SHORT COMMUNICATION

Effects of indole-3-acetic acid and auxin transport inhibitors on the style curvature of three *Alpinia* species (Zingiberaceae)

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Abstract The effects of indole-3-acetic acid (IAA) and the auxin transport inhibitors 2, 3, 5-triiodobenzoic acid (TIBA) and 1-*N*-naphthylphthalamic acid (NPA) on the style curvature of *Alpinia platychilus*, *A. blepharocalyx*, and *A. mutica* were studied. Exogenous IAA stimulated the style curvature movement of the anaflexistylous morph (ana-morph) and cataflexistylous morph (cata-morph) of three *Alpinia* species in light, but had no effect in the dark. Treatment with auxin efflux inhibitors (NPA and TIBA) before flower opening did not affect the first curvature of the two morphs in darkness; however, the subsequent second movement of the ana-morph was enhanced by NPA or TIBA, while the second movement of the cata-morph was completely inhibited. After the first curvature, NPA and TIBA treatments at 06:00 hours (before significant illumination) and 11:00 hours (after the styles were illuminated for 4 h) increased the second curvature of the ana-morph, but significantly decreased that of the cata-morph. The effect at 06:00 hours was more significant than the effect at 11:00 hours. These results suggested that auxin and auxin transport affected the style curvature in a different way in the two morphs, and two morphs had distinct mechanisms for style movement at different times.

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Introduction

Flowering plants have evolved a remarkable capacity for morphological plasticity that enables them to generate offspring by sexual means. One of the important mechanisms underlying this plasticity is style curvature, where the style bends toward or away from the anthers. Style curvature allows plants to encourage outcrossing (Li et al. 2001), to reduce sexual interference (Sun et al. 2007), or to guarantee delayed autonomous selfing (Klips and Snow 1997). To date, style curvature has been found in Passifloraceae (Jazen 1968), Marantaceae (Seed et al. 2006), Malvaceae (Klips and Snow 1997), and Zingiberaceae (Cui et al. 1996; Li et al. 2001) families. The style curvatures in these families affect the reproductive systems in different ways. The structural basis of the style movement in the Marantaceae has been studied (Claßen-Bockhoff and Pischtschan 2000), while the mechanisms of style curvature in the other three families have not been investigated. In all the style curvatures, the movement of the *Alpinia* (Zingiberaceae) style was very unique (Li et al. 2001) in that the plants with curving ability had two morphs: anaflexistylous morph (ana-morph) and cataflexistylous morph (cata-morph). The styles of each morph curve twice during flowering, the first curving beginning at midnight and the second one at about 11:00 hours. During each movement, the styles of the two morphs curve in opposite directions (Luo and Li 2010). Briefly, the styles of ana-morph move downward first, and after this movement the stigma is on the way of pollinators' visit. Then before its anthers

dehisce, the styles move upward, which avoids out-cross-ing. The styles of cata-morph move upward at first, which avoids selfing because its anthers dehisce after this move-ment; the styles then move downward which allows the stigma to be pollinated. The mechanism of these style movements is the focus of this study.

Plant movements have been divided into two broad types based on the movement mechanism: growth move-ment and turgor movement. Plant movement, no matter of what kind, is always related with auxin signaling (Krieger 1978; Friml et al. 2002). Auxin is a phytohormone that plays a master role in plant development and growth responses of plant organs to various kinds of stimuli. It is believed that the asymmetric distribution of auxin accounts for plant tropism (Muday 2001; Friml et al. 2002; Moore 2002; Tanaka et al. 2006), which is the heart of the classic Cholodny–Went hypothesis (Went and Thimann 1937). A number of molecules that are crucial for auxin redistribu-tion and auxin response have been identified (reviewed in Paciorek and Friml 2006). But the gravitropic growth of seedlings of rye does not involve the redistribution of IAA (Edelmann 2001). Similarly, auxin transport does not involve the differential growth induced by moisture gra-dients in *Arabidopsis* roots (Kaneyasu et al. 2007). In our study, we examined the effects of auxin and auxin transport inhibitors on the style curvature movements of three *Alpinia* species. Our experimental aims were to examine the effects of exogenous IAA on the movement in the two morphs, and the effects of auxin transport inhibitors on the movement at different developmental stages. In addition, because light controls the second curvature of the ana-morph (Luo and Li 2010), we assessed the effects of light when styles were treated with IAA. Through these exper-iments, we determine (1) whether auxin or auxin transport plays a role in style curvature of the three species, and (2) whether the action patterns of auxin or auxin transport are similar in different morphs, different curvature stages of one morph and in different species.

Materials and methods

Plant materials

Alpinia platychilus K. Schumann, *A. blepharocalyx* K. Schumann, and *A. mutica* Roxb. were used as the model plants. They are perennial herbs, usually 1–3 m tall. The racemes are erect on the terminals of leafy shoots and are 25 cm long or more. The flower has a very unique structure, with a conspicuous three-lobed labellum pro-duced by the fusion of two staminodes that are yellow tinged with red, and obovate. There is only one fertile stamen with two pollen sacs and the style extends through

the anther. During blooming, each inflorescence has one to five flowers opening per day, and each flowering lasts 1 day. The styles of *Alpinia* species are still able to move after the flowers are excised from the plants, so we used excised flowers for the IAA and auxin transport inhibitor treatments.

Application of chemicals

Indole-3-acetic acid (IAA, Tokyo Kasei Kogyo Co., Tokyo, Japan, 1×10^{-4} mol L^{-1}) was used as the exog-enous auxin. 1-*N*-naphthylphthalamic acid (NPA; Tokyo Kasei Kogyo Co., Tokyo, Japan, 1×10^{-4} mol L^{-1}) and 2, 3, 5-triiodobenzoic acid (TIBA; Sigma, 5×10^{-4} mol L^{-1}) were used as auxin efflux transport inhibi-tors. All chemicals were prepared at $1000\times$ concentration in dimethyl sulfoxide (DMSO). A solution with equivalent DMSO was used as a control.

We treated the flowers at three stages: before the first curvature at 23:00 hours (just before flowering); before the second curvature at 6:00 hours (before dawn); and at 11:00 hours (when the styles had been illuminated for 4 h). The bases of the flowers were dipped into small bottles that were filled with the different test solutions and incubated in light or dark at room temperature (RT). After the treat-ments, we recorded the stigma–anther angles with a digital camera.

Determination of stigma–anther angle and style curvature

The stigma–anther angle (SAA) was measured with the Screen Protractor version 4.0 (Iconico, Inc., http://www.iconico.com. Figure 1). The angle measured by the pro-tractor was denoted as α when the stigma was under the anther and β when the stigma was above the anther. We defined the style curvature as the difference between the SAAs before and after the curvature, with a positive number denoting upward curvature and a negative number denoting downward curvature. Thus, the first curvature of the ana-morph was α and the second was α + β. For the cata-morph, the first curvature was β and the second was (β + α).

Statistical analysis

The effects of IAA, NPA, and TIBA on the style curvature were analyzed using Student's two-tailed *t* tests in the SPSS 11.0 package for Windows (SPSS Inc.). Mean dif-ferences were compared by lowest standard deviations (LSD) tests. Each data point was the mean of 15 replicates ($n = 15$) and comparisons with $P < 0.05$ were considered significantly different.
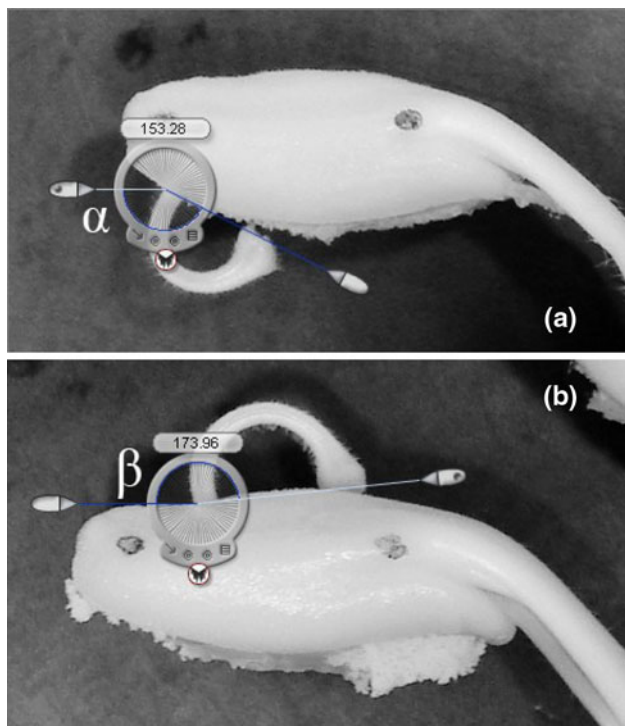
Fig. 1 Measurement of stigma–anther angle. One side of a protractor was overlapped with a line parallel with anther surface. The vertex of the protractor was the point that the style contacted with the anther surface. Another side of the protractor comprised the vertex and stigma. The angle measured by the protractor was denoted α when the stigma was under the anther, and β when the stigma was above the anther

Results and discussion

Effects of IAA on the style curvature

The style curvatures of three *Alpinia* species increased after IAA treatment in the light (Table 1). In *A. platychilus*, the first curvature of ana-morph was $-77.50 \pm 8.51°$ after control treatment (DMSO). Following IAA treatment, however, the curvature was significantly larger at $80.45 \pm 9.62°$. In cata-morph, the first curvature following control treatment was $76.45 \pm 9.98°$, but was significantly larger at $168.45 \pm 12.62°$ following IAA treatment. After IAA treatment before the second curvature, the magnitude of second curvature increased to such an extent that the stigmas touched the anthers. The style curvature of controls was $157.97 \pm 12.24°$ in ana-morph and $256.41 \pm 9.55°$ after IAA treatment; in cata-morph, the curvature was $-143.10 \pm 12.42°$ after control treatment and $-254.45 \pm 17.95°$ after IAA treatment. In the two morphs of this species, IAA treatment significantly increased the magnitude of style curvatures (t test, $P < 0.01$). Similar results were found in *A. blepharocalyx* and *A. mutica*. In addition, IAA treatment also affected the onset time of style movement in ana-morph. The control styles began to curve at about 11:00 hours, but moved before 09:00 hours after IAA treatment. The onset time of the style curvature movement of cata-morph did not change after IAA treatment (Fig. 2). The first curvature of ana-morph was upward in light, and advanced after IAA treatment.

The styles treated with IAA in darkness exhibited different movement patterns (Table 2). For the first curvature, the styles of ana-morph of *A. platychilus* curved $-78.57 \pm 9.50°$ following control treatment and $-76.83 \pm 7.09°$ in response to IAA treatment. In cata-morphs, the styles curved $76.67 \pm 7.06°$ following control treatment and $77.65 \pm 6.86°$ following IAA treatment. For the second curvature, styles of ana-morph of *A. platychilus* did not curve in the dark, whether treated with IAA or not. Similarly, the styles of cata-morph curved $-165.89 \pm 10.61°$ following control treatment and -160.55 ± 12.22 in response to IAA. There was no significant difference in

Table 1 Effects of IAA on the style curvature of three *Alpinia* species in light

The styles were sampled at 22:30 hours for the treatment of the first curvature and sampled at 06:00 hours for the second curvature. The styles were placed in light after treatment. Every treatment had 15 replications

** Indicates a statistically significant difference ($P < 0.01$) between IAA-treated styles and control styles
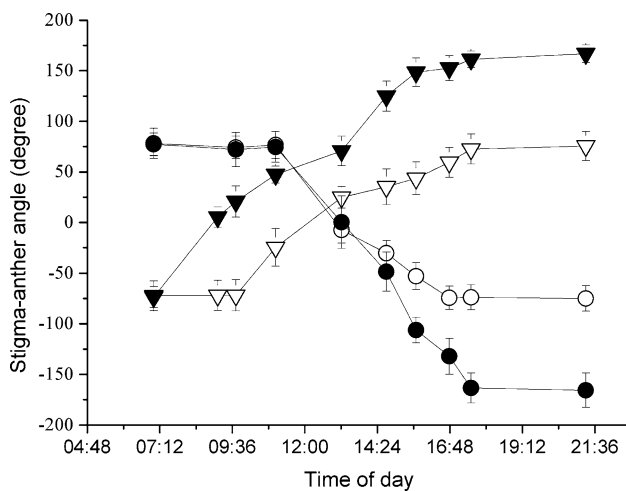
	A. platychilus	*A. blepharocalyx*	*A. mutica*
Ana-morph			
First curvature (°)			
Control	-77.50 ± 8.51	-78.22 ± 9.09	-75.36 ± 9.09
IAA	$80.45 \pm 9.62**$	$79.73 \pm 8.34**$	$76.85 \pm 10.53**$
Second curvature (°)			
Control	152.97 ± 12.24	147.46 ± 9.02	159.07 ± 13.25
IAA	$256.41 \pm 9.55**$	$237.91 \pm 7.32**$	$224.28 \pm 14.36**$
Cata-morph			
First curvature (°)			
Control	76.45 ± 9.98	73.48 ± 7.82	74.65 ± 5.05
IAA	$168.45 \pm 12.62**$	$172.25 \pm 14.61**$	$164.27 \pm 15.83**$
Second curvature (°)			
Control	-143.10 ± 12.42	-136.38 ± 10.32	-127.22 ± 11.27
IAA	$-254.45 \pm 17.95**$	$-257.28 \pm 16.32**$	$-260.72 \pm 16.48**$

Fig. 2 Time course of curvature in IAA-treated *A. platychilus* styles. Styles were sampled before dawn, treated with 10^{-4} mol L^{-1} IAA and then placed in light. *Open circles*, control styles of cata-morph; *open inverted triangle*, control styles of ana-morph; *solid circles*, IAA-treated styles of cata-morph; *solid inverted triangle* IAA-treated styles of ana-morph. Data are the means of 15 styles, and *vertical bars* represent the standard error

style curvature between control and IAA treatment in the dark ($P > 0.05$, t test).

These results indicated that auxin played a role in the style curvature of *Alpinia*, consistent with other plant movement (Hayes and Lippincott 1981; Cox et al. 2004). After application of IAA for about 15 min, the primary bean leaf blade can curve downward (Hayes and Lippincott 1981). It was hypothesized that IAA played a significant role in the differential growth of organs in response to changes in environment (Went and Thimann 1937). In the style curvature of *Alpinia*, we examined the influence of light on IAA responses because Luo and Li

(2010) found that light controlled the style curvature of ana-morph. Before the first curvature, when put in light, the styles of ana-morph curved directly upward without the first curving downward. If styles were maintained under darkness, however, they only curved downward and the second upward curvature did not occur, even after IAA treatment (Table 2). It appeared that light controlled the effect of IAA on the cell elongation of styles. Many additional studies indicated that there were links between light and auxin (Tian and Reed 2001; Casal and Yanovsky 2005; Woodward and Bartel 2005; Paul and Khurana 2008; Tao et al. 2008; Stepanova et al. 2008). Light can modulate auxin signaling and the transcription factors mediating auxin responses. As an important environmental signal, light was shown to have links with auxin signaling, which can affect differential cell growth by modulating indirectly the auxin response factors (Li et al. 2004). In the style curvature of *Alpinia*, it is possible that light acts as a "switch" allowing auxin action. Although, up to now, no direct evidence supports this opinion, some researches have indicated that light signals affect phytohormone signaling, including auxin (Lau and Deng 2010). In the dark condition, phytochromes localize mainly in the cytoplasm (Kim et al. 2000; Matsushita et al. 2003). Upon light activation, they move from the cytoplasm to nucleus where they can interact with downstream signaling components, including transcription factors. Among the transcription factors induced by light, LONG HYPOCOTYL 5 (HY5) may provide a more direct connection between light and auxin signaling. *hy5* mutants have increased hypocotyl elongation only when grown in the light (Koornneef et al. 1980). Cluis et al. (2004) found that HY5 promotes the expression of negative regulators of auxin signaling, thereby linking auxin and light signaling pathway.

Table 2 Effects of IAA on the style curvature of three *Alpinia* species in the dark

	A. platychilus	A. blepharocalyx	A. mutica
Ana-morph			
First curvature (°)			
Control	−78.57 ± 9.50	−75.86 ± 8.29	−75.63 ± 8.44
IAA	−76.83 ± 7.09	−77.53 ± 8.75	−74.73 ± 9.91
Second curvature (°)			
Control	0	0	0
IAA	0	0	0
Cata-morph			
First curvature (°)			
Control	76.67 ± 7.06	74.74 ± 4.29	75.76 ± 7.68
IAA	77.65 ± 6.86	72.46 ± 9.18	76.72 ± 5.07
Second curvature (°)			
Control	−165.89 ± 10.61	−157.33 ± 14.98	−154.08 ± 14.35
IAA	−160.55 ± 12.22	−154.96 ± 9.37	−152.09 ± 13.66

The styles were sampled at 23:00 hours for the treatment of the first curvature and sampled at 06:00 hours for the second curvature. The styles were placed in the dark after treatment. Every treatment had 15 replications

Effects of auxin inhibitors on the style curvature movement

The effects of auxin inhibitors on style movements were similar in the three *Alpinia* species (Table 3). Neither NPA nor TIBA affected the first curvature of ana-morph in darkness, but did increase the style movement of cata-morph (Table 3). Styles of ana-morph exhibited an increased second curvature after NPA or TIBA treatment, but the second movement of cata-morph was inhibited significantly by these auxin efflux inhibitors (Table 3). For example, NPA did not affect the first style curvature of the ana-morph of *A. platychilus* if applied before the first curvature (Fig. 3a), but increased the second curvature by 23.42%. For cata-morph, NPA or TIBA increased the first curvature by 62.33%, but reduced the second curvature by 89.10%. Treatment with NPA or TIBA at 06:00 hours (after the first curvature) increased the upward curve of ana-morph styles by 49.35%, but inhibited the downward movement in the cata-morph by 83.05% (Fig. 3b). If treated at 11:00 hours, however, there was a 27.16% increase in the second curve of ana-morph, but a 49.00% reduction in the second curve of cata-morph (Fig. 3c). In addition, if treated by NPA or TIBA in light, the styles of ana-morph moved upward directly and the curvature was larger than that of control.

The effects of these auxin efflux inhibitors indicated that auxin transport was involved in the style curvature.

Table 3 Effects of auxin transport inhibitors on the style curvature of three *Alpinia* species

	A. platychilus	*A. blepharocalyx*	*A. mutica*
Ana-morph			
First curvature (°)			
Control	−78.57 ± 6.50	−75.86 ± 7.29	−75.63 ± 9.44
NPA	−70.16 ± 9.83	−76.38 ± 8.85	−76.09 ± 8.02
TIBA	−79.26 ± 8.73	−76.57 ± 8.04	−75.87 ± 8.96
Second curvature (°)			
Control	157.28 ± 10.62	146.35 ± 14.98	149.45 ± 15.49
NPA	200.36 ± 15.87**	204.48 ± 15.83**	208.42 ± 17.87**
TIBA	180.68 ± 14.16**	175.56 ± 14.92**	170.26 ± 16.45**
Cata-morph			
First curvature (°)			
Control	76.98 ± 6.57	73.42 ± 9.67	74.55 ± 6.22
NPA	144.26 ± 12.22**	178.09 ± 14.65**	155.61 ± 13.67**
TIBA	123.09 ± 13.48**	120.75 ± 14.02**	120.67 ± 12.84**
Second curvature (°)			
Control	−150.75 ± 15.21	−157.46 ± 15.02	−160.46 ± 15.69
NPA	−25.69 ± 13.27**	−35.68 ± 14.16**	−40.96 ± 7.56**
TIBA	−51.35 ± 13.80**	−64.56 ± 14.01**	−75.81 ± 15.75**

The styles were sampled at 22:30 hours, treated with chemicals immediately, and then placed in the dark for first curvature. After the first curvature was complete, the styles were placed in light for the second curvature. Every treatment had 15 replications

** Indicates a statistically significant difference ($P < 0.01$) between chemical treated styles and control styles
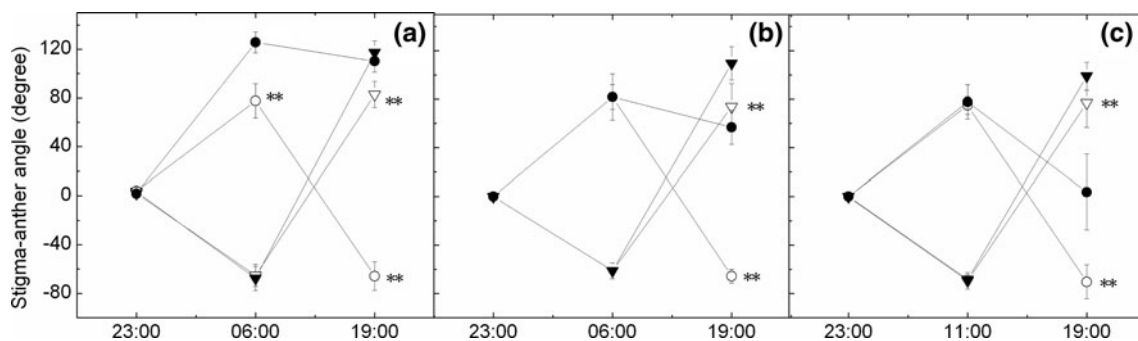

Fig. 3 Effects of 1-naphthylphthalemic acid (NPA) on *A. platychilus* style curvature. Styles were treated: **a** at 23:00 hours of the previous day (before the first curvature); **b** at 06:00 hours (before the second curvature); and **c** at 11:00 h (before the second curvature). *Open circles*, control styles of cata-morph; *open inverted triangle*, NPA-treated styles of cata-morph; *closed circles*, control styles of ana-morph; *closed inverted triangle*, NPA-treated styles of ana-morph. Data are the means of 15 styles, and *vertical bars* represent the standard error. *Double asterisks* indicate a statistically significant difference ($P < 0.01$) between experimental and control styles, using Student's two-tailed *t* test

Inhibition of basipetal IAA transport by NPA treatment can block the gravity response of *Arabidopsis* roots (Rashotte et al. 2000). NPA also had an inhibitory effect on gravitropic curvature of maize root (Zhang and Hasenstein 2000), on gravitropic curvature of protonemata of the moss *Ceratodon purpureus* (Schwuchow et al. 2001), and on phototropic curvature of hypocotyls of *Arabidopsis* (Harper et al. 2000). In our experiment, NPA and TIBA treatment increased the style upward movement of two morphs, but inhibited the second style curvature of cata-morph. These results suggest that auxin distribution in styles may be similar in the two morphs before the first curvature, with the adaxial side of the styles having more auxin than the abaxial side. In ana-morph, light may trigger auxin function, so the style curved downward in the dark but moved upward after illumination. In cata-morph, the higher auxin content in the adaxial side promoted the initial upward curvature, followed by downward movement after auxin was transported into the abaxial side.

It should be noted that IAA application in light made the styles of ana-morph move ahead, but did not affect the time course of style movements of cata-morph. In addition, NPA had distinct effects on style movements of ana-morph and cata-morph. These results indicated that the effects of auxin and auxin transport on the style curvature of two morphs were different, and the mechanisms conferring these distinct actions require further research.

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