IPGSA CONFERENCE 2010

20th International Conference on Plant Growth Substances

28th June to 2nd July 2010
Tarragona (SPAIN)

I309

CERTIFICATE OF ATTENDANCE

We hereby certify that,

MR. YUNUS EFFENDI

has attended the

20th International Conference on Plant Growth Substances

held at the Universitat Rovira i Virgili, Tarragona (Spain), on 28th June to 2 July 2010.

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	June 28 (Monday)	June 29 (Tuesday)	June 30 (Wednesday)	July 1 (Thursday)	July (Friday)
09:00	Registration (opens every day)	**P2** Hormone Biosynthesis and Transport *Shinjiro Yamaguchi (Japan)*	**P3** Hormone Perception and Signaling *Joe Kieber (USA)*	**PS09** Evolution of Plant Hormone Signaling **PS10** Root Development **PS11** Abiotic Stress **PS12** Chemical Biology	**P4** Hormones and Environment *Salomé Prat (Spain)*
09;45		*Paul Staswick (USA)*	*Bonnie Bartel (USA)*		*Moto Ashikari (Japan)*
10:30		Coffee break	Coffee break	Coffee break	Coffee break
11:00		*Tetsuya Higashiyama (Japan)*	*Zhiyong Wang (USA)*	**PS09** Evolution of Plant Hormone Signaling **PS10** Root Development **PS11** Abiotic Stress **PS12** Chemical Biology	Steve Penfield (UK)
11:30	Opening				
11:45	Silver Medal Lectures *Joanne Chory (USA)*	*Jiri Friml (Belgium)*	*Erwin Grill (Germany)*		*Luis Herrera-Estrella (Mexico)*
12:30	*Tokao Yolota (Japan)*	Lunch & Posters	Lunch & Posters	Lunch & Posters	Closing
13:00					Farewell Lunch
13:15	*Mark Estelle (USA)*				
14:00	Lunch				
15:00	**P1** Hormones and Development *Ottoline Leyser (UK)*	**PS01** Hormone Biosynthesis **PS02** Seed Development and Germination **PS03** Auxin Transport **PS04** Light Responses	**PS05** Hormone Perception and Signaling **PS06** Shoot Development **PS07** Defense responses **PS08** Systems Biology	**PS13** Hormone Interactions **PS14** Reproductive Development **PS15** Hormones and Biotechnology **PS16** Epigenetics/Small RNAs	
15:45	*Eliezer Lifschitz (Israel)*				
16:30	Coffee break	Coffee break	Coffee break	Coffee break	
17:00	*Markus Grebe (Sweden)*	**PS01** Hormone Biosynthesis **PS02** Seed Development and Germination **PS03** Auxin Transport **PS04** Light Responses	**PS05** Hormone Perception and Signaling **PS06** Shoot Development **PS07** Defense responses **PS08** Systems Biology	**PS13** Hormone Interactions **PS14** Reproductive Development **PS15** Hormones and Biotechnology **PS16** Epigenetics/Small RNAs	
17:45	*Veronica Grieneisen (UK)*				
18:30	Wellcome Reception	Tarragona Roman Ruins visit		IPGSA Business Meeting	
19:30					
20:00			congress Dinner		

ATPLA-I A PHOSPHOLIPASE A WITH FUNCTIONS IN GRAVITROPISM, PHOTOTROPISM AND ROOT TIP MOVEMENT

Yunus Effendi[1], Steffen Rietz[1,2], Katrin Radatz[1], Guenther Scherer F.E.[1*]
[1]Leibniz Universität Hannover, Institut für Gartenbauliche Produktionssysteme, Abt. Molekulare Ertragsphysiologie, Herrenhäuser Str. 2, D-30419 Hannover, Germany
[2]Max Planck Institute for Plant Breeding Research, Department of Plant Microbe Interactions, Carl von Linne´ Weg 10, D-50829 Cologne, Germany
Corresponding: scherer@zier.uni-hannover.de

Abstract
Phospholipase A enzymes cleave phospho- and galactolipids to generate free fatty acids and lysolipids that function in animal and plant hormone signaling. Here, we describe three Arabidopsis patatin-related phospholipase A (pPLA) genes AtPLAIVA, AtPLAIVB, and AtPLAIVC and their corresponding proteins. Loss-of-function mutants reveal roles for these pPLAs in roots during normal development and under phosphate deprivation. AtPLAIVA is expressed strongly and exclusively in roots and AtplaIVA-null mutants have reduced lateral root development, characteristic of an impaired auxin response. By contrast, AtPLAIVB is expressed weakly in roots, cotyledons, and leaves but is transcriptionally induced by auxin, although AtplaIVB mutants develop normally. AtPLAIVC is expressed in the floral gynaecium and is induced by abscisic acid (ABA) or phosphate deficiency in roots. While an AtplaIVC-1 loss-of-function mutant displays ABA responsiveness, it exhibits an impaired response to phosphate deficiency during root development. Recombinant AtPLA proteins hydrolyze preferentially galactolipids and, less efficiently, phospholipids, although these enzymes are not localized in chloroplasts. We find that AtPLAIVA and AtPLAIVB are phosphorylated by calcium-dependent protein kinases in vitro and this enhances their activities on phosphatidylcholine but not on phosphatidylglycerol. Taken together, the data reveal novel functions of pPLAs in root development with individual roles at the interface between phosphate deficiency and auxin signaling.

Keyword: Phospholipase, ATPLA-I, Gravitropism, Phototropism

Introduction

At first glance root tips growing full circles, so-called coils, and roots growing in a sinusoidal form (waves), seem to be ephemeral, baroque and superfluous phenomena in primary roots. Formation of coils depends on circumnutation, gravitropism and negative thigmotropism (Migliaccio and Piconese, 2001; Migliaccio et al.,2013) and occur when roots grow on a non-penetrable surface (hard agar) on a usually 60◦–45◦ tilted surface where upright is 90◦. Tilting also induces roots to grow in a wavy fashion. Roots, like shoots,move their tips in a circle-likemovement when unrestricted by soil or other obstacles (Okada and Shimura, 1990; Mullen et al.,1998; Kim et al., 2015). On 90◦ upright surfaces the circumnutation of the root tip is down-regulated by gravitropism such that the root tip becomes straightened out and the root shows no or a very weak waving pattern

(Thompson and Holbrook, 2004). On an impenetrable surface tilting of the root tip induces substantial movement to either side which, becomes “frozen” as a wave-like sinusoidal pattern with the tip moving generally down. Obviously, at some points in the wave the root tip does not perfectly point down but more or less sideways or evenup. Gravitropism recurrently will correct this to growth downward. Especially in an agravitropic mutant, when gravitropic sensing is decreased, the tip may continue to grow upward and eventually form a full circle, called coil.

Negative thigmotropism is the phenomenon that a root retracts slightly from a hard and impenetrable surface when growing down and, instead, grows sideward (Massa and Gilroy, 2003). On a surface, circumnutation movement periodically tries to press the tip onto the surface, leading to a negative thigmotropic response, as well as to lift it slightly in a periodic pattern. It was speculated that, when looking down the root, the negative thigmotropic response happens preferentially only on one side and the lifting on the other so that, in summing up many such movements, an asymmetry in the overall direction of root growing down will be induced. This way, asymmetric growth is assumed to induce the so-called slanting angle which is usually a deviation to the left from the plumb line when looking onto the plant and the surface (Migliaccio and Piconese, 2001; Migliaccio et al., 2013). Likely in conjunction with clockwise circumnutation, the root coils in the wild type grow clockwise so that decreased gravitropic control of downward growth on a tilted surface also is asymmetric with preference of one side i.e. to the left.

The first six waving and coiling mutants were first described by Okada and Shimura (1990). Although probably often not systematically collected, many mutants of root growth patterns were described thereafter (Sedbrook and Kaloriti, 2008; Migliaccio et al., 2013). Out of the waving mutants wav1 to wav6 two genes were identified as belonging to auxin physiology, the influx transport protein AUX1 as WAV5, the efflux transporter gene PIN2/EIR1 as WAV6, and WAV2 belongs to the BUD EMERGENCE 46 gene family (Mochizuki et al., 2005) which is thought to inhibit root bending. Other genes affecting waving and coiling and functioning in auxin physiology are RCN1, a protein phosphatase subunit regulating PIN protein activity (Garbers et al., 1996), AXR4, a regulator of AUX1 (Dharmasiri et al., 2006), and WAG1 and WAG2 code for protein kinases that are related to kinases which regulate PIN protein activity (Santner and Watson, 2006). The coils producing mutants mlo4 and mlo11 code for receptors in pathogen perception and were identified as being involved in thigmotropism and gravitropism regulation (Chen et al., 2009; Bidzinski et al., 2014). We described the coil producing phospholipase A mutant pplaI-1 as agravitropic and disturbed in red light physiology (Effendi et al., 2014). During this work, we realized that phyB-9 mutant roots are agravitropic and also produce strongly increased coil numbers. It was shown in a space experiment that pplaI-1 forms increased coil numbers in microgravity (Scherer and Pietrzyk, 2014). In a different group of waving and coiling mutants tubulin and tubulin-associated proteins are mutated (Sedbrook and Kaloriti, 2008; Migliaccio et al.,2013). They show as a phenotype right-handed slanting or counterclockwise coiling. Of many known root coiling or waving mutants the genes are not yet identified and probably many coiling or slanting/waving mutants were identified serendipitiously, not by systematic screening of, for instance, auxinic mutants.

The known mutant collection of coiling mutants suggested testing tools that were known from in auxin physiology and to also test them in their capacity to induce or decrease coils. The phospholipase A mutant pplaI-1 was a suitable object because it belongs to the group of auxin signaling mutants and shows weak defects in gravitropism, phototropism and red light physiology and shows moderately increased coil numbers on tilted hard agar (Effendi et al., 2014) so that increases still can be monitored. Therefore, we tested with this mutant the influence of auxin efflux and influx inhibitors, pPLA inhibitors, and red/far red light as coilinducing agents. As it is conceivable that root growth movements are integrated in the process of soil penetration (Inoue et al., 1999;Minorsky, 2003) we investigated this and found increased surface penetration rates in the pplaI-1 mutant. Taken together, the results point out auxin transport and auxin signaling as important factors in root coil formation and surface penetration.

Results

Naphthylpthalamic acid (NPA) was found as an inhibitor of gravitropism (Geissler et al., 1985) and later identified as an inhibitor of PIN protein activity (Bailly et al., 2012). When we added increasing concentrations of NPA to wild type (wt Wassilewskia) and to pplaI-1 at 1 M NPA coil formation rose from about 10% (mock) to more than 40% in pplaI-1 seedlings (Fig. 1). Induction of coils in the wt was not apparent, only at 0.1 M NPA a small increase to about 7% was found. In all mock treatments in the wt taken together no coils were observed. The root slanting angle was also markedly increased by NPA and stronger in the pplaI-1 mutant than in the wt. Despite an increased slanting angle in the wt, however, no coils were observed in the wt as were in the pplaI-1 mutant. This argues for an only loose correlation between c slanting angle and coil formation. At >0.5 M NPA roots became increasingly diagravitopic which were clearly apparent at 1 M NPA. At 5 M NPA root directions became irregular but only incomplete coils were observed (not shown). Root growth was inhibited above 1 M NPA as well as hypocotyl growth in both lines.

1-Naphthyloxyacetic acid (1-NOA) is an auxin influx transport inhibitor and 2-NOA is a weaker analog on (Imhoff et al., 2000; Parry et al.,2001).1-NOAinhibits influx transport at the auxin transporter AUX1 which is expressed in the root tip and other tissues (Swarup et al., 2001). Addition of 1-NOA induced coils already at 0.1 M strongly in the mutant pplaI-1. In the presence of 3 M 1-NOA the increase was 63% in pplaI-1 but none in the wt (Fig. 2A and B). At 1 M 1-NOA treatment by 2-NOA much weaker coil formation was observed. This reached about 40% in pplaI-1 and was almost absent (about 5%)in the wt(Fig. 2C and D). Similarly as for NPA, root slanting angles increased in the presence of either inhibitor (Fig. 2C and D). Again in the wt, despite an increase in slanting angles no coil formation was observed in the wt, only in the mutant pplaI-1. Both inhibitors inhibited root and hypocotyl growth in both lines. Auxin activates pPLA activity within about 2 min (Paul et al., 1998) and pPLA inhibitors inhibit auxin-induced elongation and gene expression (Scherer and Arnold, 1997; Scherer et al., 2007). Therefore, we tested the pPLA inhibitors HELSS and ETYA in our coiling tests (Fig. 3). Coiling increased from 0% in the mock assay to 25% at 20 M HELSS in the wt and from 23% in the mock assay to 57% at 20 M HELSS in the mutant pplaI-1. In the wt the pPLA inhibitor ETYA did neither induce coils in mock assays nor at 1 M but in pplaI-1 plants 31% coiling in mock controls and 55% coiling

with 1 M ETYA were found (Fig. 3C). The slanting angles increased at and above 5 M HELSS in pplaI-1 plants, a concentration at which coiling rates increased in pplaI-1 as well but despite some apparent increase of slanting angles in the wt no coil formation was found in the wt. Also, growth inhibition of roots and hypocotyls was small so that again, the slanting angles or root growth (inhibition) provide no explanation for the coil formation despite similar trends in both parameters. In the patatin-related phospholipase A gene pPLAI is one in a family of ten genes (Scherer et al., 2010) and the results with pPLA inhibitors with pplaI-1 indicated that pPLA genes other than pplaI-1 participate in coil formation. So we tested knockouts of all other nine genes (Labusch et al., 2013) in the coil test Several of these knockouts indeed showed increased coil numbers. Genetic redundancy in the pPLA gene family for the property of coil formation is indicated by the results.

We had tested blue and red light receptor mutants for their ability to form coils in white light and only in the phyB-9 mutant we found a strong increase in coil formation, not in phyA-211, cry1, cry2, phot1 or phot2 (Effendi et al., 2014). Therefore, we applied red, far red or white light to wt and pplaI-1 seedlings. Coils were induced by red weakly and by far red light strongly in pplaI-1 (Fig. 4). In the wt this response was much weaker. It has been suggested that root movements may help to penetrate the soil (Inoue et al., 1999; Minorsky, 2003). Since root coiling may be viewed as a kind of mobility we wanted to test the penetrating ability of the wt and pplaI-1 mutants on horizontal agar plates depending on the hardness of this surface.

Discussions

Chemicals like NPA (Geissler et al., 1985) and 1-NOA (Imhoff et al., 2000; Parry et al., 2001) affect auxin transport and affect coiling. Inhibitors of pPLA (HELSS and ETYA) inhibit auxin signal transduction and elongation (Scherer and Arnold, 1997; Scherer et al., 2007) and all these relevant inhibitors increased coil formation. Far red light (Liu et al., 2011) inhibits auxin transport and induced coiling. Rapid regulation of auxin transport is a hallmark of root gravitropism (Friml et al., 2002; Ottenschläger et al., 2003) and regulation of auxin-dependent elongation is equally important in gravitropism. The pPLA inhibitor experiments with the mutant pplaI-1 show that more pPLA's than only pPLAI participate in coil formation. Thus, our physiological results are in line with the knowledge about many known mutants of waving and coiling most of which are affected in gravitropism and auxin transport (Bennett et al., 1996; Müller et al., 1998) or are modifiers of auxin transport (Hobbie and Estelle, 1995; Garbers et al., 1996; Dharmasiri et al., 2006; Chen et al., 2009; Effendi et al., 2014) or of auxin signal transduction (Effendi et al., 2014).

Circumnutation, negative thigmotropism and gravitropism are postulated to make waving and coiling as root growth patterns (Migliaccio and Piconese, 2001; Migliaccio et al., 2013). Another explanation of root movements is provided by Tan et al. (2015) who describe them as responses to cues outside of the root. This description, however, does not include circumnutation which is autonomous. Waving and coiling can be induced in Arabidopsis by tilting agar plates from a 90◦ angle (with respect to the horizontal support) to a 60◦–45◦ (Simmons et al., 1995). Without additional stimuli e.g. high solute concentration (Buer et al., 2000) usually only mutants form coils but waves originate on a tilted surface in wt plants (Thompson and Holbrook, 2004) but not on a vertical 90◦surface.

On a 45◦ tilted surface the root tip will sense the impenetrable surface as an obstacle leading to a negative thigmotropic reaction (Massa and Gilroy, 2003). Negative thigmotropism leads the root tips to move sideward until it can grow down freely again. Though an agar surface at 45◦–60 is an obstacle to a downward growing root tip the thigmotaxis experiment by Massa and Gilroy cannot suggest a simple rule for the formation of root growth patterns like coils. Circumnutation is thought to occur also on a 45◦–60◦ surface but its consequences for root growth patterns are not known in detail. It should periodically lead to stronger contact with the surface and is probably the main component to induce slanting. Gravitropism guides the root down.

Though these three responses circumnutation, negative thigmotropism and gravitropism, are taken as a quite plausible explanation for coiling (Migliaccio and Piconese, 2001), the interactions of all three factors are not clear in detail. Potentially, a strong pressing of the root tip to the surface by circumnutation could lead to sideward growth as in negative thigmotropism. Adding circumnutation and thigmotropism up in several periodic events this could lead to asymmetrical growth to the left as itis observed when waves and a slanting angle of the root are formed. Slanting increased with all inhibitors and in red light in the wt and thi response was always stronger in the mutant but did not lead to coil induction the wt (compare Fig. 2B and D) so that the correlation of slanting - which could be based on circumnutation - and coil induction remained unclear.

Root circumnutation is correlated with periodic changes in H+ and Ca2+ activity in the root (Shabala and Newman, 1997) and activation of the proton pump is a hallmark of auxin action (Hager 2003; Takahashi et al., 2012) whereas the link of auxin to calcium physiology is much less clear (Di et al., 2015). Circumnutation of the shoot is enhanced by gravity as experiments in space showed (Brown et al., 1990;Johnson, 1997; Hatakeda et al., 2003) and, in the root, gravitropism is linked to circumnutation (Mullen et al., 1998; Minorsky, 2003; Kim et al., 2015). The clockwise tip growth direction is enhanced when gravity, by positive gravitropism, and light from above, by negative phototropism, direct the root the same direction. Clock-wise direction is decreased when light is applied form below so that both direct the root into an opposing direction (Mirza, 1987) which, however, was not tested here. The similarity in the frequencies of the waving pattern and the circumnutation pattern of roots suggested that circumnutation may cause the thigmotropic force when tactile stimulation starts (Mullen et al., 1998). In agreement with observations on shoots (Johnson, 1997) differences in growth rate did not correlate with the period of the

oscillations. However, recently the ageotropum pea mutant was identified also as a modifier of circumnutation (Kim et al., 2015) but other agravitropic mutants were not investigated under the viewpoint as potential circumnutation mutants so that circumnutation mutations or negative thigmotropism mutants are not known. Thus, the quantitative impact of these two parameters on coiling remains unclear.

After a period of sideward growth of the tip, gravitropism will lead the root tip downward so that this would shape periodically the downward growing part of the waves. Waving periodicity and shape are genetically determined i.e. were changed in several mutants. Four of these six genes were identified in waving mutants (Okada and Shimura, 1990). Two of those, AUX1 and PIN2, affect gravitropism (Bennett et al., 1996; Friml et al., 2002), one is an E3 ligase with unknown function, and one belongs to the BUD EMERGENCE 46 gene family (Mochizuki et al.,

2005).Reduced gravisensing is clearly correlated with coil formation, e.g. in the mutants pin2, aux1, and pplaI-1. In conclusion, the choices of our inhibitors and far red light experiments find a clear correlation in the properties of most of the known coiling/waving mutants as auxinic mutants related to auxin signal transduction, auxin transport and gravitropism. Root tip mobility could be related to soil penetration of the tip. Literature on root tip mobility or movements and soil penetration is scarce. Deep water rice seedling roots forming large spiral angles are more effective in colonization of soil than those with smaller ones. They make 2–3.5 rotations per day. Faster seedlings are not so efficient (Inoue et al., 1999). However, the conditions in water and a soft soil may be different from our conditions with hard agar and a comparatively dry surface. Our coiling experiments (Fig. 4) point out a role for far red light. Red light inhibits auxin transport and far red light decreases this effect (Liu et al., 2011) which could provide the link between red light and root movements, inducing coil formation as a consequence of disturbances in auxin transport. Our far red experiments, the high coiling rate of phyB-9, and the increased surface penetration of pplaI-1 (which is a coiling and red light signaling mutant (Effendi et al., 2014)) suggest as a testable speculation that a seedling shaded by green plants might bury the root tip faster in the soil than in white light

Material and Methods

Seeds for most experiments were stratified for 4 d and plated on ½ MS medium (2% (w/v) Bacto-agar) supplemented with 1% (w/v) sucrose and appropriate amounts of inhibitors in DMSO or mock. Inhibitors used were HELSS (haloenol lactone suicide substrate: E-6-(bromomethylene) tetrahydro-3-(1-naphthalenyl)-2H-pyran-2-one), 1-NOA (1-naphthoxyacetic acid), 2-NOA (2-naphthoxyacetic acid), 1-NPA (1-naphthylphtalamic acid) and ETYA (eicosatetraynoic acid). Plants were grown on petri dishes standing upright for 3 days in the light to orientthe roots and for nine additional days or as indicated tilted to 45◦ where upright is corresponding to 90◦ (16 h light: 8 h dark; 50 mol/m−2 × s−1; fluorescent tubes) at 22.5 ◦C. After scanning (CanonScan 800F;

resolution 600 dot per inch) coils were counted as percent per plate. Red and far red light experiments were done with 100% MS medium and 2% (w/v) sucrose. The higher osmotic concentration of sucrose induces more coils (Effendi et al., 2014). For three days plants were kept upright in white light (16 h light: 8 h dark; 50 mol/m−2 × s−1), after that tilted to 45◦ and kept for additional six days in red or far red (350 moles/m−2 × s−1) which was applied in an LED box at 22.5 ◦C (CLF, Plant Climatics) for another 6 days at 22.5 ◦C. For surface penetration experiments ½ MS medium was used and the agar concentrations as indicated. Surface penetration was counted by careful visual inspection of each plate separately. Parallel white light assays were kept in laboratory light as above. For statistics, percent values for one plate each were taken. Three independent experiments were made for each inhibitor concentration or irradiance with together 36–48 individuals. Error bars represent standard error.

To make a time laps movie plants on the plates were photographed with a Canon EOS D30 camera with macro lens every 20 min and pictures were combined to a movie by the program moviemaker®. Photos were taken from the backside of the plates so that in the movie sides are switched in comparison to other figures and influence of background light is noticeable. From right to left 8 seedlings can be seen, starting rightmost with a Ws wild type plant, then a pplaI-1 plant,

etc. alternating. Only pplaI-1 seedlings formed coils. In the dark period a flashlight was used. Days are indicated by the circadian cotyledon movements and elongation pulses in the early morning time. The 2% agar plates (1/2 MS) were kept at 45◦ after three days upright growth and then kept 45◦ tilted with a day-night cycle in white light (16 h/8 h) for 6 days.

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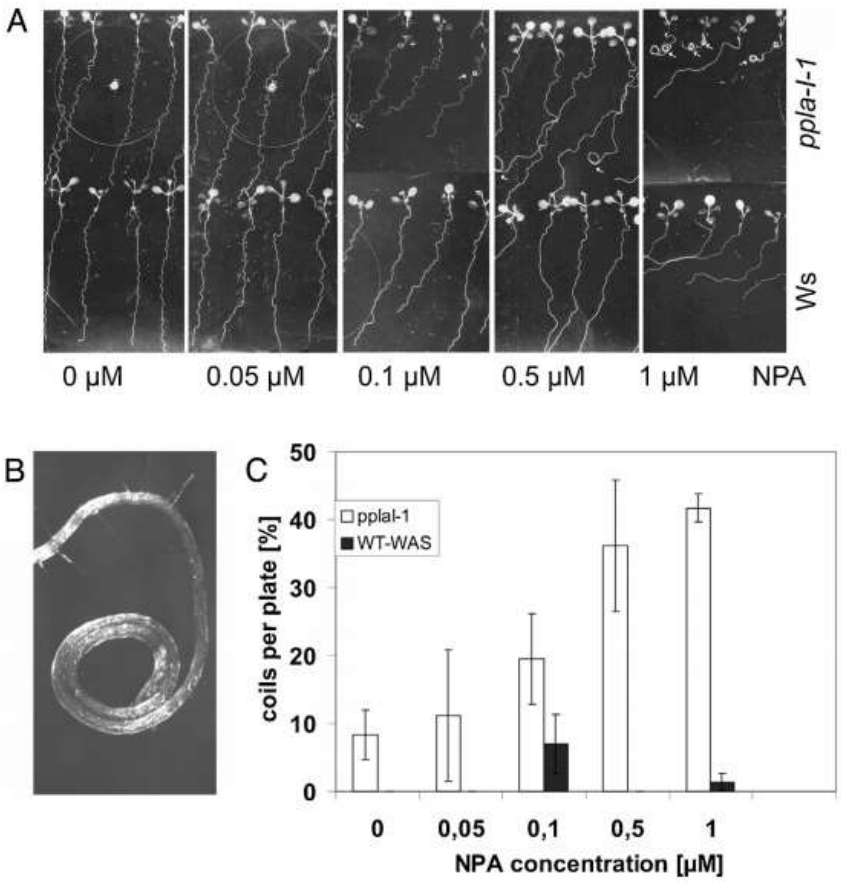

Fig. 1. Root coil formation in response to the auxin efflux inhibitor NPA. (A) Scans of seedlings. Arrows indicate coils. (B) Single coil from the mutant pplaI-1. (C) Quantification of coils

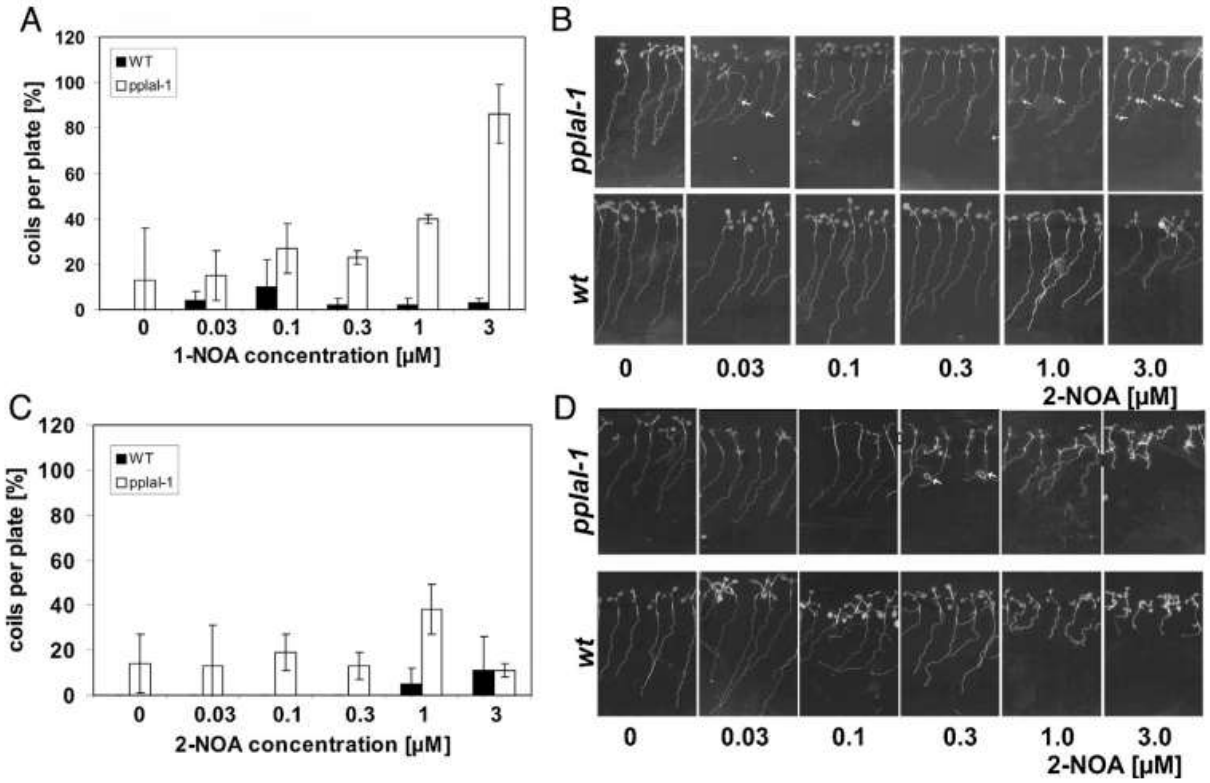

Fig. 2. Root coil formation in response to the auxin influx inhibitor 1-NOA and the analog on 2-NOA. (A, C) Quantification of coils. (B, D) Scans of seedlings. Arrows indicate coils.

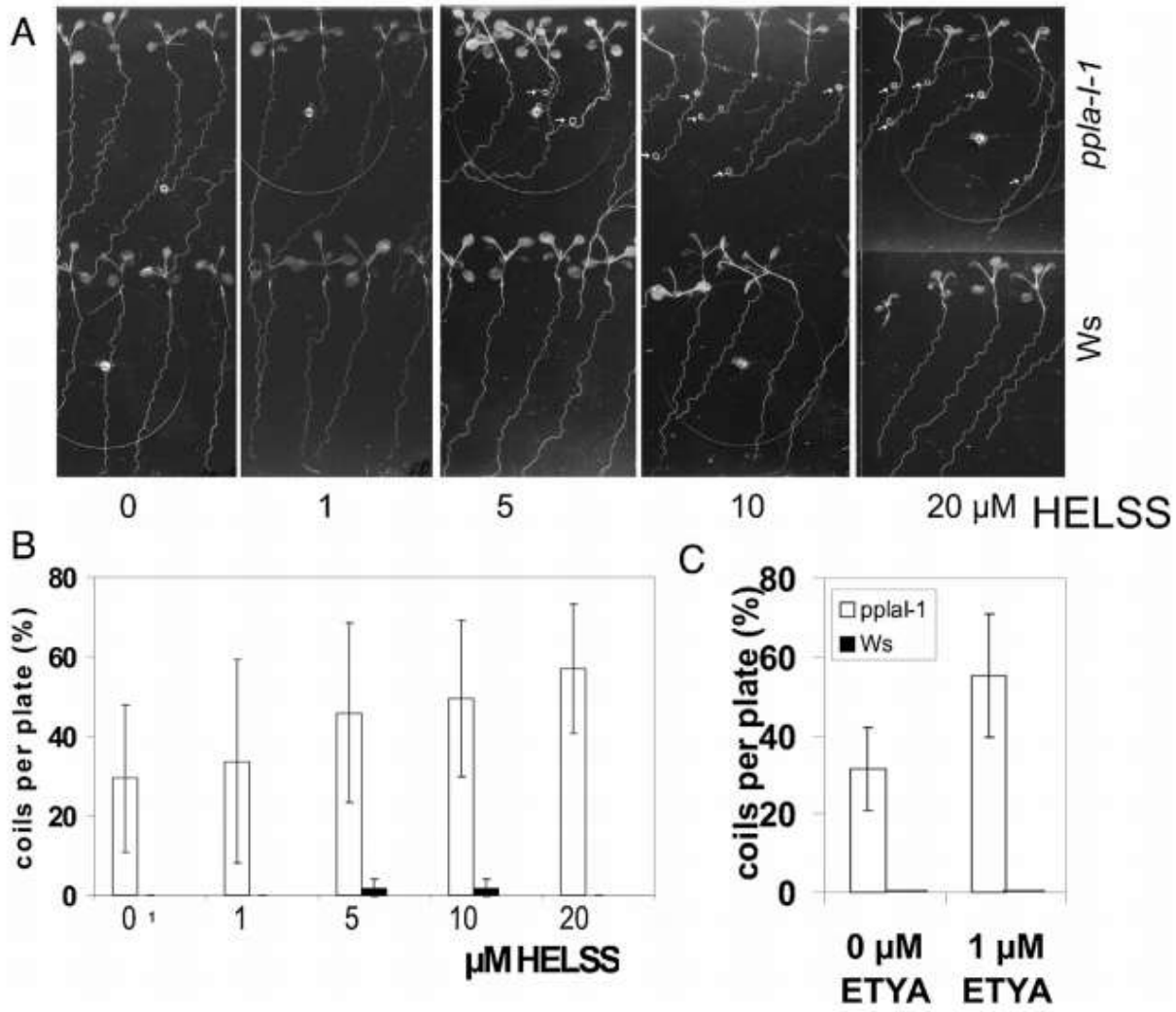

Fig. 3. Root coil formation in response to the auxin and phospholipase inhibitors HELSS and EYTA. (A) Scans of seedlings. Arrows indicate coils. (B, C) Quantification of coils.

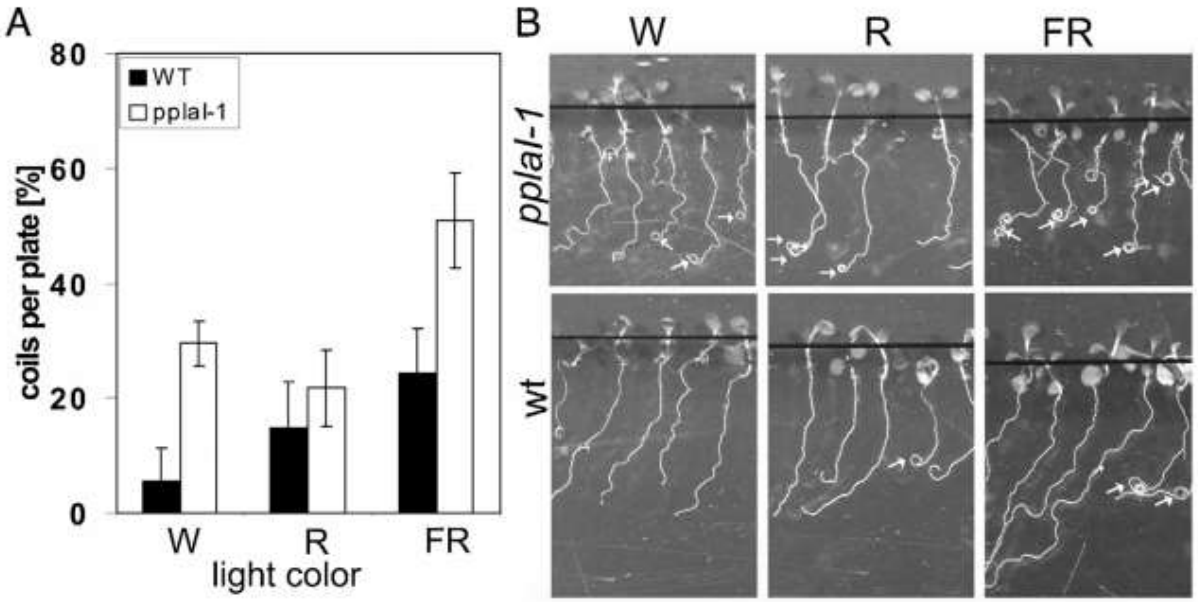

Fig.4. Root coil formation in response to the red (3 mol/m−2 × s−1 R), far red (3 mol/m−2 × s−1 FR) and white (50 mol/m−2 × s−1 W) light. (A) Quantification of coils. (B) Scans of seedlings.

PS05-18 **STRUCTURAL BASIS FOR GIBBERELLIN RECOGNITION BY ITS RECEPTOR GID1**
Miyako Ueguchi-Tanaka (Japan)

PS05-19 **MIS-REGULATION OF EARLY AUXIN-INDUCED GENES IN PHOSPHOLIPASE A KNOCKOUTS**
Corinna Labusch (Germany)

PS05-20 **CHEMICAL SCREENING AND CHARACTERIZATION OF INHIBITORS FOR GIBBERELLIN RECEPTOR**
Jung-min Yoon (Japan)

PS05-21 **A POSSIBLE CYTOSOLIC ACTIVITY FOR THE GA RECEPTOR, GID1**
Sivan Sagiv (Israel)

PS05-22 **DOMAIN REQUIREMENTS FOR DIFFERENT ROLES OF THE ETR1 ETHYLENE RECEPTOR**
Brad Binder (USA)

PS05-23 **TRANSCRIPT PROFILING OF CYTOKININ ACTION IN ARABIDOPSIS ROOTS AND SHOOTS**
Brenner Wolfram (Germany)

PS05-24 **THE IMA GENE ENCODES AN ADAPTER MINI ZINC FINGER PROTEIN REGULATING THE DEVELOPMENT OF FLORAL MERISTEM IN TOMATO.**
LEBLOND JULIE (FRANCE)

PS05-25 **QUANTITATIVE DIFFERENTIAL ANALYSIS OF PLANT PROTEOME IN A RESPONSE TO HORMONAL REGULATIONS**
Marketa Zdarska (Czech Republic)

PS05-26 **DYNAMIC STRUCTURE AND BINDING SPECIFICITY OF THE RECEIVER DOMAIN OF SENSOR HISTIDINE KINASE CKI1**
Tomas Klumpler (Czech Republic)

PS05-27 **ATPLA-I, A PHOSPHOLIPASE A WITH FUNCTIONS IN GRAVITROPISM, PHOTOTROPISM AND ROOT TIP MOVEMENTS**
Günther Scherer F.E. (Germany)

PS05-28 **AUXIN-BINDING PROTEIN1 (ABP1), THE SECOND AUXIN RECEPTOR**
Yunus Effendi (Germany)

PS05-29 **MUTATION OF TRNA SPECIFIC ISOPENTENYLTRANSFERASES AFFECTS ARABIDOPSIS PHENOTYPE**
Silvia Gajdosova (Czech Republic)