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Hormones in tomato leaf development

Ido Shwartz, Matan Levy, Naomi Ori*, Maya Bar*

The Robert H. Smith Institute of Plant Sciences and Genetics in Agriculture and The Otto Warburg Minerva Center for Agricultural Biotechnology, Hebrew University, P.O. Box 12, Rehovot 76100, Israel

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ABSTRACT

Leaf development serves as a model for plant developmental flexibility. Flexible balancing of morphogenesis and differentiation during leaf development results in a large diversity of leaf forms, both between different species and within the same species. This diversity is particularly evident in compound leaves. Hormones are prominent regulators of leaf development. Here we discuss some of the roles of plant hormones and the cross-talk between different hormones in tomato compound-leaf development.

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Contents

1. Introduction

Leaf development is highly flexible, giving rise to a wide continuum of leaf shapes. Leaves are determinate organs that go through a limited growth period before differentiating to provide for the plant. Following their initiation, leaves establish three axes of polar growth, the adaxial-abaxial, proximo-distal and medial-lateral axes (Byrne, 2012), and undergo a transient state of indeterminate growth, during which the basic shape and often the size potential of the leaf are determined, and organogenesis of lateral appendages such as leaflets occurs (Floyd and Bowman, 2010; Kaplan and Cooke, 1997). Following this morphogenetic phase the leaf expands and differentiates to reach its final size and shape. The extent of the leaf morphogenetic phase is somewhat predictable for each species, factoring in additional characteristics such as leaf position. However, leaf morphogenesis responds flexibly to the specific genetic, developmental and environmental context (Bar and Ori, 2014). The timing of the transition from morphogenesis to differentiation and the overall leaf maturation rate are fine-tuned, resulting in a wide diversity of leaf sizes and shapes that vary within and between species. Compound leaves, such as those of tomato (*Solanum lycopersicum*), are composed of multiple leaflets and are characterized by an extended morphogenetic phase, enabled by the transient maintenance of a meristematic region at the leaf margin, termed marginal blastozone (Hagemann and Gleissberg, 1996; Kaplan, 2001). Tomato leaves have a particularly long morphogenetic stage, which results in a wide range of leaf sizes and shapes and enhanced flexibility in leaf development (Bar and Ori, 2014; Bar et al., 2015; Burko and Ori, 2013).

Hormones serve many crucial functions in plant life, and are prominent factors in the regulation of leaf development. Here we discuss the role of plant hormones during compound leaf development in tomato, the regulation of hormonal pathways, and the

* Corresponding authors.
E-mail addresses: naomi.ori@mail.huji.ac.il (N. Ori), mayapiff@gmail.com (M. Bar).

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cross-talk between different hormones, with specific emphasis on the balance between morphogenesis and differentiation and on marginal patterning.

2. Auxin

Auxin plays a role in nearly all developmental processes in plants, and leaf development is no exception. Auxin coordinates the phyllotaxis of leaf initiation from the shoot apical meristem (SAM), and determines the location of serrations and the initiation of leaflets and lobes from the margin of leaf primordia. Auxin was also shown to influence leaf symmetry in both adaxial-abaxial (Pekker et al., 2005) and bilateral (Chitwood et al., 2012) patterning. Proper leaf development requires the distribution of auxin in precise locations within a specific spatiotemporal developmental context (Barkoulas et al., 2008; Ben-Gera et al., 2012; Bilsborough et al., 2011; Koenig et al., 2009). The effects of altering auxin levels or response on tomato leaf form are depicted in Fig. 1.

Formation of discrete auxin response maxima, generated by auxin biosynthesis and directional auxin transport mediated by PINFORMED1 (PIN1), occurs prior to, and is required for organ initiation at the flanks of the SAM (Benkova et al., 2003; Cheng et al., 2007; Heisler et al., 2005; Pinon et al., 2013; Reinhardt et al., 2003). Mutating *PIN1* inhibits organ initiation in Arabidopsis (Reinhardt et al., 2003) and *Cardamine hirsuta* (Cardamine) (Barkoulas et al., 2008). Chemical inhibition of polar auxin transport also interferes with leaf initiation, underscoring the importance of discrete auxin response at specific locales. Altering auxin biosynthesis by up or down regulating genes from the YUCCA family can also affect leaf development, with YUCCA down regulation reported to inhibit organ initiation in Arabidopsis, maize and petunia (Gallavotti et al., 2008; Tobeña-Santamaria et al., 2002; Zhao et al., 2001). This demonstrates a requirement for a threshold level of auxin to be available for proper leaf development. Correct phyllotaxis was hypothesized to depend on an inhibitory field generated by developing primordia (Braybrook and Kuhlemeier, 2010). One of the earliest indications of leaf initiation is the formation of an auxin maximum in the meristem. The two youngest primordia were proposed to drain auxin from the meristem, thereby determining the position of the next incipient primordium. Thus, auxin acts as an inducer of organ formation, and the postulated inhibitory fields around existing primordia are thought to result in fact from low auxin concentrations in their vicinity (de Reuille et al., 2006; Jönsson et al., 2006; Reinhardt et al., 2005; Smith et al., 2006). In *Arabidopsis*, auxin was also reported to mediate the activities of transcription factors that promote leaf initiation and early development. For example, transcription factors from the AINTEGUMENTA (ANT)-like (AIL)/PLT family were suggested to affect phyllotaxis by promoting auxin biosynthesis in the central zone of the SAM (Pinon et al., 2013). Down regulating the activity of genes from the YABBY (YAB) family of HMG-like proteins leads to defects in lamina differentiation, establishment of the leaf marginal domain, and leaf polarity, accompanied by altered distribution of auxin signalling and PIN1 (Sarojam et al., 2010).

Manipulation of the auxin pathway in tomato leaves can result in striking leaf simplification phenotypes, which may be initially surprising given the roles of auxin in the promotion of both organ initiation and organ growth. Exogenously altering auxin levels in young developing leaves affects final leaf form. For example, growing young tomato plants on media containing auxin (Fig. 1b) or auxin transport inhibitors (Fig. 1c) leads to the formation of simplified leaves. This simplification results from the abolishment of the discrete distribution of auxin response in the leaf margin, required for the formation of distinct and separated leaflets. Genetically altering endogenous auxin levels and localization also results in leaf simplification phenotypes, stemming once again from perturbations in the formation of auxin-response maxima. For example, expressing the bacterial auxin biosynthesis gene *tryptophan monooxygenase* (*iaaM*) (Romano et al., 1995) in developing tomato leaves results in leaves that are simpler than wild type leaves, with a severe reduction in secondary leaflets (Fig. 1f) (Ben-Gera et al., 2012). A closer look at some of the auxin response mutants points to defects in leaflet separation rather than lack of leaflet initiation. The tomato *ENTIRE* (*E, SlIAA9*) gene encodes a protein from the Aux/IAA family of auxin response repressors (Berger et al., 2009; Wang et al., 2005; Zhang et al., 2007). Leaves of the recessive, loss-of-function tomato mutant *entire* (*e*) have single lobed lamina with partially fused primary leaflets and no secondary leaflets (Dengler, 1984; Rick and Butler, 1956). *e* leaf primordia initiate leaflets, but these fuse rather than separating into discrete leaflets, resulting in the final *e* leaf form (Dengler, 1984; Koenig et al., 2009) (Fig. 1e). In *e* leaf primordia, E-mediated inhibition of auxin response is compromised, leading to ectopic auxin response and lamina formation between initiating leaflets: In *e* primordia, the expression of the transgenic *Arabidopsis PIN1:PIN1-GFP* reporter is upregulated, mainly in the intercalary regions between initiating leaflet primordia, and the distribution of the auxin response sensor DR5 points to expanded auxin response, spanning the entire leaf margin rather than being restricted to the sites of leaflet initiation. Interestingly, leaves subjected to auxin micro-application throughout their margins also form simplified leaves with fused primary leaflets (Ben-Gera et al., 2012; Koenig et al., 2009). These results demonstrate that an upregulation of auxin response between initiating leaflets causes ectopic lamina growth, interfering with leaflet separation. E/SlIAA9 normally functions to restrict lamina growth between developing leaflets by locally inhibiting auxin response.

Discrete auxin response locales were shown to be important for the generation of distinct leaflets in several additional species. In Cardamine, *pin1* mutants lead to simplified leaves with smooth margins, and auxin application results in ectopic expression of DR5 and ectopic lamina growth, similar to the case in tomato (Barkoulas et al., 2008). Interestingly, leaves of the *Medicago truncatula* (Medicago) *PIN1* ortholog *MtPIN10/SLM1* mutant were reported to have increased complexity and decreased marginal patterning. However, a closer look suggests that the seemingly more complex leaves may in fact result from early fusion of several leaves, each of which is simpler. Therefore, the initial effect of *pin* mutants may be leaflet fusion and decreased leaf complexity in both Cardamine and Medicago. Alternatively, this may suggest a more complex effect of auxin on leaf patterning in Medicago (Peng and Chen, 2011; Zhou et al., 2011).

The response to auxin is mediated by auxin response transcription factors (ARFs). Repression of SlARF10 by SlmiR160 was shown to be essential for auxin-mediated blade outgrowth and early fruit development in tomato (Hendelman et al., 2012). In recent work (Ben-Gera et al., 2016) we demonstrated that several ARFs, which are negatively regulated by miR160, antagonize auxin response and lamina growth in conjunction with E, acting partially redundantly but both being required for local inhibition of lamina growth between initiating leaflets. Overexpression of miR160-targeted ARFs results in increased leaf complexity coupled with reduced lamina growth (Fig. 1i), and knockdown of miR160 by Short Tandem Target Mimic also results in restricted lamina growth (Damodharan et al., 2016; Ben-Gera et al., 2016). Conversely, overexpressing miR160 causes leaf simplification and leaflet fusion (Fig. 1h). Thus, different types of auxin signal antagonists act cooperatively to ensure leaflet separation in tomato leaf margins.

Ta-siRNAs regulate another group of ARFs. ta-siRNA-targeted ARFs were shown to be involved in adaxial-abaxial patterning and

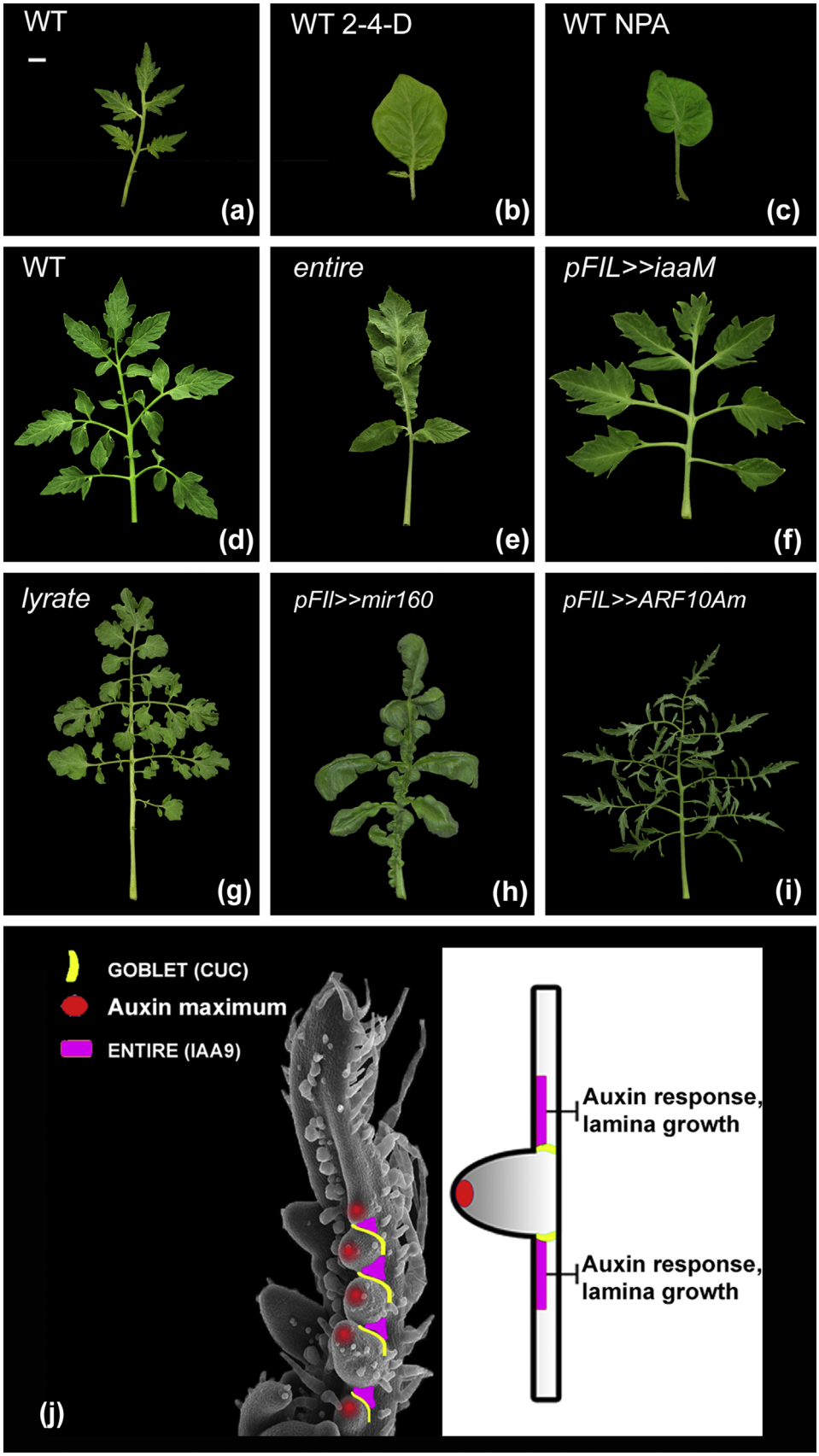

Fig. 1. Auxin in tomato leaf development. Auxin misclocalization or misexpression causes simplified leaves in tomato. (a–c) leaves grown on media as indicated. External application of the synthetic auxin analog 2,4-Dichlorophenoxyacetic acid (2-4-D, 1.5 μM) or the polar auxin transport inhibitor 1-N-Naphthylphthalamic acid (NPA, 5uM) lead to leaf simplification. (d–i) Fifth leaves of greenhouse-grown plants. (e) *entire (e)* is a recessive mutant in *E/SlIAA9* which encodes an auxin response inhibitor; (f) *pFIL > iaaM* leaves overexpress the bacterial auxin biosynthesis gene tryptophan monooxygenase; (g) *lyrate (lyr)* is a recessive mutant in the tomato *JAGGED* homolog; (h) *pFIL > mir160* leaves overexpress miR160 which downregulates 5 ARF genes in tomato; (i) *pFIL > ARF10m* leaves overexpress a form of tomato ARF10 possessing a silent mutation that makes it resistant to processing by miR160; (j) Model of the role of auxin, GOB and E during leaflet initiation and separation. Leaflet initiation and separation requires adjacent regions with enhanced and inhibited auxin response. E inhibits auxin response between leaflets and GOB specifies leaflet boundaries. Bar = 1 cm. Some images adapted from Burko and Ori (2013), copyright Springer Science+Business Media New York 2013, with permission of Springer.

heteroblasty in Arabidopsis (Hunter et al., 2006; Pekker et al., 2005; Schwab et al., 2009) and maize (Dotto et al., 2014; Nogueira et al., 2007). In species with compound leaves their effect is more pronounced and varies substantially among species, suggesting that in these species they are involved in other aspects of leaf development in addition to their effect on leaf polarity. Disrupting the ta-siRNA pathway caused increased leaf lobing but did not affect leaf complexity in Medicago (Zhou et al., 2013). In contrast, disrupting the ta-siRNA pathway in tomato underlies the "wiry" syndrome – in which leaves are simpler and very narrow (Yifhar et al., 2012). One of the *wiry* mutants is mutated in the *ARGONAUTE7* (*AGO7*) gene, required for ta-siRNA function. Conversely, overexpression of *AGO7* in tomato altered auxin responses and resulted in leaves with increased venation complexity and leaflet numbers (Lin et al., 2016). It was also reported that silencing *ARGONAUTE1* (*AGO1*) in tomato causes morphological defects in leaf adaxial-abaxial patterning and trichome development (Wang et al., 2015), coupled with significant changes in the expression of Auxin Response Factor 4 (ARF4) and Non-expressor of PR5 (NPR5), which are involved in adaxial-abaxial domain formation.

Thus, disrupting auxin distribution affects leaf and leaflet initiation, adaxial-abaxial polarity and marginal patterning in many plant species, though clearly some of the mechanisms through which auxin exerts its effects differ substantially among different species.

The transcription factor *JAGGED* (*JAG*) is a positive regulator of leaf blade growth in *Arabidopsis* (Dinneny et al., 2006; Ohno et al., 2004). *JAG* was shown to directly repress meristematic and cell cycle genes, thus promoting differentiation (Schiessl et al., 2014). The tomato *LYRATE* (*LYR*) gene, an ortholog of the *Arabidopsis* gene *JAGGED,* promotes lamina growth, and was proposed to act by modulating auxin response or distribution, as *lyrate* (*lyr*) mutants have decreased expression of *PIN1* and additional auxin related genes (David-Schwartz et al., 2009). Leaves of the recessive *lyr* mutant are smaller than wild type leaves, possessing longer petioles and petiolules, and increased complexity (Fig. 1g) (Clayberg et al., 1966).

No discussion of the roles of auxin in tomato leaf development is complete without addressing the interaction between auxin and *NO APICAL MERISTEM* (*NAM*)/CUP-SHAPED COTYLEDON (CUC) transcription factors in the formation of leaflets and lobes at the leaf margin. NAM/CUC transcription factors regulate many developmental processes including boundary specification (Aida and Tasaka, 2006; Žádníková et al., 2014). In Arabidopsis they promote leaf serrations (Hasson et al., 2011; Nikovics et al., 2006), and in tomato, the NAM/CUC gene *GOBLET (GOB)* promotes leaflet specification and separation (Brand et al., 2007). The expression of *NAM/CUC* mRNA marks the boundary between the leaf margin and the future leaflet, and NAM/CUC silencing leads to leaf simplification (Berger et al., 2009; Blein et al., 2008; Cheng et al., 2012). In Arabidopsis, a model was proposed based on genetic evidence and computational modelling, whereby CUC2 promotes PIN1 localization, while auxin in turn represses CUC2 expression, leading to regular patterns of leaf serrations (Bilsborough et al., 2011). However, in tomato auxin affects *GOB* expression in apices but not leaf primordia. Furthermore, the auxin response appears to act downstream of GOB in tomato leaf development, and it seems to be affected by both GOB and E, acting in independent pathways (Ben-Gera et al., 2012).

In conclusion, auxin affects numerous aspects of leaf development, including initiation, specification of growth axes, morphogenesis and marginal patterning. Auxin, LYR, E, mir160-targeted ARFs, and GOB collaborate to specify leaflet initiation and promote leaflet separation. A leaflet is specified by a distinct auxin response maximum, co-localized with, and possibly regulated by LYR expression, and is flanked by a distinct, precise stripe-shaped domain of GOB activity (Fig. 1j). Proper leaflet initiation and separation requires several such combined occurrences, sufficiently distant in time and space. The distinct auxin response maxima are generated by a combination of auxin accumulation, auxin transport, and inhibition of auxin response between leaflets.

3. Gibberellin

Gibberellins (GAs) are involved in many developmental processes, such as seed germination, stem elongation, trichome development, pollen maturation and flowering induction (Yamaguchi, 2008). GA can generally be viewed as a differentiation promoting hormone, responsible for “pushing through” developmental programs, and regulating the achievement of final organ forms. In leaf development, GA regulates cell proliferation and expansion, and leaf complexity. The effects of GA pathway alterations on final tomato leaf form are depicted in Fig. 2.

Increasing GA levels or GA response in tomato results in tall plants with faster maturing leaves, which are consequently simpler and paler than wild-type leaves (Bassel et al., 2008; Chandra-Shekhar and Sawhney, 1991; Fleishon et al., 2011; Gray, 1957; Hay et al., 2002; Jasinski et al., 2008; Jones, 1987; Livne et al., 2015; Van Tuinen et al., 1999). These observations suggest that GA shortens the morphogenetic stage in the leaf developmental program by promoting differentiation. As seen in Fig. 2a–c, spraying leaves with GA results in leaf simplification. Similarly, leaves of the *procera* (*pro*) mutant, in which there is a constitutive GA response due to a mutation in the single tomato DELLA-type GA-response inhibitor, have only primary leaflets with smooth margins (Fig. 2g) (Bassel et al., 2008; Fleishon et al., 2011; Jasinski et al., 2008; Jones, 1987; Van Tuinen et al., 1999). Examination of early leaf development in *pro* mutants revealed that the effect of *pro* on leaf shape results from a combination of accelerated growth during early development coupled with a delay in leaflet initiation (Jasinski et al., 2008). *pro* mutant leaves were reported to cease forming leaflets earlier than wild type leaves (Jasinski et al., 2008), indicating that GA response also inhibits late organogenic activity. Therefore, excess GA level or response leads to a delay in the initiation of morphogenesis and shortens the morphogenetic phase in tomato leaf development.

Young *pro* leaf primordia acquire an upright position earlier than the wild type. Fast growth and maturation coupled with an upright position are reminiscent of the phenotypes of a semi-dominant mutation in the TCP gene *LANCEOLATE* (*LA*), which positively affects GA homeostasis in tomato (Yanai et al., 2011). Leaves of the gain-of-function mutation *La-2* are simplified (Ori et al., 2007) (Fig. 2h). Conversely, down-regulation of *LA* and additional related genes leads to extended morphogenesis and increased leaf complexity, which is suppressed by *pro* or by GA application (Yanai et al., 2011).

Another tomato mutant reported to be affected in GA levels or response is *solanifolia* (*sf*) , which also produces simple leaves with only primary and interacalary leaflets and smooth margins (Chandra Sekhar and Sawhney, 1990). *sf* leaves also resemble GA-treated wild-type leaves, and inhibition of GA biosynthesis suppressed the *sf* simple leaf phenotype, indicating that elevated GA levels are responsible for the *sf* leaf phenotype (Chandra-Shekhar and Sawhney, 1991). Leaflet initiation is delayed in *sf* mutants, similarly to *pro* mutants. Thus, the *sf* phenotype also supports the notion of delayed and shortened morphogenesis as a result of excess GA response or levels. Identifying the affected gene in *sf* mutants will further uncover GA dynamics in tomato leaf development in the future.

Decreasing GA levels or response results in short plants with dark and in some cases more complex leaves (Koornneef et al., 1990; Livne et al., 2015; Yanai et al., 2011) (Fig. 2e–f). While some mutants with reduced GA levels (Koornneef et al., 1990) or

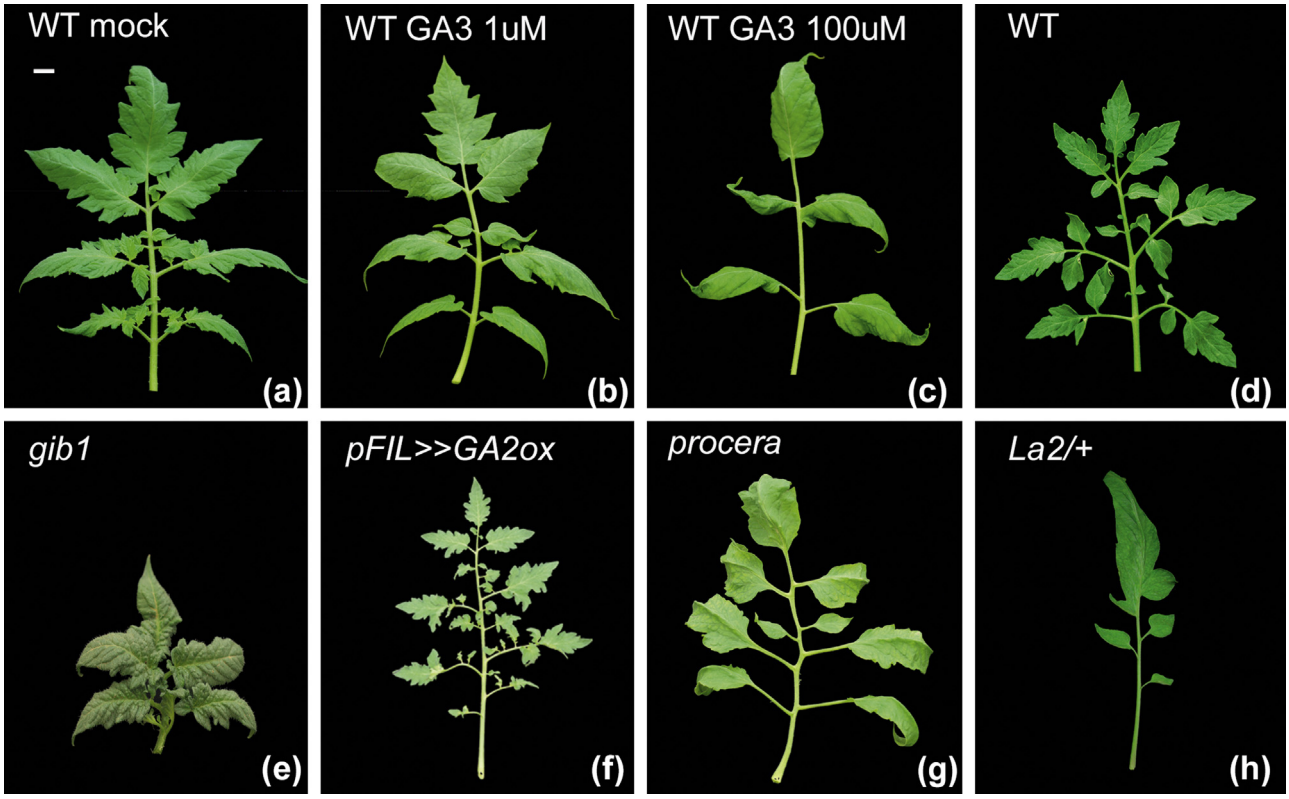

Fig. 2. Gibberellin in tomato leaf development. GA promotes leaf maturation in tomato. (a–c) Leaves sprayed with mock or GA as indicated; (d–h) Fifth leaves of greenhouse-grown plants. (e) *gib1* is a recessive GA biosynthesis mutant. (f) *pFIL≫GA2ox* leaves overexpress the Arabidopsis GA catabolic gene *GA2oxidase4*. (g) *procera (pro)* is a recessive mutant in the only tomato *DELLA* homolog, resulting in constitutive GA response. (h) *La-2/+* is a semi-dominant mutant in a CIN-TCP transcription factor whose activity is mediated by positive regulation of GA response. Increased GA levels or response leads to leaf simplification, while in some cases reduced GA levels result in more compound leaves. Bar=1 cm. Some images reproduced from Fleishon et al. (2011), copyright 2011 New Phytologist Trust.

application of the GA inhibitor paclobutrazol do not substantially affect leaf complexity, endogenously reducing internal GA levels in the leaf by overexpressing the GA catabolic gene *GA2oxidase* from a leaf-specific promoter results in a more complex and slightly darker leaf (Fig. 2f). The relatively minor effect of reducing GA levels on leaf complexity in comparison to the substantial simplification effect caused by increasing GA levels or response may suggest that GA response is normally low during early leaf development in tomato. Alternatively, severe reduction of GA levels may cause pleiotropic effects that complicate the interpretation of its effect on leaf compoundness. *GA2oxidase* appears to cause mainly extended leaflet initiation at late stages of leaf development, suggesting a stage-specific effect of GA on leaf complexity.

Interestingly, in some species elevated GA has the opposite effect of inducing more compound leaves (DeMason and Chetty, 2011; Robbins, 1957; Rogler and Hackett, 1975). For example, in pea, GA positively promotes leaf dissection in concert with auxin, by prolonging the temporal window during which acropetally initiated leaflets are produced during leaf morphogenesis (DeMason and Chetty, 2011). This exemplifies how similar effectors are modulated flexibly to achieve variable leaf forms.

4. Cytokinin

Cytokinin (CK) is also an important developmental regulator. In leaf development, CK can be viewed as a "juvenility" factor, promoting morphogenesis and delaying differentiation and senescence. The effects of manipulating the CK pathway on final tomato leaf form are depicted in Fig. 3.

CK plays an important role in SAM maintenance (Gordon et al., 2009; Kurakawa et al., 2007). The specification of leaf initiation involves complex feedback relationship between auxin and cytokinin (see below). Cytokinin also promotes the maintenance of prolonged organogenic activity at the tomato leaf margin (Shani et al., 2010). Overexpression of the CK biosynthesis gene *ISOPENTENYLTRANSFERASE 7 (IPT7)* in tomato leaves leads to the formation of highly-compound leaves (Fig. 3d), and conversely, reducing CK levels by the expression of the CK degradation gene *cytokinin oxidase* (*CKX*) results in reduced leaf complexity (Fig. 3e). Recently, we identified the affected gene in the *clausa* mutation, in which the leaf shows prolonged organogenic activity and increased complexity, as encoding a MYB transcription factor. We demonstrated that CLAUSA promotes differentiation by negatively affecting CK signalling, thus uncovering an additional instance in which heightened CK signals result in increased complexity of the tomato leaf (Bar et al., 2016). *clausa* is also known to possess up-regulated KNOX1 genes (Avivi et al., 2000; Jasinski et al., 2007). Genetic and molecular analyses have shown that CK acts downstream of KNOXI transcription factors in delaying maturation, and suggest that CK mediates the activity of KNOXI proteins in the regulation of leaf shape (Chen et al., 1997; Hareven et al., 1996; Parnis et al., 1997; Shani et al., 2009).

Exogenous application of CK has very minor leaf phenotypes in tomato (Fig. 3a,b). Leaves can become more purple in appearance due to an increase in anthocyanin accumulation, but they do not become more complex with exogenous application (Fleishon et al., 2011), likely due to "natural" CK derivatives being broken down when exogenously applied. Interestingly, in Arabidopsis exogenous CK application results in small rosette leaves with an increase in leaf serration (Greenboim-Wainberg et al., 2005).

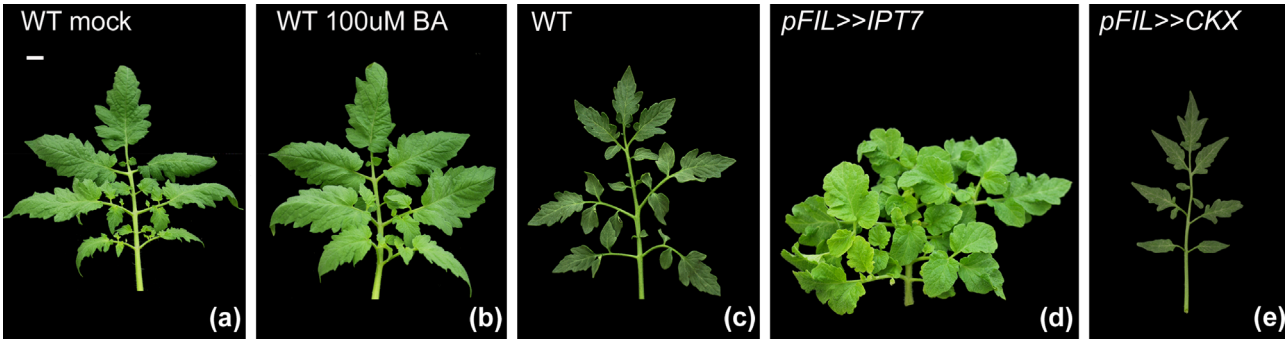

Fig. 3. Cytokinin in tomato leaf development. Endogenous CK upregulation promotes leaf morphogenesis in tomato, while exogenous CK application has little effect. (a,b) leaves sprayed with mock or CK as indicated; (c–e) Fifth leaves of greenhouse-grown plants. (d) *pFIL»IPT7* leaves overexpress the Arabidopsis CK biosynthesis gene *ISO PENTENYL TRANSFERASE7* (e) *pFIL » CKX* leaves overexpress the Arabidopsis CK catabolic gene *CK OXIDASE3*. Bar = 1 cm. Some images reproduced from Fleishon et al. (2011), copyright 2011 New Phytologist Trust.

5. Additional hormones

Reports concerning the involvement of additional hormones, such as Jasmonic acid (JA), Absiscic acid (ABA), Ethylene, and strigolactones, in tomato leaf development – are scarce. Recent works have deciphered the involvement of strigolactone in shoot branching in tomato. Similar to its effect in Arabidopsis, a decrease in strigolactone content in tomato plants leads to increased branching, and can cause plants to appear shorter and bushier as a result of excessive branching and “horizontal” rather than “vertical” growth vectors (Kohlen et al., 2012; Koltai et al., 2010). However, any effects on leaf form are too minor to quantify. JA was shown to be important in anther, pollen and seed development, but not to be crucial for additional developmental processes. A recent report concerning a tomato mutant which accumulates JA did not disclose any leaf developmental phenotypes (Garcia-Abellan et al., 2015). Similarly, the JA-insensitive tomato mutant *jai1* was also not reported to affect leaf shape although it was found to inhibit trichome development in both fruit and sepals, suggesting that JA is required for cell-differentiation processes (Li et al., 2004). This is consistent with the idea that JA does not significantly affect leaf morphogenesis, though it may be involved in differentiation of specialized cell types such as trichomes in leaves, similarly to what was reported for sepals.

Brassinosteroids (BR) affect many developmental processes by promoting elongation and differentiation (Saini et al., 2015; Singh and Savaldi-Goldstein, 2015). As such, mutations that affect BR biosynthesis or response show substantial growth aberrations, including abnormal leaf development (Altmann, 1999; Clouse and Sasse, 1998). In tomato, the recessive BR-deficient mutant *dumpy* (*dpy*) is short and has condensed, dark-green rugose leaves that are downward curling (Koka et al., 2000). Interestingly, *dpy* resembles *Curl (Cu)*, a dominant mutant in the tomato *KNOXI* gene *Tomato Knotted2 (TKN2)/Let6* (Chen et al., 1997; Parnis et al., 1997) that possess substantially increased leaf complexity (Rick and Butler, 1956; Young, 1955). *Cu* was reported to be BR insensitive (Koka et al., 2000), suggesting that KNOXI genes may affect leaf shape in part by negatively affecting BR response. Thus, lack of BR or inability to sense BR result in similar phenotypes and demonstrate that BRs s are required for proper leaf development in tomato, and that KNOXI genes, which regulate CK and GA, may also affect BR sensitivity.

Leaf development and final leaf shape are also affected by the ratio between SINGLE FLOWER TRUSS (SFT), the tomato FT homolog, often referred to as the "flowering hormone", and SELF-PRUNING (SP), a homolog of Arabidopsis TFL (Shannon and Meeks-Wagner, 1991) that acts antagonistically with SFT. A high SFT/SP ratio in the tomato leaf promotes maturation, resulting in a simplified leaf form. Interestingly, this effect is suppressed by downregulating *LANCEOLATE* through miR319 overexpression (Burko et al., 2013; Shalit et al., 2009), suggesting that the SFT/SP ratio may affect the homeostasis of additional hormones that affect leaf development, such as GA.

Ethylene has also been reported to affect developmental processes in tomato (Lashbrook et al., 1998). Transgenic tomato plants with reduced expression of multiple EIL genes, which are homologs of the Arabidopsis ETHYLENEINSENSITIVE3 (EIN3) protein, an ethylene activated transcription factor (Guo and Ecker, 2003), have reduced ethylene sensitivity, which results among other things in decreased leaf epinasty (Tieman et al., 2001). A direct connection between ethylene and tomato leaf development or leaf complexity has not been demonstrated.

A recent report links inhibited leaf growth and early leaf senescence to reduced gibberellin and auxin content and increased ABA sensitivity in leaves upon silencing of the tomato Elongator complex protein 2-like gene SlELP2L (Zhu et al., 2015). However, leaves of silenced SlELP2 plants appear to have similar complexity to wild type leaves, demonstrating that altering the balance between different hormones does not necessarily have an impact on leaf morphogenesis, despite affecting leaf growth. This indicates that leaf morphogenesis and leaf growth can be uncoupled, which will be very interesting to investigate further. In the case of more recently discovered hormones, additional research and further analyses of additional mutants and transgenic plants may uncover direct roles in leaf development.

6. Hormonal crosstalk

Developmental processes are influenced not only by the amount and distribution of individual plant hormones but, sometimes to a greater extent, by the balance between hormones. The balance between different hormones and how they interact with each other has an influence on all stages of leaf development.

A Fine coordination of local auxin and cytokinin responses regulates leaf initiation and stabilizes it. Light was shown to be essential for leaf initiation in tomato and this effect is mediated by both auxin and cytokinin (Yoshida et al., 2011). Several works led to the hypothesis that auxin and cytokinin may act synergistically in organ initiation in the SAM in Arabidopsis (Vidaurre et al., 2007; Zhao et al., 2010), in contrast to their antagonistic effects on most developmental processes (Chandler and Werr, 2015) and in shoot apical maintenance in maize (Lee et al., 2009). It would be interesting to see whether similar interactions take place during leaflet initiation in compound-leaf development. Hinting at this possibility is the crosstalk between Auxin and CK in tomato leaf

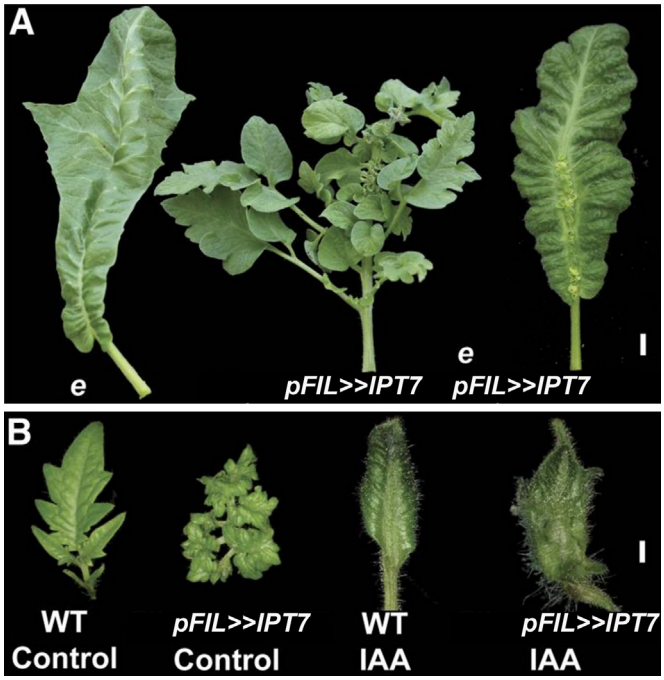

Fig. 4. Proper auxin distribution is required for the effect of CK on leaf complexity. CK regulation of tomato leaf development requires proper localization of the response to Auxin. (a) Fifth leaves of greenhouse-grown plants; (b) Leaves grown on control or Auxin (IAA, 1 mM) containing media as indicated. Bar = 1 cm. Genotypes are indicated below each leaf depicted. Images reproduced from Shani et al. (2010), copyright American Society of Plant Biologists.

development, as detailed in Fig. 4. In the absence of a properly distributed auxin response, CK is unable to significantly prolong tomato leaf morphogenesis as it can when endogenously elevated in a normal auxin response background (Shani et al., 2010) (Fig. 4). Therefore, both proper auxin content and distribution and proper CK content are required for tomato leaf elaboration.

CK maintains meristematic qualities and promotes morphogenesis, while GA promotes cell maturation and differentiation. CK and GA have been reported to possess antagonistic activities in different plant processes (Greenboim-Wainberg et al., 2005; Weiss and Ori, 2007). GA was shown to repress CK signalling, and the GA catabolic *GA2ox* gene was activated by CK (Jasinski et al., 2005). The Arabidopsis GA response inhibitor *SPINDLY* (*SPY*) was shown to interact with TCPs and positively regulate cytokinin signalling (Greenboim-Wainberg et al., 2005; Steiner et al., 2012a). Overexpression of the Arabidopsis class I TCPs *AtTCP14* and *AtTCP15* affected leaf morphology in tomato, resulting in fewer leaflets and smooth leaflet margins, and ectopic meristems on leaf petioles (Steiner et al., 2012b). Mutating SPY affects leaf shape in Arabidopsis (Steiner et al., 2012a). Interestingly, SPY was recently shown to be required for AtTCP14 and AtTCP15 stability and to affect CK sensitivity. However, SPY does not affect the activity of *AtTCP4*, the *Arabidospsis LA* homolog (see above), in *Arabidopsis* leaf development (Steiner et al., 2016). Relationships between SPY and TCP have not yet been examined in tomato, but it will be interesting to investigate the antagonistic effects of class I and class II TCPs in the regulation of hormone response and compound leaf development. GA and cytokinin were also shown to antagonize each other's response during tomato leaf morphogenesis (Fleishon et al., 2011), (Fig. 5). CK activity is required for proper leaf serration and complexity (Fig. 5e, g), while GA can inhibit the effect of CK activity on leaf morphology (Fig. 5d, k). The relationship between CK and GA in the context of the different stages of leaf development is summarized in the model presented in Fig. 5l.

KNOXI proteins regulate the balance between cytokinin, which promotes meristematic fate, and GA, which promotes differentiation (Hay et al., 2002; Jasinski et al., 2005; Scofield et al., 2013; Yanai et al., 2005). KNOXI proteins negatively regulate the expression of the GA biosynthesis gene *GA-20-oxidase* (*GA20ox*) and positively regulate the GA deactivation gene *GA-2-oxidase* (*GA2ox*) in several species (Bolduc and Hake, 2009; Hay et al., 2002; Jasinski et al., 2005; Sakamoto et al., 2001). Conversely, KNOXI proteins activate CK biosynthesis genes and promote CK accumulation in *Arabidopsis* and rice (Jasinski et al., 2005; Sakamoto et al., 2006; Yanai et al., 2005). KNOXI proteins may also affect BR signalling (see above, Farquharson (2014), Tsuda et al. (2014)). Thus, KNOXI proteins coordinate the activity of several plant hormones, enabling the balance between continuous meristematic function and organ initiation. Tomato leaves also maintain morphogenetic activity after leaf expansion, which underlies the extensive variability in tomato leaf shape. Interestingly, GA and cytokinin were both shown to modulate this late morphogenetic activity in tomato (Shani et al., 2010; Yanai et al., 2011).

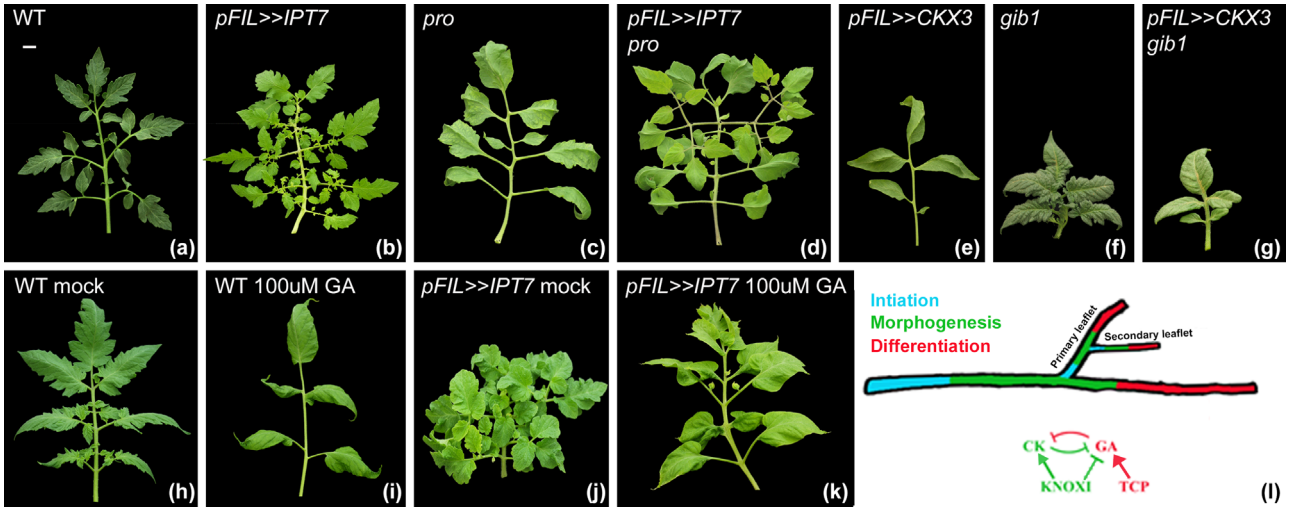

Fig. 5. Antagonistic effect of CK and GA on the morphogenetic window in tomato leaf development. (a–g) Fifth leaves- of greenhouse-grown plants; (h–k) Leaves sprayed with mock or GA as indicated. Bar = 1 cm. (l) Model summarizing the hypothesized involvement of CK and GA in the three stages of leaf development. Initiation is coded in blue, morphogenesis in green and differentiation in red. KNOXI proteins and cytokinin promote morphogenesis, and TCPs, GA promote differentiation. Some images reproduced and/or adapted from Fleishon et al. (2011), copyright 2011 New Phytologist Trust, and from Burko and Ori (2013), copyright Springer Science + Business Media New York 2013, with permission of Springer.

Table 1
Differentially regulated genes common to CK and GA treatments.

Description	Gene ID	GA FC		CK FC
Transcription factor BIM2	Solyc03g114720	2.69		6.59
Scarecrow transcription factor family	Solyc01g008910	0.21		0.09
* SlRRA1, type-A response regulators	Solyc05g006420	0.48		8.69
	GA	**FC**	**CK**	**FC**
ARF	Solyc03g120380	2.36	Solyc11g069190	0.045
SAUR	Solyc01g110680	2.25	Solyc04g052970	0.021
	Solyc01g110630	3.53		
	Solyc10g052530	2.77		
Auxin efflux transmembrane transporter activity	Solyc02g087870	2.17	Solyc05g008060	0.1
	Solyc04g007690	3.18		
SLCKX, Cytokinin oxidase/dehydrogenase	Solyc04g080820	2.36	Solyc01g088160	13.08
			Solyc04g016430	42.51
			Solyc04g080820	10.9 (24 h)
Jasmonate-amino synthetase activity	Solyc01g095580	0.37	Solyc10g009620	5.98
			Solyc07g054580	10.63

RNAseq following GA (Livne et al., 2015) and CK (Shi et al., 2013) treatments were compared using the data from Shi et al. (2013) (genes with a ± 5.65 FC in young tomato leaves following CK treatment) and the DESeq2 output from the Livne et al. (2015) data (counts were performed by HTseq and aligning was done with Tophat2 on the ITAG2.4 genome). FC – fold change.

Cross talk between different hormones can also be species specific. For example, in pea, GA causes leaf elaboration, in contrast to GA action in tomato leaves. Additionally, while auxin promotes leaf simplification in tomato, it promotes indeterminate growth in pea, and mutual positive regulation was proposed between the pea LEAFY ortholog UNI and auxin. Auxin response is reduced in *uni* mutants (Demason et al., 2013), and both GA and auxin upregulate UNI expression, thereby acting together to prolong the morphogenetic window and increase pea leaf complexity (DeMason and Chetty, 2011).

In order to further examine the crosstalk between GA and CK during tomato leaf development, we analysed and compared published RNA-seq data obtained following GA treatment from David Weiss (seedlings sprayed with 10 mg/L paclobutrazol at the time of emergence of the third leaf, three times a week for 2 weeks, followed by application of 100 μM GA3 for 1 h, or seedlings sprayed with paclobutrazol only)) (Livne et al., 2015) with RNA-seq data obtained following CK treatment (13 day old tomato leaves treated with 5 μM Benzyl Adenine (BA) or the solvent vehicle control dimethyl sulfoxide (DMSO) for 2 h) from Aaron Rashotte (Shi et al., 2013). Both treatments were applied to young tomato leaves in a similar time frame. We were interested to examine whether the antagonistic relationship between GA and CK is exhibited through shared genes with antagonistic responses between the two datasets. Two transcription factors were found to be affected similarly by GA and CK treatments. The first is *BIM2* (Table 1), which contains a bHLH-like transcription factor domain, and may be involved in regulating the plant's response to various hormonal states given its co-upregulation under both GA and CK treatments. *BIM* transcription factors were found to be involved in brassinosteroid signalling (Belkhadir and Chory, 2006; Yin et al., 2005) and *BIM1*, though not *BIM2*, was found to affect *Arabidopsis* embryogenesis through interaction with the *DRN* and *DRNL* transcription factors (Chandler et al., 2009). *BIM* was also found to be involved in shade avoidance syndrome in *Arabidopsis* (Cifuentes-Esquivel et al., 2013). A second gene affected by both CK and GA is *SCARECROW*, which has well established functions in various hormonal responses in *Arabidopsis*. The transcription factors SCARECROW (SCR) and SHORT ROOT (SHR) are members of the GRAS family. In Arabidopsis, they were found to regulate root stem cell specification and maintenance, and radial patterning (Di Laurenzio et al., 1996; Helariutta et al., 2000; Sabatini et al., 2003). Both *SCR* and *SHR* regulate quiescent centre (QC) markers (Sarkar et al., 2007) and microRNAs involved in root vascular differentiation (Carlsbecker et al., 2010). *SCR* and *SHR* are also involved in lateral root formation (Lucas et al., 2011; Malamy and Benfey, 1997), and *SCR* was reported to be induced by auxin (Moubayidin et al., 2013). There are very few reports of *SCR* activity in tomato, though it was suggested to be conserved with Arabidopsis (Ron et al., 2014). Here we show that one *SCR* family member in tomato is repressed by both CK and GA, suggesting that *SCR* may have additional roles in hormone regulation or response to hormonal balance in specific developmental processes.

Interestingly, Auxin related genes show differential expression patterns in both experiments (Table 1). For example, one Auxin Response Factor (ARF) gene shows a significant increase in expression due to GA treatment, while a different ARF shows a decrease in expression due to CK treatment. This behaviour was also observed with SAUR genes and auxin efflux trans-membrane transporter activity related genes. Additionally, a JA-amino synthetase activity gene showed a decrease in response to GA treatment, while in response to CK treatment we found a homologous gene displaying opposite regulation. These results suggest that the antagonistic relationship between CK and GA may involve auxin regulatory elements and is possibly regulated through additional hormones. Our analyses also showed that CKX genes are upregulated following both CK and GA treatment, demonstrating that the regulatory mechanism maintaining CK and GA antagonistic effects may be executed by a similar mechanism to which CK itself is negatively feedback-regulated. Interestingly, SlRRA1, a key type-A response regulator was upregulated in response to GA and down regulated in response to CK, once again suggesting that the relationship between CK and GA is regulated through CK regulation mechanisms.

Thus, while several reports have observed antagonistic relationships between CK and GA, with the data available to us we were able to uncover only a very limited number of genes which may be involved in such antagonistic effects. Due to the limited data available it is difficult to tell whether the antagonistic effect is not facilitated mainly by a direct effect on common targets, is

facilitated by a limited number of common targets with a central role, or whether different tissues or time points are needed to identify common targets. It will be interesting both to further examine the role of each hormone in leaf development and to generate additional data and examine relationships between hormones both at the systematic level and at the molecular resolution of the involvement of specific genes in hormonal regulation of developmental processes.

7. Concluding remarks

Patterning of compound tomato leaves involves the maintenance of an extended window of morphogenesis, during which distinct and separated leaflets develop. Plant hormones and the interaction between them are important regulators of these processes. The balance between GA and CK affects the extent of the morphogenetic window, and the formation of well-separated auxin maxima specify leaflet formation and separation. Each of these hormones as well as the cross-talk among them affects multiple aspects of leaf development, and further understanding of these complex interactions will require additional research.

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References

Aida, M., Tasaka, M., 2006. Genetic control of shoot organ boundaries. Curr. Opin. Plant Biol. 9, 72–77.
Altmann, T., 1999. Molecular physiology of brassinosteroids revealed by the analysis of mutants. Planta 208, 1–11. http://dx.doi.org/10.1007/s004250050528.
Avivi, Y., Lev-Yadun, S., Morozova, N., Libs, L., Williams, L., Zhao, J., Varghese, G., Grafi, G., 2000. Clausa, a tomato mutant with a wide range of phenotypic perturbations, displays a cell type-dependent expression of the homeobox gene LeT6/TKn2. Plant Physiol. 124, 541–552.
Bar, M., Ben-Herzel, O., Kohay, H., Shtein, I., Ori, N., 2015. CLAUSA restricts tomato leaf morphogenesis and GOBLET expression. Plant J. 83, 888–902. http://dx.doi.org/10.1111/tpj.12936.
Bar, M., Israeli, A., Levy, M., Ben Gera, H., Jiménez-Gómez, J.M., Kouril, S., Tarkowski, P., Ori, N., 2016. CLAUSA Is a MYB transcription factor that promotes leaf differentiation by attenuating cytokinin signaling. Plant Cell 28, 1602–1615. http://dx.doi.org/10.1105/tpc.16.00211.
Bar, M., Ori, N., 2014. Leaf development and morphogenesis. Development 141, 4219–4230. http://dx.doi.org/10.1242/dev.106195.
Barkoulas, M., Hay, A., Kougioumoutzi, E., Tsiantis, M., 2008. A developmental framework for dissected leaf formation in the Arabidopsis relative Cardamine hirsuta. Nat Genet. 40, 1136–1141.
Bassel, G.W., Mullen, R.T., Bewley, J.D., 2008. Procera is a putative DELLA mutant in tomato (Solanum lycopersicum): effects on the seed and vegetative plant. J. Exp. Bot. 59, 585–593.
Belkhadir, Y., Chory, J., 2006. Brassinosteroid signaling: a paradigm for steroid hormone signaling from the cell surface. Science 314, 1410–1411. http://dx.doi.org/10.1126/science.1134040.
Ben-Gera, H., Dafna, A., Alvarez, J.P., Bar, M., Mauerer, M., Ori, N., 2016. Auxin-mediated lamina growth in tomato leaves is restricted by two parallel mechanisms. Plant J. . http://dx.doi.org/10.1111/tpj.13188
Ben-Gera, H., Shwartz, I., Shao, M.R., Shani, E., Estelle, M., Ori, N., 2012. ENTIRE and GOBLET promote leaflet development in tomato by modulating auxin response. Plant J. 70, 903–915. http://dx.doi.org/10.1111/j.1365-313X.2012.04939.x.
Benkova, E., Michniewicz, M., Sauer, M., Teichmann, T., Seifertova, D., Jurgens, G., Friml, J., 2003. Local, efflux-dependent auxin gradients as a common module for plant organ formation. Cell 115, 591–602.
Berger, Y., Harpaz-Saad, S., Brand, A., Melnik, H., Sirding, N., Alvarez, J.P., Zinder, M., Samach, A., Eshed, Y., Ori, N., 2009. The NAC-domain transcription factor GOBLET specifies leaflet boundaries in compound tomato leaves. Development 136, 823–832.
Bilsborough, G.D., Runions, A., Barkoulas, M., Jenkins, H.W., Hasson, A., Galinha, C., Laufs, P., Hay, A., Prusinkiewicz, P., Tsiantis, M., 2011. Model for the regulation of Arabidopsis thaliana leaf margin development. Proc. Natl. Acad. Sci USA 108, 3424–3429, doi:1015162108 [pii]10.1073/pnas.1015162108.
Blein, T., Pulido, A., Vialette-Guiraud, A., Nikovics, K., Morin, H., Hay, A., Johansen, I. E., Tsiantis, M., Laufs, P., 2008. A conserved molecular framework for compound leaf development. Science 322 (80), 1835–1839.
Bolduc, N., Hake, S., 2009. The maize transcription factor KNOTTED1 directly regulates the gibberellin catabolism gene ga2ox1. Plant Cell 21, 1647–1658.
Brand, A., Shirding, N., Shleizer, S., Ori, N., 2007. Meristem maintenance and compound-leaf patterning utilize common genetic mechanisms in tomato. Planta 226, 941–951.
Braybrook, S.A., Kuhlemeier, C., 2010. How a plant builds leaves. Plant Cell 22, 1006–1018. http://dx.doi.org/10.1105/tpc.110.073924.
Burko, Y., Ori, N., 2013. The tomato leaf as a model system for organogenesis. Methods Mol. Biol. 959, 1–19. http://dx.doi.org/10.1007/978-1-62703-221-6_1.
Burko, Y., Shleizer-Burko, S., Yanai, O., Shwartz, I., Zelnik, I.D., Jacob-Hirsch, J., Kela, I., Eshed-Williams, L., Ori, N., 2013. A role for APETALA1/fruitfull transcription factors in tomato leaf development. Plant Cell 25, 2070–2083. http://dx.doi.org/10.1105/tpc.113.113035.
Byrne, M.E., 2012. Making leaves. Curr. Opin. Plant Biol. 15, 24–30. http://dx.doi.org/10.1016/j.pbi.2011.10.009.
Carlsbecker, A., Lee, J.-Y., Roberts, C.J., Dettmer, J., Lehesranta, S., Zhou, J., Lindgren, O., Moreno-Risueno, M.A., Vatén, A., Thitamadee, S., Campilho, A., Sebastian, J., Bowman, J.L., Helariutta, Y., Benfey, P.N., 2010. Cell signalling by microRNA165/6 directs gene dose-dependent root cell fate. Nature 465, 316–321. http://dx.doi.org/10.1038/nature08977.
Chandler, J.W., Cole, M., Flier, A., Werr, W., 2009. BIM1, a bHLH protein involved in brassinosteroid signalling, controls Arabidopsis embryonic patterning via interaction with DORNROSCHEN and DORNROSCHEN-LIKE. Plant Mol. Biol. 69, 57–68. http://dx.doi.org/10.1007/s11103-008-9405-6.
Chandler, J.W., Werr, W., 2015. Cytokinin-auxin crosstalk in cell type specification. Trends Plant Sci. 20, 291–300. http://dx.doi.org/10.1016/j.tplants.2015.02.003.
Chandra Sekhar, K.N., Sawhney, V.K., 1990. Leaf Development in the Normal and Solanifolia Mutant of Tomato (Lycopersicon esculentum). American Journal of Botany 77 (1), 46–53.
Chandra-Shekhar, K.N., Sawhney, V.K., 1991. Regulation of leaf shape in the solanifolia mutant of tomato (Lycopersicon esculentum) by plant growth substances. Ann. Bot. 67, 3–6.
Chen, J.J., Janssen, B.J., Williams, A., Sinha, N., 1997. A gene fusion at a homeobox locus: alterations in leaf shape and implications for morphological evolution. Plant Cell 9, 1289–1304.
Cheng, X., Peng, J., Ma, J., Tang, Y., Chen, R., Mysore, K.S., Wen, J., 2012. NO APICAL MERISTEM (MtNAM) regulates floral organ identity and lateral organ separation in Medicago truncatula. New Phytol. 195, 71–84. http://dx.doi.org/10.1111/j.1469-8137.2012.04147.x.
Cheng, Y., Dai, X., Zhao, Y., 2007. Auxin synthesized by the YUCCA flavin monooxygenases is essential for embryogenesis and leaf formation in arabidopsis. Plant Cell 19, 2430–2439.
Chitwood, D.H., Headland, L.R., Ranjan, A., Martinez, C.C., Braybrook, S.A., Koenig, D. P., Kuhlemeier, C., Smith, R.S., Sinha, N.R., 2012. Leaf asymmetry as a developmental constraint imposed by auxin-dependent phyllotactic patterning. Plant Cell 24, 2318–2327. http://dx.doi.org/10.1105/tpc.112.098798.
Cifuentes-Esquivel, N., Bou-Torrent, J., Galstyan, A., Gallemí, M., Sessa, G., Salla Martret, M., Roig-Villanova, I., Ruberti, I., Martínez-García, J.F., 2013. The bHLH proteins BEE and BIM positively modulate the shade avoidance syndrome in Arabidopsis seedlings. Plant J. 75, 989–1002. http://dx.doi.org/10.1111/tpj.12264.
Clayberg, C.D., Butler, L., Kerr, E.A., Rick, C.M., Robinson, R.W., 1966. Third list of known genes in the tomato. J. Hered. 57, 189–196.
Clouse, S.D., Sasse, J.M., 1998. BRASSINOSTEROIDS: essential regulators of plant growth and development. Annu. Rev. Plant Physiol. Plant Mol. Biol. 49, 427–451. http://dx.doi.org/10.1146/annurev.arplant.49.1.427.
Damodharan, S., Zhao, D., Arazi, T., 2016. A common miRNA160-based mechanism regulates ovary patterning, floral organ abscission and lamina outgrowth in tomato. Plant J. . http://dx.doi.org/10.1111/tpj.13127
David-Schwartz, R., Koenig, D., Sinha, N.R., 2009. LYRATE is a key regulator of leaflet initiation and lamina outgrowth in tomato. Plant Cell 21, 3093–3104.
de Reuille, P.B., Bohn-Courseau, I., Ljung, K., Morin, H., Carraro, N., Godin, C., Traas, J., 2006. Computer simulations reveal properties of the cell-cell signaling network at the shoot apex in Arabidopsis. Proc. Natl. Acad. Sci. USA 103, 1627–1632. http://dx.doi.org/10.1073/pnas.0510130103.
Demason, D.A., Chetty, V., Barkawi, L.S., Liu, X., Cohen, J.D., 2013. Unifoliata-Afila interactions in pea leaf morphogenesis. Am. J. Bot. 100, 478–495. http://dx.doi.org/10.3732/ajb.1200611ajb, 1200611 (pii).
DeMason, D.A., Chetty, V.J., 2011. Interactions between GA, auxin, and UNI expression controlling shoot ontogeny, leaf morphogenesis, and auxin response in Pisum sativum (Fabaceae): or how the uni-tac mutant is rescued. Am. J. Bot. 98, 775–791. http://dx.doi.org/10.3732/ajb.1000358ajb, 1000358 (pii).
Dengler, N.G., 1984. Comparison of leaf development in Normal (+/+), Entire (E/E), and Lanceolate (La/+) plants of tomato, Lycopersicon esculentum Ailsa Craig. Bot. Gaz. 145, 66–77.
Di Laurenzio, L., Wysocka-Diller, J., Malamy, J.E., Pysh, L., Helariutta, Y., Freshour, G.,

Hahn, M.G., Feldmann, K.A., Benfey, P.N., 1996. The SCARECROW gene regulates an asymmetric cell division that is essential for generating the radial organization of the Arabidopsis root. Cell 86, 423–433.
Dinneny, J.R., Weigel, D., Yanofsky, M.F., 2006. NUBBIN and JAGGED define stamen and carpel shape in Arabidopsis. Development 133, 1645–1655, doi:dev.02335 [pii]10.1242/dev.02335.
Dotto, M.C., Petsch, K.A., Aukerman, M.J., Beatty, M., Hammell, M., Timmermans, M. C., 2014. Genome-wide analysis of leafbladeless1-regulated and phased small RNAs underscores the importance of the TAS3 ta-siRNA pathway to maize development. PLoS Genet. 10, e1004826.
Farquharson, K.L., 2014. A rice KNOX transcription factor represses brassinosteroid production in the shoot apical meristem. Plant Cell 26, 3469. http://dx.doi.org/10.1105/tpc.114.131698.
Fleishon, S., Shani, E., Ori, N., Weiss, D., 2011. Negative reciprocal interactions between gibberellin and cytokinin in tomato. New Phytol. 190, 609–617. http://dx.doi.org/10.1111/j.1469-8137.2010.03616.x.
Floyd, S.K., Bowman, J.L., 2010. Gene expression patterns in seed plant shoot meristems and leaves: homoplasy or homology? J. Plant Res. 123, 43–55. http://dx.doi.org/10.1007/s10265-009-0256-2.
Gallavotti, A., Barazesh, S., Malcomber, S., Hall, D., Jackson, D., Schmidt, R.J., McSteen, P., 2008. sparse inflorescence1 encodes a monocot-specific YUCCA-like gene required for vegetative and reproductive development in maize. Proc. Natl. Acad. Sci. USA 105, 15196–15201. http://dx.doi.org/10.1073/pnas.0805596105.
Garcia-Abellan, J.O., Fernandez-Garcia, N., Lopez-Berenguer, C., Egea, I., Flores, F.B., Angosto, T., Capel, J., Lozano, R., Pineda, B., Moreno, V., Olmos, E., Bolarin, M.C., 2015. The tomato res mutant which accumulates JA in roots in non-stressed conditions restores cell structure alterations under salinity. Physiol. Plant. 155, 296–314. http://dx.doi.org/10.1111/ppl.12320.
Gordon, S.P., Chickarmane, V.S., Ohno, C., Meyerowitz, E.M., 2009. Multiple feedback loops through cytokinin signaling control stem cell number within the Arabidopsis shoot meristem. Proc. Natl. Acad. Sci. USA 106, 16529–16534. http://dx.doi.org/10.1073/pnas.0908122106.
Gray, R.A., 1957. Alteration of leaf size and shape and other changes caused by gibberellins in plants. Am. J. Bot. 44, 674–682.
Greenboim-Wainberg, Y., Maymon, I., Borochov, R., Alvarez, J., Olszewski, N., Ori, N., Eshed, Y., Weiss, D., 2005. Cross talk between gibberellin and cytokinin: the Arabidopsis GA response inhibitor SPINDLY plays a positive role in cytokinin signaling. Plant Cell 17, 92–102.
Guo, H., Ecker, J., 2003. Plant responses to ethylene gas are mediated by SCF EBF1/EBF2-dependent proteolysis of EIN3 transcription factor. Cell.
Hagemann, W., Gleissberg, S., 1996. Organogenetic capacity of leaves: the significance of marginal blastozones in angiosperms. Plant Syst. Evol. 199, 121–152.
Hareven, D., Gutfinger, T., Parnis, A., Eshed, Y., Lifschitz, E., 1996. The making of a compound leaf: genetic manipulation of leaf architecture in tomato. Cell 84, 735–744.
Hasson, A., Plessis, A., Blein, T., Adroher, B., Grigg, S., Tsiantis, M., Boudaoud, A., Damerval, C., Laufs, P., 2011. Evolution and diverse roles of the CUP-SHAPED COTYLEDON genes in Arabidopsis leaf development. Plant Cell 23, 54–68, doi: tpc.110.081448 [pii]10.1105/tpc.110.081448.
Hay, A., Kaur, H., Phillips, A., Hedden, P., Hake, S., Tsiantis, M., 2002. The gibberellin pathway mediates KNOTTED1-type homeobox function in plants with different body plans. Curr. Biol. 12, 1557–1565.
Heisler, M.G., Ohno, C., Das, P., Sieber, P., Reddy, G.V., Long, J.A., Meyerowitz, E.M., 2005. Patterns of auxin transport and gene expression during primordium development revealed by live imaging of the Arabidopsis inflorescence meristem. Curr. Biol. 15, 1899–1911.
Helariutta, Y., Fukaki, H., Wysocka-Diller, J., Nakajima, K., Jung, J., Sena, G., Hauser, M.T., Benfey, P.N., 2000. The SHORT-ROOT gene controls radial patterning of the Arabidopsis root through radial signaling. Cell 101, 555–567.
Hendelman, A., Buxdorf, K., Stav, R., Kravchik, M., Arazi, T., 2012. Inhibition of lamina outgrowth following Solanum lycopersicum AUXIN RESPONSE FACTOR 10 (SlARF10) derepression. Plant Mol. Biol. 78, 561–576. http://dx.doi.org/10.1007/s11103-012-9883-4.
Hunter, C., Willmann, M.R., Wu, G., Yoshikawa, M., de la Luz Gutierrez-Nava, M., Poethig, S.R., 2006. Trans-acting siRNA-mediated repression of ETTIN and ARF4 regulates heteroblasty in Arabidopsis. Development 133, 2973–2981, doi: dev.02491 [pii]10.1242/dev.02491.
Jasinski, S., Kaur, H., Tattersall, A., Tsiantis, M., 2007. Negative regulation of KNOX expression in tomato leaves. Planta 226, 1255–1263.
Jasinski, S., Piazza, P., Craft, J., Hay, A., Woolley, L., Rieu, I., Phillips, A., Hedden, P., Tsiantis, M., 2005. KNOX action in Arabidopsis is mediated by coordinate regulation of cytokinin and gibberellin activities. Curr. Biol. 15, 1560–1565.
Jasinski, S., Tattersall, A., Piazza, P., Hay, A., Martinez-Garcia, J.F., Schmitz, G., Theres, K., McCormick, S., Tsiantis, M., 2008. PROCERA encodes a DELLA protein that mediates control of dissected leaf form in tomato. Plant J. 56, 603–612.
Jones, G.M., 1987. Gibberellins and the procera mutant of tomato. Planta 172, 280–284. http://dx.doi.org/10.1007/bf00394598.
Jönsson, H., Heisler, M.G., Shapiro, B.E., Meyerowitz, E.M., Mjolsness, E., 2006. An auxin-driven polarized transport model for phyllotaxis. Proc. Natl. Acad. Sci. USA 103, 1633–1638. http://dx.doi.org/10.1073/pnas.0509839103.
Kaplan, D.R., 2001. Fundamental concepts of leaf morphology and morphogenesis: a contribution to the interpretation of molecular genetic mutants. Int. J. Plant Sci. 162, 465–474.
Kaplan, D.R., Cooke, T.J., 1997. Fundamental concepts in the embryogenesis of dicotyledons: a morphological interpretation of embryo mutants. Plant Cell 9, 1903–1919.
Koenig, D., Bayer, E., Kang, J., Kuhlemeier, C., Sinha, N., 2009. Auxin patterns Solanum lycopersicum leaf morphogenesis. Development 136, 2997–3006.
Kohlen, W., Charnikhova, T., Lammers, M., Pollina, T., Tóth, P., Haider, I., Pozo, M.J., de Maagd, R.A., Ruyter-Spira, C., Bouwmeester, H.J., López-Ráez, J.A., 2012. The tomato CAROTENOID CLEAVAGE DIOXYGENASE8 (SlCCD8) regulates rhizosphere signaling, plant architecture and affects reproductive development through strigolactone biosynthesis. New Phytol. 196, 535–547. http://dx.doi.org/10.1111/j.1469-8137.2012.04265.x.
Koka, C.V., Cerny, R.E., Gardner, R.G., Noguchi, T., Fujioka, S., Takatsuto, S., Yoshida, S., Clouse, S.D., 2000. A putative role for the tomato genes DUMPY and CURL-3 in brassinosteroid biosynthesis and response. Plant Physiol. 122, 85–98.
Koltai, H., LekKala, S.P., Bhattacharya, C., Mayzlish-Gati, E., Resnick, N., Wininger, S., Dor, E., Yoneyama, K., Yoneyama, K., Hershenhorn, J., Joel, D.M., Kapulnik, Y., 2010. A tomato strigolactone-impaired mutant displays aberrant shoot morphology and plant interactions. J. Exp. Bot. 61, 1739–1749. http://dx.doi.org/10.1093/jxb/erq041.
Koornneef, M., Bosma, T.D., Hanhart, C.J., van der Veen, J.H., Zeevaart, J.A., 1990. The isolation and characterization of gibberellin-deficient mutants in tomato. Theor. Appl. Genet. 80, 852–857. http://dx.doi.org/10.1007/BF00224204.
Kurakawa, T., Ueda, N., Maekawa, M., Kobayashi, K., Kojima, M., Nagato, Y., Sakakibara, H., Kyozuka, J., 2007. Direct control of shoot meristem activity by a cytokinin-activating enzyme. Nature 445, 652–655, doi:nature05504 [pii] 10.1038/nature05504.
Lashbrook, C.C., Tieman, D.M., Klee, H.J., 1998. Differential regulation of the tomato ETR gene family throughout plant development. Plant J. 15, 243–252.
Lee, B., Johnston, R., Yang, Y., Gallavotti, A., Kojima, M., Travençolo, B.A.N., Costa, L., da, F., Sakakibara, H., Jackson, D., 2009. Studies of aberrant phyllotaxy1 mutants of maize indicate complex interactions between auxin and cytokinin signaling in the shoot apical meristem. Plant Physiol. 150, 205–216. http://dx.doi.org/10.1104/pp.109.137034.
Li, L., Zhao, Y., McCaig, B.C., Wingerd, B.A., Wang, J., Whalon, M.E., Pichersky, E., Howe, G.A., 2004. The tomato homolog of CORONATINE-INSENSITIVE1 is required for the maternal control of seed maturation, jasmonate-signaled defense responses, and glandular trichome development. Plant Cell 16, 126–143. http://dx.doi.org/10.1105/tpc.017954.
Lin, D., Xiang, Y., Xian, Z., Li, Z., 2016. Ectopic expression of SlAGO7 alters leaf pattern and inflorescence architecture and increases fruit yield in tomato. Physiol. Plant. . http://dx.doi.org/10.1111/ppl.12425
Livne, S., Lor, V.S., Nir, I., Eliaz, N., Aharoni, A., Olszewski, N.E., Eshed, Y., Weiss, D., 2015. Uncovering DELLA-independent gibberellin responses by characterizing new tomato procera mutants. Plant Cell 27, 1579–1594. http://dx.doi.org/10.1105/tpc.114.132795.
Lucas, M., Swarup, R., Paponov, I.A., Swarup, K., Casimiro, I., Lake, D., Peret, B., Zappala, S., Mairhofer, S., Whitworth, M., Wang, J., Ljung, K., Marchant, A., Sandberg, G., Holdsworth, M.J., Palme, K., Pridmore, T., Mooney, S., Bennett, M.J., 2011. Short-Root regulates primary, lateral, and adventitious root development in Arabidopsis. Plant Physiol. 155, 384–398. http://dx.doi.org/10.1104/pp.110.165126.
Malamy, J.E., Benfey, P.N., 1997. Organization and cell differentiation in lateral roots of Arabidopsis thaliana. Development 124, 33–44.
Moubayidin, L., Di Mambro, R., Sozzani, R., Pacifici, E., Salvi, E., Terpstra, I., Bao, D., van Dijken, A., Dello Ioio, R., Perilli, S., Ljung, K., Benfey, P.N., Heidstra, R., Costantino, P., Sabatini, S., 2013. Spatial coordination between stem cell activity and cell differentiation in the root meristem. Dev. Cell 26, 405–415. http://dx.doi.org/10.1016/j.devcel.2013.06.025.
Nikovics, K., Blein, T., Peaucelle, A., Ishida, T., Morin, H., Aida, M., Laufs, P., 2006. The balance between the MIR164A and CUC2 genes controls leaf margin serration in Arabidopsis. Plant Cell 18, 2929–2945.
Nogueira, F.T.S., Madi, S., Chitwood, D.H., Juarez, M.T., Timmermans, M.C.P., 2007. Two small regulatory RNAs establish opposing fates of a developmental axis. Genes Dev. 21, 750–755. http://dx.doi.org/10.1101/gad.1528607.
Ohno, C.K., Reddy, G.V., Heisler, M.G.B., Meyerowitz, E.M., 2004. The Arabidopsis JAGGED gene encodes a zinc finger protein that promotes leaf tissue development. Development 131, 1111–1122. http://dx.doi.org/10.1242/dev.00991.
Ori, N., Cohen, A.R., Etzioni, A., Brand, A., Yanai, O., Shleizer, S., Menda, N., Amsellem, Z., Efroni, I., Pekker, I., Alvarez, J.P., Blum, E., Zamir, D., Eshed, Y., 2007. Regulation of LANCEOLATE by miR319 is required for compound-leaf development in tomato. Nat. Genet. 39, 787–791.
Parnis, A., Cohen, O., Gutfinger, T., Hareven, D., Zamir, D., Lifschitz, E., 1997. The dominant developmental mutants of tomato, Mouse-Ear and Curl, are associated with distinct modes of abnormal transcriptional regulation of a Knotted gene. Plant Cell 9, 2143–2158.
Pekker, I., Alvarez, J.P., Eshed, Y., 2005. Auxin response factors mediate Arabidopsis organ asymmetry via modulation of KANADI activity. Plant Cell 17, 2899–2910.
Peng, J., Chen, R., 2011. Auxin efflux transporter MtPIN10 regulates compound leaf and flower development in Medicago truncatula. Plant Signal. Behav. 6, 1537–1544.
Pinon, V., Prasad, K., Grigg, S.P., Sanchez-Perez, G.F., Scheres, B., 2013. Local auxin biosynthesis regulation by PLETHORA transcription factors controls phyllotaxis in Arabidopsis. Proc. Natl. Acad. Sci. USA 110, 1107–1112. http://dx.doi.org/10.1073/pnas.1213497110 [pii].
Reinhardt, D., Frenz, M., Mandel, T., Kuhlemeier, C., 2005. Microsurgical and laser ablation analysis of leaf positioning and dorsoventral patterning in tomato. Development 132, 15–26.

Reinhardt, D., Pesce, E.R., Stieger, P., Mandel, T., Baltensperger, K., Bennett, M., Traas, J., Friml, J., Kuhlemeier, C., 2003. Regulation of phyllotaxis by polar auxin transport. Nature 426, 255–260.
Rick, C.M., Butler, L., 1956. Cytogenetics of tomato. Adv. Genet. 7, 267–382.
Robbins, W.J., 1957. Gibberellic acid and the reversal of adult hedera to a juvenile state. Am. J. Bot. 44, 743–746.
Rogler, C.E., Hackett, W.P., 1975. Phase change in hedera helix: induction of the mature to juvenile phase change by gibberellin A3. Physiol. Plant. 34, 141–147. http://dx.doi.org/10.1111/j.1399-3054.1975.tb03809.x.
Romano, C.P., Robson, P.R., Smith, H., Estelle, M., Klee, H., 1995. Transgene-mediated auxin overproduction in Arabidopsis: hypocotyl elongation phenotype and interactions with the hy6-1 hypocotyl elongation and axr1 auxin-resistant mutants. Plant Mol. Biol. 27, 1071–1083.
Ron, M., Kajala, K., Pauluzzi, G., Wang, D., Reynoso, M.A., Zumstein, K., Garcha, J., Winte, S., Masson, H., Inagaki, S., Federici, F., Sinha, N., Deal, R.B., Bailey-Serres, J., Brady, S.M., 2014. Hairy root transformation using Agrobacterium rhizogenes as a tool for exploring cell type-specific gene expression and function using tomato as a model. Plant Physiol. 166, 455–469. http://dx.doi.org/10.1104/pp.114.239392.
Sabatini, S., Heidstra, R., Wildwater, M., Scheres, B., 2003. SCARECROW is involved in positioning the stem cell niche in the Arabidopsis root meristem. Genes Dev. 17, 354–358. http://dx.doi.org/10.1101/gad.252503.
Saini, S., Sharma, I., Pati, P.K., 2015. Versatile roles of brassinosteroid in plants in the context of its homoeostasis, signaling and crosstalks. Front. Plant Sci. 6, 950. http://dx.doi.org/10.3389/fpls.2015.00950.
Sakamoto, T., Kamiya, N., Ueguchi-Tanaka, M., Iwahori, S., Matsuoka, M., 2001. KNOX homeodomain protein directly suppresses the expression of a gibberellin biosynthetic gene in the tobacco shoot apical meristem. Genes Dev. 15, 581–590.
Sakamoto, T., Sakakibara, H., Kojima, M., Yamamoto, Y., Nagasaki, H., Inukai, Y., Sato, Y., Matsuoka, M., 2006. Ectopic expression of KNOTTED1-like homeobox protein induces expression of cytokinin biosynthesis genes in rice. Plant Physiol. 142, 54–62.
Sarkar, A.K., Luijten, M., Miyashima, S., Lenhard, M., Hashimoto, T., Nakajima, K., Scheres, B., Heidstra, R., Laux, T., 2007. Conserved factors regulate signalling in Arabidopsis thaliana shoot and root stem cell organizers. Nature 446, 811–814. http://dx.doi.org/10.1038/nature05703.
Sarojam, R., Sappl, P.G., Goldshmidt, A., Efroni, I., Floyd, S.K., Eshed, Y., Bowman, J.L., 2010. Differentiating Arabidopsis shoots from leaves by Combined YABBY activities. Plant Cell Online 22, 2113–2130. http://dx.doi.org/10.1105/tpc.110.075853.
Schiessl, K., Muiño, J.M., Sablowski, R., 2014. Arabidopsis JAGGED links floral organ patterning to tissue growth by repressing Kip-related cell cycle inhibitors. Proc. Natl. Acad. Sci. USA . http://dx.doi.org/10.1073/pnas.1320457111.
Schwab, R., Maizel, A., Ruiz-Ferrer, V., Garcia, D., Bayer, M., Crespi, M., Voinnet, O., Martienssen, R.A., 2009. Endogenous TasiRNAs mediate non-cell autonomous effects on gene regulation in Arabidopsis thaliana. PLoS One 4, e5980. http://dx.doi.org/10.1371/journal.pone.0005980.
Scofield, S., Dewitte, W., Nieuwland, J., Murray, J.A., 2013. The Arabidopsis homeobox gene SHOOT MERISTEMLESS has cellular and meristem-organisational roles with differential requirements for cytokinin and CYCD3 activity. Plant J. 75, 53–66. http://dx.doi.org/10.1111/tpj.12198.
Shalit, A., Rozman, A., Goldshmidt, A., Alvarez, J.P., Bowman, J.L., Eshed, Y., Lifschitz, E., 2009. The flowering hormone florigen functions as a general systemic regulator of growth and termination. Proc. Natl. Acad. Sci. USA 106, 8392–8397.
Shani, E., Ben-Gera, H., Shleizer-Burko, S., Burko, Y., Weiss, D., Ori, N., 2010. Cytokinin regulates compound leaf development in tomato. Plant Cell 22, 3206–3217, doi:tpc.110.078253 [pii]10.1105/tpc.110.078253.
Shani, E., Burko, Y., Ben-Yaakov, L., Berger, Y., Amsellem, Z., Goldshmidt, A., Sharon, E., Ori, N., 2009. Stage-specific regulation of Solanum lycopersicum leaf maturation by class 1 KNOTTED1-LIKE HOMEOBOX proteins. Plant Cell 21, 3078–3092, doi:tpc.109.068148 [pii]10.1105/tpc.109.068148.
Shannon, S., Meeks-Wagner, D.R., 1991. A mutation in the Arabidopsis TFL1 gene affects inflorescence meristem development. Plant Cell 3, 877–892. http://dx.doi.org/10.1105/tpc.3.9.877.
Shi, X., Gupta, S., Lindquist, I.E., Cameron, C.T., Mudge, J., Rashotte, A.M., 2013. Transcriptome analysis of cytokinin response in tomato leaves. PLoS One 8, e55090. http://dx.doi.org/10.1371/journal.pone.0055090.
Singh, A.P., Savaldi-Goldstein, S., 2015. Growth control: brassinosteroid activity gets context. J. Exp. Bot. 66, 1123–1132. http://dx.doi.org/10.1093/jxb/erv026.
Smith, R.S., Guyomarc'h, S., Mandel, T., Reinhardt, D., Kuhlemeier, C., Prusinkiewicz, P., 2006. A plausible model of phyllotaxis. Proc. Natl. Acad. Sci. USA 103, 1301–1306. http://dx.doi.org/10.1073/pnas.0510457103.
Steiner, E., Efroni, I., Gopalraj, M., Saathoff, K., Tseng, T.S., Kieffer, M., Eshed, Y., Olszewski, N., Weiss, D., 2012a. The Arabidopsis O-linked N-acetylglucosamine transferase SPINDLY interacts with class I TCPs to facilitate cytokinin responses in leaves and flowers. Plant Cell 24, 96–108. http://dx.doi.org/10.1105/tpc.111.093518.
Steiner, E., Livne, S., Kobinson-Katz, T., Tal, L., Pri-Tal, O., Mosquna, A., Tarkowská, D., Muller, B., Tarkowski, P., Weiss, D., 2016. SPINDLY inhibits class I TCP proteolysis to promote sensitivity to cytokinin. Plant Physiol. . http://dx.doi.org/10.1104/pp.16.00343
Steiner, E., Yanai, O., Efroni, I., Ori, N., Eshed, Y., Weiss, D., 2012b. Class I TCPs modulate cytokinin-induced branching and meristematic activity in tomato. Plant Signal. Behav. 7, 807–810. http://dx.doi.org/10.4161/psb.20606.
Tieman, D.M., Ciardi, J.A., Taylor, M.G., Klee, H.J., 2001. Members of the tomato LeEIL (EIN3-like) gene family are functionally redundant and regulate ethylene responses throughout plant development. Plant J. 26, 47–58.
Tobeña-Santamaria, R., Bliek, M., Ljung, K., Sandberg, G., Mol, J.N.M., Souer, E., Koes, R., 2002. FLOOZY of petunia is a flavin mono-oxygenase-like protein required for the specification of leaf and flower architecture. Genes Dev. 16, 753–763. http://dx.doi.org/10.1101/gad.219502.
Tsuda, K., Kurata, N., Ohyanagi, H., Hake, S., 2014. Genome-wide study of KNOX regulatory network reveals brassinosteroid catabolic genes important for shoot meristem function in rice. Plant Cell 26, 3488–3500. http://dx.doi.org/10.1105/tpc.114.129122.
Van Tuinen, A., Peters, A.H.L.J., Kendrick, R.E., Zeevaart, J.A.D., Koornneef, M., 1999. Characterisation of the procera mutant of tomato and the interaction of gibberellins with end-of-day far-red light treatments. Physiol. Plant. 106, 121–128. http://dx.doi.org/10.1034/j.1399-3054.1999.106117.x.
Vidaurre, D.P., Ploense, S., Krogan, N.T., Berleth, T., 2007. AMP1 and MP antagonistically regulate embryo and meristem development in Arabidopsis. Development 134, 2561–2567. http://dx.doi.org/10.1242/dev.006759.
Wang, H., Jones, B., Li, Z., Frasse, P., Delalande, C., Regad, F., Chaabouni, S., Latche, A., Pech, J.C., Bouzayen, M., 2005. The tomato Aux/IAA transcription factor IAA9 is involved in fruit development and leaf morphogenesis. Plant Cell 17, 2676–2692.
Wang, T., Li, R., Wen, L., Fu, D., Zhu, B., Luo, Y., Zhu, H., 2015. Functional analysis and rna sequencing indicate the regulatory role of Argonaute1 in tomato compound leaf development. PLoS One 10, e0140756. http://dx.doi.org/10.1371/journal.pone.0140756.
Weiss, D., Ori, N., 2007. Mechanisms of cross talk between gibberellin and other hormones. Plant Physiol. 144, 1240–1246.
Yamaguchi, S., 2008. Gibberellin metabolism and its regulation. Annu. Rev. Plant Biol. 59, 225–251. http://dx.doi.org/10.1146/annurev.arplant.59.032607.092804.
Yanai, O., Shani, E., Dolezal, K., Tarkowski, P., Sablowski, R., Sandberg, G., Samach, A., Ori, N., 2005. Arabidopsis KNOXI proteins activate cytokinin biosynthesis. Curr. Biol. 15, 1566–1571, doi:S0960-9822(05)00844-4 [pii]10.1016/j.cub.2005.07.060.
Yanai, O., Shani, E., Russ, D., Ori, N., 2011. Gibberellin partly mediates LANCEOLATE activity in tomato. Plant J. 68, 571–582. http://dx.doi.org/10.1111/j.1365-313X.2011.04716.x.
Yifhar, T., Pekker, I., Peled, D., Friedlander, G., Pistunov, A., Sabban, M., Wachsman, G., Alvarez, J.P., Amsellem, Z., Eshed, Y., 2012. Failure of the tomato trans-acting short interfering RNA program to regulate AUXIN RESPONSE FACTOR3 and ARF4 underlies the wiry leaf syndrome. Plant Cell 24, 3575–3589. http://dx.doi.org/10.1105/tpc.112.100222.
Yin, Y., Vafeados, D., Tao, Y., Yoshida, S., Asami, T., Chory, J., 2005. A new class of transcription factors mediates brassinosteroid-regulated gene expression in Arabidopsis. Cell 120, 249–259. http://dx.doi.org/10.1016/j.cell.2004.11.044.
Yoshida, S., Mandel, T., Kuhlemeier, C., 2011. Stem cell activation by light guides plant organogenesis. Genes Dev. 25, 1439–1450. http://dx.doi.org/10.1101/gad.631211.
Young, P.A., 1955. Curl, a mutant teratism of the tomato. J. Hered. 46, 243–244.
Žádníková, P., Simon, R., Zadnikova, P., Simon, R., 2014. How boundaries control plant development. Curr. Opin. Plant Biol. 17, 116–125. http://dx.doi.org/10.1016/j.pbi.2013.11.013.
Zhang, J., Chen, R., Xiao, J., Qian, C., Wang, T., Li, H., Ouyang, B., Ye, Z., 2007. A single-base deletion mutation in SlIAA9 gene causes tomato (Solanum lycopersicum) entire mutant. J. Plant Res. 120, 671–678.
Zhao, Y., Christensen, S.K., Fankhauser, C., Cashman, J.R., Cohen, J.D., Weigel, D., Chory, J., 2001. A role for flavin monooxygenase-like enzymes in auxin biosynthesis. Science 291, 306–309. http://dx.doi.org/10.1126/science.291.5502.306.
Zhao, Z., Andersen, S.U., Ljung, K., Dolezal, K., Miotk, A., Schultheiss, S.J., Lohmann, J. U., 2010. Hormonal control of the shoot stem-cell niche. Nature 465, 1089–1092. http://dx.doi.org/10.1038/nature09126.
Zhou, C., Han, L., Fu, C., Wen, J., Cheng, X., Nakashima, J., Ma, J., Tang, Y., Tan, Y., Tadege, M., Mysore, K.S., Xia, G., Wang, Z.Y., 2013. The trans-acting short interfering RNA3 pathway and no apical meristem antagonistically regulate leaf margin development and lateral organ separation, as revealed by analysis of an argonaute7/lobed leaflet1 mutant in Medicago truncatula. Plant Cell 25, 4845–4862. http://dx.doi.org/10.1105/tpc.113.117788tpc.113.117788 [pii].
Zhou, C., Han, L., Hou, C., Metelli, A., Qi, L., Tadege, M., Mysore, K.S., Wang, Z.-Y., 2011. Developmental analysis of a Medicago truncatula smooth leaf margin1 mutant reveals context-dependent effects on compound leaf development. Plant Cell 23, 2106–2124. http://dx.doi.org/10.1105/tpc.111.085464.
Zhu, M., Li, Y., Chen, G., Ren, L., Xie, Q., Zhao, Z., Hu, Z., 2015. Silencing SlELP2L, a tomato Elongator complex protein 2-like gene, inhibits leaf growth, accelerates leaf, sepal senescence, and produces dark-green fruit. Sci. Rep. 5, 7693. http://dx.doi.org/10.1038/srep07693.