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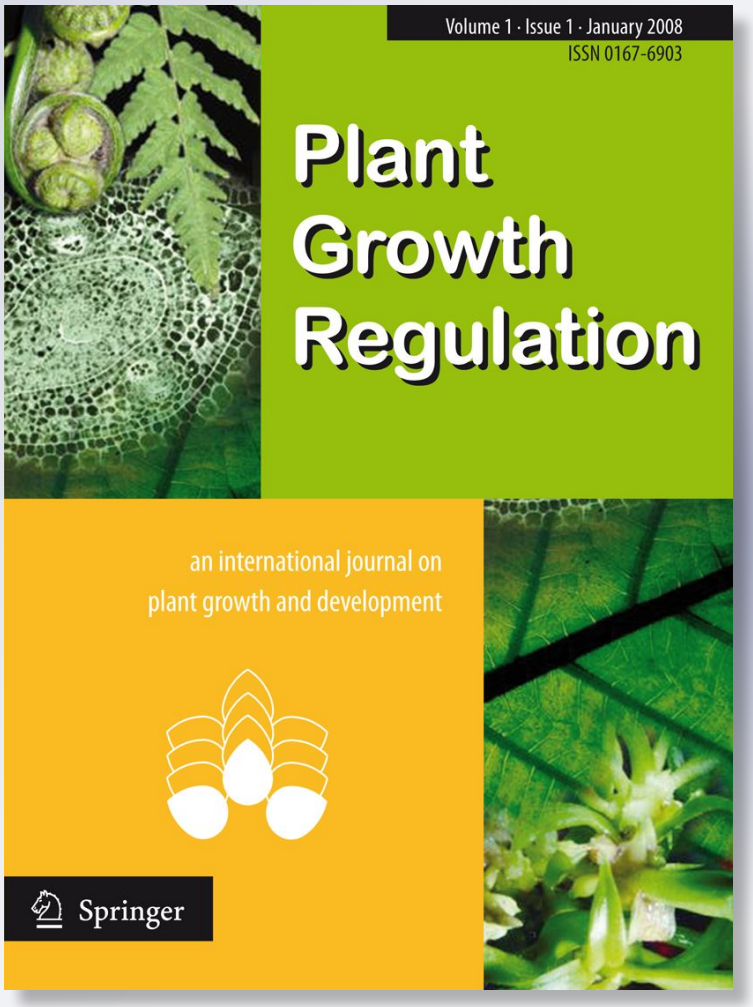
Plant Growth Regulation
An International Journal on Plant Growth and Development

ISSN 0167-6903
Volume 66
Number 2

Plant Growth Regul (2012) 66:129-136
DOI 10.1007/s10725-011-9636-4



Springer

Plant Growth Regul (2012) 66:129–136
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ORIGINAL PAPER

Sunflower root growth regulation: the role of jasmonic acid and its relation with auxins

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Received: 15 July 2011 / Accepted: 5 November 2011 / Published online: 15 November 2011

Abstract Jasmonates are lipid-derived hormones that act as signal molecules in abiotic and biotic stresses and influence several aspects of plant growth and development. In this work we have investigated the effect of jasmonic acid (JA) on the root architecture of *Helianthus annuus* seedlings and if JA and auxins interact to modulate the growth of the primary root (PR) and lateral roots (LR). The addition of μM concentrations of JA to the growing medium of sunflower seedlings decreased the growth of the PR and LR, and also reduced the number of LR. Moreover, treatment with ibuprofen, an inhibitor of JA synthesis, increased PR and LR root length causing a deep effect on root architecture. Hence, not only exogenous but also the endogenous JA regulates sunflower root growth. Microscopic analysis showed that the application of JA reduces the cortex cell length and the estimated cell production rate in root meristem while ibuprofen only affects the cell elongation. A possible interaction between JA and auxins to regulate root growth was further analyzed. We show that JA produced its phenotype even in the presence of reduced levels of auxin generated by treatment with an auxin transport inhibitor. Besides, the auxin produced its phenotype even when ibuprofen was applied. In conclusion, JA may induce primary and lateral root growth inhibition in sunflower by an auxin-independent pathway.

Keywords Auxin · *Helianthus annuus* · Jasmonic acid · Lateral root · Primary root

G. Corti Monzón (✉) · M. Pinedo · L. Lamattina · L. de la Canal
Instituto de Investigaciones Biológicas, Universidad Nacional de Mar del Plata—CONICET, Funes 3250, 7600 Mar del Plata, Argentina
e-mail: cortimonzon@mdp.edu.ar

Abbreviations

IBU	Ibuprofen
JA	Jasmonic acid
LR	Lateral roots
NAA	1-Naphthylacetic acid
NPA	N-1-Naphthylphthalamic acid
PCBI	*p*-chlorophenoxyisobutyric acid
PR	Primary root

Introduction

The root system of higher plants mainly consists of an embryonic primary root (PR) and postembryonically developed lateral roots (LR). The growth of the PR, root branching and LR formation is influenced by a wide range of environmental cues, such as nutrients and water availability in the soil (Malamy 2005). As sessile organisms, plants need to adapt to frequent changes of the environment and root plasticity is of critical importance in this process, allowing them to compete for resources in the soil. Complex physiological aspects are involved in the development of PR and LR and there are many intervening molecules, including plant hormones. Among the latter, auxin is a key player (Fukaki and Tasaka 2009; Benková and Hejátko 2009). Accumulated evidence show that the application of auxin inhibits the primary root growth (Rahman et al. 2007; Zhao and Hasenstein 2009) and stimulates LR formation (Celenza et al. 1995; Laskowski et al. 1995; Casimiro et al. 2001), whereas application of polar auxins transport inhibitors such as NPA prevent LR formation (Casimiro et al. 2001). Furthermore, mutants for auxin transport, signaling and perception show reduced LR number (Casimiro et al. 2003) while mutants that

accumulate auxin to a high level produce excess of LR (Delarue et al. 1998).

Jasmonic acid (JA) and its derivates, collectively referred to as jasmonates (JAs), are linolenic acid-derived cyclopentanone-based compounds of wide distribution in the plant kingdom (Wasternack and Kombrink 2009) that have been accepted as plant hormones. They were first characterized as potent regulators of defense responses mediating, for example, resistance to insect attack, and to certain bacterial and fungal pathogens (Turner et al. 2002; Farmer et al. 2003; Wasternack 2007). It has also been shown that JAs influence several aspects of plant growth and development, including promotion of flower and fruit development, induction of tuberization and tendril coiling, as well as inhibition of seed and pollen germination, and restriction of root growth, among others (see Wasternack 2007 for review).

In certain plant species, such as *Arabidopsis thaliana* (Staswick et al. 1992), O*ryza sativa* (Wang et al. 2002), *Allium cepa* and *Phaseolus coccineus* (Maksymiec and Krupa 2007), it has been shown that the application of jasmonates (JA or Methyl-JA) inhibits root growth. However, it has recently been shown that JA does not mediate systemic root growth responses to wounding in *A. thaliana* (Schmidt et al. 2010), while it participates in this response in *Nicotiana attenuata* (Hummel et al. 2007; Hummel et al. 2009). These results point out that the contribution of JA in many aspects of growth regulation are still unclear and can differ between species. Besides, in contrast with the effect of JA on PR length, less is known about the regulation of LR formation and LR growth by jasmonates.

The use of inhibitors of JA biosynthesis like ibuprofen (IBU) and salicylhydroxamic acid (SHAM), which block JA biosynthesis by inhibition of lipoxygenase, has provided valuable information for understanding the role of jasmonic acid in plants (Staswick et al. 1991; Nojiri et al. 1996; Oikawa et al. 2001; Zhu et al. 2006; Maksymiec and Krupa 2007). In this paper, we have analyzed the effect of JA and IBU on sunflower (*Helianthus annuus*) seedlings root architecture. Moreover, the relationship between JA and auxins to modulate PR and LR growth was investigated. Sunflower is a relevant crop frequently suffering yield losses originated by root lodging (Sposaro et al. 2008) so that studies analysing the basis of root architecture may give important clues to understand its behaviour.

Materials and methods

Plant material

Sunflower seeds (*Helianthus annuus* L, line 10347) provided by Advanta Semillas SAIC, Centro Biotecnológico Balcarce, Argentina, were surface-sterilized in 27.5 g/l sodium hypochlorite for 30 min, rinsed extensively and imbibed in water over night. They were carefully peeled and germinated in moistened filter paper for 3 days in a chamber at 25 ± 1°C and a 14 h:10 h (day:night) photoperiod. The seedlings (with a PR of approximately two cm) were then transferred to nutrient solution [KNO3 3 mM, MgSO4 0.5 mM, Ca(NO3)2 1.5 mM, KH2PO4 0.5 mM, H3BO3 25 μM, MnSO4 1 μM, ZnSO4 0.5 μM, CuSO4 0.3 μM, Na2MoO4 0.05 μM and FeNaEDTA 50 μM], supplemented or not with the hormones and/or inhibitors described later, and grown for 4 days hydroponically under controlled conditions as indicated above. The solution was maintained at a constant volume by daily additions. For longer treatments (10 days) the hydroponic solution was removed the fifth day and replaced by a fresh one.

Chemicals

Jasmonic acid (JA), Ibuprofen (IBU), 1-naphthylacetic acid (NAA) and salicylhydroxamic acid (SHAM) were from Sigma (St. Louis, MO, USA). N-1-naphthylphthalamic acid (NPA) from Chemical Services (West Chester, PA, USA). For stock solutions, JA and NAA were dissolved in 100% ethanol, IBU in 50% ethanol and NPA and SHAM in DMSO. The respective controls with ethanol and DMSO were performed and the solvent represented less than 0.02% in the seedlings growing medium.

Root length, cell length and cell production rate assays

PR and LR length were measured from images registered at the end of the treatments using ImageJ 1.38 software (http://rsbweb.nih.gov/ij/) while the number of LR was assessed under a magnifying glass. All root length data are the average of three or four independent experiments with 6 seedlings each one, and the results were analyzed using *t* test or Mann–Whitney test.

Cell length and cell production rate were estimated as indicated in Swiatek et al. (2003) and Rahman et al. (2007), with minor modifications. Briefly, images of the whole seedlings were registered and root length was measured at the beginning and the end of the experiment to obtain a value of root growth. Root elongation rate was calculated as root growth per day. Cortical cell length was measured from microscopic images of the roots captured using a digital camera attached to the microscope Eclipse E 200 (Nikon). To ensure newly matured cells were scored, the cell length was measured in longitudinal sections of the tip root region where root hairs were observed. The length of 30–40 mature cortical cells was measured from each root, with 4 roots analyzed per treatment. Cell production rate was estimated by taking the ratio of root elongation rate

and the average cell length. Data are the average of three independent experiment and the results were analyzed using *t* test or Mann–Whitney test.

Results

JA inhibits primary and lateral root growth

The effect of jasmonic acid treatment on sunflower root architecture was evaluated by incubating 3 days old seedlings with different hormone concentrations in the growing medium. As shown in Fig. 1a, b, after 4 days of treatment JA diminished the length of PR in a dose dependent manner. The length of the PR was reduced by 30% at concentrations around 40–60 μM (Fig. 1b).

In order to evaluate the role of endogenous JAs in root growth inhibition, seedlings were treated with 20 μM IBU or with this inhibitor supplemented with 40 μM JA. In agreement with the presumption that endogenous JAs contribute to growth inhibition, the treatment with ibuprofen induced the growth of the PR (Fig. 2a, b). In addition, IBU greatly increased the length of LR (Fig. 2a, c). After

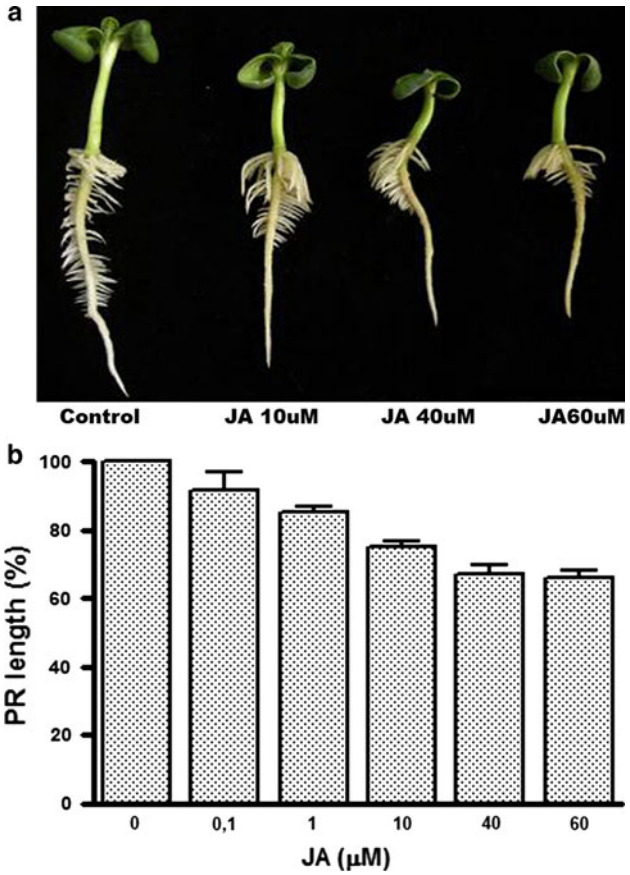

Fig. 1 Effect of JA on root architecture in sunflower seedlings. Three days old seedlings were grown in a medium supplemented with different concentration of JA during 4 days. **a** A representative image; **b** primary root (PR) length expressed as a percentage of the control. Data shown represent means ± SE ($n = 6$) for three different experiments

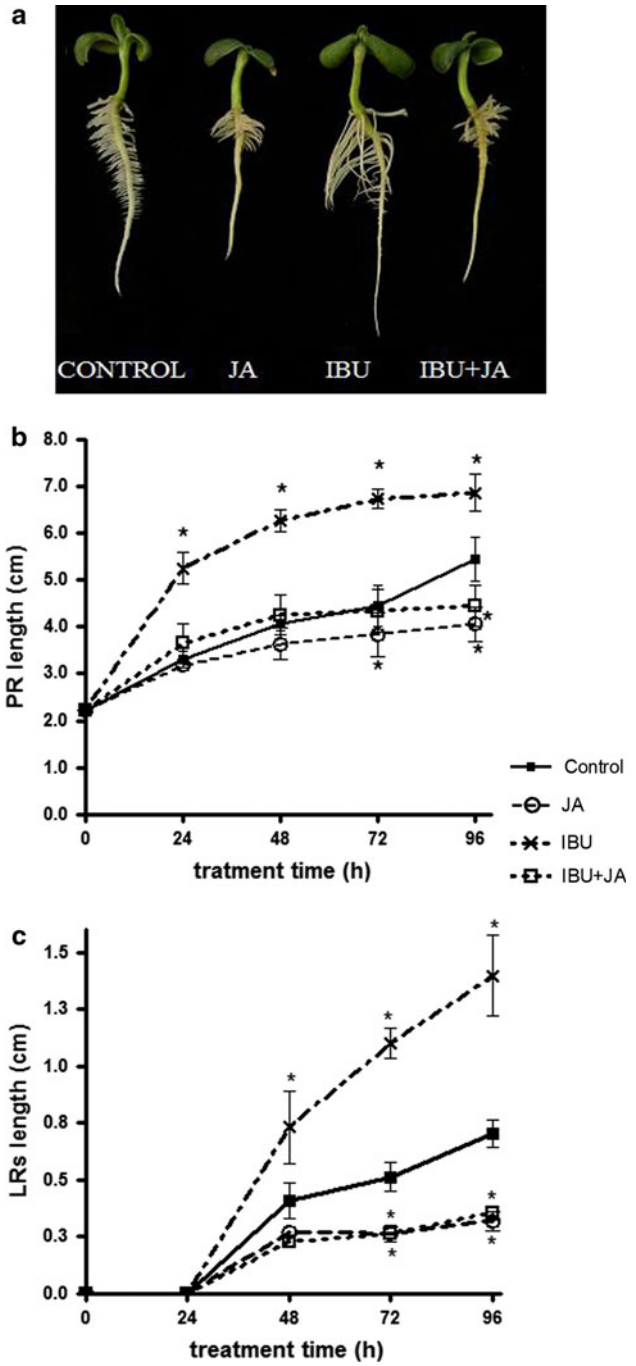

Fig. 2 Effect of a JA biosynthesis inhibition on the primary root and lateral root growth. Three days old seedlings were grown hydroponically in nutrient solution (control) or with the addition of 40 μM JA, 20 μM IBU or both, and the root length was measured every 24 h for 4 days. **a** A representative image of sunflower seedlings at the third treatment day; **b** quantification PR and **c** LR length. Data shown represent means ± SE ($n = 6$) for three different experiments. * Indicate a significant difference compared to control seedlings ($P < 0.05$)

4 days of treatment, the IBU-mediated increments in the PR and LR length compared to control seedlings were about 26 and 100%, respectively. Besides, supplementation with exogenous JA was able to revert to the phenotype of the JA-treated roots (Fig. 2a–c). These changes produced by IBU treatment in sunflower roots were also observed in plants incubated with 50–250 μM SHAM, another widely used inhibitor of JA biosynthesis (Staswick et al. 1991; Kong et al. 2005; Zhu et al. 2006; Maksymiec and Krupa 2007). After 4 days of treatment, 250 μM SHAM-induced increments of 40 and 70% in PR and LR length, respectively, compared to control seedlings (data not shown).

Since root length is the consequence of cell elongation as well as cell division, the contribution of these parameters to the JA-modulated root growth was assessed by an optical microscopy approach. Root length data were taken at the third day of treatment, where maximal differences between control and IBU-treated seedlings are observed (Fig. 2b). Analyses of PR cuts show that seedlings grown in 40 μM JA reduced the cortical root cell length and the estimated cell production rate by 30 and 40%, respectively (Table 1). On the other hand, plants treated with 20 μM IBU increased more than 100% the cell length while the cell production rate was not significantly affected. As shown in Table 1, the same tendency was observed when the analysis was performed on lateral roots. The bulk of results presented point out that endogenous jasmonates inhibit cell elongation and, as a consequence, root length.

Interestingly, different concentrations of JA starting at 10 μM decreased the number of LR. This effect is shown in Table 2 where it can be seen that 40 μM JA reduced by more than 50% the number of LR. This observation is consistent with the results presented in Fig. 1a, where it can be seen that JA allowed the emergence of LR only in the base of the PR. In fact, the proximal root region was already present when the treatment with JA was applied and showed a standard arrangement of LR while they were absent in the rest of the root (Fig. 1a). To more precisely quantify the effect of JA, the root seedling was divided in three regions for further analyses (1st, 2nd and 3rd section, Fig. 3a). Figure 3b shows that after 4 days growing in 40 μM JA, the proximal region of the root (1st third) reduced the number of LR by 47%, while in the intermediate region (2nd third) LR were practically undetected (96% of reduction). Analysis of the seedlings after 10 days growing in the treatment also revealed this inhibitory tendency (Fig. 3c, Table 2), although it can be seen that in the presence of JA the number of LR increased compared to the shorter treatment, revealing that exogenous JA did not completely block primordium formation and root emergence and growth. This observation is in agreement with the partial inhibition of meristematic cell division by exogenous JA shown in Table 1. Moreover, the application of IBU reduced the number of LR suggesting that endogenous JA might have a role in LR formation.

Table 2 Effect of JA and IBU on the number of lateral roots

Days of treatment	Treatment	Total LRs number
4	CONTROL	94 ± 4.75[a]
	JA 40 μM	32 ± 6.55[b]
	IBU 20 μM	55 ± 4.73[c]
10	CONTROL	116 ± 12.93[a]
	JA 40 μM	55 ± 12.82[b]
	IBU 20 μM	73 ± 7.75[c]

Different letters indicate a significant difference between the treatments ($P < 0.05$)

Relationship between jasmonic acid and auxins to control sunflower root growth

Auxins have been deeply analyzed in several plant species as inhibitors of primary root growth as well as promoters of lateral root formation. More recently, it was shown that auxins interact with ethylene in the control of these parameters (Swarup et al. 2007; Ivanchenko et al. 2008).

Table 1 Effect of JA on cell elongation and the cell production rate

	Treatment	Root elongation rate (cm day^{-1})	Cell length (μm)	Cell production rate (cells day^{-1})
PR	CONTROL	1.06 ± 0.29 (100)	19.02 ± 2.24 (100)	55.17 ± 8.45 (100)
	JA 40 μM	0.45 ± 0.12 (42.4)*	13.40 ± 0.88 (70.3)*	33.74 ± 9.07 (61.2)*
	IBU 20 μM	2.37 ± 0.03 (223.5)*	43.4 ± 2.05 (228.2)*	54.94 ± 3.01 (99.6)
LR	CONTROL	0.37 ± 0.02 (100)	15.12 ± 0.13 (100)	24.82 ± 1.20 (100)
	JA 40 Mm	0.14 ± 0.02 (37.8)*	13.03 ± 0.14 (86.2)*	10.35 ± 1.04 (41.7)*
	IBU 20 μM	0.72 ± 0.02 (195.3)*	35.35 ± 2.87 (233.8)*	20.45 ± 1.61 (82.4)

Values were taken at the third day of treatment

* Indicate a significant difference respect to control ($P < 0.05$). Values in brackets are the percentage of control for each column

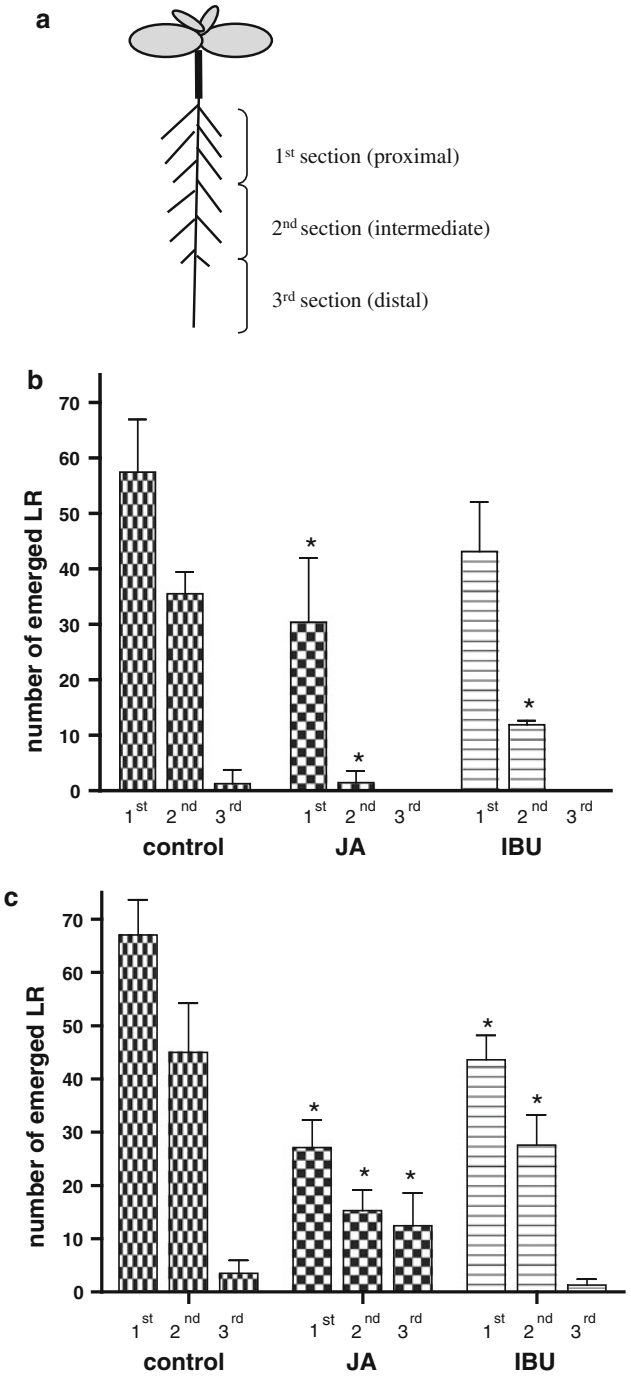

Fig. 3 Effects of JA and IBU on lateral root emergence. Three days old sunflower seedlings were hydroponically grown in nutrient solution (control) or with the addition of 40 μM JA or 20 μM IBU for 4 or 10 days and the number of emerged LR was evaluated in the proximal root region (1st section, zone in contact with the hypocotyl), intermediate region (2nd section, the intermediate zone of root) and distal region (3rd section, zone containing the root tip). **a** Drawing showing the arbitrary division of the root in thirds. **b** LR emergence upon 4 days of treatment, or **c** 10 days of treatment. Data represent means ± SE ($n = 6$) for three different experiments. * Indicate a significant difference between control and the treatments ($P < 0.05$)

To assess the impact of JA on auxin-dependent root growth we have performed a pharmacological approach by treating the seedlings with JA or IBU supplemented with the auxin transport inhibitor NPA or the synthetic auxin NAA, respectively. Since no reports are available on the effects of NPA and NAA we have first analysed their effect on sunflower. Hence, the seedlings treated with 0.1 μM NAA showed the characteristic induction of LR formation and inhibition of PR growth (Fig. 4a, b). Additionally, NAA reduced the LR growth (Fig. 4c). On the other hand, 1 μM NPA promoted PR and LR growth (Fig. 4d–f) and also reduced the number of LR (Fig. 4d), suggesting that it was able to disturb the auxin transport. In agreement with the inhibition of endogenous auxin effects, the NPA response was reverted by supplementation with exogenous NAA (not shown). To evaluate whether jasmonates and auxin could be modulating root architecture by a common pathway, combined treatments were performed. Figure 4b and c shows that NAA was able to decrease the growth of PR and LR in the presence of IBU, pointing out that auxins inhibition on root growth may not depend on the synthesis of jasmonates. Furthermore, when NPA was supplemented with JA, PR and LR growth inhibition was observed (Fig. 4e, f). This effect was seen for concentrations up to 10 μM NPA and suggest that JA induced growth inhibition does not depend on auxin transport. Similarly, the application of PCIB, an inhibitor of auxin signalling (Zhao and Hasenstein 2009), produced the same phenotype and JA-restoration pattern as NPA (not shown for briefness). Overall results indicate that JA and auxin modulate the PR and LR length in a non linear pathway.

Discussion

JA is frequently ignored as a component of the complex network operating in the root meristem (i.e., Benková and Hejátko 2009). Even if the participation of JA in the regulation of root growth has already been demonstrated in some plant species (Staswick et al. 1992; Wang et al. 2002; Maksymiec and Krupa 2007), it is generally regarded as a defence-related hormone. Here we show that JA determines sunflower root architecture in several ways as it is able to reduce both PR and LR length, as well as the number of LR. Moreover, we provide evidence on the basis of the JA-induced root growth inhibition. In fact, the addition of JA to the growing medium clearly reduced cortex root cell elongation and cell division in the PR as well as in the LR, hence supporting the inhibition of root growth. This result is in agreement with a previous report indicating that exogenously added JA could act as inhibitor

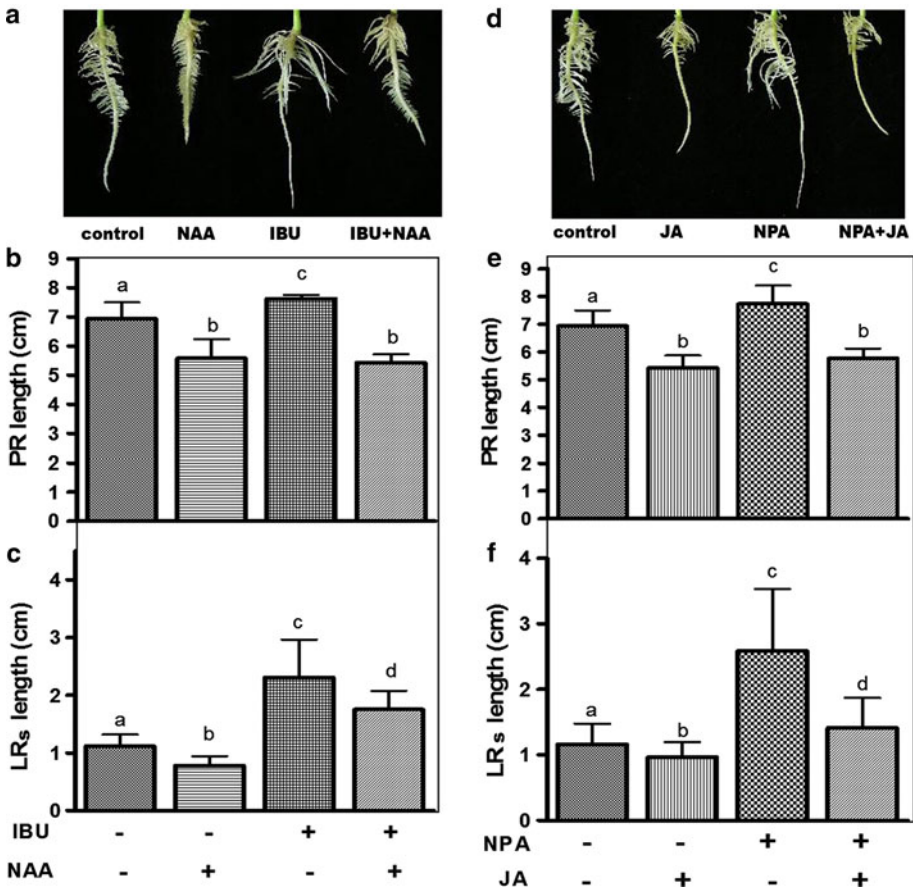

Fig. 4 Analysis of JA and auxin interaction in the regulation of the primary and lateral root growth. Three days old sunflower seedlings were hydroponically grown during 4 days with the treatments indicated and then the PR and LR were measured. **a**, **d** representative images, **b**, **e** PR and **c**, **f** LR length. The concentrations used were 0.1 μM NAA, 1 μM NPA, 40 μM JA and 20 μM IBU. Data shown represent means ± SE ($n = 6$) for four different experiments. Different letters indicate a significant difference at $P < 0.05$

of cell elongation and cell division in tobacco cells and *Arabidopsis* roots (Swiatek et al. 2003). Interestingly, when sunflower seedlings where treated with IBU to evaluate the role of endogenous JA, a significant increase of root cell elongation was observed while the cell production rate remained unchanged compared to control seedlings. This result indicates that endogenous JA concentration is able to modulate root phenotype.

Even if the exogenous application of JA is able to inhibit cell division, endogenous jasmonates do not seem to affect the frequency of meristematic cell division *in planta,* indicating that endogenous JA is more active controlling root elongation than cell division in sunflower. This assumption is also in accordance with the observation that the number of LR in sunflower seedlings is not increased by IBU treatment, suggesting that endogenous JA does not inhibit the production of LR. The effect of this inhibitor of JA biosynthesis has previously been analyzed in cell suspensions and particular tissues, but its use in a complete plant system such as sunflower seedlings provides evidence of its potential usefulness as a promoter of root elongation to decrease lodging problems in plants growing under field conditions.

It is also interesting to highlight the reduction in LR number promoted by JA. The effect of JA on LR development is barely documented and still controversial. It was shown that *Arabidopsis* and rice plants treated with jasmonates increase the number of LR (Sun et al. 2009; Wang et al. 2002), although variable responses were observed in rice depending on the root region analysed (Wang et al. 2002). Hence, the promotion of LR by JA might not be a general behaviour and could depend on the hormonal balance characteristic of each plant species.

The root phenotype produced by JA reported here resembles that of auxins, the hormone which plays a key role in root growth and development. Actually, auxins also reduce PR and LR length and some reports suggest a cross talk between the auxin and the JA pathways (Khan and Stone 2007; Staswick 2009). Thus, *Arabidopsis ANTHRANILATE SYNTHASE α1* (*ASA1*) is implicated in the jasmonate-mediated regulation of auxin biosynthesis and transport during LR formation (Sun et al. 2009). An extent of this cross talk is also exemplified by the *auxin-resistant 1(axr1)* mutant, which shows resistance to JA-inhibition of root growth (Tiryaki and Staswick 2002). AXR1 is a positive regulator shared by auxin and jasmonate responses in the proteosome-mediated signaling pathway. It has been shown that the double mutant jasmonic acid and auxin resistant (jar1-1/axr1-3) is more resistant to inhibition of root growth by MeJA than the

single mutants, therefore these genes would be involved in independent JA-mediated routes. In contrast, the resistance to the auxin IAA in the double mutant was not different from axr1-3. Thus, JA appears to act through two pathways, one linked to, and a second one independent from auxins (Tiryaki and Staswick 2002). Here, we present evidence showing that the phenotype induced by JA in sunflower roots is not prevented by an auxin transport inhibitor and, conversely, the auxin-induced phenotype does not seem to be affected by the reduction of endogenous JA levels imposed by IBU treatment. Even if our experimental system does not allow conclude on putative cross talk mechanisms between auxins and JA, it is evident that auxins are not essential for JA induced root growth inhibition in sunflower. Nevertheless, results also indicate the presence of a fine-tuned counterbalance between auxin and JA, showing the ability to generate a wide range of root phenotypes.

Root architecture is a key component determining the ability to function in anchorage and capture of soil resources. In addition to PR length, LR formation and elongation are important agronomic traits since they provide physical support to the plant and increase the absorptive area of the root system. Our results demonstrate that JA is a potent hormone, other than auxins, involved in the regulation of PR growth as well as LR growth and distribution in sunflower. Thereby, JA must be considered as a relevant factor for the vigor of the plant and its adaptation to different environmental conditions.

Acknowledgments GCM is a fellow, and LL, LDLC are members of the research career from the Argentine Research Council (CONICET). We thank S. Alemano and G. Abdala (University of Rio Cuarto, Argentina) for valuable suggestions. This work was supported by the ANPCYT (PAE-PICT N° 0016) and the University of Mar del Plata, Argentina.

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