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Grafting of tomato mutants onto potato rootstocks: An approach to study leaf-derived signaling on tuberization

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Abstract

Photoperiod controls many plant developmental responses, including tuber formation in potato (*Solanum tuberosum* L.) plants. Photoperiodic stimuli are received by phytocromes in the leaves and must be conveyed to the underground portion of the plant for the tubers to develop, but the nature of the signal responsible for this is hitherto unknown. Plant hormones are known to have a role in tuber formation, through a series of complex interactions between them and with other substances. Here, some accessions from the large collection of hormone and photomorphogenic mutants in tomato (*Lycopersicon esculentum* Mill.) were used to study the process of tuberization through grafting onto potato rootstocks. The chosen photomorphogenic mutants were *aurea* (*au*, chromophore deficient), *far red insensitive* (*fri*, PHYA deficient), *temporary red insensitive* (*tri*, PHYB1 deficient) and *high pigment* (*hp*, exaggerated phytochrome response), as well as the hormone mutants *gibberellin deficient-1* (*gib-1*), *dwarf* (*d*, brassinosteroid deficient), *diageotropica* (*dgt*, auxin insensitive), *notabilis* (*not*, ABA deficient), *procera* (*pro*, gibberellin hypersensitive). Tuber number, tuber and shoot dry weight and sprouting were quantified as a measure of the tuber induction capability of each genotype. Tomato scions were always less effective to promote tuberization than the potato scions. Among photomorphogenic mutants, the highest tuberization was achieved with the chromophore deficient (*au*). The tuber induction capability was (in decreasing order) *d*, *gib-1*, *dgt*, *not* and *pro* for hormone mutants. A clear-cut negative correlation ($r = -0.98$) was observed between dry tuber weight and dry shoot weight. Sprouting also varied to a large extent, the most sprouting-inducer was the gibberellin deficient scion. These results lead us to suggest that source–sink relationship, which is affected by both hormones and photomorphogenesis, has a pivotal role in tuber formation and that tomato scions fail to produce a substance(s) involved in the convertion of the stolon into the strong sink that forms the tuber.

Keywords: *Lycopersicon*; Phytocromes; Plant hormones; Signal transduction; *Solanum*; Source–sink relationship

1. Introduction

The process of tuberization in potato is under control of numerous environmental factors, photoperiod being arguably the most important [1]. Tuberization in many potato lines is favored by short days (SD), although the critical photoperiod may be variable among different genotypes. Thus, wild-type potato lines belonging to the Andigena group, which are cultivated at high altitudes near the Equator, typically have a critical photoperiod of only 12–13 h. In contrast, the Tuberosum group varieties, which are the result of centuries of selection that originated modern cultivars, have a critical photoperiod of 15 or more hours [2].

The effects of light on plant development are mediated by different types of photoreceptors (phytochromes, blue-UVA photoreceptors, UVB photoreceptors, chryptocromes). Phytochrome is the most thoroughly characterized, biochemically and physiologically, of these molecules [3]. It is involved in the photoperiodic responses of flowering and tuberization, as well as shade avoidance syndrome, light-dependent development of the photosynthetic apparatus and

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other morphological and biochemical processes [4]. It was demonstrated that the removal of PHYB by antisense *PHYB* gene resulted in potato tuberization in both long days (LD) and SD [5] and that the overexpression of the *PHYB* gene enhanced the inhibitory effect of LD on tuberization [6].

Even though the photoperiodic stimulus occurs in the leaf, it clearly has to be transmitted to the underground portion of the potato plant for the development of tubers to occur. The existence of such a translocable substance was demonstrated as far back as the 1950s by means of grafting experiments (reviewed in ref. [7]). However, the chemical nature of a substance capable of either inhibiting or inducing tuberization has not been hitherto discovered.

Candidate substances for leaf-derived signals that induce or repress tuberization are plant hormones. Among them, gibberellins (GAs), abscisic acid (ABA), cytokinins (Cks) and jasmonic acid (JA) are the most related to tuberization [8]. GAs have long been known to inhibit tuberization [9] and appear to play a role in the photoperiodic control of tuber formation by preventing tuberization in LD. It is remarkable that a dwarf mutant of *S. tuberosum* ssp. *andigena* that is able to tuberize in LD as well as in SD has been shown to have a partial block in its GA biosynthetic pathway [10]. GAs have also been demonstrated to induce the migration of PHOR1, a photoperiod-responsive protein, to the nucleus [11]. This could prove to be a key link in the signaling between phytocrome and plant hormones. In contrast to the clear action of GAs, the exact role of ABA remains unclear. The ABA/GA ratio was found to be high in potato plants grown in SD and low in LD and night breaks [12]. However, it was found that *droopy*, an ABA-deficient mutant of potato has no clear differences on tuberization when compared to wild-type plants [13]. As for cytokinins, it is believed that their role is to break tuber dormancy. This comes in agreement to the fact that potato plants overexpressing the *Agrobacterium ipt* gene, for cytokinin biosynthesis, present very early sprouting [14]. Jasmonic acid (JA) was the latest plant hormone shown to have an effect on tuberization [15]. Tuberonic acid, a chemically related compound, was extracted from induced potato leaves and also showed strong tuber-inducing properties in vitro assays [1]. In spite of this, neither the elevation of endogenous JA acid levels [16], nor its direct application onto potato leaves [17] had an effect on tuber induction. Furthermore, the inhibition of JA biosynthesis through salicylhydroxamic acid did not prevent tuberization under inducing conditions [18]. The hypothesis has been put forward that JA may exert its effects principally by antagonizing the effect of GA on microtubule orientation [1].

Mutants are a very powerful tool to study various developmental processes. Unfortunately, potato is not a genetically friendly model and few mutants are available in this species. Hence, the main approach to date has been the analysis of potato transgenic plants [6,14,19,20]. However, in tomato, a very closely related species of the Solanaceae family, there exists a large collection of defective mutants on phytochrome biosynthesis and response, as well as in hormone metabolism and sensitivity [21]. Tomato deficient mutants in PHYA and PHYB1 synthesis (named *far red insensitive* and *temporary red insensitive*, respectively), as well as PHYB2 deficient mutants have been isolated [22–24]. Deficient mutants in phytochrome chromophore synthesis (*aurea* and *yellow green-2*) are also available [25]. Three others photomorphogenic mutants, with exaggerated phytochrome response, named *high pigment*, *atroviolacea* and *Intense pigment* [26] exist in tomato. Hormonal tomato mutants are numerous and well-characterized. They include *procera*, with exaggerated sensitivity to gibberellin [27], *gibberellin deficient* [28], *diageotropica*, which presents altered auxin sensitivity [29], *notabilis*, an ABA-deficient mutant [30] and the brassinosteroid-deficient *dwarf* mutant [31], among many others.

In the present work, we describe a variation on the classic grafting approach to study leaf-derived signals that influence potato tuberization. We show that different tomato phytochrome or hormone-related mutants can be successfully grafted onto potato rootstocks and that they specifically affect tuberization, as well as potato root development. This simple, yet promising approach opens the possibility of using the aforementioned array of mutants to unravel the signal transduction pathway that controls tuberization.

2. Material and methods

2.1. Plant material

Seeds from tomato (*Lycopersicon esculentum* Mill.) photomorphogenic mutants *aurea* (*au*) (LA3280), *far red insensitive* (*fri*) (LA3809), *temporary red insensitive* (*tri*) (LA3808) and *high pigment* (*hp*) (LA3004), as well as hormone mutants *gibberellin deficient-1* (*gib-1*) (LA2893), *dwarf* (*d*), *diageotropica* (*dgt*) (LA1093), *notabilis* (*not*) (LA0617), *procera* (*pro*) (LA0565) were provided by Dr. Roger Chetelat (University of California, Davis, USA). Potato (*Solanum tuberosum* L) cv. Monalisa was used as rootstock. The potato plants were derived from tubers treated to break dormancy (immersion in a 10 $\mu g\ mL^{-1}$ GA solution for 15 min). Tomato seeds were sown 17 days after the breaking of tuber dormancy. The grafting was carried through 37 days after dormancy breaking. The tuberization was evaluated after 50 days after grafting. All tomato scions were mantained without flowers during the experiment to prevent fruit formation, which could represent a competing sink to potato tubers.

2.2. Grafting and cultivation

The tomato photomorphogenic and hormone mutants and potato scions were grafted onto potato stocks. The scions were prepared by cutting the stem with a razor blade below the

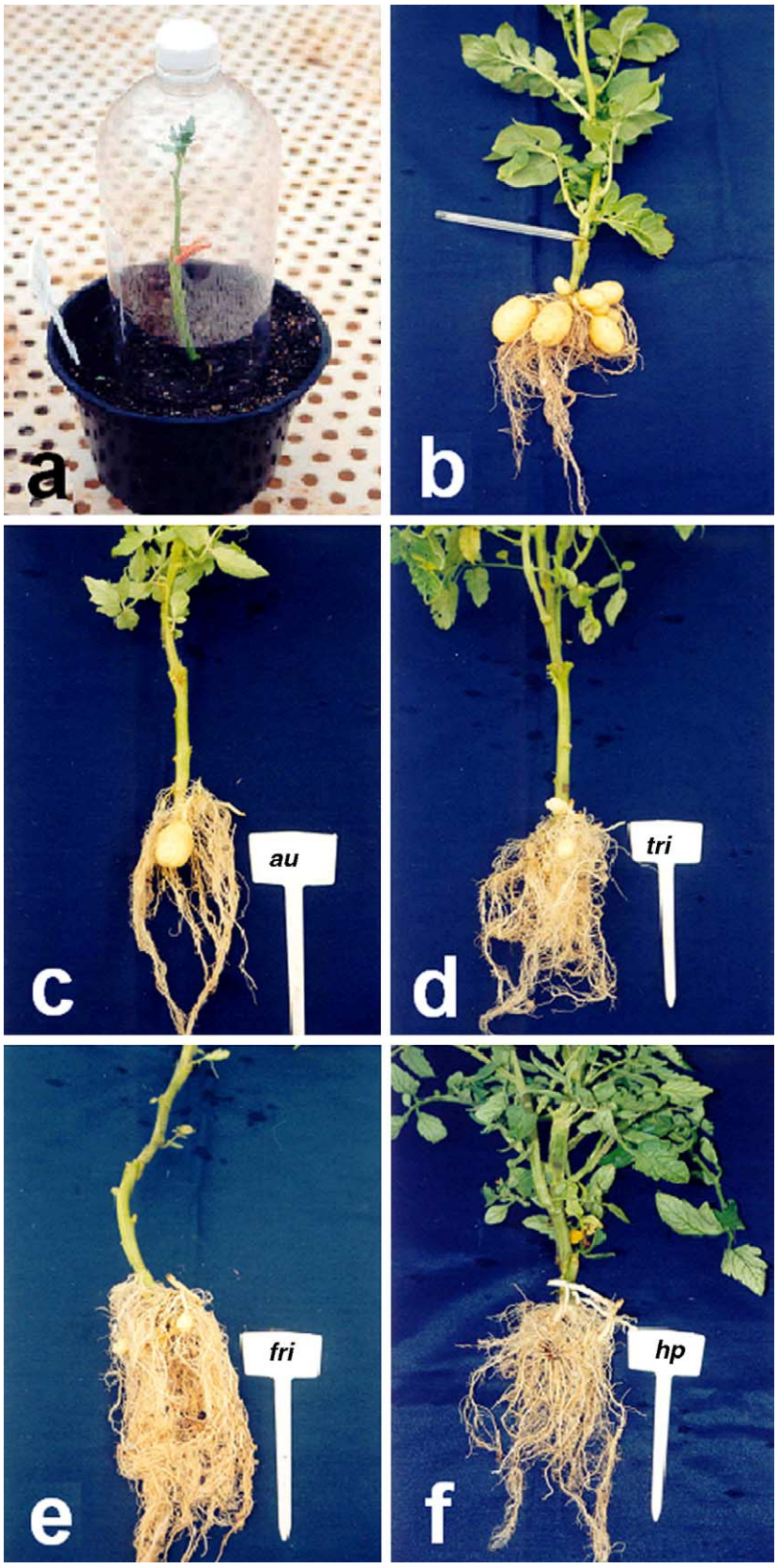

Fig. 1. Tomato scions grafted onto potato rootstocks. A sample grafting is shown in a: the plastic bottle provides the humid environment and the peg (orange) fastens scion and rootstock together. From b to f, representative plants of the following treatments (scions): potato (b), tomato genotypes *au* (c), *tri* (d), *fri* (e), *hp* (f). For abbreviations of tomato genotypes refer to Section 2. The pen in (b) indicates the local of grafting. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

second or third leaf from the apex. The stocks were prepared by cutting transversely approximately 10 cm above soil level with a razor blade. The scion to be grafted was then placed on top of the stock. The scion was cut into a wedge shape and inserted into a "V" shaped incision in the stock. The grafted plants were then placed in a vase with a transparent cover to provide a humid environment (Fig. 1a). After 1 week, the cover was removed and the plants were maintained in a greenhouse. Two liter pots were used with a commercial substrate (PlantMax HT, Eucatex, Brazil). When necessary, the plants were fertilized with a solution of NPK 20-20-20 plus micronutrients at concentration of 1 g L^{-1}. The greenhouse temperature ranged from 20 to 35 °C. A set of experiments was conducted under 13.5 h daylight for photomorphogenic mutants and 11 h daylight for hormone mutants. Both experiments represent a SD condition for the potato genotype used.

2.3. Dry weight and tuber number

The aerial parts and tubers were removed and dried at 65 °C for 2–3 days. The tubers were sliced with a razor blade, to facilitate drying. The tuber number and dry weight were measured in 8–10 plants per treatment. From these parameters, the means and the standard errors were calculated.

3. Results

3.1. Performance of grafting

All interspecific graftings performed were successful, as has been already demonstrated for tobacco [32]. Either with photomorphogenic mutants (Fig. 1) or hormone mutants (Fig. 3), tomato scions were able to grow vigorously. All tomato grafts presented a reduced tuber dry weight when compared to the potato scion (Figs. 2b and 4b). Tuber formation was even lower in photomorphogenic mutants, when compared to hormone mutants, but this could be due to the longer photoperiod used (13.5 h rather than 11 h light). Unfortunately, tomato photomorphogenic and hormone mutants are not available in the same genetic background. However, our results show clearly that independent of the mutation (and its genetic background) tomato grafts were always inhibitory for tuberization (Figs. 1 and 3). Thus, we decided that it was irrelevant to perform the wild-type tomato onto potato grafting as a control, and to use instead potato grafted onto potato as a reference. This would allow us to observe if tomato mutants reverted this inhibitory effect.

3.2. Grafting with photomorphogenic mutants

Among the photomorphogenic mutants, the *hp* (exaggerate response to phytochrome) tomato graft induced the least tuberization (Fig. 2). On the other hand, the *au* mutant,

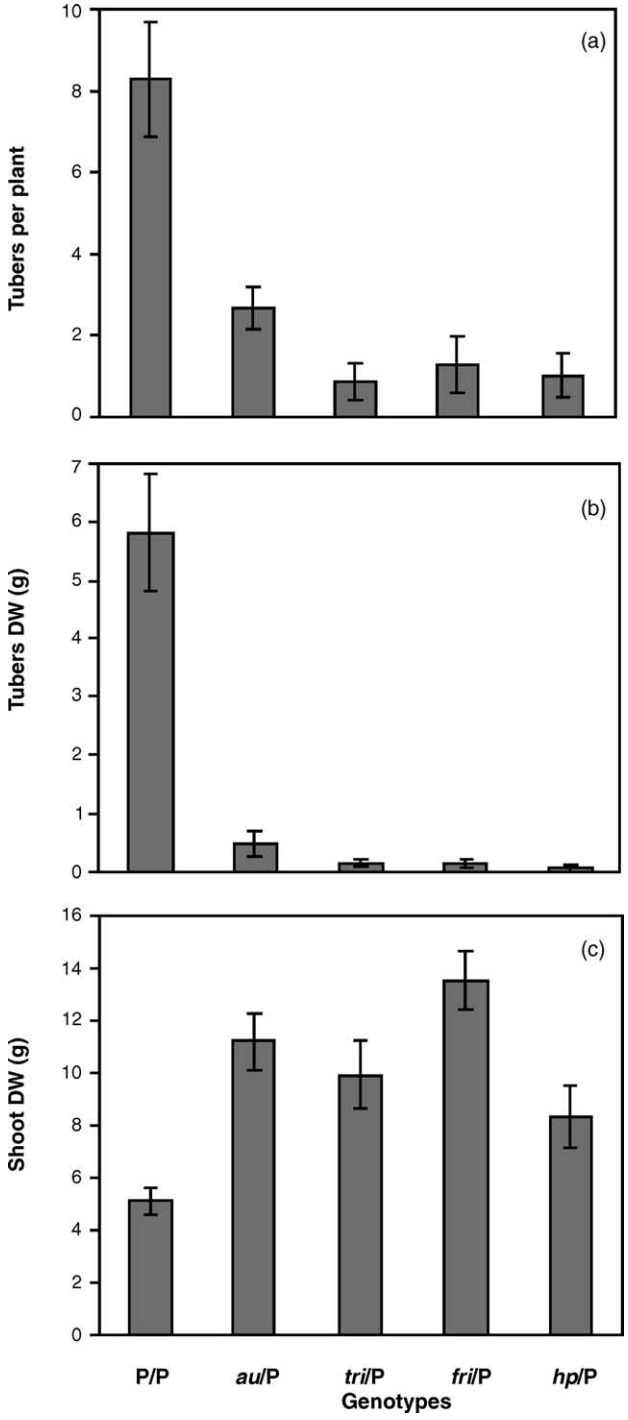

Fig. 2. Potato tuber number (a) and dry weight of tuber (b) and shoots (c) as affected by different tomato photomorfogenic mutants. The "P" symbol represents the potato scion or rootstock. The symbols *au*, *tri*, *fri* and *hp* are the tomato genotypes used as scions (refer to Section 2 for abbreviations). Data are means plus standard errors (S.E.).

which has no phytochrome activity whatsoever (considering that it is phytochrome chromophore deficient), produced significantly higher tuberization than all the other treatments (Fig. 2a and b). These results suggest that the presence of any functional phytochrome is inhibitory for tuber formation. In *S. tuberosum* ssp. *andigena* it has been shown that transgenic

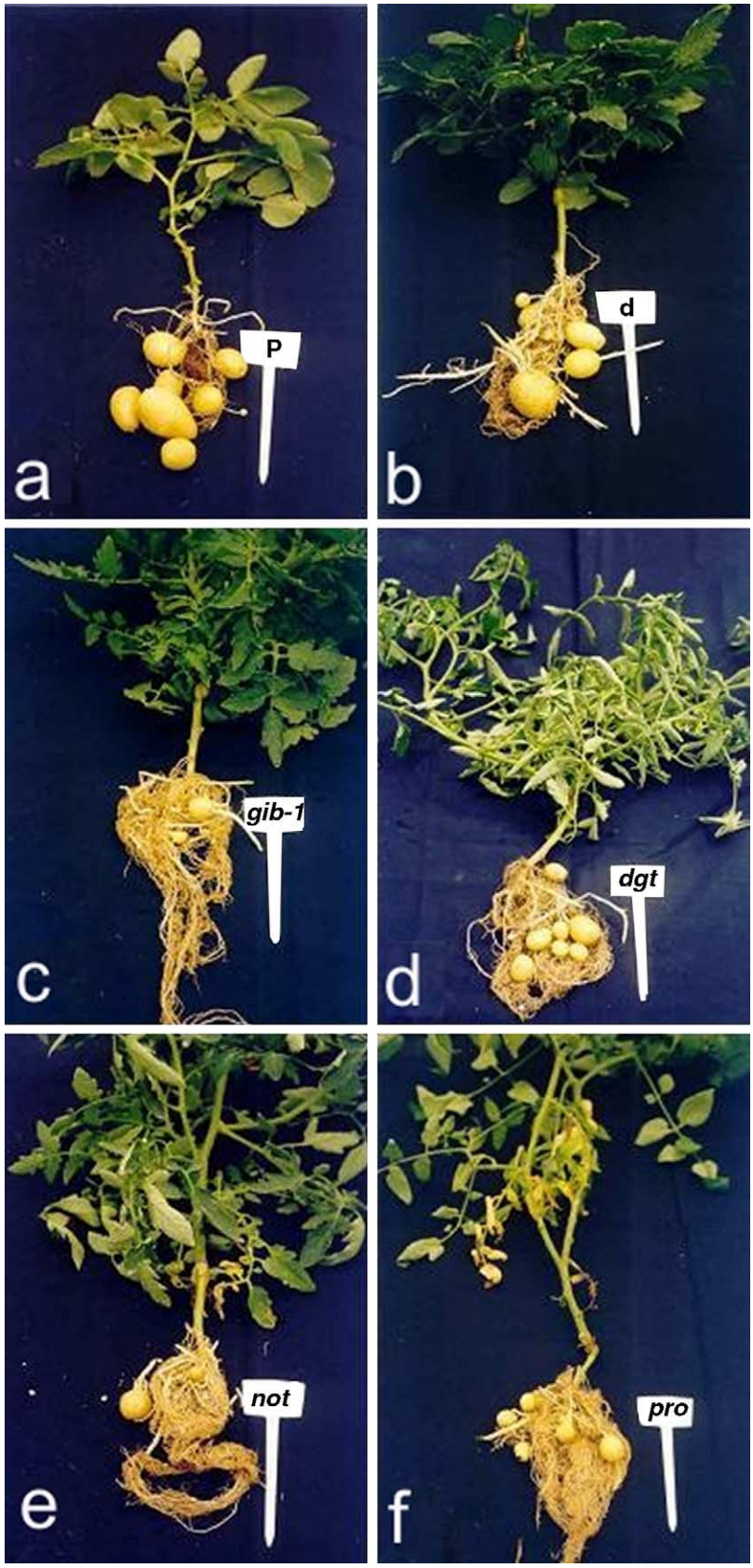

Fig. 3. Tomato scions grafted onto potato rootstocks. From (a) to (f), representative plants of the following graft combinations (scions): potato (a), tomato genotypes *d* (b), *gib-1* (c), *dgt* (d), *not* (e) and *pro* (f). For abbreviations of tomato genotypes refer to Section 2.

antisense plants for PHYB are able to tuberize in LD [19]. Similarly, Yanovsky et al. [20] using transgenic potatoes with either increased (sense transformants) or reduced (antisense transformants) phyA expression showed that this phytochrome delays tuber production in response to SD. Considering that tomato has at least five different types of phytocromes, it is not surprising that either *fri* (phyA defective) or *tri* (phyB1 defective) did not induce tuberization, since each mutant has only one of them inactivated. Furthermore, since tomato has two types of PHYB and the *tri* mutant is a phyB1 defective, one may conclude that the presence of a functional phyB2 could explain the difference between our results and those obtained in grafts with antisense phyB [7]. In all the tomato graftings the shoot dry weight was higher than the potato control (Fig. 2c), whereas in the case of tuber dry weight it was exactly the opposite (Fig. 2b). Potato root development was also more prominent when tomato was the shoot, with the root system formed in the potato grafted with the *fri* mutant clearly the largest (Fig. 1e). These results seem to indicate that, regardless of the mutation and the genetic background, tomato scions tend to divert photoassimilates to shoots and roots, but not tubers.

3.3. Grafting with hormone mutants

The tuber number was highly variable among treatments (Fig. 4a). However, a clear negative correlation can be observed when comparing the dry weight of tubers and of shoots (Fig. 4b and c). As expected, accumulation of biomass in potato took place mainly in the tubers. In hormone mutants this varied to different degrees. The *dwarf* (brassinosteroid deficient) and *gib-1* (GA deficient) mutants were the closest to the potato control, indicating that they were the most capable of inducing a strong sink in the stolons. This behavior was expected in the gibberellin-deficient mutant, but was unforeseen in the case of *dwarf*, and it could define a novel role for brassinosteroids (BRs) in tuberization. An interpretation for these results is that both GA and BR deficiency primarily reduce shoot growth, which would cause a redirection of biomass to the tubers. Consistently with this, the *dgt* mutation (low auxin sensitivity) also has a reduced shoot growth and presented enhanced tuber formation when compared to the *not* (ABA defective) and the *pro* mutants, which have a prominent shoot growth (Figs. 3 and 4c). Moreover, as *dgt* and *pro* are mutations affecting sensitivity, which would be confined to the scion and not transmitted to the potato stock, their effect on tuberization should be indirect, i.e. affecting shoot growth. The shoot growth of each mutant is consistent with what is expected for each mutation, and this is a clear evidence that it is the shoot growth that is affecting tuber growth and not vice versa.

3.4. Sprouting

In grafts with hormone mutants it was observed that tomato scions promoted (or did not inhibit) the sprouting of the new tuber formed (Fig. 5). This event was more intense when the tomato gibberellin deficient mutant (*gib-1*) was used as scion. The lower rates of sprouting were shown by tubers derived from grafts with *diageotropica* and *procera*. Potato tubers never sprouted in the plant when the scion was the potato plant itself.

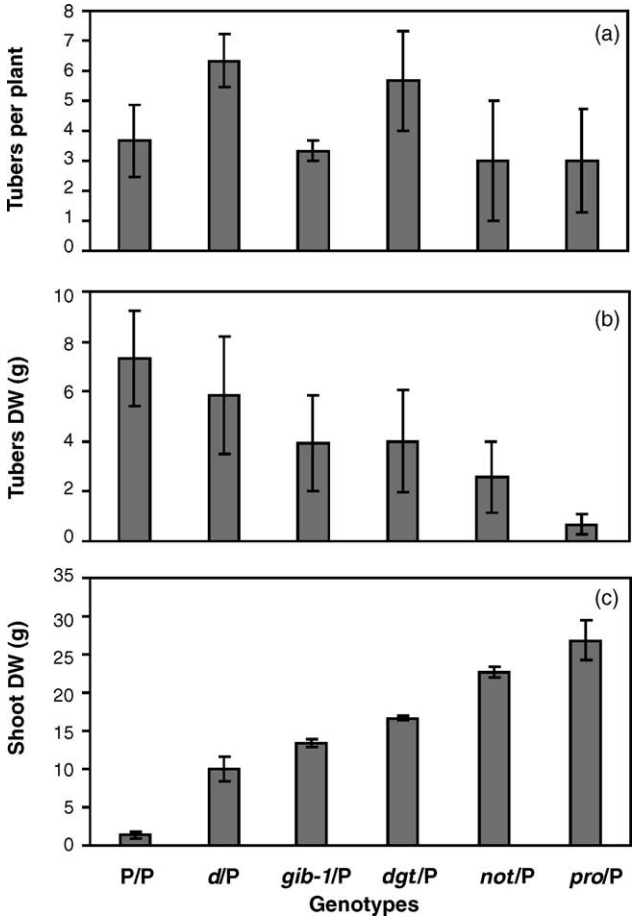

Fig. 4. Potato tuber number (a) and dry weight of tuber (b) and shoots (c) as affected by different tomato hormone mutants. The "P" symbol represents the potato scion or rootstock. Symbols *d*, *gib-1*, *dgt*, *not* and *pro* stand for the tomato genotypes used as scions (refer to Section 2 for abbreviations). Data are means plus standard errors (S.E.).

4. Discussion

We have shown here that different tomato mutants can be successfully grafted onto potato rootstocks and that they specifically affect tuberization as well as potato root development. Regardless of the genotype tested in the present work, tomato scions were always less effective in promoting tuberization than the potato scions. Inasmuch tomato is not a potato, it is not surprising that its shoot will not induce tuberization to the extent a potato does. Nevertheless, the search for the differential factor between these two species that so dramatically affects tuber formation provides an interesting opportunity to understand

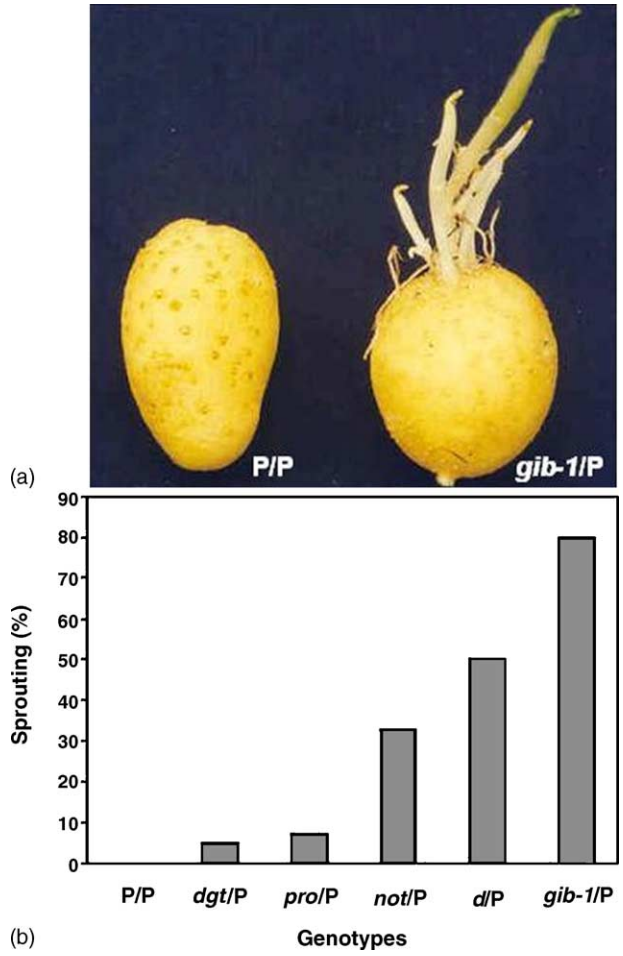

Fig. 5. Sprouting in tubers derived from potato onto potato (P/P) and hormone mutants onto potato grafts. (a) Tuber from a P/P graft (left) and from a *gib-1*/P graft (right). (b) Sprouting percentage as quantified in 3 plants per treatment.

the process of tuberization. In this sense, both sets of experiments performed here strongly suggest that an important factor affecting potato tuberization is the source–sink relationship between aboveground shoots and belowground tubers.

Although the tuber is an organ formed by specific developmental processes, it is arguably not a truly organogenic event but the conversion of pre-existent organs (stolons) into strong sinks. Thus, in the present work we could confirm specific inhibitory effects of phytochrome and gibberellins on tuberization, but, at least part of these effects seem to be mediated by source–sink relationship. In this sense, other factors that promote shoot growth, such as high soil N levels, tend to reduce tuber development, while treatments which inhibit or reduce shoot growth, such as growth retardants, promote tuber formation [2]. Furthermore, some authors have used stem cuttings to study in vitro tuber formation [9] and it is interesting to note that tuberization on such cuttings was maximal when the amount of attached stem was minimized [2] and only when sucrose is present in the culture medium [9]. Macháckova et al. [12] showed that in SD conditions, which promote tuber formation, *Solanum tuberosum* spp. *Andigena* plants have longer stems but produce a much lower mass of shoots. On the other hand, LD plants accumulate more photosynthates in aboveground parts and, in addition, are more branched with a greater number of stems [12]. These observations suggest that even the effect of photoperiod could be mediated, to a great extent, by source–sink relationship.

The results presented here suggest that tomato scions somehow fail to divert photoassimilates for tuber development. This effect could be best observed by the inverse correlation ($r = -0.98$) between tuber and shoot dry weight in the graftings with hormone mutants (Fig. 4a and c). In the case of photomorphogenic mutants the reduced degree of tuberization presented by the graftings does not allow for such a perfect correlation, but it is remarkable that while the potato control shows the lowest shoot dry weight (Fig. 2c), its tuber dry weight is the highest (Fig. 2b), again indicating an involvement of source–sink relationships. Also in the assay with photomorphogenic mutants, tomato scions seem to partition photoassimilates for potato root growth (notice root volume in Fig. 1) but they are less efficient to convert stolons into the main sink. The opposite situation occurs when the scion is the potato, which suggests that potato produces some tuber-specific sink-inducing component that is missing in the tomato scions. Tomato is a day-neutral plant and it is possible that a daylength-dependent pathway for floral/tuberization induction does not exist in this species.

The observation that non-tuber forming plants maintained in LD condition have a branched phenotype [12] indicates that tuberization parallels apical dominance, which could be also a phenomenon of source–sink relationship [33]. On this token, the stimulation of growth in the lower stolons is at the expense of the non-development of aboveground axillary buds. The tomato *lateral suppressor* (*ls*) mutation, which inhibits lateral bud development, was reported to encode a negative regulator possibly involved in GA signal transduction [34]. This observation seems to indicate that high GA levels are implicated in low branching and vice versa, which is in apparent conflict with the use of exogenous GA to sprout tubers before use as potato seeds [35]. However, breaking of dormancy and sprouting would cause the sink to be diverted from the tuber to the new dominant shoot aboveground. It is interesting to note that at 11 h daylight regime, some tomato scions had a prominent effect on the sprouting of the new tuber formed, the GA deficient mutant (*gib-1*) being the most effective (Fig. 5). Therefore, even though GA is low in the aboveground shoots of the *gib-1* mutant, the possibility that it becomes high in the belowground wild-type potato stolons in this kind of graft should be not discarded. A hypothesis to explain this is that once the tubers are formed they would be able to synthesize higher levels of GA due to the lack of initial feedback inhibition of the biosynthetic pathway from scion-derived GA.

Fig. 6. Potato leaf morphology suggestive of high gibberellin (GA) levels. From left to right, tomato leaf, tomato leaf + 100 μM GA and potato leaf. Note the smooth edged and pale green phenotype of potato and tomato + GA leaves, which could be effects of the high GA content [36]. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

In spite of the fact that potato tubers ordinary develop from underground stolons, every axillary bud on a potato stem has the potential to develop a tuber [2]. It is also well documented that the lowering of GA levels is necessary for tuberization [36]. One hypothesis to explain this differential control may be the presence of high levels of GA in aboveground shoots and low GA levels in belowground ones. High GA levels in aboveground parts could also contribute for a feedback inhibition of the biosynthetic pathway in belowground stolons. This kind of mechanism may be also operative to prevent the sprouting of the new tuber formed, and is in agreement with the results observed in GA deficient scions (Fig. 5). It is remarkable that the potato leaf resembles a tomato leaf treated with GA (Fig. 6), which could be an indirect indication that the aboveground parts of potato have high GA levels. In line with this observation, antisense phyB potato plants have an aboveground phenotype typical of a GA overproducer/hypersensitive plant, combined with an increased tuber formation in the belowground portions [37] which in turn is typical of low GA level or sensitivity. Moreover, transgenic potato plants with reduced levels of PHOR1 protein (a GA signaling component) result in early tuberization under SD, but increased levels of the PHOR1 protein were detected in the leaves of induced plants [11].

In summary, based on the results obtained in the interspecific graftings and discussed herein, we propose that although tuber formation could be a balance of different signaling pathways affected by phytochromes, plant hormones and their effects on development (such as apical dominance), a convergent point that mediates these pathways seems to be source–sink relationship. Amidst the various substances that could be translocated through phloem to a given sink are the mRNAs of homeotic knox genes [38]. This would fit to the observation that plants overexpressing knox genes have both reduced levels of GA [39] and increased levels of cytokinins [40], as well as increased tuber formation [41]. If source–sink relationship has a pivotal role in tuber formation, it is reasonable to assume that cytokinin has a central role on tuberization, since it is the main hormone class that influences sink formation [42]. This is consistent with early results showing that addition of cytokinins is necessary for in vitro tuber formation [43] and more recent work showing that transgenic potato plants expressing the *ipt* gene (and thus with increased endogenous levels of cytokinins) display a greater capacity to form tubers [14]. Thus, the wide collection of tomato developmental mutants (which includes homeotic mutants) represents a powerful tool to target the substance(s) involved in the convertion of the stolon into the strong sink that forms the tuber.

Acknowledgments

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