Plant Physiol. (1983) 71, 645–651
0032-0889/83/71/0645/07/$00.50/0

Gibberellins and Heterosis in Maize[1]

II. RESPONSE TO GIBBERELLIC ACID AND METABOLISM OF [^{3}H]GIBBERELLIN A_{20}

Received for publication July 14, 1982 and in revised form November 8, 1982

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ABSTRACT

Two maize inbreds, CM7 and CM49, and CM7 × CM49, their F_1 hybrid (which displayed significant heterosis), were examined with regard to response to exogenous gibberellin A_3 (GA_3), and in their ability to metabolize GA_{20}, a native GA of maize. The leaf sheath elongation response to GA_3 was far greater for the inbreds than for their hybrid. The inbreds also displayed significant elongation of the leaf blades in response to GA_3, whereas the hybrid was unaffected. Promotion of cell division in the leaf sheath of CM7 and the hybrid was effected by GA_3, but no promotion of cell elongation was observed in CM49, even though significant leaf sheath elongation occurred. Shoot dry weight of both inbreds was significantly increased by GA_3, but response by the hybrid in this parameter was slight and variable. Root dry weight of CM7 was significantly increased by GA_3, but was unchanged in CM49 and the hybrid. Thus, inbred shoot dry weight increases effected by GA_3 were not at the expense of the root system. Rapid metabolism of [2,3-^{3}H]GA_{20} occurred in all genotypes, although genotypic differences were observed. The hybrid had the highest rates of metabolism to GA glucosyl conjugate-like substances. Oxidative metabolism was also fastest in the hybrid, followed by CM7, and slowest in CM49, the slowest-growing inbred. Thus, rate of GA_{20} metabolism is under genetic control in normal (*i.e.* not dwarfed) maize genotypes. These results, taken together with previous reports that the hybrid has significantly enhanced levels of endogenous GA-like substances, suggest that GA play a role in the expression of heterosis in maize.

Although heterosis in yield and/or growth performance is agriculturally, horticulturally, and silviculturally important, its physiological basis has not been determined (21, 22). The involvement of plant hormones is a logical possibility inasmuch as they are known to act in regulatory roles in a wide range of processes, from seed germination through vegetative growth, reproductive development, and seed development. Heterosis has been reported for components of all of these aspects of plant growth and development (22).

In a previous paper in this series (21), we reported that increased level of endogenous GA[3]-like substances was correlated with heterosis for vigorous growth in a maize hybrid. Nickerson (13, 14) noted that responsiveness to exogenous GA_3 was correlated with degree of inbreeding in maize; inbreds were very responsive, whereas hybrids were somewhat less affected. Nickerson's (13, 14) study thus suggests that a causal role for GA may exist in heterosis. Inasmuch as maize inbreds are very responsive to exogenous GA_3, it is possible that their low endogenous GA content (21) may be one factor limiting their growth, and hence, underlying the growth depression shown by the inbreds.

Because heterosis for increased levels of endogenous GA-like substances occurs (21), it is of interest to investigate the metabolic basis for this heterosis. Is GA biosynthesis more rapid in hybrids, and/or does catabolism/conjugation proceed more slowly? Either possibility could lead to increased endogenous GA levels in the hybrids. Unfortunately, it is currently not possible to evaluate the biosynthesis of GA from GA precursors *in vivo*. However, we can examine biosynthesis of di- and tri-hydroxylated GA from monohydroxylated precursors, and we can also follow the catabolism and/or conjugation through the use of radioactive GA. The principal native GA of developing maize tassels have recently been characterized (8) and at least certain parts of the metabolic sequence have been tentatively determined (5, 9, 20). Consequently, we can examine rates of metabolism of native GA in inbreds and their hybrid.

Thus, in this second paper about GA and heterosis in maize, response to exogenous GA_3 and metabolism of [^{3}H]GA_{20} in two maize inbreds and their F_1 hybrid are described.

MATERIALS AND METHODS

Plant Materials. Two early maturing maize inbreds, CM7 and CM49, were obtained from Dr. J. Giesbrecht, Agriculture Canada Research Station, Morden Manitoba. Self-pollinations and CM7 (male) × CM49 (female) crosses were made in the summer of 1980 at the Agriculture Canada Research Station, Lethbridge, Alberta. After black layer maturity had been reached, cobs were harvested and allowed to air-dry for 1 month prior to shelling. Seeds were stored at 5°C until planting.

On January 6, 1982, five seeds of one genotype were planted 2 cm deep in each 3-L plastic pot filled with 3:1 (v:v) mixture of vermiculture and peat moss. Growth took place in a greenhouse at Toronto, Ontario (latitude 43°N) at 25/15 (±3)°C (day/night), the natural daylength being extended with 24 h low-intensity incandescent light (50 $\mu E\ s^{-1}\ m^{-2}$) to prevent sex reversals (18) of the apical inflorescence. Following emergence, seedlings were thinned to the largest three plants. Pots were watered to saturation once daily except once every 10 d when 200 ml with 0.25 g/pot of 28-14-14 (N-P-K) fertilizer was added.

Numbers of seedlings emerged were assessed daily. Numbers of leaves (*e.g.* numbers of ligules emerged from the leaf whorl), and heights to the highest extended leaf tip were measured weekly. Five plants of each genotype were harvested weekly to determine total leaf areas (measured with a Wescor LI 3000 area meter) and dry weights of roots and shoots after oven drying for 2 d at 70°C. Collodion peels were used to measure lengths of long adaxial

[1] Supported in part by Natural Sciences and Engineering Research Council Grants A-7815 and A-2585 to T. J. B. and R. P. P., respectively.

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[3] Abbreviations: GA, gibberellin(s); EtOH, ethanol; MeOH, methanol; EtOAc, ethyl acetate; C/D R GA_{20}, C/D ring rearranged GA_{20}; RC, radioactivity counting.

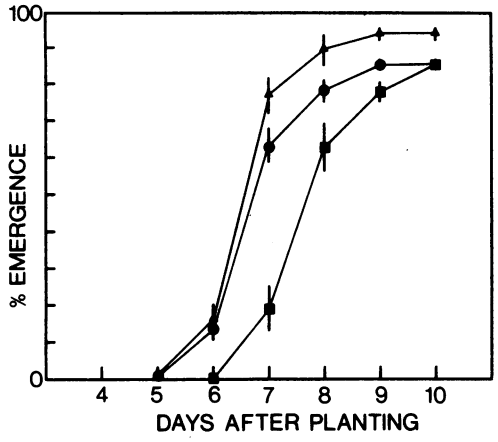

FIG. 1. Cumulative seedling emergence *versus* time for two maize inbreds (CM7 [●], CM49 [■]) and their F_1 hybrid (CM7 × CM49 [▲]) at about 25/15°C (day/night). Mean ± SE.

epidermal cells of the leaf sheath within the 10-cm region basal to the ligule of the fourth leaf. Cell number in a microscope field of view was counted as an inverse measure of cell length.

Exogenous Application of GA_3. Crystalline GA_3 was dissolved in 95% EtOH and diluted to 10% aqueous EtOH containing 0, 0.1, 0.5, or 1.0 mg GA_3/100 μl solution. On February 2 and 3, 1982, 50 μl of treatment solution was pipetted into the leaf whorl of each plant. Similar applications were carried out on February 9 and 10, 1982 on different plants. For each treatment, all three plants within a pot were treated similarly, and values from these three were averaged to produce a single experimental unit. Four replications of each treatment were carried out. Thus, 96 pots were included representing the three genotypes × two dates × four levels × four replicates, and 288 plants (96 pots × 3 plants) were studied.

After exogenous application of GA_3, heights to the highest extended leaf tip, and to all emerged ligules, were measured every 2 d and destructive sampling for shoot and root dry weights and leaf areas occurred weekly. The significance of treatments was determined by one-way analyses of variance.

Application of [^{3}H]GA_{20}. Preparation and purification of [2,3-^{3}H]GA_{20} was described previously (20). In the present study, 0.5 μCi [^{3}H]GA_{20} in 2 μl of 20% aqueous EtOH was injected into the apical meristem of each of six plants of each genotype at 10 AM on February 9, 1982. Three plants of each genotype were harvested 24 and at 48 h after application (*e.g.* six sample plants). The basal 2 cm of the shoot cylinder (which contained the terminal shoot apical meristem) was removed and immediately ground in 15 ml of 80% aqueous MeOH at −20°C. The six samples from each genotype were analyzed separately.

Chromatography of Metabolites. After 24 h of intermittant shaking at 2°C, the MeOH extracts were vacuum filtered and reduced to dryness *in vacuo* at 35°C. To promote removal of water, 20 ml of MeOH was added part way through solvent evaporation. Ten μl H_2O (to dissolve highly water-soluble components), and then 1 ml of 50:50 MeOH:EtOAc was added, and this solution was loaded onto glass-fiber filter paper discs and dried. These discs were placed on silicic acid (SiO_2) partition columns (6) (the column being made with 4.2 g Woelm SiO_2 for partition to which 20% H_2O by weight was added, shaken, and allowed to equilibrate for 7 d before use), which were stepwise eluted with 50 ml 55:45 HCOOH-saturated EtOAc:hexane, 40 ml 95:05 EtOAc:hexane, and finally MeOH. Five-ml fractions were collected and elution solvents evaporated *in vacuo*. The fractions were solubilized in MeOH, and detection of ^{3}H was performed by liquid scintillation spectroscopy. The partition column SiO_2 system will elute acidic GA (excepting GA_{32}) in the hexane:EtOAc while GA glucosyl conjugates are retained until the MeOH wash.

Radioactive fractions from the three SiO_2 partition columns of each replicate sample were bulked, and then chromatographed (1-min fractions, 1.8 ml) on reverse-phase C_{18} HPLC (12, 20). Due to the abundance of pigments in certain SiO_2 fractions, additional aliquots were removed to verify levels of radioactivity ([^{3}H]). Consequently, unequal proportions of fractions from the SiO_2 partition columns were loaded onto the C_{18} HPLC columns, and reverse-phase elution profiles (Fig. 7) must be considered as qualitative in nature; they are not quantitatively representative. For both forms of chromatography, [^{3}H]GA_{20} and authentic standards of logical acidic metabolites and of conjugates of logical acidic metabolites were analyzed for comparative purposes (20).

RESULTS AND DISCUSSION

Growth. Heterosis was observed very early in the life cycle of the hybrid, the order of seedling emergence rate was CM7 × CM49 > CM7 >> CM49 (Fig. 1). Final percentage seedling emergence was higher in the hybrid than in either parent (Fig. 1). The superior seedling emergence of the hybrid cannot be ex-

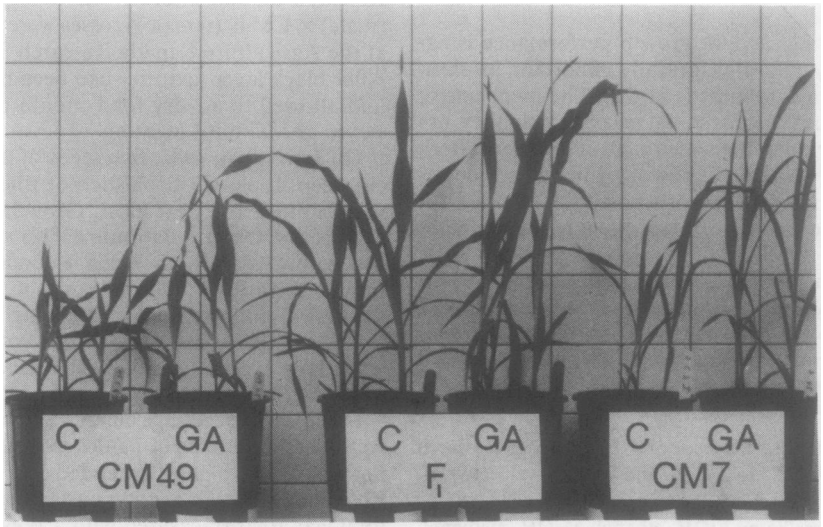

FIG. 2. Two maize inbreds and their F_1 hybrid 50 d after planting and 14 d after application of 100 μl 10% EtOH (C) or the same solution containing 0.5 mg GA_3 (+GA).

Table I. *Average Lengths of Long Adaxial Epidermal Cells of the 10-cm Region Basal to the Ligule of the Fourth Leaf, and Shoot and Root Dry Weights of Two Maize Inbreds and Their F_1 Hybrid*

Measurements were taken 14 d after the addition of 0.5 mg GA_3 or a control (C) solution (mean ± SE).

	Treatment	Cell Length	Dry Wt	
			Shoot	Root
		mm	*g*	
Inbred				
CM7	C	0.155 ± 0.003	0.450 ± 0.053	0.082 ± 0.007
	GA_3	0.161 ± 0.004	0.881 ± 0.141	0.158 ± 0.019
CM49	C	0.084 ± 0.002	0.667 ± 0.039	0.229 ± 0.035
	GA_3	0.119 ± 0.003	0.842 ± 0.043	0.216 ± 0.017
Hybrid				
CM7 × CM49	C	0.127 ± 0.003	2.007 ± 0.119	0.591 ± 0.050
	GA_3	0.151 ± 0.005	1.967 ± 0.141	0.537 ± 0.051

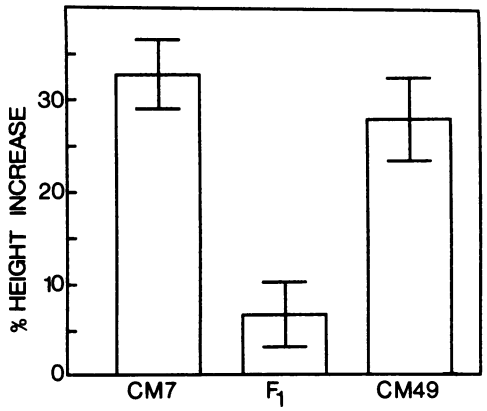

FIG. 3. Percentage change in total height of two inbreds and their F_1 hybrid 14 d after the addition of 0.5 mg GA_3. Mean ± SE.

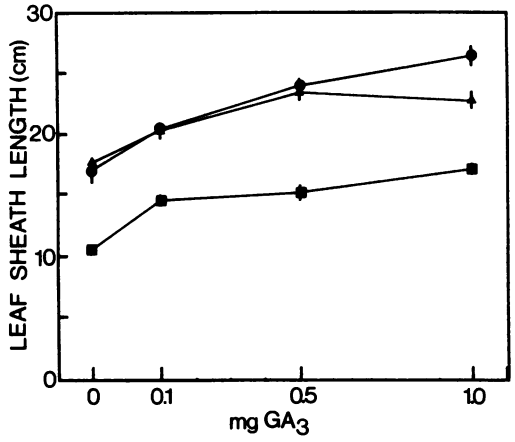

FIG. 4. Distance to uppermost ligule (*e.g.* leaf sheath length) of two maize inbred (CM7 [●], CM49 [■]) and their F_1 hybrid (CM7 × CM49 [▲]) 14 d after the addition of 0, 0.1, 0.5, or 1.0 mg GA_3. Mean ± SE.

plained simply in terms of larger seeds since hybrid seed weights (0.177 ± 0.009 g seed^{-1}) were similar to CM49 (0.192 ± 0.007 g), while CM7 seeds were smaller (0.114 ± 0.004 g). Thus, larger seeds do not necessarily support more vigorous seedlings. The similarity in seed weights for CM49 and the hybrid was expected as CM49 was the female parent. Consistent with our repeated previous observations (19, 21), growth of the hybrid continued to exceed growth of either inbred throughout the experiment (Figs. 2–4).

Response to Exogenous GA. Growth of the maize inbreds was dramatically promoted following the exogenous application of GA_3 (Figs. 2–4), while growth promotion of the hybrid by GA_3 was nominal (Figs. 2–4). The growth promotion of both inbreds by GA_3 was statistically significant ($P \geq 0.05$) at all levels of GA_3 on either date of application (data not presented). Leaf orientation of all three genotypes was changed such that leaf blades were more vertical (Fig. 2); the implications of this effect on photosynthetic efficiency of the standing crop warrant further study.

Elongation growth (expressed as a percentage) of the hybrid was only marginally altered, whereas growth of each parent was dramatic (Fig. 3). This trend is also present for absolute values; control and GA_3-treated plants under the conditions in Figure 3 average 52.3 ± 1.7 and 69.6 ± 2.0 cm for CM7, 43.6 ± 0.6 and 55.8 ± 2.0 cm for CM49, and 68.7 ± 1.6 and 73.4 ± 2.5 cm for CM7 × CM49. Thus, while GA_3 elicited an increase of 4.7 cm in height growth for the hybrid, increases in the inbreds were 17.3 and 12.2 cm for CM7 and CM49, respectively.

Growth of the leaf sheaths of all genotypes was promoted ($P \leq 0.05$) following exogenous application of GA_3 (Fig. 4). Again, growth promotion was most conspicuous in the inbreds. Elongation of the leaf sheath is one component of total plant height, the other being elongation of the leaf blades (internode elongation had not yet begun in these plants). Elongation of leaf blades was significantly promoted by GA_3 in both inbreds ($P \leq 0.05$), but remained unaffected in the hybrid.

Epidermal cell length in CM7 leaf sheath number 4 was not significantly affected by GA_3, but cell length of this region of CM49 was significantly increased (Table I). Since the leaf sheath of CM7 elongated without significant cell elongation, it is probable that increased cell division was responsible for the leaf sheath elongation. In CM49, however, the sheath elongation could be attributed largely to cell elongation (Table I). The modest sheath elongation noted in the hybrid after GA_3 application was also a result of cell elongation.

In response to GA_3, shoot dry weight of both inbreds was increased by GA_3 ($P \leq 0.05$) (Table I). Response of the hybrid was negligible and variable (Table I). The promotion of shoot growth in the inbreds was not at the expense of root growth as root dry weight was also increased by GA_3 in CM7, and remained unchanged in CM49 (Table I). Consequently, total plant dry weights of both inbreds (but not the hybrid) were promoted ($P \leq 0.05$) by the application of GA_3. Thus, almost all growth parameters were consistent in showing that exogenous GA_3 promoted growth (dry weight), particularly elongation, in these inbreds. Gibberellin A_3 had much less effect on the growth and elongation of the hybrid. Our observation that inbreds are more responsive to GA_3 than a hybrid is consistent with previous reports by Nickerson (13) and Nickerson and Embler (14).

Metabolism of [^{3}H]GA_{20}. Three principal regions of radioactiv-

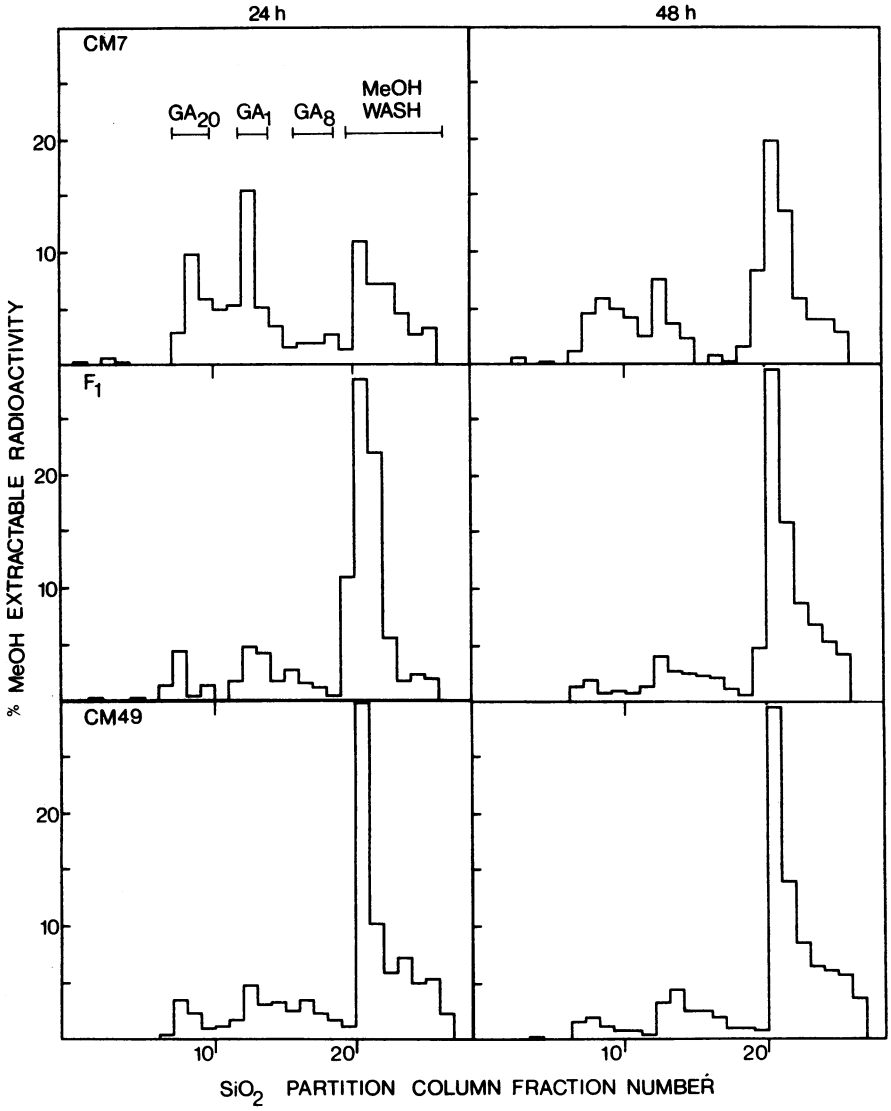

FIG. 5. Elution profiles of radioactivity ^3H from typical replicate MeOH extracts chromatographed on a stepwise-eluted SiO_2 partition column from two maize inbreds and their F_1 hybrid (age, 24 d) harvested 24 or 48 h after feeding [^{3}H]GA_{20}. Retention times of authentic standards, and fraction grouping are shown to upper left figure. Any GA glycosyl conjugates present in the methanolic extract would be eluted in the MeOH wash fraction grouping.

ity were eluted from the SiO_2 partition columns (Fig. 5). The first was coincidental with [^{3}H]GA_{20}, the second with [^{3}H]GA_1 (and other GA, including GA_{29}), and the third occurred in the MeOH wash where GA glucosyl conjugates would elute. A minor region of radioactivity eluted coincidental with [^{3}H]GA_8 (Fig. 5). In all genotypes, the amount of radioactivity in peak I ([^{3}H]GA_{20}) decreased over the 48-h period (Figs. 5 and 6). However, there were significant ($P \leq 0.05$) differences in the relative amount of radioactivity in peak I, samples from CM7 being consistently higher than CM49 and the hybrid (Fig. 6). The level of radioactivity in peak II was also considerably higher in CM7 than in CM49 and the hybrid (Figs. 5 and 6). The amount of radioactivity in the MeOH wash fraction (which would contain GA glucosyl conjugates) increased during the experimental period for all genotypes and was consistently highest in the hybrid (Fig. 6).

When fractions I and II (Fig. 6) were chromatographed on gradient-eluted C_{18} reverse-phase HPLC, at least four regions of radioactivity were eluted (Fig. 7). These were coincidental with [^{3}H]GA_8, [^{3}H]GA_1, [^{3}H]GA_{20}, and [^{3}H]C/D R GA_{20}, respectively. Amounts of radioactivity (Fig. 7) were inadequate for subsequent GLC-RC to be carried out on any of these four regions. However, these identifications based on sequential SiO_2 partition → gradient-eluted reverse-phase C_{18} HPLC are consistent with isocratic C_{18} HPLC-RC and/or GLC-RC of similar [^{3}H]GA_{20} metabolites in maize (20). The C/D R GA_{20}-like metabolite may be an experimental artifact (20), although, interestingly, only CM49 yielded detectable amounts of it (Fig. 7). The metabolic sequence of $GA_{20} \rightarrow GA_1 \rightarrow GA_8$ is both logical and consistent with previous work on several maize genotypes, including the hybrid CM7 × CM49 (5, 20). The [^{3}H]GA_8-like metabolite was observed only in the hybrid, while the [^{3}H]GA_1-like metabolite was observed in all genotypes (Figs. 5 and 7).

A number of GA glucosyl conjugate-like metabolites originating in the MeOH wash of the SiO_2 partition column were eluted from the C_{18} HPLC (Fig. 8). Subsequent analyses by isocratic C_{18} HPLC or GLC have not been performed due to limited amounts. However, it is known that GA glucosyl ether or ester conjugates are eluted from C_{18} HPLC coincidental with, or a few min prior to, the acidic GA (12). Thus, HPLC peak I and II (Fig. 8) is probably a conjugate(s) of [^{3}H]GA_8. Peak IV from HPLC (Fig. 8) probably represents a conjugate(s) of [^{3}H]GA_1. Likewise, Peak VI probably represents a conjugate(s) [^{3}H]GA_{20}, and peak VII a conjugate(s)

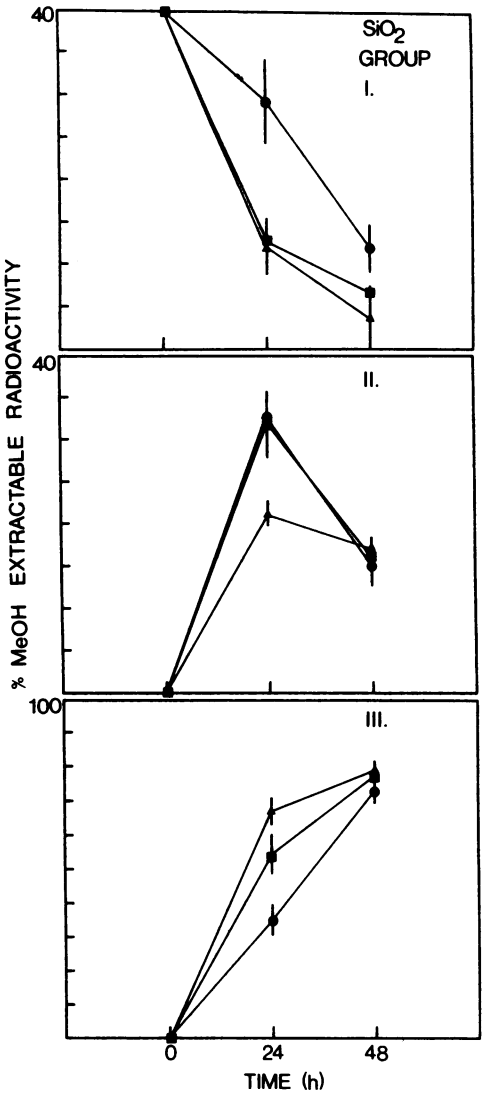

FIG. 6. Metabolism over 48 h of [^{3}H]GA_{20} into acidic and GA glycosyl conjugate-like substances by 24-d-old maize inbreds (CM7 [●] and CM49 [■]) and their F_1 hybrid (CM7 × CM49 [▲]). The SiO_2 partition column elution profile of typical replicate MeOH extracts is shown in Figure 5. Mean ± SE. SiO_2 group I would contain [^{3}H]GA_{20}, group II would contain [^{3}H]GA_1 and GA_8, whereas group III consisted of the MeOH wash.

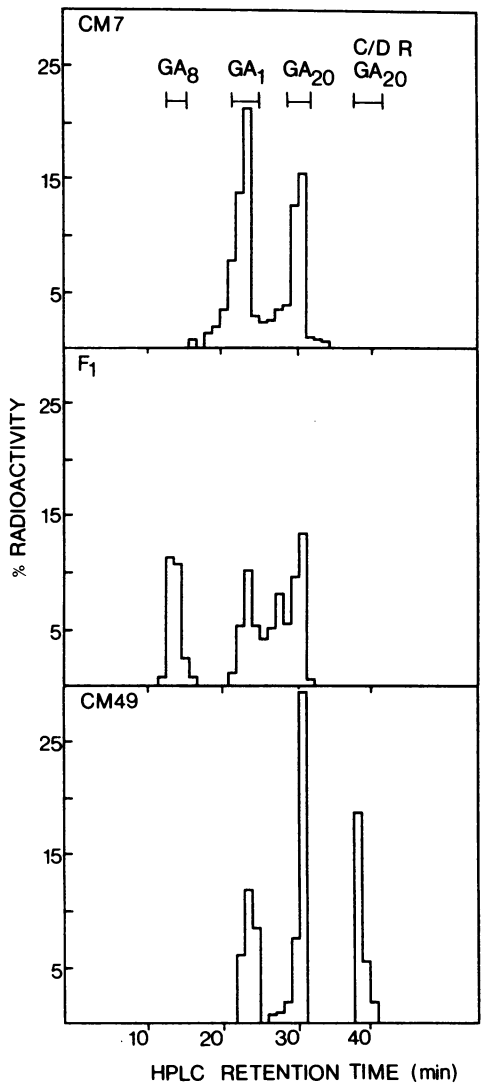

FIG. 7. Elution profile of radioactivity ^{3}H from grouped fractions I + II (Fig. 6) chromatographed on gradient-eluted reverse-phase C_{18} HPLC columns. Retention times of authentic standards are shown in top Figure. These profiles provide qualitative information only as transfers of SiO_2 fractions was not quantitative.

of [^{3}H]C/D R GA_{20} (20).

The GA_8-like metabolite (Fig. 7, peak I) occurred only in the hybrid, and the GA_8 glucosyl conjugate-like metabolite (Fig. 8, peak II) occurred only in the hybrid and CM7.

Results from SiO_2 partition (Fig. 5) and reverse-phase C_{18} HPLC (Fig. 7) were consistent, and indicated that oxidative metabolism of [^{3}H]GA_{20} was more rapid in CM7 and the hybrid than in CM49 (Fig. 6). Also, rate of apparent conjugation (Fig. 6) was greater in the hybrid than in either inbred, and greater in CM49 than in CM7 (Figs. 5 and 6).

Thus, the rate of GA metabolism is under genetic control in normal (*i.e.* not dwarfed) maize genotypes. However, the results do not explain the apparent abundance of GA in the hybrid (21). They do suggest, however, that the rate of metabolism of [^{3}H]GA_{20}, and probably that of [^{3}H]GA_1, is more rapid in the hybrid than in either inbred parent. An intriguing question would be: does increased metabolism in the hybrid reflect increased endogenous GA levels.

GA and Heterosis. The data presented herein and in Rood *et al.* (21) contributes to an understanding of the possible role of GA in heterosis in maize. Assessed in view of additional information (presented below), an integrated analysis of all information suggests that a causal association may exist between GA and hybrid vigor.

Five single gene mutants of maize have been identified which are deficient in, or contain reduced levels of GA-like substances (17). These mutants are phenotypically dwarfed and produce low grain yields. The dwarf phenotype can be totally overcome through exogenous application of GA_3 (17), and grain production of these mutants is also increased by GA_3, suggesting that a GA deficiency not only limits growth but also reduces productivity.

The most conspicuous response to exogenous application of GA_3 by normal as well as dwarf maize genotypes is an increase in internode elongation, and consequently an increase in plant height. Application of GA_3 increases whole seedling dry weight (7), and increases in fodder and grain yields have also been reported following GA_3 application (4). Thus, exogenous application of GA_3 promotes growth and yield of normal maize genotypes.

In normal genotypes, content of endogenous GA-like substances is correlated with growth rate (18, 20) and a low growing temper-

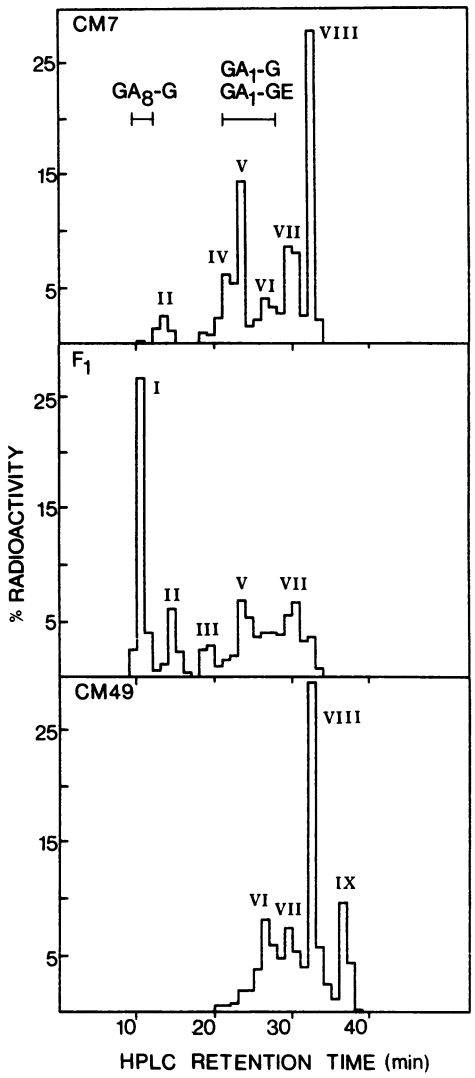

FIG. 8. Elution profiles of radioactivity ^3H from grouped MeOH wash (Fig. 6) chromatographed on gradient-eluted reverse-phase C_{18} HPLC columns. Retention times of authentic GA glucosyl conjugates are shown in top figure, and glucosyl conjugates of GA_{20} and C/D R GA_{20} would be expected to elute coincidental with or just prior to the acidic GA moiety (Fig. 7). Peaks sharing the same roman numerals had similar retention times.

ature reduces growth rate as well as levels of endogenous GA-like substances (18). The three genotypes described in the present study have now been grown under three temperature regimes, and growth rates and levels of GA-like substances were increased as growing temperature was progressively raised (18, 21). Thus, rapid growth is correlated with high levels of endogenous GA-like substances. Under favorable (warm) temperature conditions, hybrid vigor for a number of growth parameters is observed in these three genotypes (21), and endogenous GA-like substances were higher in the hybrid than in either parental inbred (21). Thus, content of GA-like substances was correlated with heterosis for superior growth.

Nickerson (13, 14) previously reported that maize inbreds are more responsive to exogenous GA_3 application than hybrids. Indeed, Nickerson further suggested that sensitivity to GA_3 was correlated with the degree of inbreeding in maize (13, 14). The results of the present study (21) support Nickerson's conclusion, show that such a relationship holds for genetically related genotypes, and are consistent with the observation that inbreds contain lower levels of endogenous GA-like substances. Hence, inbreds should be more responsive to GA application, and thus their low endogenous level of GA-like substances may be a major factor limiting growth. It is possible that the observed 'overdominance' for increased levels of GA-like substances (21) may underlie at least certain aspects of hybrid vigor in maize.

Other research also suggests that GA play a role in heterosis in maize. Parental pollen tube growth rates of germinating maize pollen are positively correlated with seedling dry weight, ear weight, and grain yield of the resultant hybrids (15). Pollen tube growth is promoted through exogenous application of GA (3, 11), and increases in endogenous GA of untreated pollen is positively correlated with increased pollen germination and rapid pollen tube growth (1, 10). Thus, the correlation between rapidity of pollen tube growth and hybrid vigor of the progeny (15) also appears interrelated with GA physiology.

In an early review, Paleg (16) concluded that GA play a role in endosperm mobilization and that this mobilization is probably correlated with the expression of heterosis. Although hybrid vigor cannot be attributed to an initial advantage of larger hybrid embryos (20), there is evidence (23) suggesting that early maize seedling performance is positively correlated with subsequent growth rate, and we noted (Fig. 1) that hybrid vigor is also displayed for early growth in maize.

Thus, maize inbreds, relative to a hybrid, are deficient in GA-like substances (21). These inbreds are also more responsive to GA_3 application than their hybrid. These results, together with the other findings (1, 3, 4, 7, 10, 11, 13–18, 21, 23) noted above, lead us to conclude that (a) low endogenous GA level is one of the more important factors limiting growth and yield of maize inbreds, and (b) the high endogenous GA level in the hybrid may provide a phytohormonal basis for at least certain aspects of heterosis in maize.

It must be noted, however, that it is unlikely that a single mechanism is responsible for all aspects of hybrid vigor. It has been suggested that enzymic polymorphism may offer a general mechanism for heterosis (2, 22), and that enzymes from a number of metabolic pathways are probably involved. The enzymic polymorphism hypothesis suggests that the presence of different isozymes in the heterozygote may broaden an individual's biosynthetic potential, thus leading to superior performance. An increase in biosynthesis of specific regulatory compounds such as GA could further amplify the benefits of enzymic polymorphism, the increased GA promoting many aspects of maize growth and development which produce the heterotic phenotype.

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