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The isolation and characterization of gibberellin-deficient mutants in tomato

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Summary. In tomato, nine independent EMS-induced mutants representing recessive mutations at three different loci (*gib-1*, *gib-2*, and *gib-3*) were isolated. Six of these have an almost absolute gibberellin requirement for seed germination and elongation growth. In addition, the leaves are darker green, smaller, and changed in structure as compared to wild type. The three other mutants, which germinate without GA, are allelic to specific, nongerminating mutants and have less severe mutant characteristics. The respective loci are situated on three different chromosomes. The genes identified by these mutants control steps in gibberellin biosynthesis, as endogenous gibberellins are strongly reduced.

Key words: *Lycopersicon esculentum* – Gibberellin – Germination – Dwarf mutants – Gene localization

Introduction

Mutants deficient in endogenous gibberellins (GAs) have been described for several plant species (reviewed by Reid 1990). All are dwarfs that can be reversed to the wild-type phenotype by applied GAs. In *Arabidopsis*, GA-deficient mutants at some loci require GA also for seed germination (Koornneef and van der Veen 1980). In cases where endogenous GAs are required for seed germination, a screen only for GA-responsive dwarfs may limit the number and types of GA-deficient mutants that can be found. In tomato, GA sensitivity has been tested extensively for the *d* mutant (Plummer and Tomes 1958; Soost 1959; Nadhzimov et al. 1988), which responds to some extent to exogeneously applied GAs but does not appear to be a true GA biosynthesis mutant (Nahzimov et al. 1988). In view of our results with *Arabidopsis* (Koornneef and van der Veen 1980), a search for GA-responsive, nongerminating mutants in the progeny of mutagen-treated tomato seeds was initiated. This resulted in the isolation of a number of such mutants (Koornneef et al. 1981). These mutants have been used to investigate the role of GAs in seed germination (Groot and Karssen 1987; Groot et al. 1988), fruit (Groot et al. 1987), and flower development (Nester and Zeevaart 1988). In these investigations, the gene symbol *ga* was used in analogy with *Arabidopsis*. However, since in tomato this gene symbol had already been used for the *galbina* mutant, it was replaced by the gene symbol *gib* (Groot et al. 1988; Nester and Zeevaart 1988). In the present report, the genetic and phenotypic characterization of these mutants and some more recently isolated mutants are described.

Materials and methods

Plant materials and mutagenic treatment

Pure line seeds of the tomato cv Moneymaker were obtained from Nunhem Seed Co. Haelen, The Netherlands. The genotype GT, which is a tomato mosaic virus resistant breeding line, similar in morphology to Moneymaker, was a gift from Deruiterzonen, Bleiswijk, The Netherlands. The linkage tester lines were provided by C. M. Rick, Davis CA, USA.

To induce mutations, seeds were submerged in a freshly prepared, unbuffered, 60-m*M* ethyl methane sulphonate (EMS) solution for 24 h in the darkness at 25 °C. After being rinsed off with tap water, M_1 plants were grown from these seeds in an unheated greenhouse in Dutch summer conditions. This treatment yielded approximately 10% completely sterile plants. In the first experiment, M_2 seeds from individual M_1 plants were harvested from the third cluster upwards. In tomato, this part of the M_1 plant is nonchimeric with few exceptions (Hildering and Verkerk 1965). In a second and third experiment, seeds were

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harvested per group of ten fertile M_1 plants from the first cluster upwards.

To select for GA-responsive mutants, M_2 seeds were sown on filter paper saturated with 15 or 50 μM GA_{4+7} (mixture of GA_4 and GA_7 = Berelex; ICI, Bracknell, UK) in 9-cm petri dishes. The seeds were incubated in the dark at 25 °C for 2 days, whereafter they were sown in soil in a heated (20–25 °C) greenhouse. Putative mutants were first selected at an early stage on the basis of their wrinkled and dark-green leaves and reduced plant height, and then tested for GA response (restoration to near wild-type phenotype). Seeds from these responders were obtained by spraying the top of the plants at least once a week with 100 μM GA_{4+7}. For the mutants described, this treatment resulted in plants of normal height, fruit, and seed set. The phenotype and responsiveness to applied GAs was tested on further generations obtained by subsequent selfing of mutant homozygotes.

Genetic characterization

Segregation ratios were determined by counting the number of wild-type and dark-green dwarfs among seedlings that had been germinated on 50 μM GA_{4+7}, as described above. The different mutants obtained were tested for allelism versus nonallelism on the basis of noncomplementation versus complementation to wild-type phenotype in their F_1s.

Linkage analysis was done in F_2 populations derived from crosses of mutants at the three loci with the linkage marker stocks obtained from C. M. Rick. In addition, some F_2 populations segregating for *gib-2* and *aurea* (*au*) or *gib-2* and *sitiens* (sit_w) mutants induced by us in the same Moneymaker background were used. Recombination frequencies were estimated by maximum likelihood procedures as described by Koornneef and Stam (1987). Map positions were calculated from the estimated recombination fractions, using the program "Genmap" written by P. Stam, which is based on the procedures described by Jensen and Jörgensen (1975).

Physiological characterization

For germination tests, six replicates of 40 seeds each were sown in 9-cm, plastic petri dishes on one layer of filter paper (No. 595, Schleicher & Schüll, Dassel, FRG) moistened with 2-ml distilled water or a solution of 10 μM GA_{4+7}. The petri dishes were placed in the dark at 25 °C for 7 days. Visible emergence of the radicle was used as a criterion for germination.

The effect of GA application on height increase was tested on plants raised from seeds imbided for 2 days in 10 μM GA_{4+7} and subsequently planted in soil in a heated greenhouse (20–26 °C) with supplementary light in Dutch winter conditions. Three weeks after sowing, the tips of the plants were treated with 50 µl of a 1-mM GA_{4+7} solution or with water. This treatment was repeated 7 and 14 days later. The increase in length between 3 and 7 weeks after sowing was used to test the effect of these treatments.

At 50 days after sowing, the chlorophyll content of fully expanded leaves was determined by extracting one gram of leaf material in 20 ml acetone. The extract obtained was transferred to a 50-ml volumetric flask and made up to volume with 80% acetone. The extraction procedure was carried out in a cold room at 2 °C under green safe-light. The absorbance of the extracts was measured (after centrifugation) in a Zeiss spectrophotometer, model PMQ II, at 646 (E_{646}) and 664 nm (E_{664}). Chlorophyll-a and -b contents were calculated using the following equations:

$$[\text{Chl-a}] = 12.7\ E_{663} - 2.7\ E_{646}$$

$$[\text{Chl-b}] = 22.9\ E_{646} - 4.7\ E_{663}$$

In addition, the fresh weight of ten leaf discs was determined. The discs were punched with a cork borer with a diameter of 4 mm. Both chlorophyll and leaf-weight determinations were performed in three replicates, each obtained from two different plants.

Growth curves of the different genotypes were determined by measuring plant height of plants that germinated after removal of the testa and endosperm at the radicle end of the seed, as described by Groot and Karssen (1987). These plants were grown under the same greenhouse conditions as described above.

Gibberellin determination

Plants of wild-type and the *gib-1* (W335), *gib-2* (W270), and *gib-3* (W182) mutants were grown in a greenhouse at 23 °C until the first flower clusters were visible. The tops of the plants down to and including the first fully expanded leaves were harvested, frozen in liquid N_2, and lyophilized.

Immature tomato fruits are known to have a high GA content (Bohner et al. 1988). In order to obtain fruits from the mutants, W270 and W335 plants were sprayed with 5 mg/l GA_7 weekly. After anthesis, GA treatment of the inflorescences was discontinued. Immature fruits with a diameter of 2–3 cm were harvested and cut in half. Fruits that contained few seeds were discarded. The fruits were frozen in liquid N_2 and lyophilized.

Extraction, purification, and fractionation by high performance liquid chromatography (HPLC) of endogenous GAs present in shoots and immature fruits were carried out as described (Koornneef et al. 1985b). The presence of GA-like substances in the HPLC fractions was determined in the *d-5* maize bioassay.

Results

Mutant isolation and mutation frequencies

Gibberellin-responsive mutants were identified by their typical dark-green leaves and reduced plant height. The mutant phenotype could be restored to wild type by spraying the plants with GA. The typical dwarf mutants needed repeated GA application for normal flowering and seed set. The seeds harvested on these plants again required GA to germinate. The semidwarf mutants were able to set seed without GA application and their seeds did not require GA for germination. In total, we found nine independently induced mutants, of which six required GA for germination and grew as typical dwarfs, and three that did not require GA for germination and grew as semidwarfs.

Mutant and mutation frequencies are presented in Table 1. In all three experiments the GA-responsive dwarf mutants were found in similar frequencies per cell.

Genetic characterization

All GA-responsive mutants behaved as monogenic recessives to wild type (Table 2). Complementation analysis revealed that the nine mutants represented mutations at three different loci named *gib-1*, *gib-2*, and *gib-3*, respectively. The three germinating mutants were alleles of loci

Table 1. Mutation frequencies for GA responsive mutants in tomato

Exp. no.	Parental genotype	No. of M_1 plants	No. of M_2 plants	No. of mutants	No. of independent mutants	Mutation frequency per cell
I	MM	844	nd	18	4	4.7×10^{-3}
II	MM	730	2,883	4	3	5.5×10^{-3}
III	GT	920	4,589	10	2	8.7×10^{-3}

nd – not recorded but 25 seeds per M_2 line were sown

Table 2. Segregation ratios in the selfed progeny of plants heterozygous for mutations at the *gib-1*, *gib-2*, and *gib-3* loci

Locus	Mutant lines		Segregation ratio			χ^2 (3:1)
	Nongerm.	Germ.	Wilde type	:	Mutant	
gib-1	W335		387	:	125	0.09
	C66			nt		
		A22		nt		
gib-2	W270		343	:	105	0.58
	A55		58	:	17	0.22
gib-3	A70		414	:	131	0.27
	B4		33	:	10	0.07
		W52	65	:	14	2.23
		W182	235	:	83	0.21

Germ. – germinating without GA application
nt – not tested

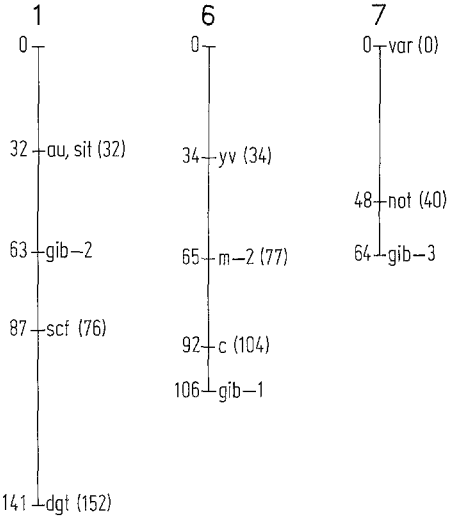

Fig. 1. Location of the *gib* loci on tomato chromosomes 1, 6, and 7. The map position of the upper marker is that on the linkage map published by Mutschler et al. (1987), whereas the other positions are derived from the data shown in Table 3. *In parentheses*, the map position according to Mutschler et al. (1987)

for which nongerminating mutant alleles were also found (Table 2).

In F_2 populations derived from crossing of mutants W335 (*gib-1*), W270 (*gib-2*), and A70 (*gib-3*) with testers that were homozygous recessive for several morphological markers with defined map positions, linkage was detected with at least one marker. These were on chromosomes 1, 6, and 7 for *gib-2*, *gib-1*, and *gib-3*, respectively. Estimates of recombination percentages on these chomosomes are presented in Table 3. The map positions calculated from these data are shown in Fig. 1.

Physiological characterization

A number phenotypic characteristics of the nongerminating mutants W335 (*gib-1*), W270 (*gib-2*), A70 (*gib-3*) and the germinating mutant W182 (*gib-3*) in comparison with their wild type (WT = cv Moneymaker) are shown in Figs. 2, 3, and 4. For the effects of GA application on some traits, see Fig. 3. Germination, which was completely reduced with most seed harvests, could be reversed by GA to almost 100%. This GA requirement for germination could be circumvented by detipping the seeds (Groot and Karssen 1987). Reduced germination and a dwarf growth habit were the most conspicuous aspects of the mutant phenotype. However, the apparently leaky *gib-1* (A22) and *gib-3* (W52 and W182) mutants showed no reduced germination and only a slightly reduced height (Fig. 3). The still darker leaf color and the slightly changed leaf morphology (Fig. 2), which represent a mild expression of similar symptoms in the other more extreme mutants, were characteristic for these mutants. The dark-green color of the mutants was not so much due to a higher chlorophyll content (Fig. 3 D), but was correlated with a changed leaf morphology, characterized by wrinkled and thicker leaves (Fig. 3 C).

The growth rate of the mutants was reduced during all stages of development (Fig. 4). Reduced plant height was due to shorter internodes (data not shown). Leaf size was reduced because leaflets were smaller in the mutants, although the morphology (number of secondary leaves, relative size of leaf incisions) was hardly different from that of the wild type (Fig. 2). For all phenotypic effects in which the mutants differed from the wild type, GA_{4+7} application resulted in reversion to wild type (Fig. 3). The aberrant flower morphology (Nester and Zeevaart 1988) was also restored to normal with a weekly spray of the plants with 100 μM GA_{4+7}, and an almost normal seed yield was obtained in a greenhouse under Dutch summer conditions.

Table 3. Estimates of recombination percentages between *gib* loci and chromosome-specific morphological markers

Chromosome 1		Chromosome 6		Chromosome 7	
Markers	$r \pm s$	Markers	$r \pm s$	Markers	$r \pm s$
sit^w – *au*	0.0 ± 6.5	*yv* – *m-2*	27.0 ± 1.9	*var* – *not*	36.9 ± 2.9
sit^w – *gib-2*	28.4 ± 3.5	*yv* – *c*	42.9 ± 2.4	*var* – *gib-3*	47.6 ± 3.4*
au – *gib-2*	25.1 ± 3.7	*yv* – *gib-1*	50.5 ± 3.2*	*not* – *gib-3*	15.3 ± 4.4
au – *scf*	41.8 ± 2.8	*m-2* – *c*	23.8 ± 1.7		
au – *dgt*	54.0 ± 3.6*	*m-2* – *gib-1*	37.0 ± 3.7		
gib-2 – *scf*	20.1 ± 5.1	*c* – *gib-1*	12.6 ± 3.4		
gib-2 – *dgt*	47.2 ± 4.3*				
scf – *dgt*	39.7 ± 2.9				

* No significant linkage

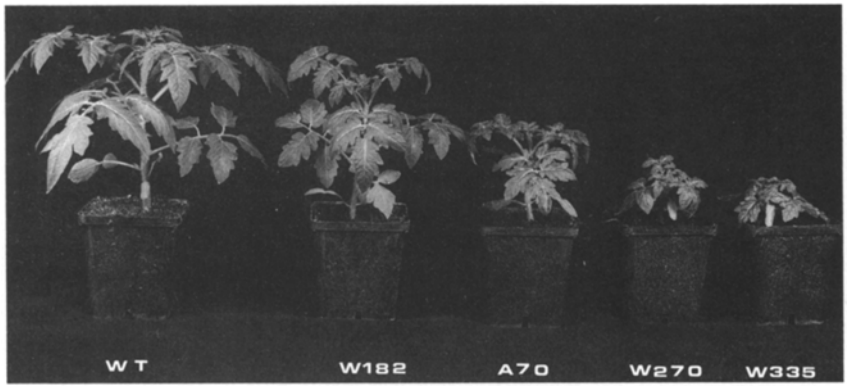

Fig. 2. Representative plants of wild type and mutants 35 days after sowing. Seeds were incubated for 2 days on 10 μ*M* GA_{4+7}, but received no GA later on

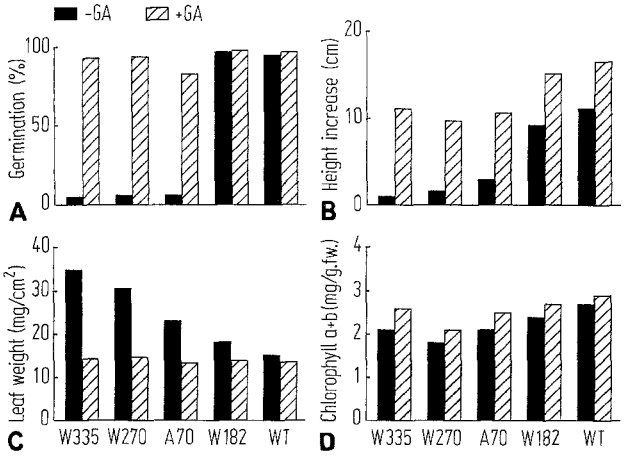

Fig. 3A–D. Some physiological characteristics of *gib* mutants as compared with wild type (cv Moneymaker) and the effect of GA application on these traits. **A** seed germination (based on six replicates of 40 seeds each); **B** height increase between the 3rd and 7th week after sowing (LSD 5%: 1.5 cm); **C** Fresh weight per unit leaf area (LSD 5%: 2.3 mg/cm^2); **D** Chlorophyll content (LSD 5%: 0.3 mg/g f.w.)

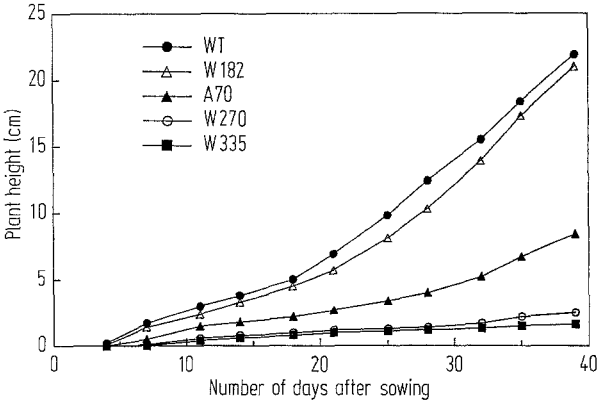

Fig. 4. Total stem length of *gib* mutants and wild-type at time intervals after sowing seeds from which the testa and endosperm at the radicle end of the seed had been removed

Endogenous gibberellin content

Comparison of the HPLC elution profiles (Fig. 5) of the extracts from wild-type and the three mutants indicated that immature, wild-type fruits contained high levels of GA, whereas W182 (*gib-3*) had low GA levels. No significant GA-like activity was detected in extracts from W335 (*gib-1*) and W270 (*gib-2*). Thus, no residual GA_7, sprayed on the W335 and W270 plants, was detected in the bioassays of these fruits (Fig. 5). The various GAs that were indicated by peaks of GA activity in the wild-type elution profile have been identified by combined gas chromatography-mass spectrometry in extracts from immature, wild-type fruits (J. A. D. Zeevaart, unpublished results).

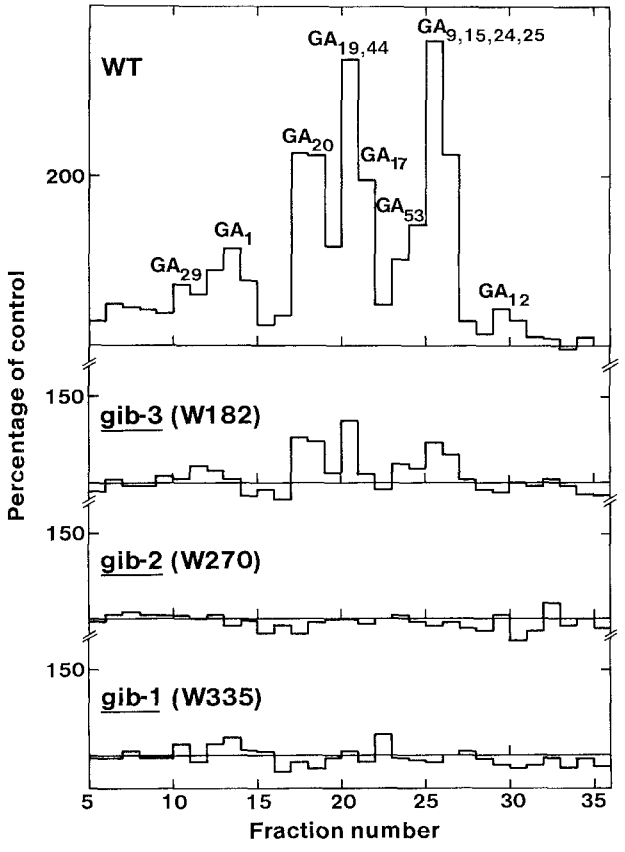

Fig. 5. Comparison of the gibberellin-like activity as detected in the *d-5* maize bioassay in acidic extracts, fractionated by HPLC, from fruits of wild-type (Moneymaker), *gib-1* (W335), *gib-2* (W270), and *gib-3* (W182) mutants. Each extract was obtained from 20 g of immature fruits. Growth of maize seedlings expressed as percentage of control (first + second leaf sheath = 41 mm)

Extracts from shoots tested in the *d-5* maize assay gave essentially the same results, except that the GA-like activity in extracts from the wild-type shoots was much lower than that from the immature fruits. In extracts from W182 shoots, low GA-like activity was detected. No activity was found in extracts from W335 and W270 shoots (data not shown).

Discussion

The relatively strong response of wild-type tomato to applied GAs complicates the classification of tomato dwarfs as GA mutants. The *gib* mutants are typical GA-responsive mutants, because all aspects of the mutant phenotype can be reversed to wild type by relatively low concentrations of applied GAs. The three mutants analyzed for GA-like activity are GA-deficient (Fig. 5). With the methods employed, GAs in extracts from the W270 (*gib-2*) and W335 (*gib-1*) were below the limit of detection, whereas in extracts of the *gib-3* mutant W182, the major peaks of GA-like activity were present, albeit much reduced in comparison with those in wild-type extracts (Fig. 5). The W182 mutant is therefore "leaky", with a growth rate close to that of wild-type (Fig. 4). Although not yet analyzed, it is likely that the GA content of the more extreme *gib-3* mutants is even further reduced. W182 (*gib-3*) and W335 (*gib-1*) have reduced activities of ent-kaurene synthetase B and A, respectively (Bensen and Zeevaart 1990). Furthermore, mutant W270 (*gib-2*) responds to GA_{12}-aldehyde, but not to ent-7α-hydroxykaurenoic acid (Zeevaart 1986). Thus, in mutants of all three loci the biochemical lesion in the GA biosynthesis pathway (Graebe 1987) is prior to GA_{12}-aldehyde.

GA-deficient mutants have been isolated and studied at the genetic and biochemical level in several plant species, such as maize, rice, pea, and *Arabidopsis;* they are blocked at specific steps of the GA biosynthesis pathway (Reid 1990). Such mutants are GA-responsive dwarfs in all species. However, only in *Arabidopsis* (Koornneef and van der Veen 1980) and tomato (Koornneef et al. 1981; Groot and Karssen 1987) is the lack of seed germination an additional characteristic of most of these mutants. A reason why GA is not required for germination in GA-deficient mutants of these other species may be either that GAs are not necessary for germination, or that they are but only at very low levels, which may still be present because these mutants are leaky.

Analysis of the *gib-1* mutant showed that the lack of germination in this mutant is due to the absence of endosperm-weakening by GAs (Groot and Karssen 1987). This weakening of the endosperm prior to radicle protrusion was found to be mediated by a GA-induced degradation by endo-β-mannanase of the mannan-rich cell walls (Groot et al. 1988).

The cellular basis of the phenotype of these GA-deficient mutants might be both a reduced cell elongation and cell division, as both processes were found to be affected by GA in tomato (Jupe et al. 1988). Apparently, lack of an adequate level of GA leads to smaller but thicker leaves (Fig. 3C). This change in leaf morphology probably explains the dark-green appearance of GA-deficient dwarfs in tomato and other plant species, as chlorophyll content per unit weight was not increased.

Although no complementation tests were performed, the tomato mutants described in this report are probably not allelic to any other reported dwarf mutant in tomato (Pelton 1964; Mutschler et al. 1987). None of the mutants at the loci: *bl, bul, Crk, cpt, d, dd, deli, div, dpy, ds, fd, Fw, in, mn, mts, na, per, rust, sd, um,* and *wd* resembled the typical morphology of the *gib* mutants, and none of these loci map at a position near one of the *gib* loci. The only exception might be *d-2*, which is located on chromosome 6 (Mutschler et al. 1987). However, this mutant resembles the phenotype of *d* mutants with relatively mild

symptoms. Mutants at the *d* locus (chromosome 2) are the only tomato dwarfs that have been tested for their response to GAs (Plummer and Tomes 1958; Soost 1959; Nadhzimov et al. 1988). Although these mutants showed a substantial stem growth response to GA, it is not considered to be a biosynthesis mutant, since normal stature and morphology are not restored and endogenous GAs are not reduced (Nadhzimov et al. 1988). The only other tomato mutant for which a reduced GA content has been observed is the *procera* mutant (Jones 1987), which resembles a wild-type plant treated with GA (Jupe et al. 1988). Apparently, this mutant is hypersensitive to GA. The *yg-6* mutant of tomato with elongated hypocotyl and internodes was claimed to be a GA overproducer (Perez et al. 1974), but was later found to be allelic to the phytochrome-deficient *aurea* mutant (Koornneef et al. 1985a; Koornneef et al. 1986). Although male sterility of the mutant *sl-2* can be reversed to fertility by GA application (Sawhney and Greyson 1979), this is most likely not a GA biosynthesis mutant, since other aspects of plant growth and development are not modified as in the case of the *gib* mutants. Further analysis of the mutants described here aims at the determination of the biochemical blocks caused by these mutations and at the use of these mutants to investigate the role of GAs in the growth and development of plants.

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