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ORIGINAL PAPER

Reduced gibberellin biosynthesis and response in fruits of the auxin insensitive *diageotropica* tomato mutant

Francesco Mignolli[1,2] · **Lorenzo Mariotti**[3] · **María Laura Vidoz**[1,2]

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Abstract

Auxin has a central role in determining tomato fruit growth and development, and most of its action is mediated by gibberellins (GAs). The *diageotropica* (*dgt*) mutant of tomato exhibits many physiological responses that are related to a defective auxin sensitivity. In this paper we investigated the effects of the *dgt* mutation on tomato gibberellin biosynthesis regulation during fruit-set and early growth of pollinated fruits. In spite of an initial accumulation of active GAs in *dgt* ovaries, their content is significantly reduced at later stages. Indeed, at the beginning of rapid fruit growth, *dgt* fruits display a lower amount of GA_1 and its direct catabolite GA_8. Consistently, transcripts of GA 20-oxidase genes (*GA20ox1*, *GA20ox2*, *GA20ox3*) are low in the mutant. Moreover, low expression of genes encoding GA catabolism enzymes (GA 2β-hydroxylases) does not lead to an increase in the amount of active GAs, supporting the hypothesis that GA 20-oxidase genes downregulation might bottleneck the synthesis of active GAs in *dgt*. Interestingly, exogenous GA_3 application has little effect on *dgt* ovaries. GA_3-treated fruits of the mutant are smaller than those of its wild type as a result of fewer and smaller pericarp cells. Consistently, GA_3 treatment in the *dgt* ovaries produces negligible effects on cell endoreduplication revealed by a lower nuclear DNA content in pericarp and locular tissue cells. The lack of DELLA-mediated constraint on GA signal in the double mutant *dgt pro* did not cause an increase in size and weight in pollinated fruits, suggesting that GA signalling is unable to overcome the inhibition of growth caused by the *dgt* mutation.

Keywords Tomato · *Diageotropica* mutant · Fruit · Gibberellin metabolism

Introduction

In tomato (*Solanum lycopersicum* L.), the transition from a static ovary to a growing fruit is characterised by the succession of three phases. After fruit-set, ovary cells increase in number on account of a high mitotic activity that is followed by a stage of cell expansion (Gillaspy et al. 1993). Several positive and negative hormonal cues are involved in regulating fruit growth and development (McAtee et al. 2013). Lines of evidence have shown that the increase of auxin content is one of the earliest events that trigger fruit-set (Dorcey et al. 2009; Mariotti et al. 2011). Indeed, IAA is produced in fertilised ovules and subsequently transported towards outer tissues, such as placenta and pericarp, through the coordinated action of auxin efflux and influx carriers (Pattison et al. 2014; Sorce et al., 2017).

Auxin perception and signal transduction are initiated following the auxin-driven recruitment of the auxin signalling repressors Aux/IAAs by the nuclear-localised receptor TIR1/AFB. Following the degradation of Aux/IAAs via 26S proteasome, the repression on auxin responsive genes is released making their transcription possible (Salehin et al. 2015). Spontaneous fruit-set in tomato has been obtained by altering the expression of some auxin signalling components. Indeed, when the transcription of Aux/IAA9 (*SlIAA9*) is suppressed with an antisense construct or, as in the *entire* mutant, a truncated peptide version is encoded, spontaneous fruit initiation is triggered (Wang et al. 2005; 2009; Zhang et al. 2007; Mignolli et al.

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✉ María Laura Vidoz
malauravidoz@gmail.com

[1] Instituto de Botánica del Nordeste (IBONE), UNNE-CONICET, 3400 Corrientes, Argentina

[2] Facultad de Ciencias Agrarias, UNNE, 3400 Corrientes, Argentina

[3] Dipartimento di Scienze Agrarie, Alimentari e Agro-Ambientali, Università di Pisa, 56124 Pisa, Italy

2015). Other auxin signalling elements have emerged as new players involved in tomato fruit formation. Particularly, the Auxin Response Factors 7 (SlARF7), 9 (SlARF9) 5 (SlARF5) have been shown to modulate tomato ovary cells divisions and expansion (de Jong et al. 2011; 2015; Liu et al. 2018).

Gibberellins (GAs) represent a class of plant hormones that counts 136 different structures whose biosynthesis is summarised in Fig. S1. Physiologically, GAs exert major control in organ elongation and, in certain cases, in cell divisions. In addition, GAs regulate the physiological switch between vegetative to reproductive development, pollen fertility and seed germination (Hedden and Thomas, 2012). Together with auxin, GAs actively participate in fruit growth and development (Vriezen et al. 2008; Li et al. 2020; Shinozaki et al. 2020) since exogenous application of GA_3 or silencing the GA signal repressor SlDELLA trigger parthenocarpic fruit formation, whereas the inhibition of GA biosynthesis strongly hinders fruit growth (Serrani et al. 2007a, 2008; Martí et al. 2007; Carrera et al. 2012). The fact that GA metabolism and signal are modulated in response to auxin indicates that tomato fruit formation actually depends on auxin and GA crosstalk (Serrani et al. 2008; Tang et al. 2015). Indeed, genes involved in GA biosynthesis (GA 20-oxidases) and in GA catabolism (GA 2β-hydroxylases) are, respectively, induced and repressed in auxin-treated ovaries or in auxin signalling repressor mutants (Serrani et al. 2008; Mariotti et al. 2011; Mignolli et al. 2015). Similarly, in *SlARF7* and *SlARF5* RNA interference lines of tomato, GA responsive genes are upregulated, indicating a control of GA signalling by auxin (De Jong et al. 2011; Liu et al. 2018). Although it has been suggested that auxin acts upstream of GAs in regulating tomato fruit-set, recent pieces of evidence indicated that GAs are able to modulate auxin signalling (Hu et al. 2018; Mignolli et al. 2019).

Since its first physiological description, the tomato *diageotropica* (*dgt*) mutant has been considered an auxin insensitive mutant (Zobel 1973). Along with several auxin-related responses such as root and shoot gravitropism, hypocotyl elongation, apical dominance and lateral root formation, also primary metabolism, such as photosynthesis and respiration, is controlled by DGT (Kelly and Bradford 1986; Coenen et al. 2002; Batista-Silva et al. 2019). The *DGT* locus encodes a cyclophilin (LeCYP1) that travels via phloem from shoot to roots as a signalling molecule (Oh et al. 2006; Spiegelman et al. 2017). The *dgt* mutation has also been shown to negatively affect tomato fruit formation since it reduces seed number, fruit set rate and fruit size (Balbi and Lomax 2003). Mignolli et al. (2012) have found out that auxin signalling transduction is dramatically impaired in auxin-treated *dgt* fruits, confirming the positive function of *DGT* in auxin signal transduction in fruit. Furthermore, the *DGT* gene seems to be involved in mediating the auxin-induced GA biosynthesis, acting as a positive regulator (Mignolli et al. 2019).

The objective difficulty in blocking the auxin signal or biosynthesis with a pharmacological approach (Fukui and Hayashi 2018), makes the *dgt* mutant a valid tool to dissect the role of auxin in tomato. To the best of our knowledge, no information is available about the effect of a reduced auxin perception on GA metabolism in fruits. Analysis of endogenous GAs and GA metabolism gene expression have allowed us to demonstrate that DGT plays a role as a positive modulator of GA biosynthesis. In addition, since neither exogenous application of GA_3 nor a constitutive GA signal are capable of restoring a normal fruit phenotype in *dgt,* we suggest that DGT might also be implicated in processes that override the role of GAs in fruit growth and development.

Materials and methods

Plant material and ovary treatments

Seeds of tomato (*Solanum lycopersicum* L.) cv. Ailsa Craig (AC) were obtained from the Tomato Genetics Resource Center (University of California, Davis, CA, USA). Seeds of d*iageotropica* (*dgt*) mutant, backcrossed into AC genetic background, were donated by Dr. C. Coenen (Allegheny College, Meadville, PA, USA). Double mutant *dgt pro* was obtained as described by Mignolli et al. (2019). Some phenotypical characteristics of *dgt pro* are reported in supplemental material (Fig. S1 and Table S1).

Plants were grown under greenhouse conditions as reported by Mignolli et al. (2012). Only four flowers per truss were left in order to limit fruit competition. Flowers were emasculated at pre-anthesis (one day before anthesis) which is equivalent to 0 DAP (days after pollination) in order to prevent self-pollination. Once emasculated, flowers were manually pollinated using pollen from AC plants for both genotypes. Ovaries/fruits were collected at different time points from pollination (from 0, to 8 DAP). Samples were immediately stored at − 70 °C up to analyses.

Similar to Serrani et al. (2007b), treatments with the gibberellin biosynthesis inhibitor LAB198999 (3,5-dioxo-4-butyryl-cyclohexane carboxylic acid ethyl ester; BASF) were performed by applying on 2 DAP ovaries 10 µl of 2 mM LAB198999 dissolved in 1% ethanol and 0.1% Tween 20 solution. An equal volume of solvent was used as mock. Gibberellin application was carried out on emasculated flowers at pre-anthesis with 10 µl of 0.2 µg $µl^{-1}$ GA_3 (Sigma-Aldrich, St. Louis, MO, USA) dissolved in 1% ethanol and 0.1% of Tween 20 solution. Equal volume of solvent was used as mock treatment.

Quantification of endogenous GAs

Endogenous GAs were determined in pollinated ovaries and fruits of AC and *dgt* from 0 to 8 DAP. Extraction, purification and GAs determination through GC–MS/MS were performed according to Mariotti et al. (2011).

Histology and ploidy level determination

Histological analysis was carried out on fruits treated with GA_3 or a mock solution, according to Gonzalez and Cristóbal (1997). Fruits of AC and *dgt* were sampled after 4 days from the treatment, immediately fixed in a formaldeyde:ethanol:acetic acid (4:50:5 v/v) and dehydrated in xylene:ethanol solution series. Transversal sections 10 µm thick were stained with safranin-fast green. Sections were observed with a Leica DM LB2 microscope and microphotographs were taken with a Leica ICC50HD digital camera (Leica, Wetzlar, Germany).

Nuclear DNA content was assessed in pericarp and locular tissue of GA_3-treated fruits after 10 days from treatment according to Mignolli et al. (2012). Mean of C value (MCV) was calculated according to Serrani et al. (2007a).

RNA extraction and gene expression analysis

Total RNA extraction, purification and conversion into cDNA from ovaries and fruits were performed according to Mignolli et al (2012). Expression analysis of GA metabolism genes was carried out using TaqMan Universal PCR Master Mix (Applied Biosystems) by using specific probes and primers as reported by Mariotti et al. (2011). Transcript levels of all genes were normalised with the expression of *SlEF1α*. Each sample derived from a pool of at least five fruits. Gene accession numbers and primer sequences were reported in Mignolli et al. (2015).

Statistical analysis

Analysis of variance (one-way ANOVA, Tuckey post-test) and Student *t*-test were performed using the software GraphPad Prism 8.0 (GraphPad Software Inc., San Diego, CA, USA).

Results

Pollinated fruits of *dgt* grew less and had lower fresh weight compared with pollinated ovaries of AC. From 6 to 8 DAP, fruit weight increased 7.5 times in AC but only 3.2 times in *dgt* (Fig. 1a). In order to assess the role of GAs in *dgt* fruit growth, we treated pollinated ovaries with the inhibitor LAB198999, which is known to block the last steps of GA biosynthesis (Rademacher 2000). While LAB198999 application determined a significant reduction of fruit weight in AC (more than 2.5 times), no statistically significant difference was observed between mock- and LAB-treated *dgt* fruits (Fig. 1b).

To establish whether the *dgt* mutation alters GA metabolism, concentrations of GAs from the early 13-hydroxilation pathway (GA_{19}, GA_{20}, GA_1, GA_3, GA_8 and GA_{29}), which is the most representative pathway in tomato (Fos et al. 2000; Serrani et al. 2007a, b; Garcia-Hurtado et al. 2012), were quantified. After an initial increase, GA_{19} content steadily declined in *dgt*. However, levels of GA_{19} from 4 to 8 DAP were higher in *dgt* than in AC (Fig. 1c). Levels of GA_{20} did not change substantially in *dgt* in comparison to AC (Fig. 1d). In both genotypes, they decreased at 2 DAP to rise again at 4 DAP. Singularly, the content of GA_1 and GA_3 in pre-anthesis ovaries and at 2 DAP were higher in *dgt* than in AC. However, levels of GA_1 in *dgt* were lower than in AC fruits at 8 DAP (Fig. 1e, f). Levels of GA_8 (the GA_1 catabolite) were high during the first 2 days from pollination in *dgt* but, at 6 to 8 DAP, its levels were 2 and 4 times lower than in AC (Fig. 1g). The content of GA_{29} (the GA_{20} inactive form) increased in both genotypes after pollination; however, a sharp decrease after 4 DAP was observed in AC. The amount of GA_{29} did not decrease and was significantly higher than in AC in fruits of *dgt* at 6 and 8 DAP (Fig. 1h).

Real time PCR analysis was performed in order to establish whether the *dgt* mutation alters the expression of GA metabolism genes. The expression of *SlGA20ox1* and *SlGA20ox3* was similar in both genotypes from 0 to 4 DAP but, following, the expression of both genes in *dgt* failed to increase. On the contrary, the expression of *SlGA20ox-1*and *SlGA20ox3* in AC abruptly increased after 8 and 6 DAP, respectively (Fig. 2a, c). *SlGA20ox2* gene showed a two-fold increase in AC fruits between 2 and 6 DAP but its expression was barely detectable in *dgt* fruits throughout the 8 days (Fig. 2b). In AC and *dgt*, *SlGA3ox1* and *SlGA3ox2* transcripts peaked in ovaries at pre-anthesis stage but plummeted thereafter. Both genes were relatively more expressed in *dgt* at 0, 2 e 4 DAP but reached a similar level to AC at 6 DAP. In AC, the expression of *SlGA3ox1* and *SlGA3ox2* from 2 to 8 DAP was kept extremely low (Fig. 2d, e). Among the genes encoding GA 2β-hydroxylases, the expression pattern of *SlGA2ox1* in *dgt* was slightly higher than AC after 2 and 4 DAP (Fig. 2f). On the contrary, while *SlGA2ox2* transcript levels were higher in *dgt* ovaries at pre-anthesis stage and sharply decreased after pollination, they remained higher than in AC from 2 to 6 DAP (Fig. 2g). *SlGA2ox3*, *SlGA2ox4*, and *SlGA2ox5* were downregulated soon after pollination in both genotypes; yet, an upsurge in their expression was observed in AC at 6 and 8 DAP (Fig. 2h–j).

With the aim of testing *dgt* ovary responsiveness to active GAs, we treated emasculated unpollinated ovaries with an

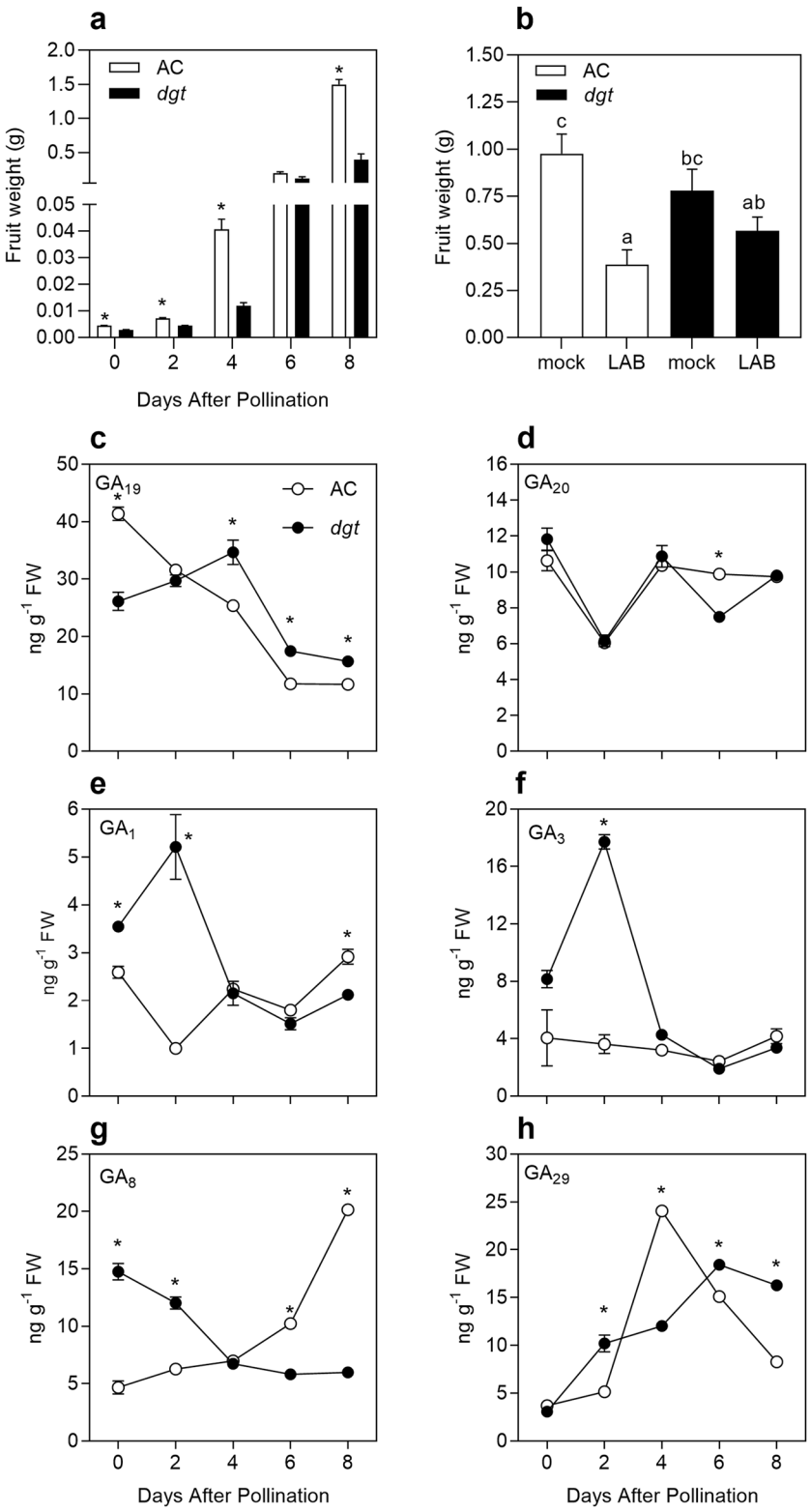

Fig. 1 Weight of fruits of AC and *dgt* collected after 8 days from manual pollination (**a**). Each point represents a mean ± SEM of 20 to 90 ovaries/fruits. Asterisks indicate significant differences between AC and *dgt* (Student's *t*-test, $P < 0.05$). Effect of the GA biosynthesis inhibitor LAB198999 on pollinated AC and *dgt* fruit growth (**b**). Manual pollination was carried out at pre-anthesis stage and application of LAB198999 or mock solution was performed 2 days later. Fruits were harvested at 8 days from pollination (or 6 days from mock/LAB198999 treatment). Data are means of 20 fruits ± SEM. Different letters indicate statistical differences according to one-way ANOVA Tuckey post-test ($P < 0.05$). Endogenous GA content in pollinated AC and *dgt* fruits (**c**–**h**). Samples were collected from 1 day before anthesis (0 DAP) to 8 days after pollination. Analyses were carried out through GC–MS/MS as reported in Materials and Methods. Data are means ± SEM (n = 3). Asterisks indicate significant differences between AC and *dgt* (Student's *t*-test, $P < 0.05$)

optimal dose of GA_3 and we measured fruit weight and some cellular parameters. GA_3 treatment triggered fruit growth in both genotypes, albeit *dgt* fruits were smaller and weighted less than AC ones (Fig. 3a–e). Histological observations showed that GA_3-treated fruits of *dgt* had thinner pericarps as a result of fewer cell layers and reduced cell size (Fig. 3f–h). In order to assess whether the *dgt* mutation also altered ploidy level in GA_3-treated fruits, flow cytometry

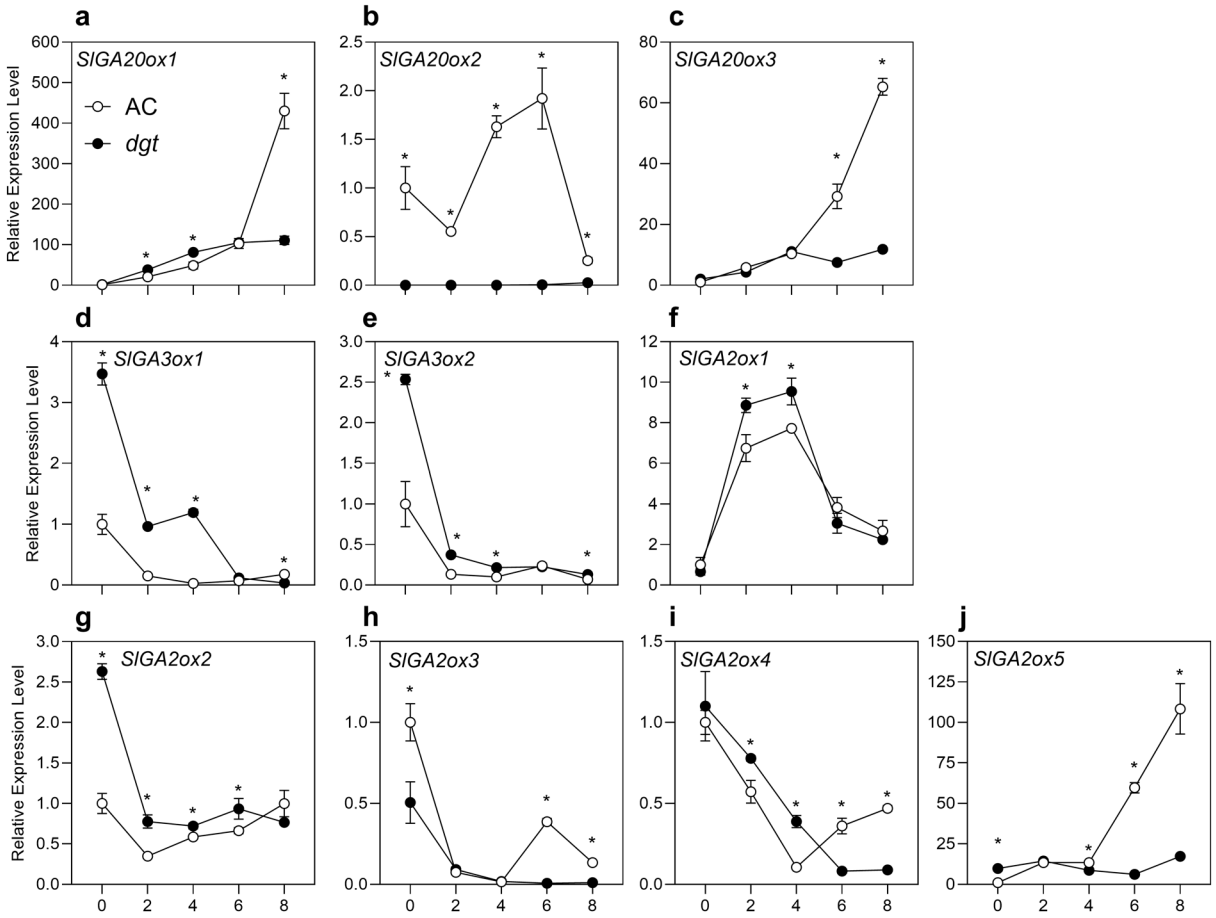

Fig. 2 GA biosynthesis genes expression in developing AC and *dgt* fruits (**a**–**e**). Relative expression of GA 20-oxidase (**a**–**c**) and GA 3β-hydroxylase (**d**, **e**) gene family were measured in ovaries and fruits from 0 to 8 DAP. Relative expression of GA catabolism genes, GA 2β-hydroxylases (**f**–**j**). Transcript levels were normalized to the *SlEF1α* expression. Value at 0 DAP in AC was set to 1 for each gene, and all other values were calculated relative to this. Data are mean ± SD (n = 3). Asterisks indicate significant differences between AC and *dgt* (Student's t-test, $P < 0.05$)

analysis of pericarp and locular tissue was performed. The effect of GA_3 on cell endoreduplication in *dgt* was less marked than in AC (Fig. 3i–l) since no 32 C nuclei were detected in *dgt* pericarp and the MCV values in pericarp and locular tissues were significantly lower than in AC (Fig. 3j, l).

PROCERA (PRO) is the tomato DELLA protein and its mutation *pro*, confers a constitutive activation of the GA signal (Jasinski et al. 2008). We sought to determine whether the *dgt* fruit phenotype could be reverted by the *pro* mutation. Analysis of some vegetative traits of the double mutant *dgt pro* indicates that plant height and mean internode length were only partially rescued while stem diameter, number of leaves, leaf area, leaf perimeter and leaf pigments content did not differ from the *dgt* parent (Table S1). Notably, leaf shape of *dgt pro* displayed the reduced lobing of the main leaflets typical of *pro* leaf phenotype (Fig. S2). As far as fruit phenotype is concerned, 30-day-old pollinated fruits of the double mutant have similar ellipsoid shape as in *pro* but both size and weight are statistically identical to *dgt* (Fig. 4).

Discussion

Fruit growth and development in tomato depend on a tightly regulated interplay between auxin and GAs (Koshioka et al. 1994; Serrani et al. 2007b, 2008; Mariotti et al. 2011; Hu et al. 2018; Mignolli et al. 2019). Our data confirmed that the *dgt* lesion dramatically alters fruit growth and development (Fig. 2a; Balbi and Lomax 2003; Mignolli et al. 2012). We tested the hypothesis that the reduced auxin sensitivity in *dgt* adversely affects GA biosynthesis and hence fruit growth. However, when ovaries of *dgt* were treated with the GA biosynthesis inhibitor LAB198999, fruit growth was practically unaffected (Fig. 1b). Since GA biosynthesis inhibition has stronger effects on parthenocarpic mutants whose

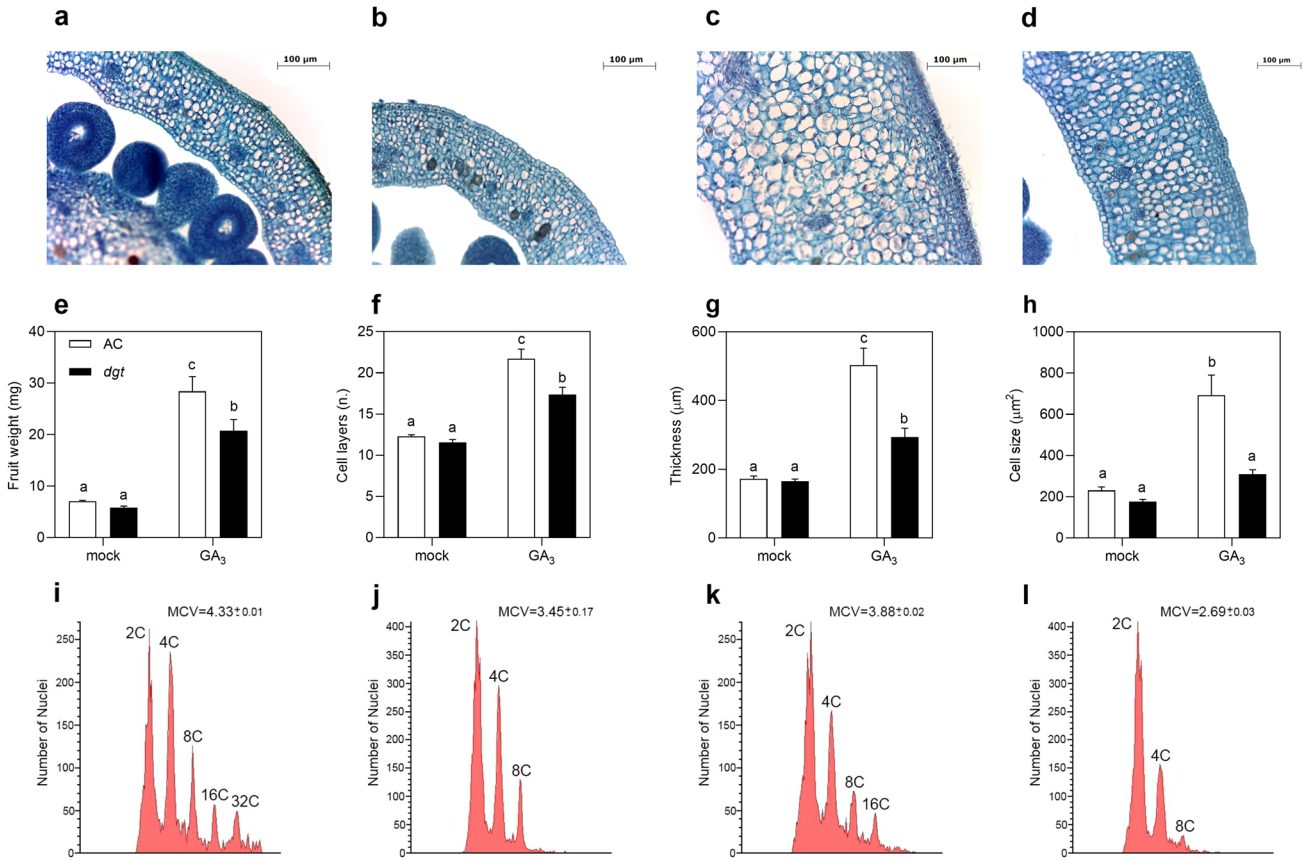

Fig. 3 Microphotographs of transversal sections of pericarps of mock- and GA_3-treated fruits of AC (**a**, **c**) and *dgt* (**b**, **d**). Fruits were emasculated at pre-anthesis and treated either with a mock solution or with 2 µg GA_3. Fruits were collected after 4 days from the treatment. Fruit weight (**e**), number of pericarp cell layers (**f**), pericarp thickness (**g**) and pericarp cell size (**h**) in fruit of AC and *dgt* treated with mock or 2 µg ovary^{-1} GA_3. Each bar represents the mean of 4 biological replicates ± SEM. Different letters indicate statistical differences according to one-way ANOVA Tuckey post-test ($P < 0.05$). Ploidy level in GA_3-treated fruits of AC (**i**, **j**) and *dgt* (**k**, **l**). Nuclear DNA content was analysed in pericarp (**i**, **k**) and in locular tissue (**j**, **l**) of fruits after 10 days from GA_3 treatment. Mean of C value (MCV) was calculated from measurements performed on a pool of 5 fruit in two independent experiments ± SEM

fruits growth largely depend on GAs (Fos et al. 2000, 2001; Olimpieri et al. 2007), our findings could indicate that, in pollinated *dgt* fruits, GAs are either synthesised in low concentrations or/and that they have little effect on fruit growth. Surprisingly, the early accumulation of high amounts of GA_1 and GA_3 in *dgt* ovaries (Fig. 1e, f) results neither in spontaneous fruit set nor in steeper growth rate (Fig. 1a), indicating that the *dgt* ovary might not sense this initial peak of active GAs. Consistently, exogenous GA_3 produces smaller fruits with fewer cells in the pericarp in *dgt* (Fig. 3a–h) compared with AC. Since fruit size is highly correlated with pericarp cell nuclear DNA content (Chevalier et al. 2011), smaller cell area in GA_3-treated *dgt* fruits reflects their lower ploidy levels (Fig. 3i–l).

Our data showed that DGT is actively involved in regulating GA metabolism in pollinated tomato fruits. Despite the early upregulation of GA 3β-hydroxylase genes after pollination, which may account for the early high content of GA_1 and GA_3, the overall GA biosynthesis in *dgt* seems to be limited by the low induction of GA 20-oxidases (Fig. 2a–e). Growing evidence reveals a role for GA 20-oxidases as one of the rate limiting steps in active GA synthesis in tomato fruits (Serrani et al. 2007b; Mariotti et al. 2011; García-Hurtado et al. 2012). In fact, some authors indicated that a concerted action of GA 20-oxidases is necessary to regulate the growth of tomato fruits (Xiao et al. 2006; Olimpieri et al. 2007; 2010). Although no significant change in GA_{20} content was detected in *dgt* (Fig. 1d), its precursor GA_{19}, was not depleted as fast as in AC (Fig. 1c), which indicates a slower conversion rate into GA_{20}. In addition, *SlGA20ox1* and *SlGA20ox3* are not upregulated in *dgt* at 6 and 8 DAP, and *SlGA20ox2* shows no expression whatsoever (Fig. 2a–c). The presence of an auxin-responsive element in the tomato *GA20ox1* gene promoter (Martí et al. 2010) and the little induction of *GA20ox1* in auxin-treated *dgt* fruits (Mignolli et al. 2019) support the idea that DGT positively regulates the expression of GA 20-oxidases genes.

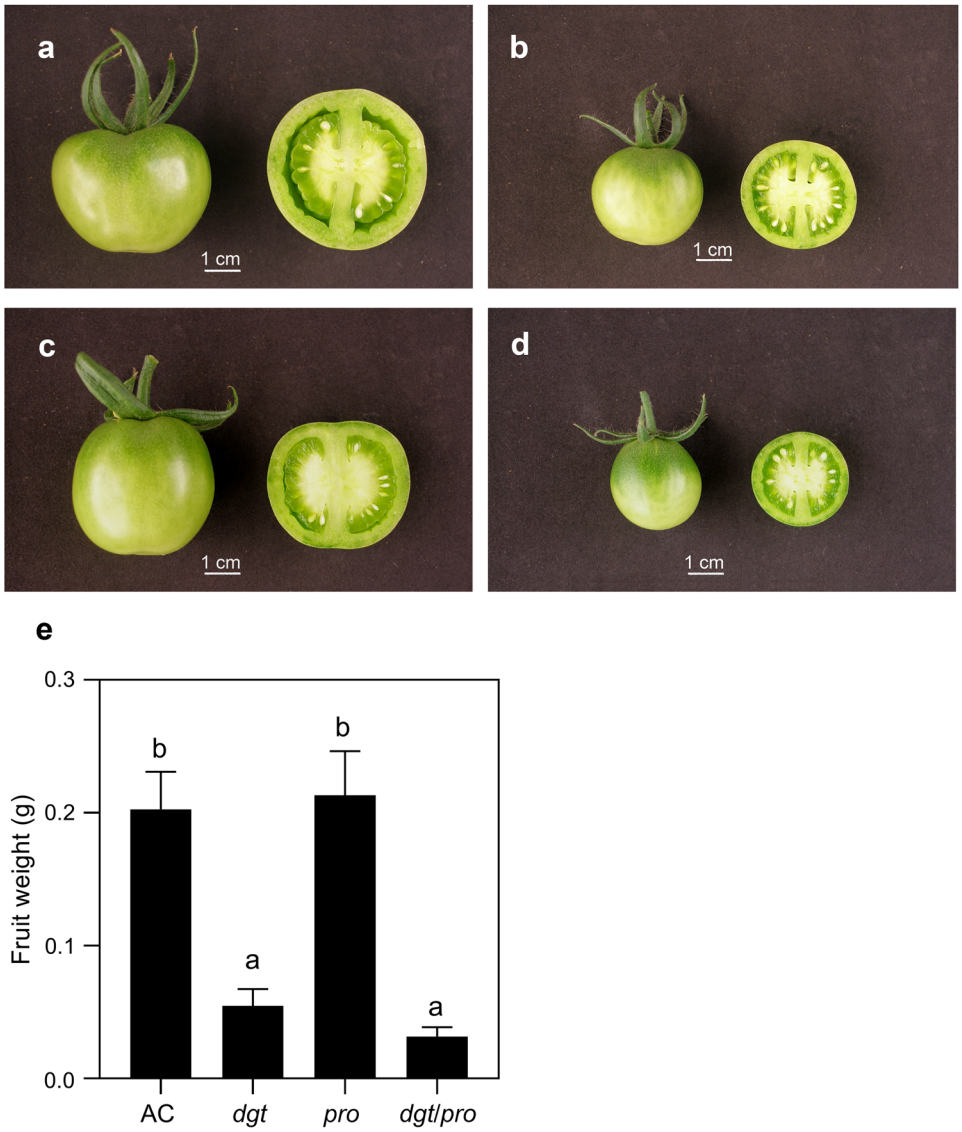

Fig. 4 Pollinated AC (**a**), *dgt* (**b**), *pro* (**c**) and *dgt pro* (**d**) fruits collected after 30 days from manual pollination. Weight of fruits after 30 days after pollination (**e**). Data are means of 20–30 fruits ± SEM. Different letters indicate statistical differences according to one-way ANOVA Tuckey post-test ($P < 0.05$)

Along with GA biosynthesis, endogenous GAs homeostasis is controlled by GA catabolic processes (Thomas et al. 1999). Unlike AC, *dgt* fruits accumulate significantly lower quantities of GA_8 but higher amounts of GA_{29} at 6 and 8 DAP (Fig. 1g, h). Being GA_8 the record of the earlier GA_1 (Coles et al. 1999) and GA_{29} the inactive form of GA_{20}, we can infer that the GA flux through GA_1 could be diminished in the mutant at the beginning of the rapid fruit growth phase. Since the moderate induction of *SlGA2ox3*, *SlGA2ox4* and *SlGA2ox5* (Fig. 2h–j) in *dgt* at 6 to 8 DAP does not contribute to increase the level of active GAs, we believe that this could be the effect of a feedforward regulation in response to a relatively low active GA_1 supply. Indeed, in *Arabidopsis,* active GAs upregulated the expression of *AtGA2ox1* and *AtGA2ox2*, whereas their deficiency promoted the transcription of *PsGA2ox1* and *PsGA2ox2* in pea shoots according to a positive feedforward control (Thomas et al. 1999; Elliott et al. 2001).

In conclusion, our data indicate that the *dgt* mutation slows down active GAs biosynthesis in pollinated fruits by preventing the upregulation of the GA 20-oxidases and, at the same time, limits the effect of active GAs (i.e. GA_3) on fruit growth. However, it seems unlikely that these findings may account for the reduced fruit size in the mutant. If the phenotype of the *dgt* fruit was the result of an attenuated GA signalling, we would have expected them to grow more in presence of a constitutively active GA signalling. In fact, the lack of the protein DELLA in the double mutant *dgt pro* does not result in bigger fruits than in *dgt* (Fig. 4). This leads us to think that, regardless of the abundance of active GAs or GA responsiveness, the GA-induced response in tomato ovaries may only be partial in the *dgt* mutant. Interestingly, fruit

respiration and sugar metabolism are severely affected in *dgt* resulting in impaired cell growth (Batista-Silva et al. 2019; 2022). It is therefore conceivable that primary metabolism constraint in *dgt* overrules the effect of active GAs or GA signalling on fruit growth.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10725-022-00921-x.

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Author contributions FM and MLV conceived the experiments. LM performed endogenous gibberellins analyses while FM carried out gene expression and histological analyses. FM and MLV wrote the paper. All authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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