Gibberellin-Deficient Dwarfs in Potato Vary in Exogenous GA_3 Response When the ga_1 Allele Is in Different Genetic Backgrounds

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ABSTRACT

Gibberellins (GAs) are involved in internode elongation and other important processes such as seed germination, flowering, maturation, tuberization, and tuber dormancy. The discovery of GA-deficient mutants enabled further study of the role of these hormones in many plant processes. GA-deficient mutants lack the ability to produce adequate amounts of gibberellin for normal growth, resulting in a rosette type growth and short internodes. The *ga_1* mutant allele was introduced into various genetic backgrounds including different *Solanum* species and ploidies. Diploid GA-deficient genotypes were obtained by crossing haploid *Solanum tuberosum* ssp. *andigena* with *Solanum chacoense*. The progeny was then bulked and intermated to produce F_2 individuals. Tetraploid GA-deficient genotypes were obtained by crossing *S. tuberosum* ssp. *andigena* with *Solanum sucrense* and with *Solanum gourlayi*. The two resulting progenies were then bulked and intermated. Diploid and tetraploid GA-deficient genotypes were grown on MS media containing different levels of gibberellin (GA_3). Plant height and visual observations were made as a way to assess the response of these genotypes to GA_3. Concentration of 0.1 µM GA_3 and lower failed to restore normal plant height in both diploid and tetraploid genotypes. Normal plant height was restored in most of the GA-deficient genotypes when concentrations between 0.8 and 1.2 µM GA_3 were used. We found some important differences between these genotypes: (1) the level of GA_3 to restore normal plant height varies among the GA-deficient genotypes, some needed more GA_3 than others to grow normally; (2) the time to respond to the presence of GA_3 in the media differs between the GA-deficient genotypes, (3) tetraploid genotypes exhibited normal growth and internode length in response to GA_3, while diploid genotypes tended to show a rosette-type growth at the apical end. These results suggest that *ga_1* mutants can be affected by a series of modifier genes and/or iso-alleles. The importance of variable response to GA among dwarf individuals is two fold: (1) experiments measuring GA response should choose and clonally multiply one genotype to ensure uniform optimal response to GA application; and (2) variation between *ga_1* mutant phenotypes could be used to characterize GA-response modifier genes.

RESUMEN

Las giberelinas (GAs) están involucradas en el crecimiento internodal y en otros procesos importantes como germinación de semillas, florecimiento, maduración, tuberización y dormancia del tubérculo. El descubrimiento de mutantes deficientes en GA ha permitido estudiar el rol de estas hormonas en muchos procesos en la planta. Los mutantes deficientes en GA carecen de la habilidad de producir cantidades adecuadas de giberelina para tener un crecimiento normal, resultando en un crecimiento tipo roseta y espacio internodal corto. El alelo mutante *ga_1* fue introducido en varios materiales genéticos, incluyendo diferentes especies de *Solanum* y

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ABBREVIATIONS: GA, gibberellin; GC-MS, gas chromatography-mass spectrometry; MS, Murashige-Skoog; PAR, photosynthetically active radiation

diferentes ploidías. Genotipos diploides deficientes en GA fueron obtenidos cruzando haploides de *S. tuberosum* ssp. *andigena* con *S. chacoense*. La progenie fue después combinada y entrecruzada para producer individuos F_2. Genotipos tetraploides deficientes en GA fueron obtenidos cruzando *S. tuberosum* ssp. *andigena* con *S. sucrense* y con *S. gourlayi*. Las dos progenies resultantes fueron combinadas y entrecruzadas. Los genotipos diploides y tetraploides deficientes en GA fueron cultivados *in vitro* en medio de cultivo MS conteniendo diferentes niveles de giberelina (GA_3). La altura de la planta y observaciones visuales fueron utilizadas como parámetros para evaluar la respuesta de los genotipos a GA_3. Concentraciones de 0.1 µM GA_3 y menores no restauraron la altura normal de la planta en los dos tipos de genotipos, diploide y tetraploide. La altura normal de la planta fue restaurada en la mayoría de los genotipos deficientes en GA cuando las concentraciones utilizadas fueron entre 0.8 y 1.2 µM GA_3. Este estudio encontró diferencias importantes entre estos genotipos: (1) el nivel de GA_3 necesario para restaurar la altura normal de la planta varía entre los diferentes genotipos deficientes en GA, algunos necesitan más GA_3 que otros para crecer normalmente; (2) el tiempo en el cual la planta responde a la presencia de GA_3 en el medio es diferente entre los genotipos deficientes de GA; (3) los genotipos tetraploides exhibieron crecimiento y espacio inter-nodal normal en respuesta al GA_3 presente en el medio de cultivo, mientras que los diploides tendieron a mostrar un crecimiento tipo roseta en el extremo apical de la planta. Estos resultados sugieren que los mutantes *ga₁* pueden estar afectados por una serie de modificadores genéticos y/o iso-alelos. La importancia de la presencia de modificadores y/o isoalelos son dos: (1) experimentos que miden la respuesta a GA deben elegir y multiplicar clonalmente un solo genotipo para asegurar una respuesta óptima y uniforme a la aplicación de GA; y (2) la variación fenotípica entre los mutantes *ga₁* puede ser utilizada para caracterizar los modificadores genéticos que pueden estar involucrados en la respuesta a GA.

INTRODUCTION

Gibberellin (GA) hormones act throughout the life cycle of plants, influencing seed germination, stem elongation, flower induction, anther development, and seed and pericarp growth (Hooley 1994; Swain and Olszewski 1996). Furthermore, GAs are known to mediate environmental stimuli, which modify the flux through a GA-biosynthetic pathway (Hedden and Kamiya 1997). In potatoes, gibberellins have been shown to be involved in such important processes as seed germination, flowering, maturation, tuber dormancy, and tuberization. Exogenous applications of GA have long been used to break dormancy in true seeds (Simmonds 1963; Spicer and Dionne 1961), enhance flowering (Pavek and Stallknecht 1974; Ross et al. 1979), inhibit tuber formation (Hammes and Nel 1975), and break tuber dormancy (Coleman 1987; Smith and Rappaport 1961).

Bamberg and Hanneman (1991) first reported a gibberellin-related dwarfing locus in potato. Parents from *Solanum tuberosum* Groups Andigena and Tuberosum were found to produce dark green progeny, with very short internode resulting in rosette-type growth. These were designated to be dwarf individuals, which could be completely restored to normal growth and appearance by exogenous GA_3 (Bamberg and Hanneman 1991). Test crosses indicated that this phenotype was explained by the action of a single locus *ga₁*, the dwarfing phenotype being conferred by the nulliplex or completely recessive condition (*ga₁ ga₁ ga₁ ga₁*) (Hanneman and Bamberg 1991). Later, Van den Berg et al. (1995) found a 25-fold reduction of the amounts of GA_1 in the *ga₁* dwarfs compared to the wild type. These authors reported that a block of GA biosynthesis in the *ga₁* mutant occurs between GA_{12} and GA_{53}. Further screening of a broad sample of Group Andigena populations found this dwarfing allele in 14 of 120 populations in the US Potato Genebank (with a minimum of 0.2% to a maximum of 27.7% frequency). These results indicated that the dwarf allele is not particularly rare in potato (Bamberg 1999), although *ga₁* has not been reported in wild species.

Dwarf plants, having the same morphological characteristics described by Bamberg and Hanneman (1991), were also reported in *S. tuberosum* cv Pito (Valkonen et al. 1999). They found very low amounts of all analyzed GAs in the dwarfs, indicating a block in an early part of the GA biosynthesis pathway. Without a genetic analysis, they described "*pito*" as a recessive dwarfing gene in cv Pito.

Using dwarf plants obtained in an F_2 population of a cross between *Solanum chacoense* and *Solanum phureja*, Kimura and Hosaka (2002) mapped a dwarfing gene, named ga_2, on the most or near distal end of chromosome 7. Segregation analyses of the F_2 and backcross populations suggested that the observed dwarfism was controlled by a single recessive gene and transmitted from the *S. phureja* parent. Dwarf plants studied by Kimura and Hosaka (2002) could be restored to normal phenotype by exogenous treatment with GA.

The use of these GA mutants has lead to studies on the regulation of the GA biosynthetic pathway at the molecular level. For example, by using the ga_1 dwarf mutant from Bamberg and Hanneman (1991), Carrera et al. (1999) isolated three cDNA clones encoding potato GA 20-oxidases. GA 20-oxidase activity is suggested to be one of the principal points of regulation in the GA biosynthetic pathway. The characterization of these cDNA clones showed that they encode functionally identical enzymes with different patterns of tissue-specific expression. Carrera et al. (1999) also used these mutants to study the regulation of GA biosynthesis by photoperiod. Currently, the GA 20-oxidase genes isolated by Carrera et al. (1999) are being used to study the regulation of transcript levels of these genes by light and phytochrome B (Chen et al. 2003; Rosin et al. 2003; Jackson et al. 2000).

In view of the importance that these GA-deficient mutants have and their current wide use in plant research, we sought to determine if the genetic background of the plant in which ga_1 is expressed significantly influences the response to exogenous GA. If so, as mentioned above, it might be useful to select and clonally maintain the most sensitive GA-deficient genotypes for use as experimental tools, and further examine the modifier genes presumably responsible for the difference in sensitivity of the different dwarf genotypes. Preliminary experiments showed that the incorporation of GA_3 in sterile culture media provides a convenient and consistent bioassay of GA response by measuring plantlet elongation (Martin and Bamberg 1990). The present study used that system to evaluate the exogenous GA_3 response of the ga_1 allele in different genetic backgrounds.

MATERIALS AND METHODS

Plant Material and Growing Conditions

Materials used were those available from the US Potato Genebank and not intentionally developed for this experiment. The original source of the ga_1 allele is *S. tuberosum* ssp. *andigena* PI 347773, the dwarf phenotype being discovered in progeny of this tetraploid population and cv Superior as a female parent. To broaden the genetic background, vigor, and fertility of dwarfs, these dwarfs had been crossed as females with bulk pollen from compatible tetraploid species *Solanum gourlayi* and *Solanum sucrense*. The resulting hybrids were selected and intermated, producing the population from which 4x dwarfs tested in this experiment were obtained. Tetraploid *S. tuberosum* ssp. *andigena* hybrids heterozygous at the dwarfing locus had also been used to produce diploid progeny by maternal haploid extraction by the *S. phureja* pollinator 1.22 method (Ross 1986). Introgression of wild species had also been conducted at the diploid level to increase vigor and fertility, this time using bulk pollen of the diploid wild species *S. chacoense*. The resulting heterozygous *S. tuberosum* ssp. *andigena-S. chacoense* F1 hybrids had been bulk intermated to produce a segregating diploid family from which the 2x dwarfs used in this experiment were obtained. These materials were not chosen with the intent of isolating the effect of ploidy or contribution of any particular wild species, but to represent dwarfs in the most diverse genetic background offered by the US Potato Genebank.

Each GA-deficient genotype was clonally propagated on MS media (Murashige and Skoog 1962) with 3.0% sucrose, from single-node stem sections in cultured tubes (Pyrex N° 9820) for 5 to 6 weeks. Sterile culture tubes were maintained under a continuous photoperiod at 20±2 C with 70 µmol $\bullet m^{-2} \bullet s^{-1}$ PAR (measured at plant level with a lightmeter Model LI-185A, Li-Cor, Lincoln, NE) from cool-white fluorescent lamps (Sylvania/GTE, Danvers, MA).

In Vitro GA_3 treatments

Five- to six-week-old plantlets were clonally propagated from single-node stem sections into culture tubes with 5mL of MS media containing 0 to 10 µM GA_3 and kept under the same culture conditions as described above. GA_3 stock solution was filter sterilized and was added after autoclaving the media. Four replications were used for each GA_3 concentration tested. Gibberellin requirements were assessed based on plant growth over time in response to the GA_3 concentration present in the media. Plant growth was evaluated by measuring plant height (from the base of the plant to the apical meristem) over 5 weeks. Weekly measurements were taken from outside the tube (without opening the culture tube).

Data Analysis

A repeated measures (day) 2-way ANOVA (GA_3 and genotype) with interaction and replication was performed. In order to account for the autocorrelated errors due to repeated measures, an AR(1) error structure was used in the SAS MIXED procedure (SAS Institute Inc. 1999). AR(1) is a first order autoregressive term. LSD analysis was performed using Proc Mixed Mean Separation Formatting according to Saxton (1998). This macro formats pair-wise differences from SAS Proc MIXED, created by the PDIFF option on the LSMEANS statement. The differences are used to create groups of similar means, represented by letters a, b, etc. (Saxton 1998).

RESULTS AND DISCUSSION

An initial screening with a wide range of GA_3 concentrations (0, 0.001, 0.01, 0.1, 1, and 10 µM) showed that all GA-deficient genotypes started to respond to the GA_3 present in the media at a *minimum* of about 0.1 µM (Figure 1). Concentrations below 0.1 µM GA_3 had little or no effect on the plant height in either the diploid or the tetraploid genotypes, but response was dramatic at and above 0.1 µM GA_3. These differences were verified from the visual appearance at harvest, which was 42 days of growth in vitro (Figure 2). On the other hand, *optimal* rapid growth was achieved at about 1.0 µM GA_3. At 10 µM GA_3 however, abnormal growth was observed in all GA-deficient genotypes. Overdosed plants showed axillary shoot growth and abnormal growth (Figure 3). Axillary shoot growth indicates that at 10 µM GA_3 concentration, apical dominance was not maintained.

To detect differences in the *minimum* concentration of GA_3 needed for plant response, we tested all GA-deficient genotypes at 0, 0.025, 0.05, 0.075, and 0.1 µM GA_3. The results are shown in Table 1. With the exception of one genotype (2x-9), all GA-deficient genotypes reached their maximum plant height at 0.1 µM GA_3. In all the diploid genotypes except 2x-9, the difference between the plant height observed at 0.075 and 0.1 µM GA_3 was highly significant ($P \leq 0.01$). Among the tetraploids, all five genotypes had plant heights significantly higher at 0.1 µM GA_3 when compared to the plant height at 0.075 µM GA_3 ($P \leq 0.01$). This means that these genotypes responded to the increment of GA_3 in the media. Overall, GA-deficient genotype 2x-9 was the only one significantly more responsive to the GA_3 present in the media, being able to reach its maximum plant height under

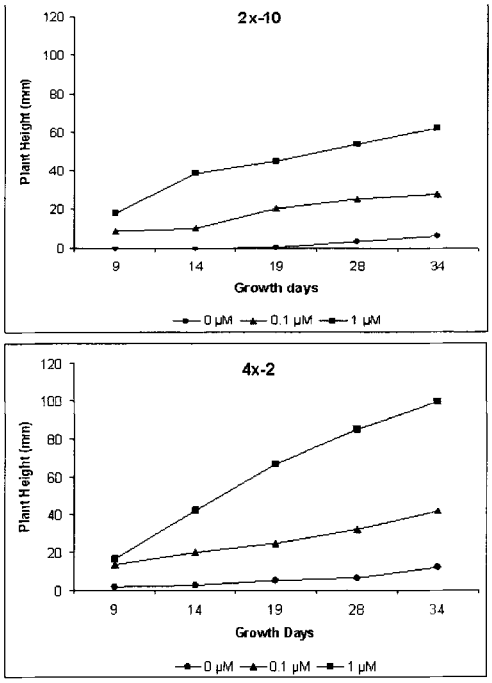

FIGURE 1.
Average plant height measured over time in the presence of varying concentrations of GA_3 (0 to 10 µM). One diploid and one tetraploid GA-deficient genotype are shown as examples. Averages taken over four plantlets.

FIGURE 2.
Example of a diploid and tetraploid GA-deficient genotype grown on MS media containing different concentrations of GA_3 (0 to 1.0 µM). Plants were harvested after 42 days of growth.

lower amounts of GA_3 (0.075 µM GA_3) compared to the other genotypes (0.1 µM GA_3).

Table 1 gives the mm of height per time per GA_3 treatment (response index) for all the genotypes tested. From these results we see that genotypes 2x-9 and 4x-15 have a high response index; the former because it responded to a lower dose of GA_3, and the latter because it reached its maximum height significantly earlier when compared to the others. These results suggest that there is significant variation between these dwarfs for the response time to GA_3. All genotypes reached 50% of their maximum plant height between 12 and 17 days of growth. Nevertheless, with these low concentrations of GA_3, both diploid and tetraploid genotypes retained most of the features of the dwarf phenotype.

To detect differences in the GA_3 needed to restore *optimal* growth with normal plant appearance, we tested all genotypes at concentrations around 1 µM GA_3: 0.7, 0.8, 0.9, 1.0, and 1.2 µM. The results are shown in Table 2. All genotypes took between 13 and 18 days to reach 50% of their maximum plant height. As was true at much lower GA_3 concentrations reported in Table 1, genotypes 2x-9 and 4x-15 exhibited a significantly greater response to GA_3 than the relatively unresponsive genotypes 2x-4 and 4x-12.

TABLE 1—*Differences in GA_3 sensitivity of diploid and tetraploid GA-deficient genotypes grown at doses around the minimum needed for response: 0, 0.025, 0.05, 0.075, and 0.1 µM GA_3. Plants were harvested after 42 days. Averages were taken over four replicates.*

Genotype	A µM GA_3 for max. height at 42 days (µM)	B[1] Max. height reached at 42 days (mm)	C[2] Growth days to reach max. height (d)	B/(A•C)[3] Response Index Height per day per µM GA_3 ($mm•d^{-1}•µM^{-1}$)
2x-4	0.100	38 c	42 a	9.0 b
2x-9	0.075	48 b	38 a	16.8 a
2x-10	0.100	45 b	42 a	10.7 b
2x-12	0.100	53 a	38 a	13.9 ab
4x-2	0.100	54 bc	42 a	12.9 ab
4x-5	0.100	62 a	42 a	14.8 ab
4x-12	0.100	38 d	40 a	9.5 b
4x-15	0.100	55 b	35 b	15.7 a
4x-17	0.100	51 c	40 a	12.7 ab

[1]LSD_{05} (diploid genotypes) = 3.2
LSD_{05} (tetraploid genotypes) = 3.7
[2]LSD_{05} (diploid genotypes) = 6.2
LSD_{05} (tetraploid genotypes) = 3.6
[3]LSD_{05} (diploid genotypes) = 5.0
LSD_{05} (tetraploid genotypes) = 5.5

While all GA-deficient genotypes reached normal plant height, clear differences were observed in the appearance of the plants. Most tetraploid genotypes showed normal appearance and internode length at the GA_3 level that restored normal height. However, all the diploid genotypes showed a shortening of the internode length at the apical end as the plant grew further away from the GA_3-containing media (Figure 4). This effect resulted in plantlets that were normal in height but with a rosette-type growth around the apical area (i.e., with short internodes typical of dwarfs untreated with GA). Thus, translocation of GA_3 within the shoot and/or the

FIGURE 3.
Example of a diploid and tetraploid GA-deficient genotype grown on MS media containing 10 µM GA_3. Plants show abnormal growth: absence of apical dominance.

TABLE 2—*Differences in GA_3 sensitivity of diploid and tetraploid GA-deficient genotypes grown at doses around the* optimal *for plant growth with normal appearance: 0.7, 0.8, 0.9, 1.0, and 1.2 µM GA_3. Plants were harvested after 42 days. Averages were taken over four replicates.*

Genotype	A µM GA_3 for max. height at 42 days (µM)	B[1] Max. height reached at 42 days (mm)	C[2] Growth days to reach max. height (d)	B/(A•C)[3] Response Index Height per day per µM GA_3 ($mm•d^{-1}•µM^{-1}$)
2x-4	1.2	102 c	42 a	2.0 b
2x-9	0.9	126 a	37 a	3.8 a
2x-10	0.8	82 d	40 a	2.6 ab
2x-12	1.2	110 b	42 a	2.2 b
4x-2	1.2	123 ab	38 ab	2.7 b
4x-5	1.2	131 a	37 b	2.9 ab
4x-12	1.2	120 bc	40 ab	2.5 b
4x-15	0.8	113 c	40 ab	3.5 a
4x-17	1.0	98 d	42 a	2.3 b

[1]LSD_{05} (diploid genotypes) = 6.5
LSD_{05} (tetraploid genotypes) = 8.7
[2]LSD_{05} (diploid genotypes) = 8.2
LSD_{05} (tetraploid genotypes) = 4.9
[3]LSD_{05} (diploid genotypes) = 1.5
LSD_{05} (tetraploid genotypes) = 0.7

FIGURE 4.
Example of a diploid and tetraploid GA-deficient genotype grown on MS media containing 0.7 to 1.2 µM GA_3. Plants were harvested after 42 days of growth.

translocation of the signal from GA_3 in the media may also be variable among GA-deficient genotypes.

Our results show that there are some important differences between GA-deficient genotypes:

1) The level of GA_3 to restore normal plant height varies between the GA-deficient genotypes, some needing more GA_3 than others to grow normally.
2) The time of response to the presence of GA_3 in the media differs between the GA-deficient genotypes, some responding within a week of growing in the presence of GA_3; others taking longer.
3) Tetraploid genotypes exhibit normal growth and internode length in response to GA_3, while diploid genotypes tend to elongate and show a rosette-type growth at the apical end. This distinction could reflect a feature of ploidy, like different cell sizes, or simply the different genetic backgrounds of 4x and 2x materials tested here.

These results have both theoretical and practical implications. The one phenotype that has been referred to as GA-deficient mutant or dwarf, which segregates like a single locus (ga_1), shows significant GA_3-response variation in different genetic backgrounds. These results suggest that ga_1 mutants can be affected by modifier genes and/or iso-alleles. In addition, there might be environmental interactions with the genetic component. Different temperatures and light conditions (intensity and length of photoperiod) might promote even more differences in GA responsiveness. All these issues should be considered in future research that uses these mutants.

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