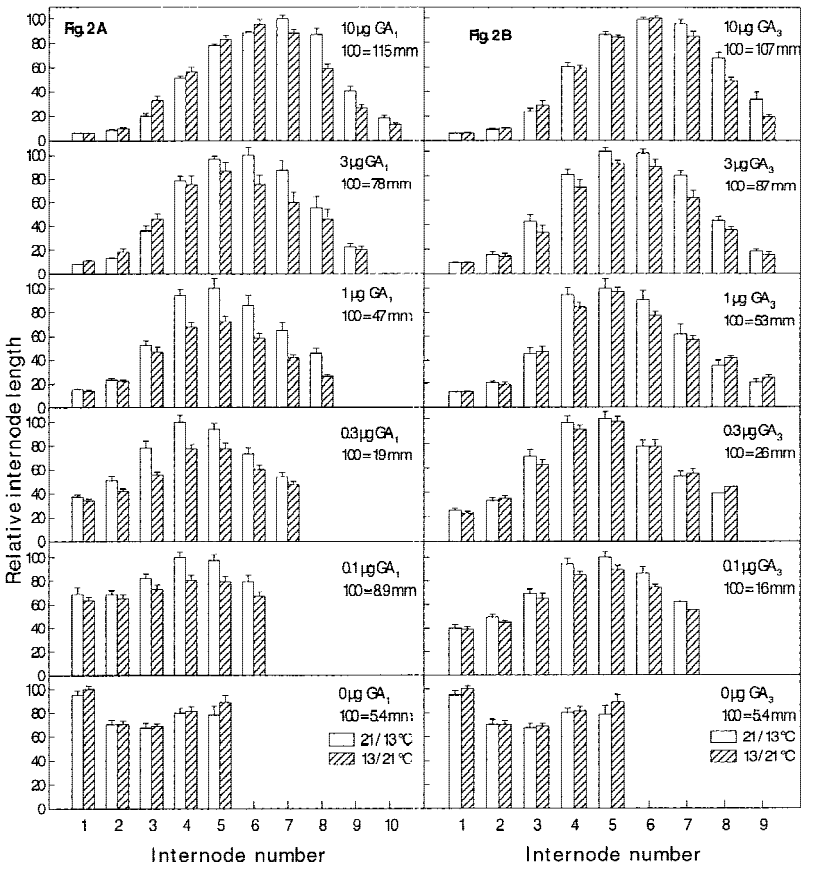


**Fig. 2.** Relative response in internode length to increasing doses of $GA_1$ (*panel A*) and $GA_3$ (*panel B*) in *P. sativum* dwarfed with paclobutrazol and grown for 14 days under DT/NT 21/13°C (positive DIF) or 13/21°C (negative DIF). Internodes are counted from the second foliage leaf where the GAs were applied. *Bars* indicate S.E. ($n \geqslant 9$, normally 11).

chemical by spraying the plants daily. Under these conditions, we found no differences in the response pattern to $GA_1$ and $GA_3$ in prohexadione-treated plants grown under the two temperature regimes (Table 4, Fig. 3) supporting our hypothesis of an impact of temperature alternations on the rate of inactivation of $GA_1$.

This hypothesis is supported further by quantitative analysis of endogenous GAs in pea. Compared with positive DIF, levels of $GA_1$ and its immediate precursors were reduced by negative DIF, whereas the ratio of $GA_8$ to $GA_1$ was enhanced (Grindal et al. 1998). This is consistent with the suggestion of a faster inactivation of $GA_1$ by a 2β-hydroxylation to $GA_8$ under negative than positive DIF. This indirect evidence needs to be confirmed by metabolic studies of labeled $GA_1$ in plants grown under the two opposite temperature regimes. Further, both untreated plants and plants treated with growth inhibitors need to be included in such studies to account for the feedback mechanisms of $GA_1$ on GA biosynthesis (Hedden and Kamiya 1997). To our knowledge, no environmental factor other than DIF has been suggested to affect the inactivation of $GA_1$.

In *Campanula*, inhibition of stem elongation by negative DIF was accompanied not only by decreased levels of $GA_1$, but also by increased levels of 2β-hydroxylated $GA_{53}$ (Jensen et al. 1996). Analysis of endogenous GA in pea showed a higher ratio of $GA_{29}$ to $GA_{20}$ (Grindal et al. 1998), also a step representing a 2β-hydroxylation under negative than positive DIF. Together, these observations make it interesting to investigate further the influence of DIF on GA 2β-hydroxylations in general.

**Table 4.** Relative increase in stem length in response to $GA_1$ and $GA_3$ under negative (DT/NT 13/21°C) compared with positive DIF (DT/NT 21/13°C) and the number of foliage leaves developed after 14 days in *P. sativum* dwarfed with prohexadione-calcium. S.E. was at the most ±0.3 for number of leaves ($n \geqslant 7$, normally 9). Relative increase in stem length for control plants treated with paclobutrazol is given in Table 3 (replication 3).

| $GA_n$ | DT/NT (°C) | Dose of GA applied (µg) 0 | 0.3 | 1 | 3 |
|---|---|---|---|---|---|
| Increase in stem length | | | | | |
| $GA_1$ | | 86 | 96 | 93 | 94 |
| $GA_3$ | | | 88 | 98 | 102 |
| No. of leaves | | | | | |
| $GA_1$ | 21/13 | 5.1 | 6.6 | 7.3 | 7.7 |
| | 13/21 | 5.7 | 7.3 | 7.6 | 7.7 |
| $GA_3$ | 21/13 | | 7.0 | 7.3 | 7.7 |
| | 13/21 | | 6.9 | 7.5 | 7.7 |

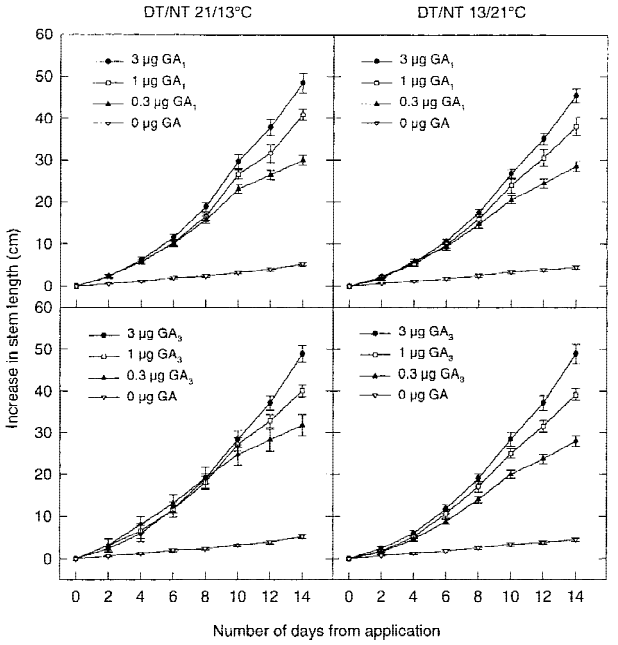


**Fig. 3.** Increase in stem length in response to $GA_1$ and $GA_3$ in *P. sativum* treated with prohexadione-calcium and grown for 14 days under DT/NT 21/13°C (positive DIF) or 13/21°C (negative DIF). *Bars* indicate SE ($n \geq 7$, normally 9).

Comparison of the response to $GA_1$ with that to its immediate precursors $GA_{20}$ and $GA_{19}$ did not indicate temperature regulation of the conversion of $GA_{19}$ to $GA_{20}$ or $GA_{20}$ to $GA_1$ (Table 2). This is in agreement with the results of Grindal et al. (1998) who found no influence of temperature alternations on these steps based on the determination of endogenous GA levels in pea.

Three µg of $GA_3$ leveled out the difference between negative and positive DIF in plants not treated with any growth inhibitor (Fig. 1), whereas 10 µg was necessary to get the same elongation response to $GA_1$ in paclobutrazol-treated plants (Table 2, Fig. 2). Together with the lack of a DIF response in the *la cry*$^s$ pea mutant (Grindal et al. 1998), which expresses a slender phenotype reflecting a constitutive response to GA (Potts et al. 1985), these findings indicate a poor response to DIF in plants having a GA response close to the saturation.

In summary, our findings support the hypothesis of a more rapid inactivation of $GA_1$ to $GA_8$ in pea plants grown under negative than positive DIF. The tissue sensitivity to available bioactive GAs cannot alone account for the altered stem elongation in peas in response to daily temperature alternations.

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