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Gibberellins in *Citrus sinensis:* A Comparison Between Seeded and Seedless Varieties

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Abstract. The gibberellin (GA) content of the reproductive organs of *Citrus sinensis* (L.) Osb., cv. Blanca Comuna and the seedless variety, Salustiana, were examined by combined gas chromatography–mass spectrometry (GC/MS) at different stages of development. Gibberellins A_1, A_{20}, and A_{29} were identified in the reproductive buds of both cultivars 21 days prior to anthesis and in fruits 35 days after anthesis by comparison of their mass spectra and Kovats retention indices with those of standards. In addition, three uncharacterized isomers of GA_1 were detected, one in buds and two in fruits. The presence of GA_4 in both tissues, and of GA_8 in the reproductive buds, was indicated by the occurrence of characteristic ions at the expected retention times, although their spectra were too weak for full identification. Vegetative shoots of cv. Salustiana contained gibberellins A_1, A_{19}, A_{20}, and A_{29}, and the unidentified isomer of GA_1 present in reproductive buds. The presence of trace amounts of gibberellins A_8 and A_{17} was also indicated. Although the two varieties did not differ qualitatively in the GAs present during flower and fruit development, the seedless variety contained slightly greater amounts. The concentrations of gibberellins A_1, A_4, and A_{20} were determined by gas chromatography–selected ion monitoring (GC/SIM) throughout ovary development and early fruit growth. In both varieties, the maximum GA_1 concentration occurred at anthesis. Highest concentrations of gibberellins A_{20} and A_4 were found in fruit 35 days after anthesis, although the GA_1 concentration at this stage remained low.

The importance of gibberellins (GAs) in reproductive development is now well accepted (Goodwin 1978, Pharis and King 1985). In *Citrus,* exogenous GA_3 increased fruit set in self-incompatible mandarins (Soost and Burnett 1961), and application of GA_3 to pistils resulted in greater mobilization of metabolites to young ovaries, a process which is apparently essential for fruit set and development (Powell and Krezdorn 1977). It has been suggested that fruit development in seedless and seeded varieties of Clementine mandarins was controlled by a balance between abscisic acid (ABA) and auxin-like substances and ABA and GA-like substances, respectively (Garcia-Papi and Garcia-Martinez 1984).

Attempts have been made to study the relationship between the endogenous GA content and fruit development in *Citrus,* although in most cases, the limitations of the methods used restrict the reliability of the results. The first chemical characterization of a GA from *Citrus* was reported by Kawarada and Sumiki (1959) who, on the basis of infrared spectra and physiological properties, identified GA_1 in water sprouts. Khalifah et al. (1965) detected three GA-like substances in young fruits, two of which were tentatively identified as GA_1 and GA_9, based on Rf values, biological properties, and fluorimetry. Wiltbank and Krezdorn (1969) detected GA_1 and GA_3 spectrofluorimetrically during early fruit growth. All subsequent studies with *Citrus* fruit have relied on bioassay (see Goldschmidt 1976 and references therein, Kuraoka et al. 1977), and the results have indicated that fruits approaching maturation contain less GA-like activity than younger fruits. Recently, the identification by combined gas chromatography–mass spectrometry (GC/MS) of eight GAs, including GA_1 and GA_{20}, in vegetative shoots of *Citrus sinensis* was reported by Poling and Maier (1988).

We describe herein the GC/MS identification of

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GAs in developing flowers, fruit, and vegetative buds of *Citrus sinensis* and changes in concentration of three physiologically important GAs during reproductive development of a seeded and seedless genotype of this species.

Materials and Methods

Plant Material

Reproductive organs from the seeded variety cv. Blanca Comuna of sweet orange [*Citrus sinensis* (L.) Osb.] and its parthenocarpic mutant, cv. Salustiana, were selected at random at the following reproductive stages, as described for *Citrus* by Frost and Soost (1968): stage A, bud probably containing pollen mother cells before the prophase of the first meiotic division [−21 days after full bloom (DAFB)]; stage C, ovary at the stage of young pollen (−7 DAFB); stage E, ovary at pollination (0 DAFB); stage F, ovary at petal fall (7 DAFB); stage I, fruit at the time of normal fruit drop (35 DAFB). Vegetative shoots from cv. Salustiana, consisting of 8-mm shoot apices with a pair of attached growing leaves, were sampled at −21 DAFB. All samples were frozen immediately in liquid nitrogen, lyophilized, and stored at −20°C until analysis.

Extraction and Purification Procedure

Five or 10 grams dry weight of each sample were homogenized in cold 80% aqueous methanol (MeOH) (1 g/10 ml) and the homogenate stirred overnight at 4°C. The extract was filtered and the residue washed with MeOH (three times in 10 ml). The combined filtrate and washings were reduced to the aqueous phase in vacuo at 34°C, an equal volume of 0.1 M KPi buffer at pH 3.0 added, and the pH adjusted to 2.5 with H_3PO_4. The aqueous extract was partitioned against ethyl acetate (EtOAc) (three times in equal volumes), the combined EtOAc phases reduced in volume, and partitioned against 0.1 M KPi buffer, pH 8.5 (three times in equal volumes). The combined aqueous phases were adjusted to pH 2.5 with 1 N HCl and partitioned against EtOAc (three times in equal volumes), which was then washed twice with water at pH 3 (1 ml/20 ml EtOAc), and evaporated to dryness. The dried extract was dissolved in 0.1 M KPi buffer at pH 4.5 (5 ml), the pH adjusted to 8.0 with 1 M KOH, and the solution applied to a column of polyvinylpyrrolidone (PVP, 0.1 g/2 g sample). Further washes with 0.1 M KPi buffer at pH 8.0 (two times in 5 ml) were applied to the column, the total eluate was adjusted to pH 2.5 with H_3PO_4, and passed through a C_{18} Sep-Pak cartridge. The cartridge was washed with 5-ml portions of 5% acetic acid and then water, and the GAs eluted with 80% MeOH–water (5 ml). Further purification was achieved by anion-exchange chromatography. The dried eluate from Sep-Pak was redissolved in a few drops of MeOH, water at pH 8 (5 ml) was added, and the pH of the solution was carefully readjusted to above 7 with 1 N KOH. The solution was applied to a column of QAE Sephadex-A25 (1 × 5 cm) that had been preequilibrated with 0.5 M Na formate and washed with four volumes water. After application of the sample, the column was washed with water at pH 8 (three times in 5 ml) and the GAs eluted with 0.2 M formic acid (four times in 5 ml), which were combined and reduced to dryness in vacuo.

Reverse-Phase High-Performance Liquid Chromatography (HPLC)

The purified extracts were dissolved in 30% aqueous MeOH (0.5 ml), injected onto an ODS Hypersil (5 μm) column (250 × 4.9 mm i.d.), and eluted at 1 ml/min with a linear gradient of 20–100% MeOH in aqueous acetic acid (50 μl/L) over 40 min using a Kontron HPLC System 600. Fractions were collected at 1-min intervals.

Bioassays

HPLC fractions were assayed for GA-like activity using the barley endosperm (Jones and Varner 1967) and the Tan-ginbozu dwarf rice (Martin 1971) assays.

Qualitative Analysis by GC/MS

In order to determine recoveries and elution volumes on HPLC, the original homogenate was spiked with approximately 800 Bq [1,2-$^3H_2$]GA_1, [1,2-$^3H_2$]GA_4 (Amersham International plc, Arlington Heights, Illinois, USA), [1,2,3-$^3H_3$]GA_{20} (purchased from Prof J. MacMillan, University of Bristol) and [2,3-$^3H_2$]GA_9 (gift from Dr A. Crozier, University of Glasgow). Dried HPLC fractions were dissolved in MeOH, combined in eight groupings based on the retention volumes of the internal standards, and methylated with ethereal diazomethane. Residual sugars were removed from the methylated samples by adding water (0.5 ml) and partitioning against EtOAc (three times in 0.5 ml). The combined organic phases were dried, the extracts transferred to glass ampoules, and trimethylsilylated with *N*-methyl-*N*-trimethylsilyltrifluoracetamide (MSTFA) (5 μl) at 90°C for 30 min. Derivatized samples were analyzed using a Kratos MS80RFA GC/MS system. The samples (1 μl) were co-injected with 0.1 μl of a solution of Parafilm in hexane (for determining Kovats retention indices (Gaskin et al. 1971)) into a fused, silica wall-coated open tubular (WCOT) BP-1 capillary column (25 m × 0.32 mm × 0.33 μm film thickness) at an oven temperature of 50°C with the injector split valve closed. After 0.5 min, the split (50:1) was opened and after 1 min the oven temperature was increased at 20°C/min to 240°C and then at 4°C/min to 295°C. The He inlet pressure was 0.04 MPa and the injector and interface temperatures were 220 and 250°C, respectively. After 12 min positive ion electron impact mass spectra were acquired, scanning from 700–50 atomic mass units (amu) at 1 s/mass decade. The electron energy was 70 eV and the source temperature 200°C.

Quantitative Analysis by Gas Chromatography–Selected Ion Monitoring (GC/SIM)

Quantitative analysis of GA_1, GA_4, and GA_{20} was accomplished by isotope dilution. In addition to the ^3H-labeled internal standards listed above, [$^2H_2$]GA_1, [$^2H_1$]GA_{20} (gifts from Prof J. MacMillan, University of Bristol), and [$^2H_2$]GA_4 (synthesized by the Wittig reaction, see Hedden 1987) were added to the tissue homogenate. HPLC fractions containing GA_1, GA_{20}, or GA_4 were analyzed separately using a Hewlett Packard 5890 gas chromatograph coupled to a 5970 Mass Selective Detector. Derivatized samples (1 μl) were injected into a fused silica WCOT bonded OV-1 capillary column (25 m x 0.2 mm × 0.33 μm film thick-

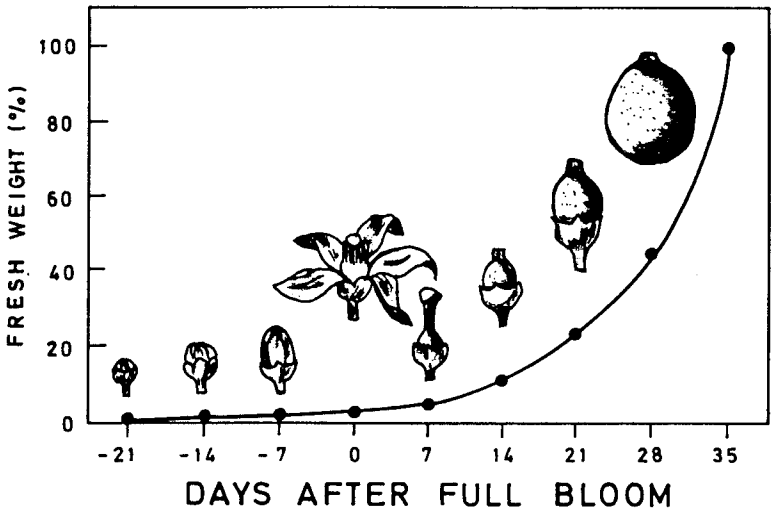

Fig. 1. Growth of reproductive organs (cumulative fresh wt as % weight at 35 DAFB) of *Citrus* during stage I and early stage II.

ness), using the temperature program described above except that the starting temperature was 60°C. The He inlet pressure was 0.11 MPa and the injector, interface, and MS source temperatures were 220, 270, and 200°C, respectively. Ions were monitored with dwell times of 0.1 s as follows: for $GA_1/[^2H_2]GA_1$ methyl ester trimethylsilyl ether (MeTMS), m/z 508, 506, 448, 376; for $GA_4/[^2H_2]GA_4$ MeTMS, m/z 420, 418, 291, 289, 286, 284; and for $GA_{20}/[^2H_1]GA_{20}$ MeTMS, m/z 419, 418, 403, 375. The concentrations of GA_1, GA_4, and GA_{20} in the original extract were determined from the peak area ratios 506/508, 284/286, and 418/419, respectively, by reference to the calibration curves. The other ions were monitored to confirm the identity of the compounds being analyzed.

Results

Fruit Growth

Citrus fruit exhibit a sigmoidal growth curve which can be divided into three stages (Bain 1958). Stage I is a period of cell division with slow growth and includes flowering. Stage II is characterized by rapid cell enlargement and stage III is the maturation period during which the growth rate decreases progressively. The growth of *Citrus sinensis* fruit in stage I and early stage II is illustrated in Fig. 1.

Identification of GAs

The identities of GAs in reproductive tissues of Salustiana and Blanca Comuna were determined at three stages of development: flower bud at 21 days before anthesis (stage A), ovary at petal fall 7 days after anthesis (stage F), and fruit at 35 days after anthesis (stage I) (Table 1). Gibberellins A_1, A_{20}, and A_{29} were identified by comparing mass spectra and Kovats retention indices with those of authentic standards (Table 2). Very low levels of GA_8 were detected in the reproductive buds. The presence of GA_4 was suggested by dilution of added $[^2H_2]GA_4$ as determined by GC/SIM. It was not possible to confirm its identity by full-scan GC/MS because of its low concentration and the presence of high levels of co-eluting contaminants. The fruit also contained two components with mass spectra indicative of dihydroxy C_{19} GAs, but which did not correspond to any available reference spectra. Their identity, therefore, was not established. They eluted later from the reverse-phase HPLC column than GA_1 and had shorter GC retention times (Table 2). The component with the longer GC retention time was present also in the young ovaries.

The presence of GAs in the vegetative apex of cv. Salustiana was examined using the dwarf rice and barley aleurone bioassays on HPLC fractions, as well as by GC/MS. Compounds active in the rice assay co-eluted with $[^3H]GA_1$ and $[^3H]GA_{20}$, and with $[^3H]GA_1$ in the barley aleurone assay (Fig. 2). GC/MS analysis of the vegetative apices showed the presence of gibberellins A_1, A_8, A_{17}, A_{19}, A_{20}, and A_{29} and a third unidentified dihydroxy-C_{19} GA, which was also present in the reproductive bud (Table 1). This compound had a similar HPLC retention time to GA_1, but eluted considerably earlier from the GC column (Table 2).

Quantification of GAs

The concentrations of GA_1, GA_{20}, and GA_4 were measured by GC/SIM using ^2H-labeled internal standards. Vegetative shoots contained no detectable GA_4, but significant levels of GA_1 (0.8 ng g^{-1}

Table 1. Distribution of GAs identified by GC/MS during early reproductive development of *Citrus sinensis* cv. Blanca Comuna and Salustiana, and in vegetative shoots of cv. Salustiana.

	Reproductive organs						Vegetative organs
	Salustiana			Blanca Comuna			Salustiana
Gibberellin	Bud	Ovary	Fruit	Bud	Ovary	Fruit	Shoot
GA_{20}	X	X	X	X	X	X	X
GA_1	X	X	X	X	X	X	X
GA_{29}	X	ND	X	X	ND	X	X
GA_8	X	ND	ND	X	ND	ND	X
GA_4[a]	X	X	X	X	X	X	ND
GA_{19}	ND	ND	ND	ND	ND	ND	X
GA_{17}	ND	ND	ND	ND	ND	ND	X
Di-OH-C_{19}-GA (KRI = 2554)	X	ND	ND	X	ND	ND	X
Di-OH-C_{19}-GA (KRI = 2586)	ND	X	X	ND	X	X	ND
Di-OH-C_{19}-GA (KRI = 2523)	ND	ND	X	ND	ND	X	ND

KRI, Kovats retention index; X, present; ND, not detected.
[2] Detected by GC/SIM.

Table 2. Comparison of Kovats retention indexes (KRIs) and mass spectra of GAs in reproductive and vegetative tissues of *Citrus sinensis* cv. Blanca Comuna (BC) and Salustiana (SA) with those of authentic compounds (RS = reference spectra).

GA	Source	Tissue	HPLC (min)	KRI	Relative ion abundance
GA_{29}	BC	Reproductive bud	6–10	2685	M^+506(100), 491(13), 375(18), 303(19), 207(27)
GA_{29}	SA	Reproductive bud	6–10	2687	M^+506(100), 491(10), 375(13), 303(14), 207(26)
GA_{29}	RS			2680	M^+506(100), 491(10), 375(15), 303(15), 207(35)
GA_1	BC	Reproductive bud	11–15	2676	M^+506(100), 491(12), 448(21), 377(8), 313(11)
GA_1	SA	Reproductive bud	11–15	2678	M^+506(100), 491(18), 448(23), 377(8), 313(20)
GA_1	RS			2676	M^+506(100), 491(13), 448(22), 377(15), 313(17)
GA_{20}	BC	Developing fruit	16–20	2508	M^+418(100), 403(19), 375(51), 359(12), 301(16)
GA_{20}	SA	Developing fruit	16–20	2507	M^+418(100), 403(15), 375(37), 359(15), 301(15)
GA_{20}	RS			2512	M^+418(100), 403(16), 375(45), 359(14), 301(16)
GA_{19}	SA	Vegetative shoot	21–25	2612	M^+462(100), 434(100), 402(25), 375(48), 374(50)
GA_{19}	RS			2612	M^+462(10), 434(100), 402(41), 375(57), 374(59)
GA_8	BC	Reproductive bud	6–10	2818	—[a]
GA_8	SA	Reproductive bud	6–10	2820	—[a]
GA_8	RS			2818	—[a]
GA_{17}	SA	Vegetative shoot	21–25	2595	—[a]
GA_{17}	RS			2598	—[a]
Di-OH C_{19}-GA	SA	Vegetative shoot	11–15	2554	M^+506(100), 491(7), 448(17), 390(13), 375(10)
Di-OH C_{19}-GA	SA	Developing fruit	21–22	2586	M^+506(85), 491(14), 448(100), 390(53), 375(42)
Di-OH C_{19}-GA	SA	Developing fruit	21	2523	M^+506(67), 491(6), 448(100), 390(14), 377(40)

The data correspond to the most intense spectra obtained from the different tissues analyzed.
[a] Molecular ions and most abundant fragment ions were detected at the given KRIs, but their intensities were too low for reliable relative abundancies to be obtained.

fresh wt) and GA_{20} (6.5 ng g^{-1} fresh wt) were present. The changes in concentration of these GAs during ovary and early fruit development are shown in Fig. 3. The patterns of change for all three GAs are similar in the two cultivars, although levels were generally higher in the seedless variety (Salustiana). The highest concentration of GA_1 occurred at anthesis, whereas GA_4 and GA_{20} concentrations were highest in developing fruit and lowest in the ovaries at petal fall.

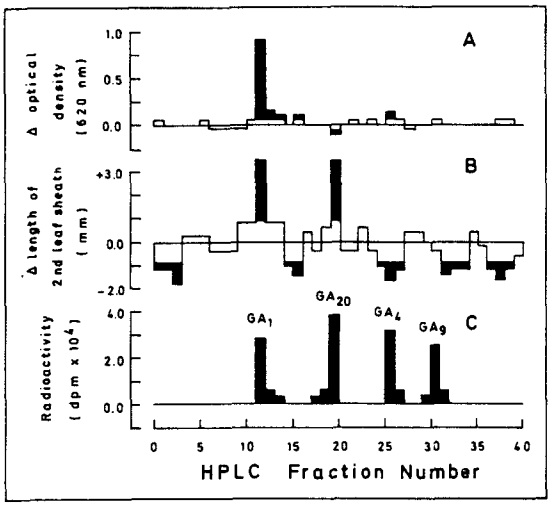

Fig. 2. Gibberellin-like activity of HPLC fractions from an acidic EtOAc extract of vegetative apices of *Citrus sinensis* cv. Salustiana, equivalent to 5 g dry wt. Each HPLC fraction (9 of 20) was assayed on **(A)** the barley aleurone bioassay and **(B)** the dwarf rice bioassay. **(C)** Radioactivity present in each HPLC fraction due to the addition of ^{3}H-labeled internal standards as determined by counting the remaining aliquot (1 of 10).

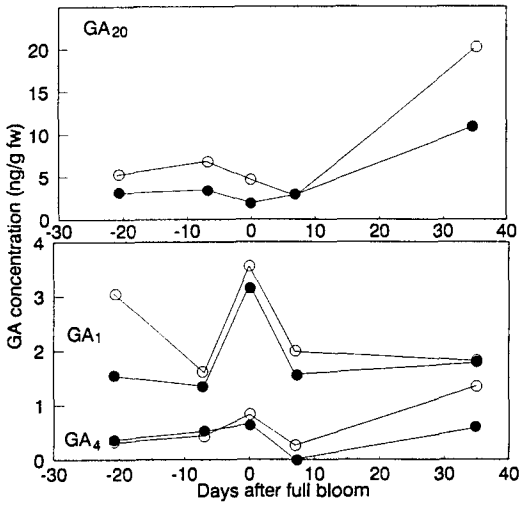

Fig. 3. Concentration of GA_1, GA_{20}, and GA_4 determined by GC/SIM throughout the early development of the reproductive organs from *Citrus sinensis* cv. Salustiana (seedless) (–○–) and Blanca Comuna (seeded) (–●–).

Discussion

The GAs present in vegetative shoots, GA_1, GA_8, GA_{17}, GA_{19}, GA_{20}, and GA_{29}, are members of the 13-hydroxy GA pathway, which is considered to be the major GA biosynthetic pathway in vegetative tissues. These GAs were also identified in shoots of Navel oranges by Poling and Maier (1988), who in addition identified GA_{44} and iso-GA_3.

The concentration of GA_{20} was higher in vegetative shoots than in reproductive buds, which contained more GA_1 and GA_4. Furthermore, the C_{20}-GAs, GA_{19} and GA_{17}, were not detected in the flower buds. This indicates that the conversion of GA_{20} to GA_1 was enhanced in reproductive buds of *Citrus* and supports the conclusion of Moore et al. (1986), that, in sugarcane, the rate of GA biosynthesis is higher in reproductive than in vegetative shoots. These workers gave no indication of the relative levels of GA_{20} in the two tissue types.

The GAs in reproductive tissues of the seeded and seedless cultivars were qualitatively and quantitatively similar throughout the developmental stages studied, with the seedless cultivar containing slightly higher levels of GA_1, GA_{20}, and GA_4 (Fig. 3). In general, GAs in fruit are concentrated in the seeds (Goodwin 1978), and fruit which have been prevented from setting seeds have much lower levels of GAs than fruit with seeds, as for example in pea (Garcia-Martinez et al. 1987) and pear (Martin et al. 1982). However, fruit that naturally set parthenocarpically have been found to contain higher levels of GA-like substances than seeded fruit (Gil et al. 1972, Ito et al. 1969, Iwahori et al. 1968) and this may explain their tendency to set in the absence of pollination or fertilization.

In both cultivars the concentration of GA_1 was highest at anthesis, at which time GA_4 levels also peaked, but GA_{20}, the precursor to GA_1, was at a relatively low level. In the latest developmental stage of fruits to be analyzed, at 35 days after anthesis, the concentrations of GA_{20} and GA_4 were high. GA_1 levels did not increase at this stage. This period corresponds to the stage in the development of most fruit when extremely high amounts of GAs accumulate, usually in the seeds (Goodwin 1978). The function of these GAs is unknown. In contrast, GAs present during the initial stages of fruit growth are probably involved in cell expansion in the fruit, as suggested for pea (Garcia-Martinez et al. 1987) and tomato (Bohner et al. 1988). The apparent increase in GA_1 production around anthesis may be sufficient to trigger fruit set and early fruit development in *Citrus* and would explain how these processes are stimulated by a single application of GA at this time (Soost and Burnett 1961, Powell and Krezdorn 1977).

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