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Temperature Interactions with Growth Regulators and Endogenous Gibberellin-like Activity during Seedstalk Elongation in Carrots[1]

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ABSTRACT

Stecklings (roots) of three cultivars of carrots (*Daucus carota* L.) were vernalized 10 weeks at 5 C and subsequently grown at each of three greenhouse night/day temperature regimes: high (27/32 C), medium (21/27 C), and low (15/21 C). Floral differentiation occurred first in the easy bolting cv. Scarlet Nantes, intermediate in cv. Danvers 126, and last in cv. Royal Chantenay. Stem elongation arising from the subapical meristematic region always preceded floral differentiation. Extractable gibberellin-like activity in carrot stem apices increased from harvest during the 10-week vernalization period, then remained constant even though floral differentiation and stem elongation occurred during an additional 20-week cold storage period. Low temperature had both an inductive and a direct effect on reproductive development depending on length of low temperature exposure.

After 10 weeks vernalization at 5 C, high greenhouse temperature severely reduced ultimate seedstalk height and the endogenous gibberellin-like activity decreased rapidly during the first 3 weeks in the greenhouse. At the low greenhouse temperature, activity remained fairly constant during the 10-week sampling period. Changes in endogenous gibberellin-like activity were related with stem elongation, but not with floral initiation. Exogenous gibberellic acid (GA_3) applied following vernalization prevented the inhibitory effect of high greenhouse temperature on seedstalk elongation and resulted in seedstalk heights comparable to untreated controls grown at the low greenhouse temperature. Exogenous applications of succinic acid-2,2-dimethylhydrazide and chlormequat reduced seedstalk height of carrot plants grown at the medium and low greenhouse temperatures to that of untreated controls grown at high temperature. Exogenous growth regulators and greenhouse temperature affected seedstalk elongation, but did not affect the number of plants that flowered.

Flowering of most herbaceous plants involves a complete alteration of the developmental processes of the shoot apical meristem, in which the formation of leaves and internodes ceases, and the flowers and associated appendages are initiated. Normal flower formation in rosette species is generally associated with rapid elongation of the stem which has its origin in the subapical zones of the shoot meristem (13, 20). The interaction of endogenous phytohormones, which are markedly influenced by various environmental conditions, is an important regulatory factor. Although flower formation and stem elongation appear to occur simultaneously, these processes may be neither related nor influenced by the same factors (13, 25, 26). Flower initiation may precede stem elongation in some species whereas the opposite may be true in other species.

The carrot, a rosette plant in the vegetative stage, normally produces an elongated, branched seedstalk 120 to 160 cm tall following vernalization during which the apical bud is exposed to temperatures below a critical threshold for a requisite period of time (2, 9, 19). Several authors have reported on flower differentiation in the carrot (1, 12, 24), but only one presented data on seedstalk growth. Tsukamoto *et al.* (24) showed that the early stages of differentiation occurred during macroscopic seedstalk development, but failed to emphasize the relation of subapical meristem elongation to differentiation.

Endogenous gibberellins regulate cellular activity in the subapical meristem, the zone responsible for shoot histogenesis in caulescent and elongating rosette plants (11, 20). Lona (15) and Wellensiek (26) showed conclusively that GA[3] promoted only stem elongation in rosette species and that stem elongation did not always coincide with floral initiation. These results have been confirmed more recently with other plant species (21, 22, 28). Growth retardants which inhibit GA biosynthesis also reduce stem elongation (14, 20–22). Low temperature treatments have resulted in both quantitative increases and qualitative changes in GA levels of several plant species (11, 22, 23). Although the significance of this response in the reproductive development was not clear, a direct relationship between GA level and reproductive activity has often been assumed.

Relatively high greenhouse temperatures following the vernalization period have been shown to reduce seedstalk elongation in certain carrot cultivars, although the plants flowered and matured normal main umbels (6, 9, 19). Hiller and Kelly (9) found that during the first 6 weeks following vernalization a high greenhouse temperature dramatically reduced the ultimate seedstalk height with no effect on flowering. This was apparently a devernalization effect on seedstalk elongation but not on flowering, opposite to most plant species studied to date (13).

The objectives of the research reported here were to: (*a*) study the effect of exogenous applications of growth regulators on stem elongation and floral development of carrots under different greenhouse temperatures following vernalization; (*b*) determine the endogenous GA-like activity in the apical tissue of carrots during vernalization and subsequent reproductive development under the various greenhouse temperature regimes; and (*c*) relate the GA-like activity with anatomical changes in the apical buds during reproductive development.

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[3] Abbreviations: GA(s): gibberellin(s); SADH: succinic acid-2,2-dimethylhydrazide; CCC: chlormequat; FAA: formalin-acetic acid-ethyl alcohol.

MATERIALS AND METHODS

Plant Materials. Carrot (*Daucus carota* L.) cvs. Royal Chantenay, Danvers 126, and Scarlet Nantes were field-grown and harvested in September. Some roots were planted directly into the greenhouse while other roots were stored at 5 C before planting in the greenhouse. Complete cultural and vernalization details were previously published (9).

Exogenous Growth Regulators. Based on results from a preliminary study, aqueous solutions of GA_3, 100 and 1,000 μg/ml, and SADH, 2,000 and 5,000 μg/ml, were applied (1 ml per plant at each application) directly on the apical leaves twice weekly during the first 6 weeks following vernalization. Foliar application of CCC caused severe damage and variable results in the preliminary study; therefore, CCC, 500 and 1,500 mg/plant, was applied as a root drench, half of the final concentration 2 days after potting and the remainder 3 weeks later. Ten plants were used per treatment in each greenhouse temperature regime 15/21, 21/27, and 27/32 C (night/day). Weekly measurements were made on the main seedstalk from the time of visible elongation until flowering and growth had ceased. This experiment was repeated for 2 years with similar results.

Endogenous GA-like Activity. Measurements were made on plants at harvest and after 5-, 10-, 20-, and 30-week storage at 5 C. In the same experiment, plants were stored for 10 weeks at 5 C and then grown at each of three greenhouse temperature regimes stated above. Plant samples were collected weekly for a 10-week period. Each sample consisted of 1-cm cubes from 20 shoot apices with all but the small primordial leaves removed. Measurable GA-like activity was not found in young or old leaves, in edges of the crown surrounding the apical portion of the plant, or in other portions of the root. Immediately upon collection, each sample was weighed, placed in polyethylene bags, and stored at −18 C for later extraction and purification.

Plant samples were extracted in cold (<0 C) 80% (v/v) methanol (50 ml methanol to 1 g tissue) in a VirTis homogenizer for 3 min. The homogenate was filtered under vacuum and extraction with fresh methanol was repeated on the residue two more times. Combined methanol extracts were reduced to the aqueous phase *in vacuo*, made to a standard volume, and centrifuged 30 min at 27,000*g*. The supernatant was adjusted to pH 8.3 with 10% (v/v) NH_4OH and partitioned three times with equal volumes of methylene chloride. The methylene chloride phase removed pigments, lipids, and nonpolar compounds and was discarded. The aqueous phase was adjusted to pH 3 with 3 N HCl and partitioned three times with equal volumes of ethyl acetate. The combined ethyl acetate phases were evaporated *in vacuo*. Further purification and separation of the GA-like activity were by a modified column chromatography procedure (5, 18) using stepwise elutions of increasing concentrations of 1-butanol in *n*-hexane. Preliminary tests showed that $GA_{4/7}$ were eluted in the 3 and 5% fractions and GA_3 was eluted in the 30% fraction and that recovery of reference GAs was 95 to 98% using these methods. The 3% + 5%, 10% + 20%, 30%, and 40% (v/v) fractions were collected for bioassay.

A slightly modified lettuce (*Lactuca sativa* L. cv. Butter King) hypocotyl bioassay (7) was used as the principal test in determining GA-like activity. The column fractions were bioassayed in triplicate at three levels representing 50, 100, and 500 mg fresh weight for a dose response curve comparison with the standard curve (8). Known levels of GA_3 standards in triplicate accompanied each bioassay test (Table I). Known levels of GA_4 and GA_7 standards were also examined for their response and reference in the lettuce hypocotyl bioassay. A modified dwarf rice bioassay (17) was used on selected plant samples for comparison and confirmation of results from the lettuce hypocotyl bioassay. Each column fraction was bioassayed in triplicate at two levels representing 500 and 1,000 mg fresh weight.

Table I. Lettuce hypocotyl length in response to known concentrations of GA_3 in the lettuce hypocotyl bioassay.

Concentration of GA_3 (μg/ml)	Net hypocotyl length (mm)[z]
0.0005	2.5
0.0015	4.1
0.005	5.5
0.025	9.0
0.05	10.4
0.25	12.5
0.5	13.8
2.5	15.5
5.0	17.0
25.0	17.6
50.0	18.1
100.0	18.4
Dunnett's Allowance (4) at 0.95	0.9

[z] Mean length of 15 lettuce seedlings in each of 10 replications minus length of the water control.

Histological Studies. Samples of shoot apices were collected periodically from field harvest through the cold storage period and during the first 8 weeks in the greenhouse following vernalization. The shoot apices were fixed in FAA, and later dehydrated, imbedded in paraffin, sectioned and stained with safranin-fast green or periodic acid-Schiff's reaction (10). Sections 5 to 8 μm thick were observed with a light microscope to determine the stage of development of the apical meristem.

RESULTS AND DISCUSSION

Exogenous Growth Regulators. Similar results from two separate experiments showed that exogenous applications of growth regulators greatly affected the ultimate seedstalk height of the three carrot cultivars when treated following a 10-week vernalization period at 5 C (Table II). The untreated plants grown at 15/21 C following vernalization exhibited normal seedstalk growth and height, but the ultimate seedstalk height was shorter in the untreated plants grown at the higher greenhouse temperatures as has been previously reported (9). The cv. Scarlet Nantes bolted quickest and had the tallest seedstalks whereas Danvers 126 was intermediate and Royal Chantenay was slowest to bolt and had the shortest seedstalk at the high temperatures. This response agrees with previous reports (2, 9) and may have some relationship with the endogenous GA-like activity and histological data discussed later. Main umbel development and seed set were not affected by the postvernalization temperature as was previously reported (9, 19).

Application of GA_3 to the carrot plant increased seedstalk height of all three cultivars at every temperature while SADH and CCC decreased seedstalk height in every case. At the high greenhouse temperature (27/32 C), GA_3 increased the ultimate seedstalk height of the carrots comparable to the height of untreated plants grown at the low (15/21 C) temperature. Thus, exogenous applications of GA_3 prevented the inhibitory effect of high temperature on elongation and ultimate seedstalk height observed in the untreated plants. Conversely, SADH and CCC reduced seed-

Table II. The effect of exogenous applications of growth regulators[z] and 3 greenhouse temperatures on carrot seedstalk height.

Greenhouse Temp. (C)	Growth Regulator	Seedstalk Height (cm)[y] Royal Chantenay	Danvers	Scarlet Nantes
15/21	Untreated	73 ± 4.7	55 ± 3.5	91 ± 4.2
	GA 100ug/ml	123 ± 10.7	116 ± 6.3	133 ± 10.1
	GA 1000ug/ml	121 ± 7.3	122 ± 7.6	159 ± 8.0
	SADH 5000ug/ml	19 ± 3.9	22 ± 4.9	26 ± 4.3
	CCC 1500 mg/plant	18 ± 4.2	26 ± 4.8	26 ± 5.2
21/27	Untreated	19 ± 5.5	33 ± 5.0	57 ± 6.5
	GA 100ug/ml	86 ± 7.8	120 ± 8.0	127 ± 10.0
	GA 1000ug/ml	110 ± 4.8	140 ± 6.1	133 ± 10.9
	SADH 5000ug/ml	8 ± 1.7	11 ± 3.2	21 ± 2.4
	CCC 1500 mg/plant	9 ± 1.8	11 ± 3.2	20 ± 3.9
27/32	Untreated	10 ± 1.3	26 ± 3.5	33 ± 3.6
	GA 100ug/ml	53 ± 3.1	40 ± 2.0	61 ± 6.8
	GA 1000ug/ml	71 ± 4.4	49 ± 4.2	89 ± 4.6
	SADH 5000ug/ml	4 ± 0.5	4 ± 0.7	13 ± 2.0
	CCC 1500 mg/plant	6 ± 0.5	4 ± 0.4	14 ± 2.2

[z]The growth regulator and greenhouse temperature treatments were following the 10-week vernalization period at 5 C.
[y]Mean height of 20 plants per treatment ± standard error of the mean.

stalk height at the low greenhouse temperature comparable to the untreated material grown at the high temperature. There were no significant differences between the two concentrations of either growth retardant and so only one concentration is presented in Table II.

The exogenous growth regulators also influenced the rate of seedstalk elongation, determined by the weekly measurements, but did not affect the number of plants which flowered. Elongating seedstalks in GA_3-treated plants were macroscopically visible 2 to 4 weeks before those of the untreated plants, and the GA_3-treated plants elongated more rapidly than those not treated. The main umbel on untreated plants developed as the seedstalk elongated, but on GA_3-treated plants the seedstalks had elongated to nearly their ultimate height before the main umbel unfolded. The GA_3 affected only the rate of development of the umbel not the time of initiation. This was previously reported for carrots (3) and other species (15, 16, 22, 28). In contrast to GA_3, SADH and CCC significantly delayed the appearance of visible seedstalks and slowed the rate of growth and appearance of flowers 2 to 3 weeks compared to the untreated plants. In many treated plants, umbel development was visible before any measurable seedstalk growth was apparent, similar to the sessile umbels in untreated plants which resulted at high greenhouse temperatures (9). These growth retardants did not affect the number of plants which flowered or any characteristics of the main umbel. Reduction of final stem height without influencing percentage of flowering has been reported for growth retardants in other species (14, 16, 21, 22).

Histological Studies. The development of the seedstalk and flowers was divided into eight stages (Fig. 1), similar to those reported by Tsukamoto *et al.* (24), but with more emphasis on the subapical elongation. The vegetative apex of the carrot had a small, slightly convex meristem (stage I). Elongation in the subapical zone was initiated before any morphological change occurred at the apex of the growing point (stages II and III compared to stage IV). The subapical meristematic zone is responsible for stem elongation in reproductive rosette and caulescent plants (13, 20); therefore, stem elongation was initiated before floral differentiation began. In addition, it was found that floral differentiation did not commence until the time the seedstalk was 5 to 10 cm long which agreed with previous reports (1, 24). Physiological changes in the apex were not always detected histologically. For example, carrots stored 5 weeks at 5 C did not flower when grown at 27/32 C while those stored 10 weeks at 5 C flowered although there were essentially no noticeable microscopic differences in the meristems after 6- and 9-week storage at 5 C (Fig. 2B).

Later stages of differentiation (stages V–VIII) were observed in carrots stored 30 weeks at 5 C (Fig. 2B). In fact, seedstalks 5 to 15 cm in length were observed in several of these plants, particularly the cv. Scarlet Nantes. Thus, low temperature had both an inductive and a direct effect on carrots depending on the length of exposure. This had been previously indicated for carrots (2) and a number of plant species (13) but disagrees with the report by Kruzhilin and Shvedskaya (12) that differentiation occurred only after carrots had been returned to warm temperatures following vernalization. However, these investigators considered morphological changes in the apical meristem of young seedlings and plants vernalized only 60 days, which may explain some of the discrepancy.

Endogenous GA-like Activity. All three carrot cultivars showed some GA-like activity at harvest. The activity increased during 5 to 10 weeks at 5 C, but tended to level off during the longer storage periods of 20 and 30 weeks (Table III). These results from the lettuce hypocotyl bioassay were confirmed in the dwarf rice bioassay. Similar increases in GA-like activity during vernalization treatments have been reported for various species (11, 21–23). The fast bolting Scarlet Nantes had significantly greater activity

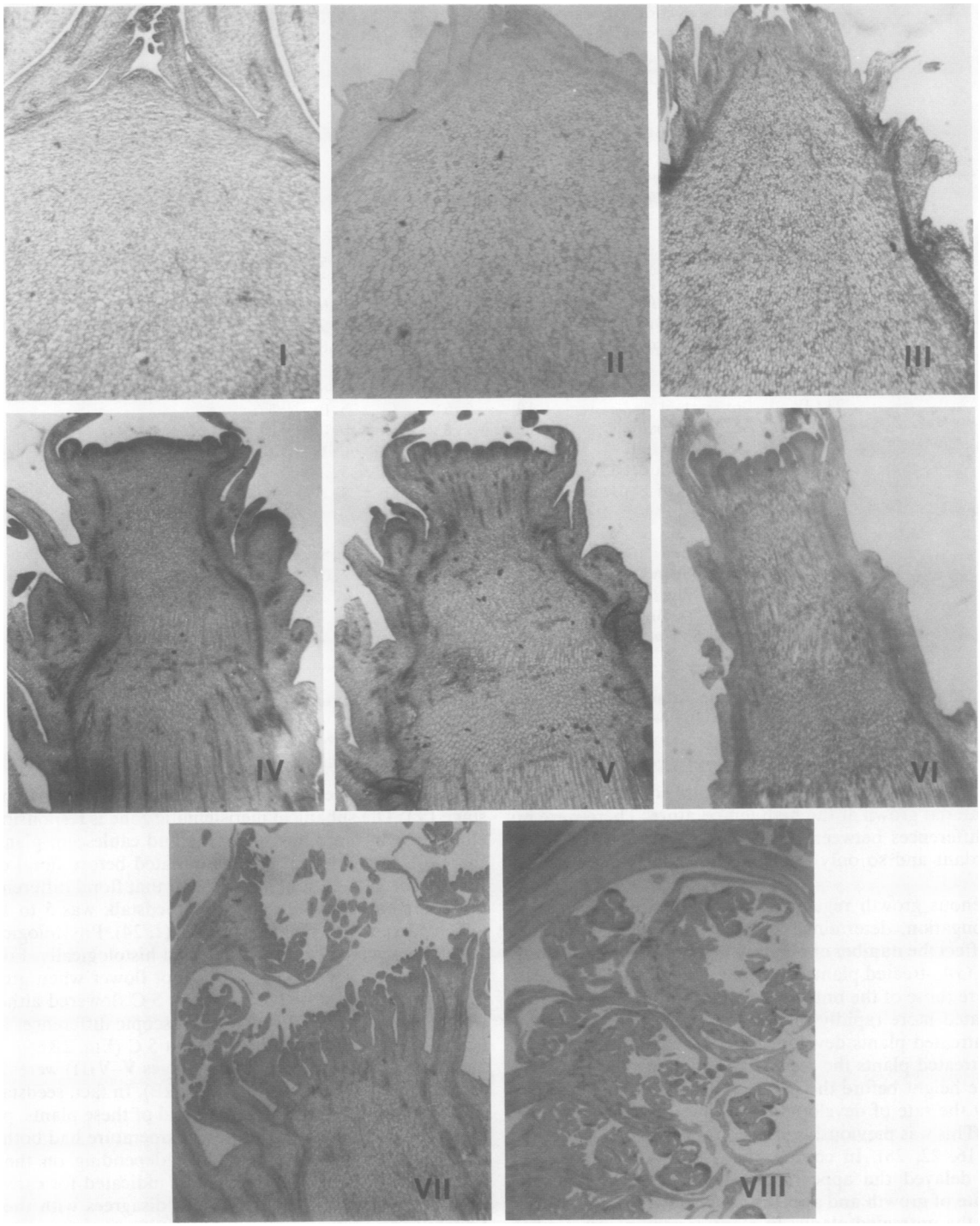

FIG. 1. Early stages of seedstalk and floral development in the carrot (× 100). Stage I: vegetative apex—growing point slightly convex; stage II: growing point broad and beginning to raise; stage III: elongated growing point (conical shape) with domed apex; stage IV: differentiation of involucral bract with flattened growing point; stage V: umbellet differentiation; stage VI: completion of umbellet differentiation and formation of bractlet of involucel; stage VII: floral differentiation on umbellets; stage VIII: completion of floral differentiation.

than the slower bolting Danvers 126 and Royal Chantenay (Table III). Cultivar differences in GA-like activity have been reported for other species (11, 14, 23).

The greenhouse temperature following vernalization had a marked effect on qualitative and quantitative changes in GA-like activity (Table IV). During the storage period and the first 3 weeks in the greenhouse, activity was found for all three cultivars only in the 30% column fraction, corresponding to GA_3 or other GAs chromatographically similar. The cv. Scarlet Nantes showed significant activity only in this 30% fraction throughout the entire 10-week greenhouse sampling period, but after 4 weeks Royal Chantenay and Danvers 126 showed additional activity in the 3% + 5% column fraction (Table IV), corresponding to $GA_{4/7}$ or other GAs chromatographically similar. This $GA_{4/7}$-like activity increased in Royal Chantenay at 21/27 C and the GA_3-like activity decreased until the end of the 10-week sampling period, but at 15/21 C the GA_3-like activity remained high even though the $GA_{4/7}$-like activity increased until the end of the sampling period.

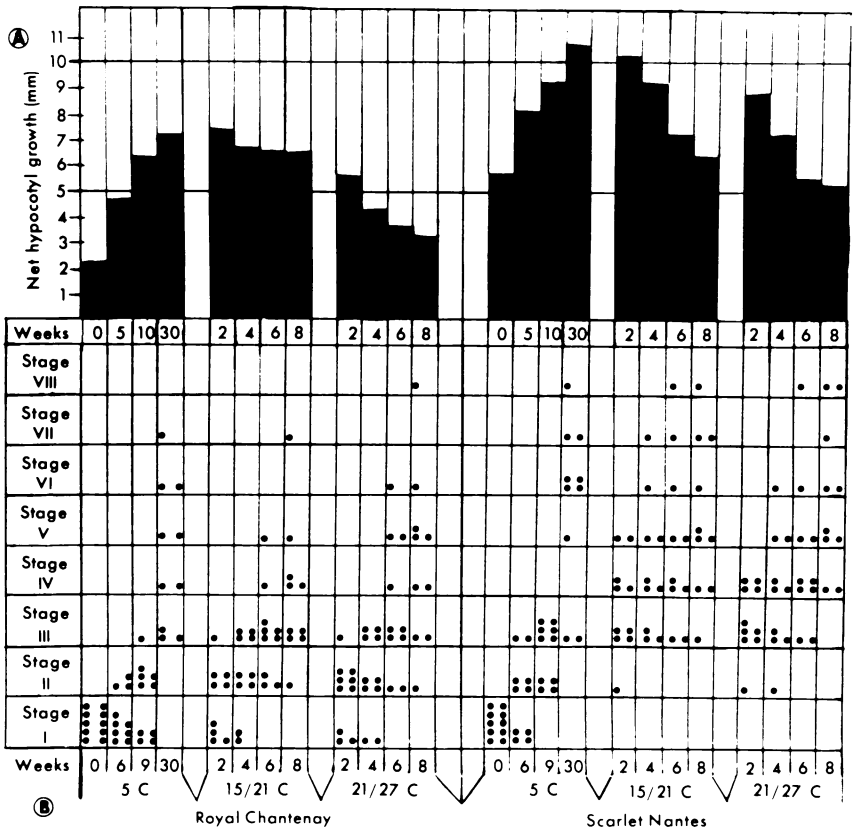

FIG. 2. GA-like activity and stage of reproductive development of carrot apices in Royal Chantenay and Scarlet Nantes stored at 5 C and subsequently grown at two greenhouse temperatures following 10 weeks at 5 C. A: net hypocotyl growth in lettuce bioassay from 30% column fraction, corresponding to GA_3-like activity or other GAs chromatographically similar. Dunnett's allowance (4) at 0.95 for Royal Chantenay was 0.5 mm and for Scarlet Nantes was 0.7 mm; B: stage of carrot apex development for corresponding temperature regime and time period. Each lot represents one plant.

Table III. GA-like activity in apex samples of three carrot cultivars collected after different vernalization periods at 5 C as determined in the lettuce hypocotyl bioassay.[z]

Weeks at 5 C	Net Hypocotyl Length (mm)[y] Royal Chantenay	Danvers 126	Scarlet Nantes
0	2.0	0.7	5.5
5	4.3	2.5	7.8
10	6.4	4.1	9.8
20	7.1	4.5	10.3
30	7.1	4.7	10.7
Dunnett's Allowance (4) at 0.95	0.5	0.4	0.7

[z]Each sample consisted of 20 carrot apices bioassayed for the level representing 500 mg fresh weight of tissue from the 30% column fraction. Significant activity was not found in the other column fractions.

[y]Mean length of 15 lettuce seedlings in each of 3 replications minus length of the water control.

At 27/32 C there was no significant $GA_{4,7}$-like activity at any time in the three cultivars.

The relationship of exogenous GA_3 to seedstalk elongation was dramatic, but the relationship of endogenous GA was not as clear-cut. The often assumed relation of GA to floral differentiation was not found in this study. There was a marked increase in GA_3-like activity during the first 5 weeks at 5 C (Fig. 2A) with little change in the apical meristem (Fig. 2B). Storage for 30 weeks caused further increase in GA_3-like activity and there was considerable floral differentiation with seedstalks 10 to 15 cm long. In the 15/21 C greenhouse following vernalization, Royal Chantenay began floral differentiation at 6 weeks (stage IV and later) (Fig. 2B), but the GA_3-like activity was the same as after 10 weeks at 5 C. In contrast, floral differentiation at 21/27 C started about the same time as at 15/21 C, but the GA_3-like activity was much lower at 21/27 C than at 15/21 C. Seedstalks were about 15 cm tall after 8 weeks at 15/21 C, but were not long enough to measure at 21/27 C, thus seedstalk height, but not floral differentiation, correlated well with GA_3-like activity. Scarlet Nantes always had higher GA_3-like activity and the changes in this activity at 5 C were similar to Royal Chantenay. The GA_3-like activity in Scarlet Nantes decreased with time at each greenhouse temperature, but was always lower at 21/27 C than at 15/21 C (Fig. 2A). After 8 weeks the seedstalks were about 15 cm at 21/27 C and about 30 cm at 15/21 C, again correlating with GA_3-like activity. The rate of floral differentiation was not affected by the greenhouse temperature (Fig. 2B). Floral differentiation of Danvers 126 was intermediate between Royal Chantenay and Scarlet Nantes, yet it had the lowest GA_3-like activity of the three cultivars (Table IV), providing further evidence of the independence of floral differentiation and GA_3-like activity.

These studies have shown that high temperatures following

Table IV. GA-like activity in apex samples collected after periods of growth at three greenhouse temperatures following 10 weeks vernalization at 5 C as determined in the lettuce hypocotyl bioassayed.[z]

Greenhouse Temp. (C)	Weeks	Net Hypocotyl Length (mm)[y] Royal Chantenay 3+5[x]	Royal Chantenay 30	Danvers 126 3+5	Danvers 126 30	Scarlet Nantes 3+5	Scarlet Nantes 30
15/21	1	0.3	7.0	0.1	4.2	0.6	9.9
	2	0.3	7.1	0.2	4.3	0.9	10.9
	3	0.3	6.9	0.3	4.0	0.3	9.4
	4	0.7	6.8	0.7	3.7	0.4	9.0
	5	1.2	6.9	1.2	3.5	0.3	8.2
	6	2.0	6.8	1.4	3.4	0.3	7.0
	8	2.8	6.6	1.2	3.3	0.3	6.2
	10	3.7	6.4	1.0	3.0	0.3	5.8
21/27	1	0.5	6.1	0.3	3.9	0.7	9.6
	2	0.3	5.5	0.3	3.8	1.5	8.8
	3	0.4	4.3	0.5	3.6	0.8	8.5
	4	2.1	4.2	0.9	3.3	1.0	7.2
	5	5.1	3.8	1.5	3.0	0.6	5.1
	6	5.3	3.7	2.1	2.7	0.6	5.4
	8	4.9	3.1	1.8	2.5	0.4	5.1
	10	4.7	2.8	1.6	2.4	0.1	4.8
27/32	1	0.1	4.9	0.3	3.6	0.2	8.8
	2	0.5	4.2	0.3	3.3	0.5	7.9
	3	0.4	3.9	0.6	3.2	0.3	7.4
	4	0.7	3.5	0.4	2.9	0.5	6.1
	5	0.6	3.1	0.5	2.5	0.7	4.9
	6	0.3	2.8	0.1	2.5	0.7	4.9
	8	0.3	1.9	0.3	2.2	0.6	4.8
	10	0.1	1.5	0.1	2.1	0.5	4.6
Dunnett's Allowance (4) at 0.95		0.5		0.4		0.7	

[z] Each sample consisted of 20 carrot apices bioassayed for the level representing 500 mg fresh weight of tissue.

[y] Mean length of 15 lettuce seedlings in each of 3 replications minus length of the water control.

[x] The fractions from the column chromatography procedure: 3% + 5% and 30% (v/v 1-butanol in n-hexane). Significant activity was not found in the other column fractions.

vernalization decreased carrot seedstalk elongation and endogenous GA-like activity, but exogenous GA_3 applied at the high temperature produced seedstalk height comparable to low temperature. Seedstalk height was reduced by CCC and SADH comparable to the high temperatures, suggesting that these growth retardants influenced the level of endogenous GA-like activity during carrot seedstalk elongation. CCC has been shown to decrease endogenous GA-like activity in several plants and to inhibit GA biosynthesis (11, 14, 21, 22). SADH is believed to interfere with GA activity (11, 14) and inhibit biosynthesis of GA precursors (27).

Determination of the endogenous GA-like activity by the extraction method used in this study indicated the level of activity in the plant tissue at that moment, but provided no information on the turnover of endogenous GAs (11). The marked reduction in GA_3-like activity measured at higher temperatures may have been the result of an increased rate of plant growth and metabolism, changes in sensitivity of receptor sites to GA, conversion or destruction of endogenous GA, or decreased biosynthesis. There are four interesting aspects of this study which suggest that determination of the endogenous GA turnover would be enlightening. First, Scarlet Nantes samples collected shortly after vernalization showed a decrease in GA_3-like activity at all three greenhouse temperatures, whereas the Royal Chantenay samples decreased only at the two higher greenhouse temperatures and did not change at 15/21 C. This was found in both bioassay procedures. The anatomical studies indicated that stem elongation in Scarlet Nantes occurred during this period of rapid decrease in GA_3-like activity, but Royal Chantenay did not initiate seedstalk elongation until 3 to 4 weeks later. Second, Scarlet Nantes always had higher activity in the GA_3-like fraction and no significant activity in the $GA_{4/7}$ fraction compared to Royal Chantenay and Danvers 126, but yet Scarlet Nantes initiated seedstalk elongation first, which related to its natural fast bolting characteristic, and had the tallest seedstalks. Third, higher levels of $GA_{4/7}$-like activity were found at 21/27 C than 15/21 C in both Royal Chantenay and Danvers

126, but ultimate seedstalk height was always less at 21/27 C, suggesting that GA_4, GA_7, or similar GAs may not be present or involved in carrot seedstalk growth. Fourth, the endogenous GA_3-like activity in Danvers 126 was the lowest of the three cultivars and decreased at a uniform and parallel rate at all three temperatures. The rates of bolting, seedstalk elongation, and ultimate seedstalk height for this cultivar were always intermediate to the other cultivars. These factors indicate that the rate of GA turnover may differ naturally among the cultivars, or be influenced differently by temperature, and may be equally or more important than the total GA level present.

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