J Plant Growth Regul (1993) 12:41–46

Journal of
Plant
Growth
Regulation

Distribution of Endogenous Gibberellins in Vegetative and Reproductive Organs of *Brassica*

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Received October 28, 1992; accepted February 8, 1993

Abstract. Recognizing the physiological diversity of different plant organs, studies were conducted to investigate the distribution of endogenous gibberellins (GAs) in *Brassica* (canola or oilseed rape). GA_1 and its biosynthetic precursors, GA_{20} and GA_{19}, were extracted, chromatographically purified, and quantified by gas-chromatography-selected ion monitoring (GC-SIM), using $[^2H_2]$GAs as internal standards. In young (vegetative) *B. napus* cv. Westar plants, GA concentrations were lowest in the roots, increased acropetally along the shoot axis, and were highest in the shoot tips. GA concentrations were high but variable in leaves. GA_1 concentrations also increased acropetally along the plant axis in reproductive plants. During early silique filling, GA_1 concentrations were highest in siliques and progressively lower in flowers, inflorescence stalks (peduncles plus pedicels), stem, leaves, and roots. Concentrations of GA_{19} and GA_{20} showed similar patterns of distribution except in leaves, in which concentrations were higher, but variable. Immature siliques were qualitatively rich in endogenous GAs and GA_1, GA_3, GA_4, GA_8, GA_9, GA_{17}, GA_{19}, GA_{20}, GA_{24}, GA_{29}, GA_{34}, GA_{51}, and GA_{53} were identified by GC-SIM. In whole siliques, GA_{19}, GA_{20}, GA_1, and GA_8 concentrations declined during maturation due to declining levels in the maturing seeds; their concentrations in the silique coats remained relatively constant and low. These studies demonstrate that GAs are differentially distributed in *Brassica* with a general pattern of acropetally increasing concentration in shoots and high concentration in actively growing and developing organs.

Gibberellins (GAs) are involved in the regulation of many aspects of shoot growth and development in *Brassica* (Rood et al. 1990b, Zanewich et al. 1990) and other crop plants (Pharis and King 1985, Phinney 1985). The role of endogenous GAs in the control of shoot elongation has been well documented (Phinney 1985) for many plants, and reduced stature is a phenotypic consequence in GA-deficient or GA-insensitive *Brassica* mutants (Rood et al. 1989b, 1990b, Zanewich et al. 1991). Additionally, reproductive development is retarded and anthesis is delayed or does not occur in GA-deficient *Brassica* dwarfs (Rood et al. 1989b, Zanewich et al. 1990, 1991). Consistent with this, the application of triazole plant growth retardants that block GA biosynthesis can prevent or inhibit *Brassica* flowering in addition to retarding shoot elongation (Rood et al. 1989a).

Studies of the physiological role of GAs in plant growth and development frequently involve qualitative and/or quantitative analyses of endogenous GAs. Major portions of shoots, whole shoots, or even whole plants are often extracted for GA determinations. However, such procedures will obscure any tissue- or organ-specific GA distribution and will dilute GAs from GA-rich organs with relatively GA-deficient, metabolically less-active tissues. Such dilution could prevent meaningful analyses of GA level or concentration.

Differences in GA distribution in several plants including pea (Smith et al. 1992), maize (Murofushi et al. 1991), rice (Takahashi 1990), *Silene* (Talon and Zeevaart 1990), and oat (Kaufman et al. 1976) have been recognized. To investigate the distribution of GAs within *Brassica* plants, studies were performed to determine the GA distribution in vegetative and reproductive organs of *Brassica*. Since GA_1 is probably a principal bioactive GA in *Brassica* (Hedden et al. 1989, Rood et al 1987, 1989b), the studies focused on analyses of GA_1 and two of its biosynthetic precursors, GA_{20} and GA_{19}. Additionally, the major endogenous GAs in the GA-rich immature siliques (including seeds) were investigated.

Materials and Methods

Plant Materials and Growth

Seeds of *Brassica napus* cv. Westar were planted in 15 cm pots filled with Metro mix (W. R. Grace & Co., Ajax, Ontario). Seedlings were subsequently thinned to one healthy plant per container. Plants were grown at 23 ± 4°C in the University of Lethbridge greenhouse (latitude 49.6°N), watered daily, and provided with continuous light from high-pressure sodium vapor lights positioned 1.3 m above the plants [260 μmol s^{-1} m^{-2} photosynthetically active radiation; Reflector PL90M (medium) N400, P.L. Light Systems Canada, Inc.]. Plants were fertilized as required with water-soluble 20-14-14 (N-P-K) fertilizer with supplemental trace elements (Professional Gardener Co., Ltd., Calgary, Alberta).

Twenty eight-day-old Westar plants, which were still vegetative, were dissected into the following parts: (1) shoot tips (containing the apical meristem, small leaf primordia, and subtending stem to provide approximately 5 mm long segments); (2) medial stems (stems between the shoot tip and cotyledons); (3) hypocotyls; (4) roots (primary and some secondary roots); (5) young leaves (those leaves nearest the shoot tip which had not yet fully expanded and had short petioles); (6) expanded leaves (those leaves with large blades and completely elongated petioles; and (7) old leaves (those leaves nearest the base of the plant which were senescing).

Another group of Westar plants was harvested 9 weeks after planting and separated into: immature siliques, flowers (about 1 day postanthesis), inflorescence stalks (peduncles plus pedicels), stems, leaves (all nonsenescent leaves), and roots. Material for each replicate was collected from five plants (dry weights from 1.3–39 g).

Siliques at various developmental stages were collected over two 45-day periods, beginning July 31, 1989 and July 18, 1990 from Westar plants grown in an irrigated field plot at the Agriculture Canada Research Station, Lethbridge. Criteria for judging silique developmental stage were length, degree of filling, and color. Immature siliques (stage 1) were green, 1–3 cm long, and had no seeds or tiny, moist, green seeds. In some instances the stigmas were still present. Stage 2 siliques were green and elongating and had small green "watery" seeds. Siliques which were still green but with full seeds were categorized as stage 3. Stage 4 siliques had coats which had started to yellow or ripen, and hard, greenish-brown seeds. Mature siliques (stage 5) were dry, yellow, greater than 5 cm long, appeared full, and contained hardened black seeds. The dry weights for immature silique samples ranged from 2–10 g and for seeds from 0.89–1.8 g.

Endogenous GA Analyses

Endogenous GAs were extracted and purified by step-elution (Rood et al. 1983) silicic acid (SiO_2) partition chromatography (Durley et al. 1972) followed by reversed-phase C_{18} high-performance liquid chromatography (HPLC) (Koshioka et al. 1983). HPLC samples were methylated and silylated (Rood et al. 1987) and analyzed using a Hewlet-Packard 5890 Series II GC, containing a 15 m × 0.25 mm DB-5 fused silica column (J&W Associates) with a 0.25 μm film of polymethyl (5% phenyl) siloxane. Head pressure of the carrier gas (He) was 265 kPa, and the resulting flow rate was 1.4 ml min^{-1}. Samples were introduced by cool on-column injection into a 10 cm long mega bore precolumn. At injection, the column head pressure was 28 kPa and the temperature was 60°C. Following a 30 s delay at 60°C, the following temperature program was used: a rapid temperature ramp of 25°C min^{-1} to 200°C, a decreased rate of temperature ramp of 5°C min^{-1} to 270°C, and a final rapid temperature ramp of 20°C min^{-1} to 300°C (transfer line from gas chromatograph to mass detector at 300°C). Selected ion monitoring programs were used and ion fragments were detected using a Hewlet-Packard 5970 mass selective detector.

To quantify endogenous GA levels, 10–20 ng each of [17,17-$^2H_2$]GA_{19}, [17,17-$^2H_2$]GA_{20}, [17,17-$^2H_2$]GA_1, and [17,17-$^2H_2$]GA_8 standards (all greater than 99% enrichment) from L.N. Mander, Australian National University, were added during extraction. The amounts of endogenous GA_{19}, GA_{20}, GA_1, and GA_8 were calculated from the peak area ratios of 434/436, 418/420, 506/508, and 594/596 respectively, using a modified version of the equation for isotopic dilution analysis described by Fujioka et al. (1986).

Three separate growth experiments consisting of two or three replicates were independently analyzed for endogenous GA content of different organs from Westar (two replicates for vegetative plants and six replicates for reproductive plants). Endogenous GAs of developing siliques were analyzed in two replicates for each of five developmental stages from each of the two growing seasons, 1989 and 1990 (four replicates per stage in total). Five replicates were analyzed for endogenous GA content of seeds and silique coats.

For the identification of GAs from immature siliques, 2 g samples from silique harvest 1 were purified by SiO_2 and C_{18} HPLC. HPLC fraction groupings were derivatized and analyzed by GC-SIM, probing appropriate fractions for specific GAs as indicated in Table 3 in addition to $GA_{5,7,12,13,25,27,36,44,70,77,85}$ and 2β-OH GA_{53}, relying on Kovats Retention Indices (Gaskin et al. 1971) and ion abundances of authentic standards or from published reports. For identification, eight ions were normally monitored but only five characteristic ions are included in Table 2.

Results and Discussion

GA Distribution in Vegetative Seedlings

GA_1 was detected in extracts from all parts of the seedling axis, including roots, in which GA concentrations were consistently low (Fig. 1). Shoot tips, regions of extensive cell proliferation, had the highest GA_1 concentrations, while stem concentrations were somewhat lower. Thus, within the plant axis, GA_1 concentration increased acropetally. A similar axial distribution of GA_1 has been recently reported for *Pisum* (Smith et al. 1992).

GA_1 concentrations in leaves were generally high but variable (Table 1). Leaves which had already undergone expansion typically had the highest GA_1 concentrations, young actively growing leaves had the lowest concentrations, and older senescing leaves had intermediate GA_1 concentrations. The leaves did not exhibit acropetally increasing concentrations of GA_1 as had been demonstrated in pea (Smith et al. 1992). In contrast to pea, the young uppermost *Brassica* leaves had relatively low GA_1 concentrations.

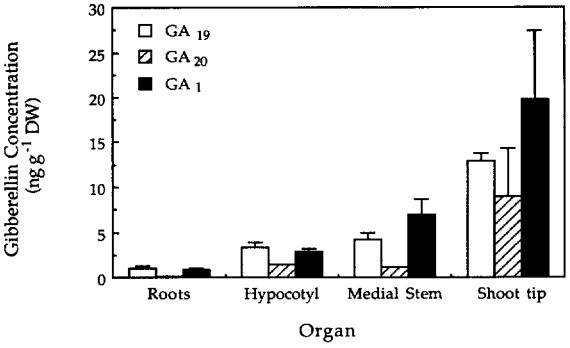

Fig. 1. Gibberellin concentration (ng g^{-1} dry weight) in different organs of 28-day-old (vegetative) *Brassica napus* (canola cv. Westar) plants. Values represent means of two replicates + SE.

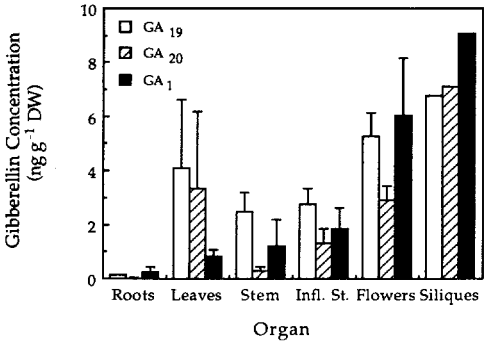

Fig. 2. Gibberellin concentrations (ng g^{-1} dry weight) in different organs of 64-day-old *Brassica napus* (canola cv. Westar) plants during early silique-filling. Infl. St. indicates the inflorescence stalk that includes peduncles plus pedicels. Values represent means of five replicates + SE, except for siliques.

Table 1. Endogenous gibberellin (GA) concentration in leaves from 28-day-old (vegetative) *Brassica napus* cv. Westar plants (standard errors are included).

	GA concentration (ng g^{-1} dry weight)		
Leaves	GA_{19}	GA_{20}	GA_1
Young	3.8 ± 0.1	5.6 ± 3.0	13.1 ± 6.2
Expanding	1.8	6.7 ± 2.0	34.6 ± 23.3
Old (senescing)	3.0 ± 1.3	3.9 ± 0.2	23.5 ± 5.4

Two immediate metabolic precursors of GA_1, GA_{20} and GA_{19}, were also most concentrated in shoot apical regions and progressively less concentrated in stems and roots (Fig. 1). Although GA_{20} and GA_{19} concentrations were both consistently lower than GA_1, GA_{19} concentrations were greater than GA_{20} concentrations in the plant axis. However, unlike the high concentrations of GA_{20} that have been reported in the upper leaves of pea (Smith et al. 1992), concentrations of GA_{20} in canola leaves were lower than those of GA_1 (Table 1). Additionally, GA_{19} concentrations were also low in the leaves. Previous observation of lower GA concentrations in canola or oilseed rape shoots (Hedden et al. 1989, Rood et al. 1989a) probably resulted from analyses of large shoot samples that contained substantial amounts of metabolically less-active, mature tissues combined with more vigorous younger tissues.

GA Distribution in Reproductive Plants

The pattern of distribution of GA_{19}, GA_{20}, and GA_1 in reproductive plants was similar to that observed in the vegetative seedlings. Concentrations of all three GAs were highest in the apical tissues that had differentiated into the reproductive organs (Fig. 2). Comparing the reproductive structures, concentrations of the three GAs tended to be highest in immature siliques (including seeds), intermediate in the flowers, and lower in the inflorescence stalks (peduncles and pedicels). The stems generally contained lower concentrations of GAs than the reproductive organs, and the lowest GA concentrations occurred in the roots, similar to the findings in the seedlings. GA concentrations in the leaves were also variable in the reproductive plants. GA_1 concentration in the leaves was lower than in other shoot parts (Fig. 2).

Endogenous GAs in Siliques and Seeds

In the reproductive plants, GA concentrations were highest in the immature siliques (Fig. 2). To investigate changes of GA concentrations in developing siliques, weekly harvests were conducted to obtain siliques at five developmental stages. During this sequence of development, GA_{19}, GA_{20}, and particularly GA_1 concentrations progressively declined with age (Fig. 3). Consequently, the concentrations of these free GAs, and particularly free GA_1, were very low in the mature siliques. García-Martínez et al. (1987) also found qualitative and quantitative differences in GAs in pea pods and seeds at different developmental stages.

To differentiate between the endogenous GA contribution of the seeds and the silique coats, seeds were dissected from immature (stage 1) and mature (stage 5) siliques. Concentrations of GA_{19}, GA_{20}, GA_1, and GA_8 were consistently low in the silique coats regardless of harvest timing (Fig. 4). In

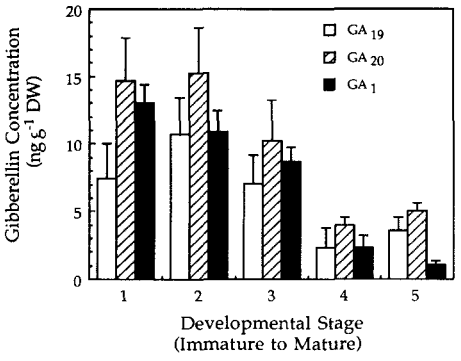

Fig. 3. Gibberellin concentrations (ng g^{-1} dry weight) of *Brassica napus* (canola cv. Westar) siliques at different developmental stages. Values represent means of four replicates + SE for tissue harvested from plants growth in field tests at Lethbridge in 1989 and 1990.

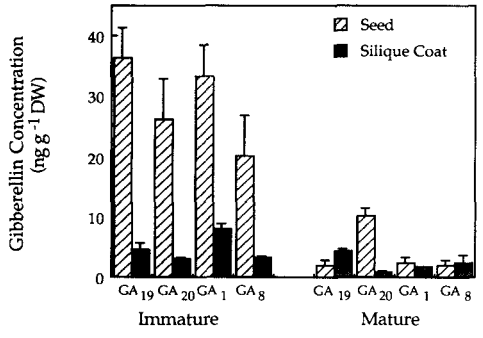

Fig. 4. Gibberellin concentration (ng g^{-1} dry weight) of immature (stage 1) and mature (stage 5) *Brassica napus* (canola cv. Westar) seeds and silique coats. Values represent means of 2–5 replicates + SE from plants grown in field tests at Lethbridge in 1990.

contrast, the immature seeds had GA concentrations which were significantly (ANOVA, $p \leq 0.0325$) higher than those in the mature seeds. This is consistent with numerous reports which indicate that the levels of GAs present in immature seeds of various plants are generally high (Takahashi et al. 1986, Sponsel 1987). Further, García-Martínez et al. (1991) have noted that GA concentrations are substantially higher in ovules than in pods of pea.

The immature seeds contained higher concentrations of all measured GAs relative to the mature seeds. GA_{19}, GA_{20}, GA_1, and GA_8 concentrations were, respectively, 18.2-, 9.9-, 13.6-, and 2.6-fold higher in immature than mature seeds. The mature seeds contained more GA_{20} than the other GAs, an observation that corresponds to recent findings with the *Brassica napus* cultivar Parkland (H. Imeson, K. Zanewich, and S. Rood, unpublished results).

Since GA_{19}, GA_{20}, and GA_1 concentrations were high in immature siliques, the occurrence of other endogenous GAs in that plant part were subsequently investigated. GC-SIM analyses were focused to probe for specific GAs that are native to *Brassica* (Hedden et al. 1989, Rood et al. 1987) or to other crucifers, *Arabidopsis* (Talon et al. 1990) and *Thlaspi* (Metzger and Mardaus 1986), as well as other GAs that are metabolically associated. Thirteen GAs were detected (Table 2), including 10 that had been previously identified from stems and apices (Rood et al. 1987) or whole shoots (Hedden et al. 1989). The three additional GAs—GA_4, GA_9, and GA_{53}—are members of GA biosynthetic pathways previously proposed for *Brassica* (Hedden et al. 1989, Rood et al. 1987). GAs which were investigated but not detected included $GA_{5,7,12,13,25,27,36,44,70,77,85}$ and 2β-OH GA_{53}.

Of particular interest is the presence of GAs characteristic of both the early 13-OH and non-13-OH GA biosynthetic pathways. Based on the ease of detection by GC-SIM and, hence, apparent abundance of GA_4, GA_9, GA_{24}, GA_{34}, and GA_{51}, it would appear that the non-13-OH GA biosynthetic pathway could be a dominant pathway in the immature siliques.

In apparent contrast to vegetative shoots (Hedden et al. 1989; Rood et al. 1987), GA_4 and its precursor, GA_9, were readily detected and hence apparently abundant in immature siliques. GA_4 has been previously shown to be abundant in rice anthers (Kobayashi et al. 1988) and maize tassels (Murofushi et al. 1991), prompting the proposal that it may be involved in reproductive development. Further, Takahashi (1990) has presented evidence for the organ specificity of 13-OH versus non-13-OH GAs in rice. Further studies of the abundance and role of 13-OH versus non-13-OH GAs in vegetative and reproductive organs and tissues of *Brassica* are warranted.

The observation that GAs are concentrated differentially in organs of both vegetative and reproductive *Brassica* plants is consistent with results from pea (Smith et al. 1992), *Silene* (Talon and Zeevaart 1990), rice (Kobayashi et al. 1988), and *Avena* (Kaufman et al. 1976). In these other plants, concentrations of GAs were also found to be high in shoot tips, providing a consistent pattern of high GA concentration in these centers of growth and developmental activity. Further, the studies provide evidence of acropetally increasing concentration of GAs, with highest levels in shoot tips or reproductive organs. The observation of lowest concentrations of GAs in *Brassica* roots suggests the pattern of decreasing concentration down the plant axis.

Table 2. MeTMSi gibberellins (GAs) identified by capillary gas chromatography-selected ion monitoring (GC-SIM) from *Brassica napus* cv. Westar immature siliques.

GA	HPLC fraction	KRI[a]	Ion *m/z* and (relative abundance)				
GA_1	21–24	2709	506 (100)	491 (8)	448 (18)	416 (8)	390 (6)
GA_3	21–24	2739	504 (100)	489 (6)	445 (9)	431 (7)	347 (8)
GA_4	35–37	2564	418 (9)	390 (6)	386 (19)	289 (66)	284 (100)
GA_8	10–14	2831	594 (100)	579 (7)	565 (3)	553 (5)	535 (12)
GA_9[b]	38–40	2390	298 (100)	270 (61)	243 (36)	227 (30)	226 (36)
GA_{17}	31–34	2625	492 (73)	460 (34)	432 (33)	401 (21)	373 (21)
GA_{19}	31–34	2650	462 (9)	447 (7)	434 (100)	431 (15)	402 (43)
GA_{20}	28–30	2534	418 (100)	403 (14)	375 (47)	359 (20)	301 (25)
GA_{24}[b]	38–40	2513	314 (78)	286 (60)	285 (71)	226 (100)	225 (93)
GA_{29}	15–18	2711	506 (100)	491 (14)	477 (3)	447 (3)	389 (11)
GA_{34}	31–34	2699	506 (100)	459 (7)	431 (6)	416 (6)	288 (19)
GA_{51}	35–37	2568	403 (4)	386 (28)	343 (13)	328 (42)	284 (100)
GA_{53}	38–40	2538	448 (47)	419 (5)	389 (17)	251 (41)	235 (31)

[a] Kovats Retention Index. Samples were analyzed on a DB-5 capillary column.
[b] MeGA.

The observed moderately high concentrations of GAs in stems is relevant to the observation that this organ is highly GA-responsive. Stem elongation is a normal consequence of GA application. Elongation may also occur through the action of the single gene mutation seen in the *Brassica* mutant, *elongated internode*, which has accelerated GA_1 biosynthesis and in some conditions elevated GA_1 levels in the stems (Rood et al. 1990a). Conversely, depressed stem elongation is a primary characteristic of the GA-deficient mutant *rosette* Rood et al. 1989b). Similarly, the application of plant growth retardants that block GA biosynthesis particularly inhibit stem elongation in *Brassica* (Hedden et al. 1987, Rood et al. 1989a). Thus, it is probably physiologically relevant that endogenous GA concentration is reasonably high in the GA-responsive organ, the stem.

In summary, the present study demonstrates greater than 10-fold differences in GA concentration among different *Brassica* organs. Increased concentrations of endogenous GAs upward along the plant axis were observed in both seedlings and reproductive plants, with highest concentrations in the reproductive plants observed in immature seeds. Further, complete siliques were qualitatively as well as quantitatively rich in endogenous GAs. These observations emphasize the need to consider differential distribution of endogenous GAs in plants for an accurate understanding of GA physiology.

Acknowledgments. We express our thanks to Keith Topinka at the Lethbridge Agriculture Canada Research Station for his help in providing canola plants from which siliques could be harvested. This research was funded by a National Research Council of Canada Industrial Research Assistance Program grant in collaboration with the United Grain Growers and Allelix Crop Technologies.

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