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Dwarf Mutants of *Brassica:* Responses to Applied Gibberellins and Gibberellin Content

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Abstract. Eight rapid-cycling *Brassica* genotypes differing in height were treated with gibberellins (GAs) by syringe application to the shoot tip. The height of two genotypes of *Brassica napus*, Bn5-2 and Bn5-8, and *B. rapa* mutants, *dwarf 1* (*dwf1*) and *dwarf 2* (*dwf2*), was unaffected by exogenous GA_3 at dosages up to 0.1 μg/plant, a level which increased shoot elongation of normal genotypes. Thus, these dwarf mutants are "GA-insensitive." In contrast to the *B. napus* dwarfs, two *B. rapa* mutants, *rosette* (*ros*), and *dormant* (*dor*), elongated following GA_3 application. The dwarf *ros* was most sensitive, responding to applications as low as 1 ng GA_3/plant. Furthermore, *ros* also responded to GA_1 and some of its precursors with decreasing efficacy: $GA_3 > ent$-kaurenoic acid $\geq GA_1 > GA_{20} \geq GA_{19} = GA_{44} \geq GA_{53}$. Endogenous GAs were measured by gas chromatography–selected ion monitoring using $[^2H_2]$GA internal standards for calibration, from shoots of the GA-insensitive genotypes Bn5-2, Bn5-8 which contained the *B. napus* mutant *dwarf 1*, and from a normal genotype Bn5-1. Concentrations of GA_1 and GA_{20} averaged 3.2- and 4.6-fold higher, respectively, and GA_{19} levels also tended to be higher in the dwarfs than in the normal genotype.

The study of single-gene dwarf mutants of a range of plants has provided valuable information regarding gibberellin (GA) physiology in a range of processes (Phinney 1985, Reid 1990). GA-deficient mutants are dwarfs which are typified by two characteristics: (1) stem elongation is dramatically promoted through the application of bioactive GAs, and (2) they contain reduced levels of endogenous GAs. In contrast to these GA-responsive dwarfs, certain other dwarf mutants cannot be "cured" through GA treatment. Such mutants are classified as GA-insensitive (Reid 1986, 1990, Scott 1990). The genetic lesion in these mutants might involve modifications to the GA-response mechanism and possibly changes to a GA receptor.

Recently, we described a triplet of rapid-cycling *Brassica* genotypes with differences in height and GA physiology. The dwarf *rosette* (*ros*) is GA-deficient (Rood et al. 1989), whereas *elongated internode* (*ein*) is an overgrowth mutant with accelerated internode elongation and increased GA biosynthesis (Rood et al. 1990a, Zanewich et al. 1990). A comparison of GA physiology and metabolism in these two mutants and in other tall and short genotypes may provide additional insight into the role of GAs in the regulation of growth and development in *Brassica*. Thus, in the present study, we describe the response of a number of single-gene dwarf mutants of *Brassica* to exogenous GA_3, and report on the endogenous GA levels in two of these mutants.

Methods and Materials

Plant Material and Growth

The studies involved three genotypes of rapid-cycling *Brassica napus; B. napus* normal (Bn5-1, Crucifer Genetics Cooperative 5-1); Bn5-2, a line homozygous for *dwarf 1* (CrGC 5-2; *dwf1/dwf1*); and the segregating line Bn5-8 which also contains *dwf1* but with radish (*Raphanus sativus*) cytoplasm (CrGC 5-8; genotype: *dwf1/dwf1:DWF1/dwf1*, genomic designation: R1aacc). The *dwf1* heterozygote is a partial dwarf, whereas the homozygote is an extreme dwarf. The study also involved five genotypes of *B. rapa* (syn. *B. campestris*) designated *B. rapa* normal (CrGC 1-1); *rosette* (*ros/ros*, CrGC 1-7); *dormant* (*dor/dor*, 218149); *dwarf* 1 [*dwf1/dwf1*, CrGC 1-10 (not the same as *B. napus dwf1*)]; and *dwarf 2* (*dwf2/dwf2*, CrGC 1-21). These mutant genotypes had arisen spontaneously in rapid-cycling *Brassica* populations (Williams and Hill 1986).

Seeds were planted in 4 × 4 × 12 cm plastic root trainers containing Sunshine mix (Fisons Western Corp., Vancouver,

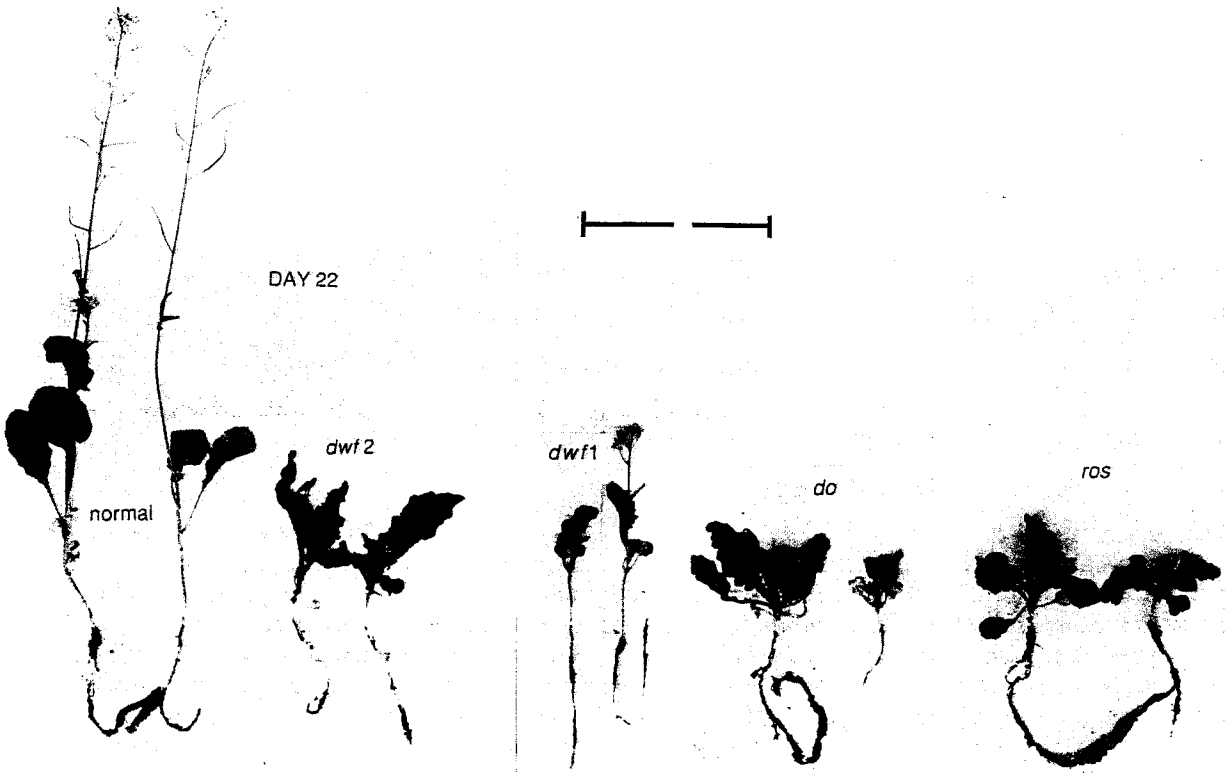

Fig. 1. Untreated, 22-day-old *Brassica rapa* genotypes (left to right): normal, *dwf2*, *dwf1*, *dor*, and *ros*. The scale bar represents 10 cm.

B.C.). Plants were grown in the University of Lethbridge greenhouse (latitude 49.6°N), watered daily, and provided with 24 h of light from high-pressure sodium vapor lights [Reflector PL90M (medium) N400, P.L. Light Systems Canada Inc.] 1.33 m above plants which provided about 100 $\mu E\ s^{-1}\ m^{-2}$.

GA Treatments

GA concentrations of 0, 1.0×10^{-5}, 1.0×10^{-4}, 1.0×10^{-3}, 1.0×10^{-2}, or 1.0×10^{-1} μg GA_3 in 0.5 μl 95% ethanol (EtOH) were applied by syringe to the shoot tip of 8-day-old *Brassica* seedlings of each genotype. This experiment was performed on three separate occasions with 5, 5, and 10–30 replicates, respectively. Results are presented from the third experiment and are generally consistent with results from the other trials. To clarify the sensitivity of *B. rapa dwf1* to exogenous GA_3, a fourth study involving normal *B. rapa dwf1* and *ros* was subsequently conducted with 10 additional replicates.

In a subsequent experiment *ent*-kaurenoic acid (KA), GA_{53}, GA_{44}, GA_{19}, GA_{20}, GA_1, and GA_3 were applied by syringe to the shoot tip of 7-day-old *ros* plants at concentrations of 0, 1.0×10^{-3}, 1.0×10^{-2}, or 1.0×10^{-1} μg GA in 0.5 μl 95% ethanol. Eight to 10 plants were included for each treatment and 30 plants were treated with 95% ethanol only to serve as experimental controls. A second study was conducted involving only GA_3, KA, and control to confirm the efficacy of KA. GAs were obtained from Professor R. P. Pharis and were greater than 90% pure. Treatments were evaluated by measuring the following growth parameters: height, leaf blade length, petiole length, dry weight, and leaf area, the latter using a Li-Cor (LI-3000) photometric area meter with conveyer assembly.

Statistical analyses of data involved one- and two-factor ANOVAs with GA treatment being the principal factor investigated. When ANOVAs indicated significant treatment effects, subsequent paired comparisons were made using the Fisher PLSD test with a 95% confidence interval.

Endogenous GA Content

Endogenous GAs were extracted and analyzed as previously described (Rood et al. 1989, 1990b). Between 12 and 18 fourteen-day-old stems (including apices but with leaves removed) were harvested from each genotype (dry weights ranging from 0.0282–0.2430 g). Extracts were purified by silicic acid partition chromatography and reversed-phase high-performance liquid chromatography. $[^2H_2]GA_1$, $[^2H_2]GA_{19}$, and $[^2H_2]GA_{20}$ were added as internal standards at initial extraction which enabled quantitative analyses by gas chromatography–mass spectrometry with selected ion monitoring. Two replicates from three independent experiments were separately extracted and analyzed for each genotype for GA_1, two replicates from two experiments were analyzed for GA_{20}, and only two replicates from one experiment were analyzed for each genotype for GA_{19}.

Results and Discussion

Growth of Untreated Dwarf Mutants

The single-gene dwarf mutants demonstrated dis-

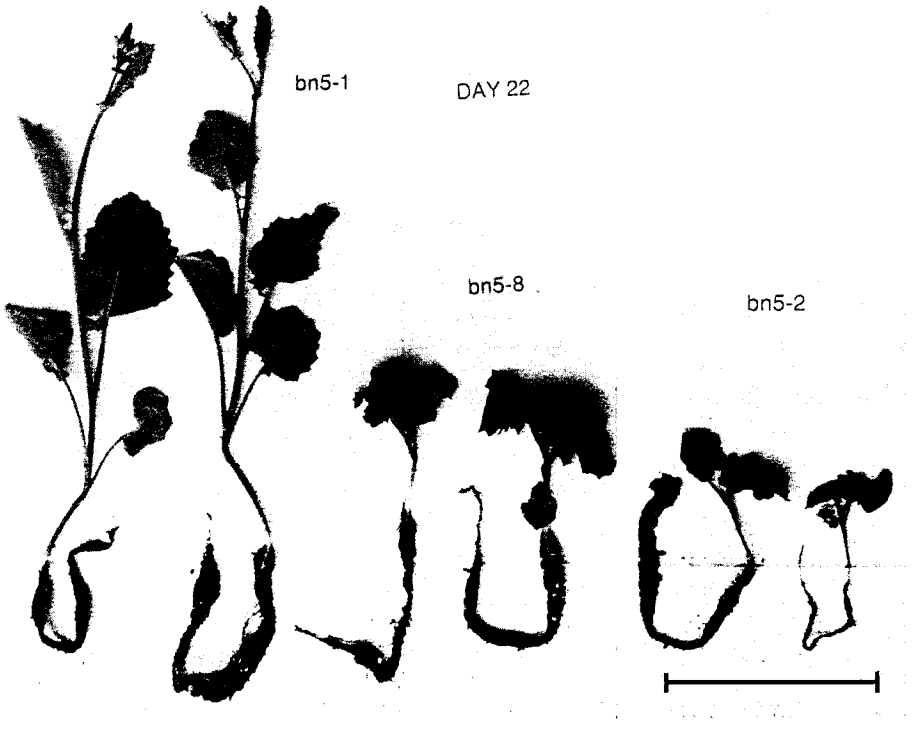

Fig. 2. Untreated, 22-day-old *Brassica napus* genotypes (left to right): normal Bn5-1, dwarfs Bn5-8 and Bn5-2. The scale bar represents 10 cm.

tinctive phenotypes (Figs. 1 and 2) with differences in height, leaf area, and shoot dry weight.

The genotypes ranking from tallest to shortest for *B. rapa* were normal > *dwf2* = *dwf1* > *dor* = *ros* and for *B. napus* were normal > Bn5-8 = Bn5-2 (Figs. 1 and 2; Table 1). Differences in height were due to differences in internode elongation; leaf numbers did not vary substantially across the genotypes (Zanewich et al. 1990 and unpublished observations).

Leaf area was not correlated with plant height (Table 1). In *ros* and *dor* genotypes there was little change in leaf area relative to the normal line. Leaf dry weights were also unchanged from the normal line, although stem dry weights were reduced (Table 1). Thus, in these two mutants, stem growth was reduced but leaf growth was relatively unaltered.

In contrast, *B. rapa dwf2* had much larger leaves than the normal line (Table 1). There was no change in total shoot dry weight (Table 1), reflecting a change in growth allocation between stems and leaves in this genotype.

The phenotype of the mutant *dwf1* was the most distinctive (Fig. 1). Leaf area was markedly reduced and total shoot dry weight was less than one third of the normal line (Table 1). Normal plants treated with the triazole inhibitor of GA biosynthesis, paclobutrazol (PP333) (Rood et al. 1989), resemble *ros* rather than *dwf1*.

Phenotypes of the *B. napus* mutants were characterized by reduced height and stem dry weight (Table 1). However, leaf area was slightly reduced in Bn5-2 and the same trend toward reduced leaf area was also observed in Bn5-8. In terms of relative growth changes, both were quite similar to the *ros* and *do* genotypes of *B. rapa*.

Responses of Six Dwarf Mutants to Exogenous GA_3

As has been previously observed, the application of GA_3 induced internode elongation in *B. rapa* mutants *ros* and *dor* (Table 2). A growth response to exogenous GA_3 is consistent with our previous observation of decreased endogenous levels of GA_1 and GA_3 in *ros* (Rood et al. 1989). In some experiments, the height of *dwf2* was slightly promoted by GA_3, although to a much lesser extent than in *dor* or *ros*. The influence of GA_3 on *dwf1* was minor and inconsistent. There was no indication of increased elongation of the *B. napus* dwarfs, even with 100 ng GA_3, a level which increased the height of normal *B. napus* (Table 2). Collectively, these results suggest that only *ros* and *dor* are GA-sensitive, whereas the other dwarfs are generally GA-insensitive.

Influence of Different GAs on the GA-Deficient Dwarf, Rosette

The dwarf *ros* is extremely sensitive to exogenous

Table 1. Shoot characteristics of 22-day-old dwarf mutants of *Brassica*.[a]

	Height (cm)	Leaf area (cm^2)	Dry weight (g)		Ratio leaves/stem
			Stem	Leaves	
Brassica rapa					
Normal	29.9 ± 1.4 a	19.6 ± 3.2 bc	173.6 ± 19.3 a	64.2 ± 11.0 b	0.37
dwf2	9.2 ± 1.6 b	41.6 ± 9.9 a	115.3 ± 20.0 b	116.8 ± 21.8 a	1.01
dwf1	9.2 ± 1.3 b	8.0 ± 1.9 c	34.7 ± 6.8 c	28.6 ± 4.9 c	0.82
dor	5.1 ± 0.8 c	19.7 ± 2.8 b	47.9 ± 7.8 c	50.0 ± 6.1 bc	1.04
ros	3.4 ± 0.5 c	21.2 ± 3.8 b	51.4 ± 5.2 c	66.4 ± 7.1 b	1.29
Brassica napus					
Normal	27.2 ± 1.1 a	54.8 ± 6.9 a	270.2 ± 24.6 a	179.9 ± 21.9 a	0.67
Bn5-8	6.1 ± 0.5 b	41.3 ± 8.2 ab	78.0 ± 8.4 b	140.9 ± 15.9 a	1.81
Bn5-2	5.6 ± 0.5 b	30.9 ± 3.5 b	76.4 ± 9.0 b	133.1 ± 15.6 a	1.74

[a] For each species within a column, values followed by the same letter do not differ significantly ($p < 0.05$).

Table 2. Height of 16-day-old *Brassica* genotypes untreated or treated with GA_3 8 days after planting.

	Height (cm)			
	Untreated	10 ng GA_3	100 ng GA_3	p[a]
Brassica rapa				
Normal	13.9 ± 1.5 a[b]	15.2 ± 1.3	14.9 ± 1.0	NS[c]
dwf2	2.4 ± 0.3 b	2.2 ± 0.3	2.8 ± 0.3	NS
dwf1	4.2 ± 0.4 b	6.0 ± 0.5	5.4 ± 0.3	0.0365
dor	1.0 ± 0.2 c	1.7 ± 0.2	2.6 ± 0.5	0.001
ros	0.7 ± 0.1 c	0.9 ± 0.1	1.8 ± 0.2	0.0016
Brassica napus				
Normal	7.4 ± 0.5 a	7.6 ± 0.5	9.3 ± 0.8	0.0294
Bn5-8	2.4 ± 0.2 b	2.5 ± 0.2	2.8 ± 0.2	NS
Bn5-2	2.6 ± 0.2 b	2.8 ± 0.2	3.0 ± 0.2	NS

[a] Probability from one-way ANOVA for each genotype.
[b] For a species, values followed by the same letter do not differ significantly ($p < 0.05$).
[c] NS, nonsignificant.

GA_3, requiring only 100 pg/plant for a detectable response under controlled conditions. A linear response existed between the log concentration of exogenous GA_3 applied and the corresponding height increment (Fig. 3) resulting in the function: height = 13.36 + log(GA_3 concentration) with a regression coefficient (r) of 0.996 ± 0.004. A quadratic regression coefficient was 0.997 ± 0.004, which was not a significant improvement over the linear regression. Due to its quantitative response, *ros* may be useful for the bioassay of GAs from semi-purified plant extracts. This *Brassica* dwarf might be a useful complement to dwarf rice and dwarf maize assays (Crozier and Durley 1983), since it involves a dicotyledon and both growth and development (flowering) are promoted (Rood et al. 1989).

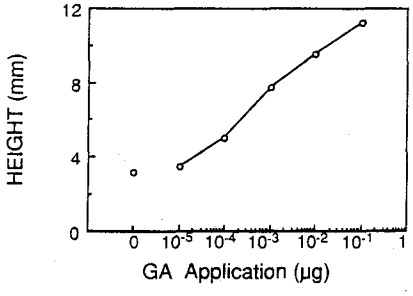

Fig. 3. Dose–response curve of *ros* treated with GA_3.

The principal endogenous GAs of *Brassica* have been recently identified (Hedden et al. 1989, Rood et al. 1987). The most abundant bioactive GAs (Rood et al. 1987) in shoots are members of the early-13-hydroxylation biosynthetic pathway. This pathway leads to GA_1, the probable effector GA for shoot elongation in maize, pea, and rice (Phinney 1985). In *Brassica*, as in these other plants, GA_1 is formed from GA_{20} which, in turn is formed from GA_{19} (Rood et al. 1990a). The origin of GA_{19} in *Brassica* has not been determined, but it is probably

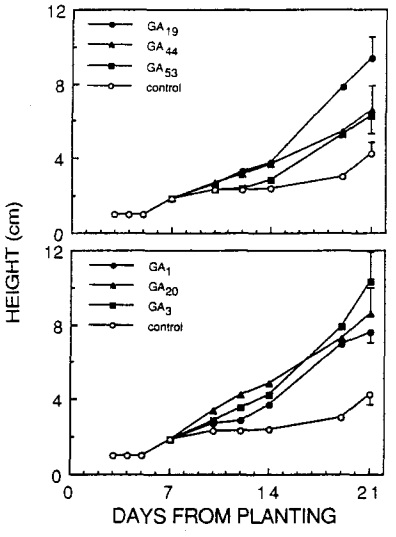

Fig. 4. Height of *ros* treated 7 days after planting with 100 ng of GA_3, GA_1, or biosynthetic precursors of GA_1.

formed from GA_{53} via GA_{44} (Graebe 1987). GA_{53} has not yet been identified in *Brassica* but its presence has been postulated (Hedden et al. 1989).

The mutant *ros* is apparently deficient in GA_1 (Rood et al. 1989) and to determine at what point in the biosynthetic pathway a biosynthetic block exists, GA_1 and its precursors, GA_{20}, GA_{19}, GA_{44}, and GA_{53}, were applied. Additionally, KA, a precursor which is a four steps prior to GA_{53} (Graebe 1987), was also applied. GA_3 was also tested for comparison.

The dwarf *ros* was responsive to all of the applied putative biosynthetic precursors of GA_1 (Fig. 4). Treated plants were significantly taller than control plants (e.g., height at day 21, ANOVA, df = 7, F = 3.995, p = 0.0009), possessed longer leaf blades (F = 3.256, p = 0.0029), and longer petioles (F = 4.326, p = 0.0.0002). Treatments tended to promote leaf area and stem dry weights but significant effects ($p < 0.05$) for these characteristics were only detected following the application of GA_1 or GA_3.

The exogenous application of GA_1 precursors was intended to provide an index of sensitivity of *ros* to different GAs and indicate the location of a block in GA biosynthesis. Since ANOVAs indicated highly significant effects of GA treatment on height, leaf blade, and petiole lengths, subsequent paired comparisons were performed to compare efficacies of various GAs.

By day 14, 6 days after GA application, GA_{20}-treated plants were taller than controls or plants treated with GA_{53}. At day 21, plants treated with GA_3 were significantly taller than plants treated with GA_{53} or control plants and plants treated with

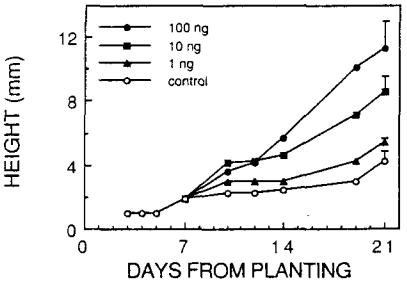

Fig. 5. Height of *ros* untreated and treated 7 days after planting with various levels of kaurenoic acid (KA).

KA were significantly taller than control plants and plants treated with GA_1, GA_{19}, GA_{44}, or GA_{53} (see also Fig. 5).

A two-way, repeated measures ANOVA involving height of experimental plants at days 14 and 21 indicated both highly significant effects of GA treatment and of date (growth effects) and a significant interaction of treatment × date (df = 7, F = 2.753, p = 0.0136). This indicates that the GAs did not uniformly influence height increment over time. Instead, some GAs such as GA_{20} had more rapid effects while responses to other compounds were delayed.

Petiole length was significantly promoted by day 21 by all compounds applied, including GA_{53}, which had the least influence on stem height. GA_3 was most potent at increasing petiole length, being significantly more effective than other treatments, including GA_1 or KA. Finally, leaf length was also generally promoted by GA treatment, with GA_1 being significantly more effective than GA_{19}, GA_{20}, GA_{44}, or GA_{53}.

The effects on height, leaf blade length, and petiole length may be grouped to determine relative efficacies of the GAs on elongation of *ros*. There was a progressive decline in efficacy of the earlier putative GA_1 precursors resulting in the following efficacy ranking: $GA_3 > GA_1 > GA_{20} \geq GA_{19} = GA_{44} \geq GA_{53}$.

These results do not demonstrate an abrupt reduction in efficacy but instead suggest that a block in the biosynthetic pathway in this genotype probably occurs prior to GA_{53}. The progressive decline in efficacy of GA_1 precursors is similar to findings with dwarf mutants of maize (Phinney 1985).

Interestingly, KA was more potent than early 13-hydroxylated GAs, GA_{53}, or GA_{44}, in inducing stem or leaf elongation (Fig. 5). This was surprising since KA might be metabolized through those GAs to produce GA_1 and/or GA_3, possible effector GAs for shoot elongation (Phinney 1985). KA was recently found to be much more active than GA_{53} and as

Table 3. Endogenous GA_1, GA_{20}, and GA_{19} concentrations in stems of 14-day-old *Brassica napus* seedlings.

	GA_1	GA_{20} (ng/g dry wt tissue)	GA_{19}
Normal	12.4 ± 2.1 b[a]	5.0 ± 0.3 b	4.7 ± 1.6 a
Bn5-8	40.0 ± 8.1 a	25.2 ± 4.5 a	7.8 ± 0.8 a
Bn5-2	39.5 ± 5.6 a	20.4 ± 2.2 a	5.8 ± 2.6 a

[a] Within a column, values followed by the same letter do not differ significantly ($p < 0.05$).

active as GA_{20}, in promoting stem elongation of *Thlapsi,* another crucifer, prompting Metzger (1990) to propose that GAs other than GA_1 may be important for thermoinduced stem elongation in that plant.

The efficacy of KA suggests a biosynthetic block prior to KA, which might make *ros* biochemically equivalent to the *d5* mutant of maize (Phinney 1985), d_x mutant of Tan-ginbozu dwarf rice, *lh or lx* mutants of pea, and *ga* tomato mutant (Reid 1990). Plants in which the GA biosynthetic pathway is blocked at an early stage respond to a broad range of exogenous GAs and hence, these mutants are useful for GA bioassays. Thus, *ros* may be useful as a bioassay plant, for it is both very sensitive and responds to a broad range of GAs.

Endogenous GAs of Brassica napus *Mutants*

The phenotypic differences between *ros* and *dor* and the other *B. rapa* mutants, *dwf*1 and *dwf*2, suggest that these latter mutations do not directly modify the GA level or response. However, both *B. napus* mutants, Bn5-8 and Bn5-2, resemble *ros* and hence, these GA-insensitive lines were further studied to investigate the possibility that they involve modifications to the GA response mechanism. If this was the case, it might be predicted that they would have increased endogenous GA levels, similar to some other GA-insensitive dwarfs which phenotypically resemble GA-deficient dwarfs, *D8* of maize (Fujioka et al. 1988) and possibly, *Rht* of wheat (Lenton et al. 1987).

Differences in GA_1 concentration (or level per stem) were statistically significant (ANOVA, $F = 7.42$, $p = 0.006$) with both Bn5-2 and Bn5-8 containing 3.2-fold higher concentrations than the normal line, Bn5-1 (Table 3). Concentrations of GA_{20} were also significantly ($F = 13.06$, $p = 0.033$) higher in the dwarf mutants. GA_{19} concentrations were not statistically significantly ($p < 0.05$) different in the three genotypes, although the dwarfs tended to have higher concentrations, the same pattern was observed for GA_1 and GA_{20} (Table 3).

Both *B. napus* dwarf genotypes contain the mutant gene, *dwf1* (note that the *B. napus dwf1* mutant is not the same as the *B. rapa dwf1* mutant). However, the two genotypes have different cytoplasms and Bn5-8 is a segregating mixture of the dwarf heterozygote, *DWF1/dwf1,* and the slightly more severe dwarf homozygote, *dwf1/dwf1*. The *B. napus dwf1* gene demonstrates incomplete dominance.

A higher GA_1 content of the GA-insensitive *B. napus* dwarfs suggest that the *dwf1* mutation might be similar to mutations of other GA-insensitive dwarfs, *D8* of maize (Fujioka et al. 1988), and *Rht* of wheat (Lenton et al. 1987). Quantitatively, the apparent 3.2-fold GA_1 enrichment of *dwf1* is considerably less than the 50-fold increase of *D8* maize but quite similar to the 2.9-fold increase in *Rht1*. It is interesting that these three mutants are dominant or incompletely dominant in contrast to the GA-deficient dwarf mutants which are generally recessive (Phinney 1985, Reid 1986, Rood et al. 1989).

Thus, in the present study a number of single-gene dwarf mutants of two species of *Brassica* were studied. Only the *B. rapa* mutants *ros* and *dor* appear to be GA-deficient dwarfs with the metabolic block of *ros* appearing to be early in the GA biosynthetic pathway. The *B. napus* lines Bn5-2 and Bn5-8, containing the mutant *dwf1* are "GA-insensitive" and have elevated levels of endogenous GAs. These two types of dwarf mutants, GA-deficient and GA-insensitive, are physiologically similar to dwarf mutants of other plants, such as maize, pea, rice, and wheat, an observation which suggests that GA physiology may be fundamentally similar in a range of crop plants.

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