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SHORT COMMUNICATION

Strigolactones' Effect on Root Growth and Root-Hair Elongation May Be Mediated by Auxin-Efflux Carriers

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Abstract Strigolactones are a new group of plant hormones that play a pivotal role in the regulation of aboveground plant architecture. However, the mechanisms governing their regulation of plant growth and development are unknown. We characterized the effect of a synthetic strigolactone (GR24) on tomato (*Solanum lycopersicon*) roots and present evidence for its relationship with the plant hormone auxin. We demonstrate that strigolactones interfere with the inhibitory effect of exogenously applied auxin on root elongation. This GR24-induced root elongation is conveyed via an increase in root cell length accompanied by a reduction in cell diameter, and it occurs despite strigolactone's reduction of cell division (detected as reduction of *CYCB1;1* transcript). In addition, high concentrations of strigolactone lead to asymmetric root growth and inhibition of root-hair elongation. Exogenous application of NAA or IAA was unable to restore symmetric root growth and root-hair elongation in the presence of strigolactone. However, application of NPA, an auxin-efflux inhibitor, did restore root-hair elongation in the presence of strigolactone. Similarly, exogenous application of 2,4-D, a synthetic auxin that is not secreted by efflux carriers, restored root-hair elongation and symmetric growth in the presence of strigolactone. Nevertheless, 2,4-D was unable to prevent root elongation by strigolactones. Therefore, strigolactones' effect on root growth and root-hair elongation appears to be mediated via an effect on auxin-efflux carriers. Nevertheless, more than one mechanism may govern strigolactones' effect on root growth.

Keywords Strigolactone · Auxin · Root · Cell elongation · Symmetric growth · Root hair

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Introduction

Today, strigolactones are considered a new group of plant hormones or their biosynthetic precursors (Gomez-Roldan and others 2008; Umehara and others 2008). They are produced in many plants and their synthesis-associated genes are present in all plants (Klee 2008). Years ago, strigolactones were identified as inducers of witchweed germination (Cook and others 1966) and then, in a number of studies, as signals for plant interactions with both witchweed and mycorrhizal fungi (for example, Akiyama and others 2005; Matusova and others 2005; Bouwmeester and others 2007; Besserer and others 2008; Goldwasser and others 2008; Yoneyama and others 2008). Strigolactone production has been demonstrated in many plant species (for example, Sato and others 2005; Gomez-Roldan and others 2008; Umehara and others 2008), mainly in the roots (Foo and others 2001), derived from the carotenoid pathway (Matusova and others 2005) via the activity of various oxygenases (Gomez-Roldan and others 2008; Umehara and others 2008 and references therein).

Very recently, strigolactones have been suggested to play a pivotal role in the regulation of aboveground plant architecture by inhibiting shoot branching; this was deduced from studies of *Arabidopsis*, pea, and rice mutants defective in strigolactone production or perception (Gomez-Roldan and

others 2008; Umehara and others 2008). However, the mechanisms underlying the effects of strigolactones on plant growth remain elusive.

In this article we examine the effect of a synthetic strigolactone (GR24), previously shown to have biological activity (Gomez-Roldan and others 2008; Umehara and others 2008), on tomato root growth. Roots, unlike shoots, are simple structures with an indeterminate growth pattern and consequently can serve as a model for studies of hormones and their functions (for example, Teale and others 2008). An investigation of strigolactones' effects on root growth and development could promote an understanding of the mechanisms by which strigolactones participate in the control of plant architecture.

Based on their effect on root and root-hair growth, we suggest that strigolactones affect auxin-efflux carriers, thereby regulating auxin flux from root cells. However, there may be more than one mechanism governing strigolactones' influence on root growth.

Materials and Methods

Plant Material and Growth Conditions

Tomato (*Solanum lycopersicon*) cv. M82 (Eshed and others 1992) seedlings were surface-sterilized, immersed in sterile distilled water for 2 h, and placed on 1% water agar in 9-cm Petri dishes (50 seeds per Petri dish). Dishes were placed horizontally in the dark at 25°C for 72 h to induce germination. Germinated seeds were placed on half-strength Murashige and Skoog (MS) agar medium supplemented with 1.5% (w/v) sucrose in Petri dishes containing auxins as follows: indole-3-acetic acid (IAA) at a concentration of 10^{-8} M, 1-naphthalenacetic acid (NAA) at 7×10^{-9} M, and 2,4-dichlorophenoxyacetic acid (2,4-D) at 1×10^{-7} M. These concentrations were determined in a preliminary experiment, and the lowest concentrations exerting a significant effect on root length were applied. The synthetic strigolactone GR24 (Johnson and others 1981) was applied at concentrations of 0.027, 0.27, 0.54, 1.35, 2.7, 8.1, 13.5, and 27 μM (the latter for root-growth symmetry, root-hair elongation, and NAA experiments only). The plates were placed vertically to allow gravitropic root growth along the surface of the agar under constant fluorescent lighting (100 μmol m^{-2} s^{-1}) at 25°C. Root length at 0, 24, and 48 h of incubation was marked on the plates. Gravitropic stimulus was induced by rotating the growth plates 90° after 24 h of incubation. Experiments were repeated four times; each treatment within each experiment included five replicates with four germinated seedlings per replicate. Means of replicates were subjected to statistical analysis by multiple-range test ($p \leq 0.05$) using the JMP statistical package (SAS Institute, Cary, NC).

Determination of Cell Length

Cell length was determined in roots of cv. M82 grown as described above on half-strength MS medium plates. Root segments that grew on plates between 24 and 48 h and segments of their curved sites (for the 27-μM GR24 treatment only) were sectioned, separated, and placed on glass slides. Using a Leica DMLB light microscope (Leica Microsystems GmbH, Wetzlar, Germany), pictures were taken with a Leica DC200 camera of three separate roots from each treatment, at six different locations along the root segment. In all pictures, the focal plane was adjusted to focus on the first cell layer of the cortex beneath the root epidermis. IMAGEJ (http://rsbweb.nih.gov/ij/) was used to quantify cell length. At least 30 cells were measured from each image. Means of replicates were subjected to statistical analysis by multiple-range test ($p \leq 0.05$) using the JMP statistical package.

Root Cross Sections and Determination of Cell Number and Root Diameter

Root segments that grew on plates between 24 and 48 h, as described above, were fixed and sectioned using a Vibratome microtome (Series 1000 Sectioning System, Technical Products International, O'Fallon, MO), as described previously (Gal and others 2006). Sections were placed on glass slides. Using a Leica DMLB light microscope, pictures were taken with a Leica DC200 camera of eight separate roots from each treatment, with three different cross sections along the mature part of the root segment for each root. Cortex cells were counted and root diameter was measured using IMAGEJ. Means of replicates were subjected to statistical analysis by Student's t test ($p \leq 0.05$) using the JMP statistical package.

Determination of Root-Hair Number and Length

For examination of root-hair number and length, roots were grown as described above on plates containing GR24 at a concentration of 0 (control) or 27 μM. Following 24 h of growth, seedlings were gently transferred to new plates containing IAA (10^{-8} M), NAA (7×10^{-9} M), 1-N-naphthylphthalamic acid (NPA, 5 μM), dimethyl sulfoxide (DMSO, 0.5% v/v, the concentration used to dissolve NPA), or 2,4-D (10^{-7} M), and 0 (control) or 27 μM GR24. Roots were examined on plates using a confocal microscope (Leica MZFLIII). Pictures were taken with a Leica DC200 camera of six separate roots from each treatment at 24 h of growth. At 24 h of growth, cells were generated on

0 (control) or 27 μM GR24 and exposed as meristematic cells to auxin or NPA (or DMSO) treatments. The number of root hairs was determined for 500 μm of root segment in each picture taken, and root-hair length was measured for 20 different root hairs within each picture using IMAGEJ. Experiments were repeated four times; each treatment within each experiment included five replicates with four germinated seedlings per replicate. Means of replicates were subjected to statistical analysis by multiple-range test ($p \leq 0.05$) using the JMP statistical package.

Determination of CyclinB1 Transcription Level

We used the steady-state level of CyclinB1 (*CYCB1;1*) transcript as a marker for cell-cycle activity in tomato primary roots (reviewed by Dewitte and Murray 2003). For *CYCB1;1* quantitative PCR experiments, the root tip (10 mm), grown as described above on half-strength MS medium plates for 52 h (end of experiment), was sectioned with a scalpel. Primary roots of four seedlings were pooled and RNA was extracted using TRI reagent (MRC, Cincinnati, OH). DNase treatment, reverse transcription, and quantitative real-time PCR were performed as described previously by Gal and others (2006). The primers used for amplification of the *CYCB1;1* gene fragment were as follows: (forward) 5′-CCA AAG GAG CAT ATT GTG GAC ATT-3′ and (reverse) 5′-TCG TTT ATC TCA GGC TGT GAA TCA A-3′. Tomato 17S ribosomal RNA (GenBank accession No. X51576) was used as an internal control, with specific primers (forward) 5′-CTGAGAAACGGC-TACC-3′ and (reverse) 5′-GACTCATAGAGCCCGG-3′, respectively. Three biological (in each primary root from four seedlings) and two technical replicates were performed for each hormonal treatment. Ratios of gene expression between two examined treatments were determined using the ΔΔCt method (Applied Biosystems manual, Carlsbad, CA) for each biological replicate. Means and standard deviations of the ratios were calculated from the three biological replicates. Means of replicates were subjected to statistical analysis by multiple-range test ($p \leq 0.05$) using the JMP statistical package.

Results and Discussion

We examined the effect on root morphology of a synthetic strigolactone-type isomer (GR24), previously shown to have biological activity similar to that of endogenous strigolactones on plant morphology (Gomez-Roldan and others 2008; Umehara and others 2008). The synthetic strigolactone affected root growth: roots treated with GR24 exhibited shorter and fewer root hairs than control roots (detailed below); however, at GR24 concentrations ranging from 0.027 to 13 μM, only a small and insignificant increase in the length of the primary root was evident (not shown).

Auxin is an established effector of root elongation, and when applied exogenously, it has been shown to reduce root length in a concentration-dependent manner (for example, Hobbie and Estelle 1995). Moreover, auxin has been suggested to be involved in strigolactone's effect on shoot architecture (Ongaro and Leyser 2008; Ferguson and Beveridge 2009). In our system, addition of auxin (10^{-8} M IAA) to the medium caused a significant decrease in primary root elongation relative to controls (Fig. 1A); this was associated with a significant decrease in cell length (Fig. 1B). To find a possible connection between the effects of auxin and strigolactones, we applied GR24 exogenously at increasing concentrations (ranging from 0.027 to 13.5 μM) in the presence of 10^{-8} M IAA and measured the effect on root length. High concentrations of exogenously applied GR24 were able to eliminate the

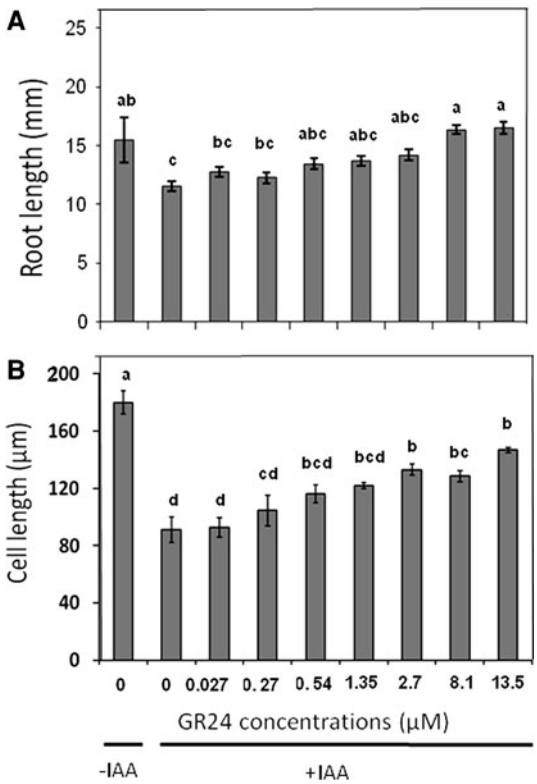

Fig. 1 Length of primary root and root cell in the presence or absence of auxin (IAA) and different concentrations of the synthetic strigolactone GR24. (**A**) Primary root length (mm) and (**B**) primary root-cell length (μm) of *Solanum lycopersicon* M82 roots on an agar plate in the presence (+IAA, 10^{-8} M) or absence (-IAA) of auxin and different concentrations of the synthetic strigolactone GR24. Experiments were repeated four times, in each $n = 20$. Error bars represent standard deviation; different lowercase letters above bars represent significantly different means (multiple-range test; $p \leq 0.05$)

Table 1 Relative levels of *CYCB1;1* transcription in primary roots of *Solanum lycopersicon* M82

Compared root-growth conditions*	Relative steady-state levels of *CYCB1;1* transcript
IAA (10^{-8} M) + GR24 (2.7 μM) vs. IAA (10^{-8} M)	0.055 ± 0.034^{a}
IAA (10^{-8} M) + GR24 (8.1 μM) vs. IAA (10^{-8} M)	0.089 ± 0.032^{a}
IAA (10^{-8} M) + GR24 (2.7 μM) vs. control	0.008 ± 0.004^{b}
IAA (10^{-8} M) + GR24 (8.1 μM) vs. control	0.013 ± 0.002^{b}
IAA (10^{-8} M) vs. control	0.152 ± 0.032^{c}

* Control = no IAA or GR24 was applied; GR24 = synthetic strigolactone; IAA = auxin

[a,b,c] Different superscript indicates significant difference ($p \leq 0.05$)

Table 2 Root curvature in primary roots of *Solanum lycopersicon* M82

Growth conditions*	Degree from stem
Control	172 ± 4^{a}
GR24 (27 μM)	$102 \pm 14^{c,d}$
IAA (10^{-8} M)	171 ± 4^{a}
GR24 (27 μM) + IAA (10^{-8} M)	91 ± 15^{d}
NAA (5 x 10^{-9} M)	$164 \pm 6^{a,b}$
GR24 (27 μM) + NAA (5 x 10^{-9} M)	$133 \pm 15^{b,c}$
2,4-D (10^{-7} M)	172 ± 7^{a}
GR24 (27 μM) + 2,4-D (10^{-7} M)	$156 \pm 7^{a,b}$
Control following gravitropic stimulation (at gravitropic site)	41 ± 8^{e}
GR24 (27 μM) following gravitropic stimulation (at gravitropic site)	44 ± 18^{e}

* Control = no auxin, NPA, or GR24 was applied; GR24 = synthetic strigolactone

[a–e] Different superscript indicates significant difference ($p \leq 0.05$)

suppressive effect of 10^{-8} M IAA on primary root length (Fig. 1A).

Increments in root length obtained by applying strigolactone in the presence of exogenously applied auxin may result from an increase in cell length, cell number, or both. High concentrations of exogenously applied GR24 were able to reverse the suppressive effect of 10^{-8} M IAA on cell length (Fig. 1B) but led to a reduction in *CYCB1;1* transcription, suggesting reduced cell division (Table 1).

In addition, in the presence of exogenously applied auxin, roots treated with 13.5 μM GR24 had a significantly ($p \leq 0.05$) smaller diameter than IAA-treated roots (505 ± 18 μm for IAA-treated roots vs. 321 ± 29 μm for IAA + GR-treated roots) and had a lower number of cells in their cross-section than IAA-treated roots, although this difference was not significant (123 ± 5 for IAA and 107 ± 6 for IAA + GR). Hence, strigolactone's effect on root elongation is probably mediated via cell elongation and, to some extent, cell organization in the presence of exogenously applied auxin rather than via cell division.

The lack of a strigolactone effect on roots in the absence of exogenously applied auxin may be a result of homeostasis that is maintained at endogenic auxin concentrations (that is, an ability to "buffer" strigolactone effect is retained); however, a thorough understanding of these phenomena has yet to be achieved.

Moreover, under high concentrations of strigolactone (27 μM), $85 \pm 10\%$ of the roots exhibited distortion of linear root growth (none of the roots exhibited such distortion in controls, Table 2). This distortion was associated with asymmetric cell length where the roots curve (Fig. 2a, b). The exogenous supply of IAA failed to suppress the asymmetric root growth under high concentrations of strigolactone (Table 2). Although this root response was similar to an abnormal gravitropic response, under these conditions, roots were able to respond to a gravitropic stimulus (Fig. 2c and Table 2).

Auxin-flux carriers are regulators of root asymmetric growth (for example, gravitropism) (for example, Lucas and others 2008). Therefore, we hypothesized that strigolactone may affect auxin transport. This hypothesis is supported by the idea raised recently by Ongaro and Leyser (2008) that strigolactones may influence shoot architecture via their effect on auxin transport. To further examine this possibility, we looked at strigolactone's effect on auxin-influx carriers by examining root and cell length once roots had been exposed to NAA. Cellular IAA levels are controlled by both influx (for example, AUX1) and efflux carriers (for example, PINs; for example, Marchant and others 1999), whereas NAA, rather than being brought in by auxin-influx carriers, is thought to enter the cells through diffusion, while its level is regulated by an efflux carrier (Delbarre and others 1996; Marchant and others 1999). If the strigolactone effect on roots in the presence of exogenously applied IAA is mediated by auxin-influx carriers, we would expect this effect to be reduced once NAA was supplied exogenously. The extent of increase in root length (Fig. 3) in the presence of strigolactone was found to be similar to that in the presence of exogenously applied NAA (5×10^{-9} M) and exogenously applied IAA. Also, similar to the effect of GR24 in the presence of exogenously applied IAA, GR24 in the presence of exogenously applied NAA leads to an increase in cell length (214 ± 40, 167 ± 29, and 286 ± 59 μm were measured for control [in which no auxin or GR24 was applied], NAA only, and NAA + GR24-treated root cells, respectively). Moreover, exogenously applied NAA failed to suppress the

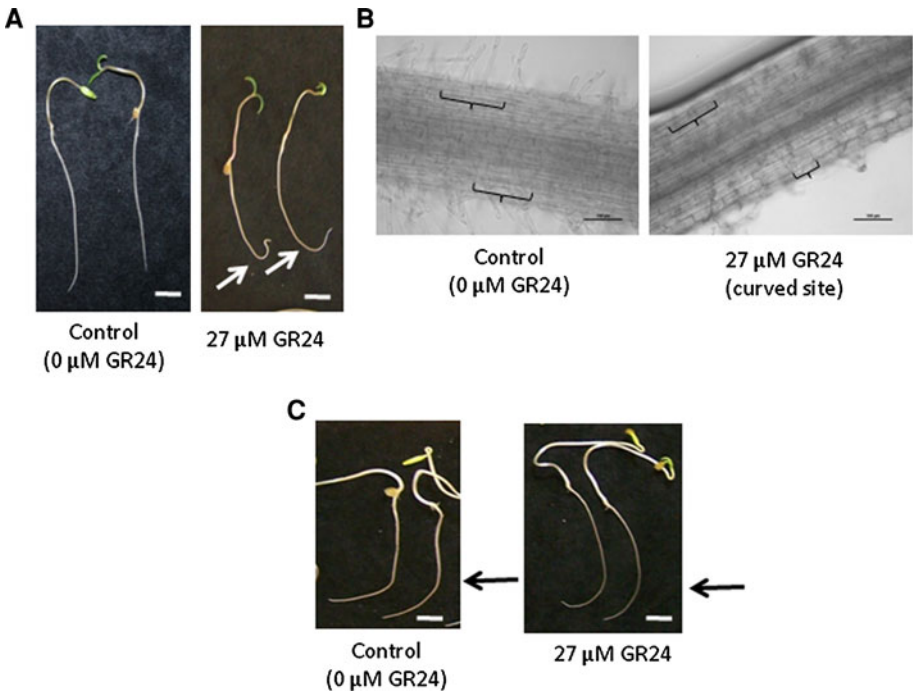

Fig. 2 Root growth and asymmetric root-cell length in the presence or absence of high concentrations of the synthetic strigolactone GR24. **a** Examples of growth of *Solanum lycopersicon* M82 roots on agar plates, in the presence or absence of strigolactone (27 µM GR24). Arrows denote curved sites. Scale bars = 10 mm. **b** Microscopic examination of cortex cells (first layer beneath the epidermis) in control roots and at the curved sites of 27 µM GR24-treated roots. Cell size is emphasized by brackets. Scale bars = 100 µm. **c** Examples of growth of *S. lycopersicon* M82 roots on agar plates in the presence or absence of strigolactone (27 µM GR24), and following gravitropic stimulus. Arrows denote root length at which growth plates were rotated 90°. Scale bars = 10 mm

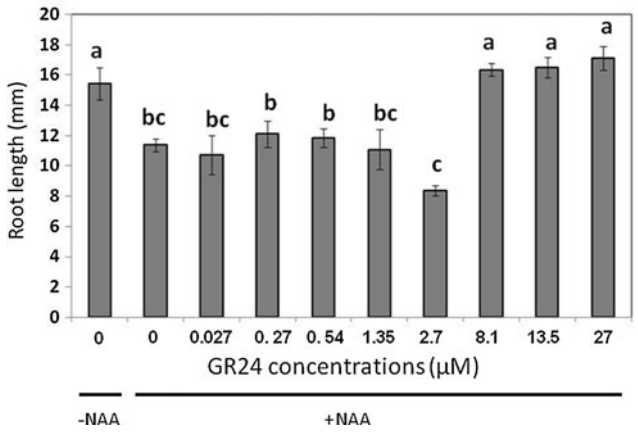

Fig. 3 Primary root length (mm) of *Solanum lycopersicon* M82 roots on an agar plate in the presence (+NAA; 5×10^{-9} M) or absence (-NAA) of auxin and different concentrations of the synthetic strigolactone GR24. Experiments were repeated four times, in each $n = 20$. Error bars represent standard deviations; different lowercase letters above bars represent significantly different means (multiple-range test; $p \leq 0.05$)

distortion in linear root growth under high concentrations of strigolactone (Table 2). Therefore, it is not likely that strigolactone's influence on root growth is mediated by auxin-influx carriers.

Although strigolactones' effects are not mediated by auxin influx, they may be mediated by auxin-efflux carriers, thereby affecting auxin flux and root growth, because cellular IAA levels are controlled by both influx and efflux carriers (for example, Marchant and others 1999). To examine this hypothesis we studied root-hair length, which is affected by cellular auxin levels: increased levels of auxin are associated with increased root-hair elongation and vice versa (for example, Pitts and others 1998). Roots treated with GR24 exhibited shorter and fewer root hairs than control roots (Fig. 4). This effect of GR24 was most pronounced in the 27-µM GR24 concentration. Hence, this GR24 treatment was further examined, as detailed below.

Supplementing IAA or NAA to GR24-treated roots failed to restore root-hair number and length (Fig. 4), further supporting the suggestion that GR24 does not affect auxin-influx carriers. However, exogenous application of NPA, an inhibitor of auxin-efflux carriers (for example, Cande and Ray 1976; Blilou and others 2005), to GR24-treated roots restored root-hair number and length (Fig. 4). This strigolactones' effect is especially apparent with exogenous application of IAA; only application of a combination of NPA and IAA, and not application of IAA only, to the GR24-treated roots led to restoration of root-hair number and length (Fig. 4). Although the complex

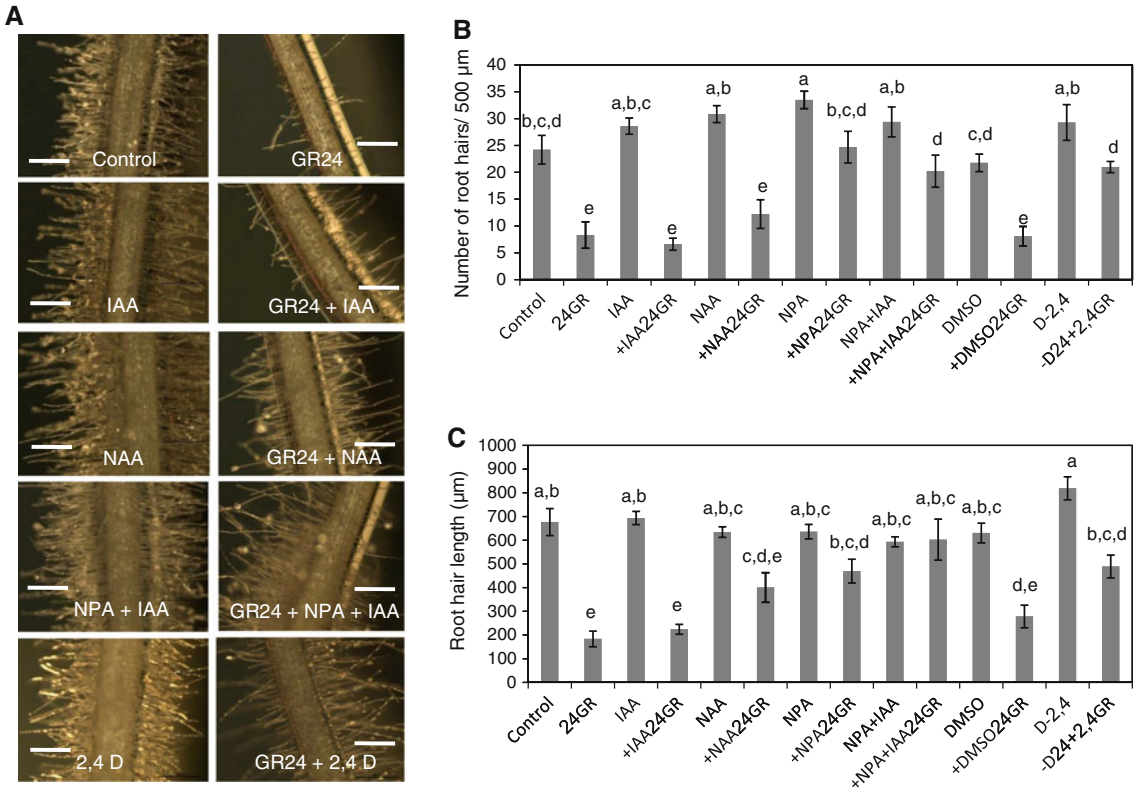

Fig. 4 **A** Examples of roots treated with GR24, auxin (IAA, NAA, or 2,4-D), or NPA, or their combination. Scale bars = 500 µm. **B** Root-hair number and **C** root-hair length in roots treated with GR24, auxin (IAA, NAA, or 2,4-D), or NPA, or their combination. Concentrations used: 10^{-8} M IAA, 5×10^{-9} M NAA, 10^{-7} M 2,4-D, 27 µM GR24. All hormonal concentrations were determined in preliminary experiments as the lowest concentrations with a significant effect on root length; DMSO effect on root hairs was examined at the concentration used for NPA dissolution. Experiments were repeated four times, in each $n = 20$. Error bars represent standard deviations; different lowercase letters above bars represent significantly different means (multiple-range test; $p \leq 0.05$)

experimental designs may lead to complex interpretations, these results suggest that strigolactones affect auxin-efflux carriers (PIN proteins among others; Vieten and others 2007). These proteins are the targets of NPA; once these targets are blocked by NPA, strigolactones' effect on root-hair number and elongation is abolished and root phenotype is restored to that of the untreated roots. DMSO, which was used to dissolve NPA, had no significant effect on root-hair elongation at the examined root segment (Fig. 4).

These findings suggest that when strigolactone is present in high concentrations, it enhances auxin efflux. However, in the *Arabidopsis* strigolactone-synthesis-deficient mutant *max1* (Booker and others 2005; Umehara and others 2008), auxin transport is enhanced and PIN1 transcription induced (Bennett and others 2006). Also, in the rice strigolactone-synthesis-deficient mutant d27, the treatment with NPA showed a remarkable reversion to WT phenotype, suggesting that the tillering phenotype of d27 may be correlated with an enhanced polar auxin transport (Lin and others 2009). It may be that similar to the contradictory effects of auxin on root growth (induction and inhibition recorded for different concentrations of auxin; for example, Hobbie and Estelle 1995), at lower, physiological concentrations, strigolactones inhibit auxin efflux; either absence of or excess of strigolactone facilitate it.

Interestingly, in some cases, most notably in GR24 + NPA + IAA-treated roots, root hairs were partially restored to only one side of the root (Fig. 4A). Similar to root curving, this may reflect the postulated asymmetric growth under high concentrations of GR24, but it may also result from the complexity of experimental designs that may lead to side effects on root growth. Moreover, in GR24-treated roots that were exposed to NPA (or auxin) only as mature tissue, root hairs were not restored (not shown). This may be a result of either an effect of GR24 on root-hair elongation that cannot be reversed by NPA or auxin, or loss of the ability of mature root tissue to respond to root-hair elongation signals.

The synthetic auxin 2,4-D is brought by auxin-influx carriers into the cell, where it accumulates, unable to exit (Delbarre and others 1996). Hence, we expected that the

effects of 2,4-D on root growth would not be influenced by the presence of strigolactone. Our results demonstrated that indeed 2,4-D is able to better restore root-hair elongation (Fig. 4) than is IAA or NAA, and it is able to restore symmetric root growth (Table 2). However, 2,4-D failed to prevent root elongation by GR24 (root length with exogenously applied 10^{-7} M 2,4-D: 8.6 ± 1.1 mm; root length with exogenously applied 10^{-7} M 2,4-D and 13.5 μM GR24: 20.8 ± 0.6 mm).

To summarize, these results suggest that synthetic strigolactone (GR24), a non-natural strigolactone-type isomer previously shown to have biological activity (Gomez-Roldan and others 2008; Umehara and others 2008), may affect auxin-efflux carriers. However, this may not be the only path by which strigolactones affect plant growth regulation. This notion is in line with recent suggestions of strigolactones' role, deduced from studies of shoot morphology: Strigolactones have been suggested to be regulators of auxin transport (Ongaro and Leyser 2008) or secondary messengers of auxin signaling (Brewer and others 2009; Ferguson and Beveridge 2009).

Further work will be needed to test whether these newly identified hormones have a role in root development. Moreover, the effects of strigolactone on root growth are probably associated with root responses not only to auxin, but to other plant hormones that affect root architecture as well (Teale and others 2008).

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