RESEARCH PAPER

Interactions between jasmonates and ethylene in the regulation of root hair development in Arabidopsis

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Abstract

Root hair formation is an important model with which to study cell patterning and differentiation in higher plants. Ethylene and auxin are critical regulators of root hair development. The role of jasmonates (JAs) was examined in Arabidopsis root hair development as well as their interactions with ethylene in this process. The results have shown that both methyl jasmonate (MeJA) and jasmonic acid (JA) have a pronounced effect on promoting root hair formation. However, the effect of MeJA and JA on root hair formation was blocked by ethylene inhibitors Ag+ or aminoethoxyvinylglycine (AVG). The stimulatory effects of MeJA and JA were also diminished in ethylene-insensitive mutants etr1-1 and etr1-3. Furthermore, the JA biosynthesis inhibitors ibuprofen and salicylhydroxamic acid (SHAM) suppressed 1-aminocyclopropane-1-carboxylic acid (ACC)-induced root hair formation, and decreased the root hairs in seedlings of the ethylene over-producing mutant eto1-1. These results suggested that JAs promote root hair formation, through an interaction with ethylene.

Key words: Ethylene, jasmonates, root hair.

Introduction

Root hairs are tip-growing tubular extensions that develop from a subset of specialized epidermal cells called trichoblasts (Dolan et al., 1994; Galway et al., 1994). They increase the root surface area and absorptive capacity for water and nutrients. They also play a critical role in anchoring the plant to the soil and serve as the interface between the plant and a range of fungal and bacterial symbionts (Clarkson, 1985; Dolan et al., 1994; Ridge, 1995, 1996; Hofer, 1996; Peterson and Farquhar, 1996).

Root hair development has been used as an important model to study the mechanisms of cell patterning and differentiation in higher plants (Schiefelbein, 2000). Mutational analysis revealed that several genes in Arabidopsis function in the specification of root epidermal cell types. Among these, the TTG (Galway et al., 1994; Berger et al., 1998; Walker et al., 1999), GL2 (Rerie et al., 1994; Di Christina et al., 1996; Masucci and Schiefelbein, 1996), and WER (Wada et al., 1997; Hung et al., 1998; Lee and Schiefelbein, 1999) genes are the best characterized.

Hormones are involved in the regulation of root hair development. Studies on Arabidopsis mutants, such as axr1 and ctr1, indicated that auxin and ethylene function in root hair initiation. The wild-type CTR1 gene encodes a Raf-like protein kinase that negatively regulates the ethylene signal transduction pathway (Kieber et al., 1993). The ethylene response mutant ctr1 possesses ectopic root hairs on their atrichoblasts, producing very few root hairs (Dolan et al., 1994). In wild-type Arabidopsis, the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) induces ectopic root hair formation (Tanimoto et al., 1995; Masucci and Schiefelbein, 1996; Pitts et al., 1998), whereas aminoethoxyvinylglycine (AVG, an ethylene biosynthesis inhibitor), and Ag+ (an ethylene action inhibitor) reduce root hairs (Masucci and Schiefelbein, 1994; Tanimoto et al., 1995). The defect of root hair initiation in the mutant rhd6 can be rescued by the application of ACC and indole-3-acetic acid (IAA) (Masucci and Schiefelbein, 1994). Moreover, the auxin response mutants aux1, axr1, axr2, and axr3 are all abnormal in root hair formation (Lincoln et al., 1990; Wilson et al., 1990; Okada and Shimura, 1994; Leyser et al., 1996). These results suggest that both ethylene and auxin are critical regulators of root hair development.

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Abbreviations: ACC, 1-aminocyclopropane-1-carboxylic acid; AVG, aminoethoxyvinylglycine; JA, jasmonic acid; JAs, jasmonates; MeJA, methyl jasmonate; SHAM, salicylhydroxamic acid.

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Jasmonates (JAs) are a family of cyclopentanone derivatives that originated from linolenic acid via an inducible octadecanoic pathway. Generally, jasmonic acid (JA) and methyl jasmonate (MeJA) are referred to as the most potent substances among derivatives of JAs (Turner et al., 2002). JAs play important roles in the responses of plants to insect-driven wounding, various pathogens, and abiotic stresses (Farmer and Ryan, 1992; McConn et al., 1997; Wasternack and Parthier, 1997; Thomma et al., 1999; Wasternack and Hause, 2002). They also regulate a variety of developmental processes, such as inhibition of seed germination and root growth (Staswick et al., 1992), promotion of tuber formation, tendril coiling, fruit ripening, and senescence (Creelman and Mullet, 1997). In addition, JAs are required for pollen development and anther dehiscence (Feyns et al., 1994; McConn and Browse, 1996; Sanders et al., 2000; Park et al., 2002).

In this study, JAs are reported to be involved in the regulation of root hair development in Arabidopsis. As both JAs and ethylene have been shown to activate synergistically a set of defence responses against pathogens and herbivores (Feyns and Parker, 2000; McDowell and Dangl, 2000; Glazebrook, 2001; Thomma et al., 2001; Lorenzo et al., 2003), the relationships between JAs and ethylene in the control of root hair formation were also examined.

Materials and methods

Plant materials and growth conditions
Arabidopsis wild type (ecotype Columbia) and mutants etr1-1, etr1-3, and eto1-1 were used.

Plant seedlings were cultured as described by Estelle and Somerville (1987). The culture medium consisted of 5 mM KNO₃, 5 mM NH₄NO₃, 2 mM MgSO₄, 2 mM CaSO₄, 2.5 mM KH₂PO₄, 70 μM H₃BO₃, 14 μM MnCl₂, 1 μM ZnSO₄, 0.5 μM CuSO₄, 10 μM NaCl, 0.2 μM Na₂MoO₄, and 40 μM FeEDTA, and solidified with 0.8% (w/v) agar. Suc (43 mM) and MES (4.7 mM) were included, and the pH was adjusted to 5.5. The seedlings were surface-sterilized by immersing in 5% (v/v) NaOCl for 5 min and 96% (v/v) 35% H₂O₂ for 1 min, followed by four rinses in sterile water. The sterilized seeds were placed onto Petri dishes containing Murashige–Skoog medium containing 3% SUC and 1% agarose solution. Hand-cut sections from the root hair zone were stained with toluidine blue, and one cell layer each was analysed using a BH₂ Olympus microscope. The measurements were repeated at least three times. Statistical significances of differences between mean values were analysed by using SPSS.

Results

Impact of JAs on root hair formation

In order to investigate the effect of JAs on root hair formation, 4-d-old wild-type Arabidopsis seedlings were transferred to agar medium supplemented with MeJA or JA, the most potent derivatives of JAs. As shown in Fig. 1, JAs

![Dose-response curves of JAs on root hair density in wild-type Arabidopsis seedlings.](https://example.com/fig1)

**Fig. 1.** Dose–response curves of JAs on root hair density in wild-type Arabidopsis seedlings. The seedlings were grown for 4 d in agar medium and then transferred to fresh agar medium (control) or medium supplemented with JA or MeJA at the indicated concentrations. Root hair densities were determined after 48 h of the treatment. The values represent the means of 15 seedlings, and error bars represent SE (P < 0.05).
induce root hair formation in a dose-dependent manner. Two days after treatment, seedlings incubated in MeJA at concentrations ranging from 0.01–10 μM or JA at concentrations ranging from 0.1–10 μM exhibited a significant increase in root hair density. At a concentration of 1 μM, the numbers of root hairs increased by 2.5-fold and 4-fold in the presence of JA and MeJA, respectively. When the concentrations of MeJA or JA were increased to 10 μM a maximum number of root hairs were formed. However, at such a concentration root elongation was severely inhibited. Therefore, a concentration of 1 μM was used for all further experiments.

Subsequently, the time-courses of root hair formation in response to JAs were conducted in wild-type seedlings. Figure 2A shows that the root hair densities increased as early as 12 h after JAs application and continued to increase up to 72 h, compared with the untreated control. The formation of root hairs after JAs application was restricted to the root differentiation zone (Fig. 2B). MeJA exhibited a stronger effect on the promotion of root hair formation than JA (Figs 1, 2) and, as a consequence, was used for all subsequent experiments.

To verify the role of ethylene in *Arabidopsis* root hair formation, 4-d-old wild-type seedlings were transferred to fresh culture medium with or without the ethylene precursor ACC. In the presence of ACC root hair formation was promoted at concentrations ranging from 0.01 to 10 μM (Fig. 3A). In a time-course experiment (Fig. 3B), 1 μM ACC exhibited an increased effect on root hair density from 12 h to 72 h after treatment, compared with the control. These data support previous observations that ethylene stimulates the development of root hairs in *Arabidopsis*.

*Effect of MeJA on the activation of trichoblast cells*

As JAs could inhibit root elongation, the possibility that the ability of JA to increase root hair density might be the
consequence of trichoblast cell activation or the inhibition of root elongation was examined. When 4-d-old wild-type seedlings were supplied with 1 μM MeJA the primary root length was decreased by 44.8% (Table 1), whereas the total number of root hairs was increased more than 2-fold compared with control maintained in the absence of added MeJA (Table 1). These data suggest that MeJA acts by increasing the number of root hairs.

In Arabidopsis, root hairs are formed from specific epidermal cells (trichoblasts) located over the intercellular space between underlying cortical cells, i.e. cells in the H position, while cells (atrichoblasts) located directly over a single cortical cell (in the N position) do not form hairs (Dolan et al., 1994). Based on the calculation of trichoblast length and the number of trichoblast files in these data (Table 1), root hair densities of control and MeJA-treated roots were expected to be 40.8 and 64.8 per mm root length, respectively. However, the observed root hair densities were 7.8 and 30.5, respectively, suggesting that not all of the trichoblasts developed root hairs under either control or MeJA treatment. In the control condition, 19.12% of epidermal cells in the H position developed into root hairs, while MeJA treatment increased the percentage to 47.06%. These data reveal that MeJA has a stimulatory effect on the activation of trichoblast cells for root hair formation.

It is known that ectopic root hairs can occur on cells in the N position with ACC treatment (Tanimoto et al., 1995). This was confirmed in our experiments (Fig. 4C). It was also found that both ACC and MeJA could induce branched hairs, and in MeJA-treated seedlings, more root hairs were branched. The branched hairs occurred either at bulges or from the sides of growing hair cells. Some of these branches underwent further branching. The induction of

Table 1. Effect of MeJA on root hair density and root length

<table>
<thead>
<tr>
<th></th>
<th>Control</th>
<th>MeJA (1 μM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Root hair numbers</td>
<td>90.7±2.04</td>
<td>196.6±12.3</td>
</tr>
<tr>
<td>Root length (mm 2d⁻¹)</td>
<td>11.6±0.02</td>
<td>6.4±0.14</td>
</tr>
<tr>
<td>Length of trichoblasts (μm) (L)</td>
<td>195.5±4.5</td>
<td>123.1±1.2</td>
</tr>
<tr>
<td>Number of trichoblasts mm⁻¹</td>
<td>5.1</td>
<td>8.1</td>
</tr>
<tr>
<td>Root (U=1000/L)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of H cells per cross-section</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>Theoretical hair density (no. of</td>
<td>40.8</td>
<td>64.8</td>
</tr>
<tr>
<td>hairs mm⁻¹ root) (T=U×N)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed hair density (no. of</td>
<td>7.8</td>
<td>30.5</td>
</tr>
<tr>
<td>hairs mm⁻¹ root) (O)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% H cells forming hairs (PH)</td>
<td>19.12</td>
<td>47.06</td>
</tr>
<tr>
<td>Calculated PH=(O/T)×100%</td>
<td>0.72±0.13</td>
<td>6.68±0.79</td>
</tr>
<tr>
<td>Branched root hair (%)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig. 4. Effects of MeJA and ACC on root hair development of wild-type Arabidopsis seedlings. Cross-sections of a control root (A), MeJA-treated root (B), and ACC-treated root (C). Micrographs of a control root (D) and MeJA-treated root (E, F). Asterisks indicate the presence of ectopic root hairs. Arrows indicate the branched root hairs. (A, B, C) Bar=10 μm, (D, E, F) bar=50 μm.
branched hair formation may be a novel function of MeJA on root hair development.

**Interactions between MeJA and ethylene on root hair formation**

The above data have revealed that a JAs-dependent mechanism exists in the regulation of root hair formation. To explore the interactions between ethylene and JAs on root hair formation, use has been made of inhibitors of ethylene action (Ag⁺) and biosynthesis (AVG), as well as the ethylene-insensitive mutants *etr1-1* and *etr1-3*.

When wild-type seedlings of *Arabidopsis* were grown in the medium with 1 μM MeJA and either AVG or Ag⁺ for 48 h, root hair formation was inhibited (Fig. 5). Ag⁺ at concentrations ranging from 1.25 μM to 10 μM (Fig. 5A) and AVG from 0.08 μM to 10 μM (Fig. 5B) were able to antagonize the effects of MeJA on root hair density significantly. In the presence of 2.5 μM Ag⁺ or 2 μM AVG, the root hair density was decreased to 10.04% and 12.80% of that with MeJA treatment, respectively. A morphological analysis (Fig. 5C) also showed that both 2.5 μM Ag⁺ and 2 μM AVG had the capacity to block the effect of MeJA on root hair formation.

To clarify the role of ethylene in MeJA-induced root hair formation further, the responsiveness of ethylene-insensitive *Arabidopsis* mutants *etr1-1* and *etr1-3* to MeJA was investigated. The mutant seedlings were grown either under control condition or in the presence of 1 μM MeJA. As shown in Fig. 6, 1 μM MeJA had no significant effect on the root hair formation of *etr1-1* seedlings. MeJA treatment did increase root hair density in *etr1-3* mutants, but the effect was substantially decreased compared with wild-type seedlings. These results indicate that MeJA-induced root hair formation is suppressed by mutations in ethylene perception, and that the gaseous plant hormone is a prerequisite for JAs function.

**Impact of JA biosynthesis inhibitors on ethylene-induced root hair formation**

JAs and ethylene have been reported to induce synergistically defence responses to a variety of pathogens (Xu *et al.*, 1994; Penninckx *et al.*, 1998). To determine whether ethylene-induced root hair formation requires JAs, the effects of the JA biosynthesis inhibitors, ibuprofen and SHAM (a known inhibitor of lipoxygenase in jasmonate biosynthesis in plant cells) (Nojiri *et al.*, 1996) were tested on root hair formation in wild-type seedlings in the presence of ACC, and in the ethylene over-producing mutant *eto1-1*.

As shown in Fig. 7, ethylene-induced root hair formation in wild-type *Arabidopsis* seedlings was suppressed by ibuprofen at concentrations ranging from 5 μM to 20 μM

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**Fig. 5.** The effects of ethylene inhibitors on suppression of MeJA-induced root hair formation in wild-type *Arabidopsis* seedlings. The seedlings were grown for 4 d in agar medium and then transferred to the medium supplemented with 1 μM MeJA in the presence or absence of Ag⁺ (A) or AVG (B). After 48 h the root hair densities were determined. The values represent the means of 15 seedlings, and error bars represent SE (*P* <0.05). (C) Root morphology of MeJA-treated seedlings in the presence or absence of 2.5 μM Ag⁺ or 2 μM AVG. Bar=1 mm.
or by SHAM at a concentration of 50 lM (Fig. 7B). When the seedlings were treated with 20 lM ibuprofen or 50 lM SHAM, the root hair densities were decreased to 10.87% and 67.61%, respectively, of that supplied with 1 lM ACC alone. No significant effect of SHAM was observed at low concentrations. The root morphology (Fig. 7C) also showed that both 20 lM ibuprofen and 50 lM SHAM partially inhibited ACC-promoted root hair formation.

To test the involvement of JAs in ethylene-stimulated root hair formation further, the ethylene over-producing Arabidopsis etr1-1 and etr1-3 seedlings. The seedlings were grown for 4 d and then transferred to fresh medium in the presence or absence (control) of 1 lM MeJA. After 48 h the root hair densities were determined. The values represent the means of 15 seedlings, and error bars represent SE. Bar=1 mm.

(Fig. 7A), or by SHAM at a concentration of 50 lM (Fig. 7B). When the seedlings were treated with 20 lM ibuprofen or 50 lM SHAM, the root hair densities were decreased to 10.87% and 67.61%, respectively, of that supplied with 1 lM ACC alone. No significant effect of SHAM was observed at low concentrations. The root morphology (Fig. 7C) also showed that both 20 lM ibuprofen and 50 lM SHAM partially inhibited ACC-promoted root hair formation.

To test the involvement of JAs in ethylene-stimulated root hair formation further, the ethylene over-producing Arabidopsis mutant eto1-1 was examined. Mutant plants were supplemented with or without ibuprofen or SHAM. As shown in Fig. 8, both 20 lM ibuprofen and 50 lM SHAM significantly decreased the root hair density in eto1-1 mutants. Compared with wild-type, eto1-1 mutant exhibited a 6-fold increase in root hair density. Increased root hair density in eto1-1 mutants was antagonized by ibuprofen or SHAM application. Ibuprofen treatment at 20 lM reduced root hair formation by 63.69%, whereas 50 lM SHAM reduced root hair density by 46.33% in eto1-1 mutant.

The activity of MeJA to overcome the inhibitory effects of ibuprofen and SHAM was also tested. Table 2 shows that exogenous 10 µM MeJA was able to rescue partially the inhibitory effects of ibuprofen and SHAM on root hair formation in both ACC-treated wild-type and eto1-1 seedlings. These data suggest that the specific effects of these two chemicals on reducing root hair formation were at least partially due to the inhibition of JA biosynthesis besides their own pharmacological effects.

Discussion

Both genetic analyses using mutants with altered responses to ethylene (Kieber et al., 1993) or to auxin (Wilson et al., 1990; Leyser et al., 1996), and physiological experiments using exogenous IAA, auxin transport inhibitors, ACC, or ethylene inhibitors (Masucci and Schiefelbein, 1994; Okada and Shimura, 1994; Pitts et al., 1998) have supported the roles of auxin and ethylene in controlling root hair initiation and growth. Moreover, there have been several reports on the interactions between ethylene and auxin in these processes. Rahman et al. (2002) found that Arabidopsis mutants that have defects in ethylene signaling also had reduced sensitivity to auxin-driven root hair initiation and elongation. Takahashi et al. (2003) examined the hormonal regulation of cortical microtubule (CMT) randomization by auxin and ethylene in lettuce seedling roots, and found that auxin is essential for CMT randomization, and that ethylene may promote the induction by auxin of CMT randomization in hair-forming cells. In the present study, it was found that plant growth substances, JAs, strongly induced root hair formation in Arabidopsis, probably via an interaction with ethylene.

There exist several possible mechanisms accounting for the increase in root hair density (Ma et al., 2001a). Firstly, more trichoblast files may be initiated. Secondly, the occurrence of trichoblasts with branched root hairs may contribute to an increase in root hair density. Thirdly, atrichoblasts may be recruited into trichoblasts during root hair development under certain conditions. Alternatively, all of the above three conditions may occur in combination. These results suggest that the initiation of more trichoblast cells into root hairs may be an important cause of MeJA-induced root hair development. In addition, the induction of branched hair formation may be a novel function of MeJA on root hair development.

It was investigated whether JAs activate root hair formation via ethylene, and it was found that the effects of JAs were abolished in the ethylene-insensitive mutants etr1-1 and etr1-3, or by ethylene action (Ag+) or biosynthesis inhibitors (AVG). Furthermore, it was found that JA biosynthesis inhibitors, ibuprofen and SHAM, repressed ACC-driven or eto1-1-induced root hair formation. Collectively, these data support a role for the interaction between JAs and ethylene in the regulation of root hair development in Arabidopsis.
Interactions between JAs and ethylene have been proposed to contribute to a variety of responses of plants to abiotic and biotic stresses or developmental cues. Both positive and negative interactions have been described. The positive interactions are the involvement of these two hormones in the induction of plant defence responses. JAs and ethylene have been shown to induce synergistically the expression of a wide range of defence genes including \textit{PR1b}, \textit{PR5} (osmitin), \textit{PDF1.2}, the basic chitinase gene \textit{CHI-B}, a hevein-like protein gene, and proteinase inhibitors (PIN) genes. (Xu et al., 1994; O’Donnell et al., 1996; Penninckx et al., 1998; Norman-Setterblad et al., 2000; Ellis and Turner, 2001). A convergence point between JAs and ethylene pathways was represented by the transcriptional activation of \textit{ETHYLENE TRANSCRIPTION FACTOR1} (ERF1), a transcription factor that regulates the expression of pathogen response genes that prevent disease progression (Lorenzo et al., 2003). The expression of \textit{ERF1} was activated rapidly by ethylene or JAs and could be activated synergistically by both hormones. Furthermore, over-expression of \textit{ERF1} could rescue the defence response defects of \textit{coi1} (coronatine insensitive1) and \textit{ein2} (ethylene insensitive2) by restoring PR gene expression, suggesting that \textit{ERF1} is a key downstream element of both ethylene and jasmonate signalling pathways for the regulation of defence response genes. By contrast, in the wound response, the oligosaccharide-mediated repression of the JA-dependent signalling pathway was exerted through the production and perception of ethylene in the locally damaged tissue. This negative interaction between JA and ethylene allows the establishment of the correct spatial pattern of systemically induced genes in plants reacting to injury (Rojo et al., 1999). Another example of negative interaction occurs in development. \textit{Arabidopsis} seedlings germinated in the dark in the presence of ethylene display the triple-response that includes an exaggerated apical hook (Kieber et al., 1993), which can be suppressed by JA in a \textit{COI1}-dependent manner (Ellis and Turner, 2001). In this report, it is demonstrated that root hair formation in \textit{Arabidopsis} involves the concerted action of ethylene and JAs. These results support a positive interaction between JAs and ethylene in the regulation of root hair formation.

Recently, the emerging evidence indicated that JA and auxin might use a similar signalling mechanism. Tiryaki and Staewick found that an \textit{Arabidopsis} mutant defective in JA response, \textit{axr1-24}, was allelic to the auxin signalling...
The effects of MeJA inhibitors on (A) root hair densities and (B) root morphology of Arabidopsis eto1-1 seedlings. The seedlings of the eto1-1 mutant were grown for 4 d and then transferred to fresh medium in the presence or absence (control) of ibuprofen and SHAM. After 48 h, root hair densities were determined. The values represent the means of 15 seedlings, and error bars represent SE. Bar=1 mm.

**Fig. 8.** The effects of MeJA inhibitors on (A) root hair densities and (B) root morphology of Arabidopsis eto1-1 seedlings. The seedlings of the eto1-1 mutant were grown for 4 d and then transferred to fresh medium in the presence or absence (control) of ibuprofen and SHAM. After 48 h, root hair densities were determined. The values represent the means of 15 seedlings, and error bars represent SE. Bar=1 mm.

Table 2. Activity of MeJA on the inhibitory effects of ibuprofen and SHAM on root hair formation

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Root hair density (number/mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Wild type</strong></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>7.1±0.9</td>
</tr>
<tr>
<td>ACC</td>
<td>40.1±3.9</td>
</tr>
<tr>
<td>ACC+ibuprofen</td>
<td>20.6±0.8</td>
</tr>
<tr>
<td>ACC+ibuprofen+MeJA</td>
<td>27.7±3.1</td>
</tr>
<tr>
<td>ACC+SHAM</td>
<td>28.8±3.0</td>
</tr>
<tr>
<td>ACC+SHAM+MeJA</td>
<td>35.2±1.8</td>
</tr>
<tr>
<td><strong>eto1-1</strong></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>36.9±0.1</td>
</tr>
<tr>
<td>Ibuprofen</td>
<td>12.6±0.4</td>
</tr>
<tr>
<td>Ibuprofen+MeJA</td>
<td>25.3±1.6</td>
</tr>
<tr>
<td>SHAM</td>
<td>24.7±2.8</td>
</tr>
<tr>
<td>SHAM+MeJA</td>
<td>31.9±3.2</td>
</tr>
</tbody>
</table>

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