

DIFFERENTIAL EFFECTS OF AUXIN POLAR TRANSPORT INHIBITORS ON ROOTING IN SOME CRASSULACEAE SPECIES

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Abstract

Effects of auxin polar transport inhibitors, 2,3,5-triiodobenzoic acid (TIBA), 1-*N*-naphthylphthalamic acid (NPA) and methyl 2-chloro-9-hydroxyfluorene-9-carboxylate (morphactin IT 3456), as a lanolin paste, on root formation in cuttings of some species of Crassulaceae, such as *Bryophyllum daigremontianum*, *B. calycinum*, *Kalanchoe blossfeldiana* and *K. tubiflora*, were studied. Cuttings of these plants were easily rooted in water without any treatment. TIBA and morphactin IT 3456 completely inhibited root formation in the cuttings of these plants but NPA did not when these inhibitors were applied around the stem below the leaves. When TIBA and morphactin were applied around the stem near the top, but leaves were present below the treatment, the root formation was observed in *B. calycinum* and *K. blossfeldiana* but in a smaller degree than in control cuttings. These results strongly suggest that endogenous auxin is required for root formation in cuttings of Crassulaceae plants. The differential mode of action of NPA is discussed together with its effect on auxin polar transport.

Key words: *Bryophyllum daigremontianum*, *B. calycinum*, cuttings, *Kalanchoe blossfeldiana*, *K. tubiflora*, rooting, auxin, 2,3,5-triiodobenzoic acid, 1-*N*-naphthylphthalamic acid, morphactin IT 3456

Abbreviations: IAA – indole-3-acetic acid, IBA – indole-3-butyric acid, NAA – naphthalene-3-acetic acid, TIBA – 2,3,5-triiodobenzoic acid, NPA – 1-*N*-naphthylphthalamic acid, morphactin IT 3456 – methyl 2-chloro-9-hydroxyfluorene-9-carboxylate, morphactin HFCA – 9-hydroxyfluorene-9-carboxylic acid

INTRODUCTION

Rooting in cuttings is a useful method to propagate plants easily. To promote rooting, many adventitious roots in cuttings are required. The process of adventitious root formation can be divided into three stages: root induction in which molecular and biochemical changes occur before any cytological event, root initiation when the first anatomical modifications take place, and protrusion, corresponding to the emergence of root primordia. Auxin indole-3-acetic acid (IAA) is one of essential endogenous hormones known to play the most important role in the formation of adventitious roots [1]. Exogenous auxins, IAA, indole-3-butyric acid (IBA) and naphthalene-3-acetic acid (NAA) are widely used in the promotion of rooting cuttings.

Auxin has been well known to play a crucial role in many aspects and development in plants [2]. Auxin moves from the shoot apex to the root tip between plant cells through a combination of membrane diffusion. Carrier- and/or facilitator-mediated transport has been shown to modulate both auxin biosynthesis and auxin movement [3,4]. The auxin polar transport generates auxin maxima and gradients within tissues that are instrumental in the diverse regulation of various plant developmental processes, including elongational growth, organogenesis, vascular tissue formation, embryogenesis, tropisms and many other processes, including root formation in cuttings as described above [4].

Compounds such as 1-*N*-naphthylphthalamic acid (NPA), 2,3,5-triiodobenzoic acid (TIBA), methyl

2-chloro-9-hydroxyfluorene-9-carboxylate (morphactin IT 3456), and 9-hydroxyfluorene-9-carboxylic acid (morphactin HFCA) have been well known to be effective auxin polar transport inhibitors affecting many physiological and developmental processes in plants. Several studies have shown the inhibition of rooting and inhibition of auxin transport in many plants (*Cucumis sativus*, *Helianthus annuus*, *Dianthus caryophyllus*, *Salix tetrasperma*, *Vigna radiata*, *Pisum sativum*, *Forsythia x intermedia*, *Syringa vulgaris*) after application of NPA and TIBA [5–10]. Morphactin IT 3456 also inhibited adventitious root formation in cuttings of *Pisum sativum* [11], hypocotyl cuttings of *Impatiens balsamina* [12] and stem cuttings of *Salix tetrasperma* [13]. The plantlet root emergence from epiphyllous plantlets on excised leaves of *Bryophyllum marnierianum* was completely inhibited by TIBA, but shoot growth was not significantly inhibited by TIBA, whereas NPA had almost no effect on plantlet root development on leaves [14]. However, adventitious root growth in cuttings of *Bryophyllum marnierianum* was inhibited both by TIBA and NPA when cuttings were incubated with their basal ends in the presence of these compounds [14]. These results suggest that the effects of auxin polar transport inhibitors depend on plant species and/or its growth situation. Auxin transport inhibitors interfere with basipetal polar transport of auxin and in this way change auxin distribution, resulting in perturbations in plant development. Generally, various effects of auxin transport inhibitors have been proposed to be caused, at molecular level, by interference with the auxin-efflux carrier and/or facilitator, but the detailed mechanism remains unclear whether or how blockage of the efflux of auxin by the inhibitors is involved in the effects of these inhibitors on physiological and developmental processes in plants [15].

Recently we have found differential effects of auxin polar transport inhibitors on rooting in cuttings of some Crassulaceae plants. Here, we report the differential effects of auxin polar transport inhibitors, TIBA, NPA and morphactin IT 3456, on root formation in cuttings of *Bryophyllum daigremontianum*, *B. calycinum*, *Kalanchoe blossfeldiana*, and *K. tubiflora*. The differential mode of action of NPA compared to that of TIBA and morphactin IT 3456 is intensively discussed focusing on their mode of inhibitory action on auxin polar transport as well.

MATERIALS AND METHODS

Young cuttings of some Crassulaceae species, *Bryophyllum daigremontianum*, *Bryophyllum calyci-*

num, *Kalanchoe blossfeldiana* and *Kalanchoe tubiflora*, were prepared and subjected to rooting in distilled water in natural light conditions in a greenhouse with shading, if necessary. Cuttings with a length of 8–9 cm were kept separately in 100 ml Erlenmeyer flasks with change of water every 3 days. Auxin transport inhibitors, TIBA, NPA and morphactin IT 3456, at concentrations of 0.2 % (w/w) and sometimes 0.5 % (w/w) in lanolin paste, were applied as a ring around the lower side of the stem under all leaves of the cutting, or a ring around the upper side of the stem near the top of cuttings. The experiments were carried out in different seasons in the year, mainly on January 23, July 28 and September 1 or 5.

Rooting was visually observed every day after starting the experiments and the number of initiated roots was calculated. Based on the observations, the effects of the chemicals were evaluated. Ten cuttings were used for each treatment and the experiments were repeated 3 to 5 times. TIBA, NPA and morphactin IT 3456, purchased from Aldrich, Trade TCI Mark and Celamerck GmbH and Co. KG, Germany, respectively, were used without any further purification.

RESULTS

Young cuttings of all these species, *Bryophyllum daigremontianum*, *Bryophyllum calycinum*, *Kalanchoe blossfeldiana* and *Kalanchoe tubiflora*, were easily rooted in water without any additional treatment and sprouting of roots was visible in about one week (Fig. 1). The main sprouted roots formed many lateral roots (Fig. 1). TIBA and morphactin IT 3456 completely inhibited root formation in cuttings of these plants when these inhibitors were applied as a ring around the lower side of the stem under all leaves of the cutting (Fig. 1, Table 1). When TIBA and morphactin were applied as a ring around the upper side of the stem near the top of cuttings, root formation was observed in cuttings of *B. calycinum* and *K. blossfeldiana*, but to a much smaller extent as compared to that in control cuttings (Fig. 2, Table 2). Cuttings of *B. tubiflora* and *B. daigremontianum* were not used in this kind of experiment. On the other hand, NPA did not inhibit rooting in cuttings of *B. daigremontianum*, *B. calycinum*, *K. blossfeldiana* and *K. tubiflora* when NPA was applied using the two methods described above (Figs. 1 and 2, Tables 1 and 2). These results strongly suggest that endogenous auxin produced and/or restored in the regions below the treatments of TIBA and morphactin and also NPA is required for root formation in cuttings.

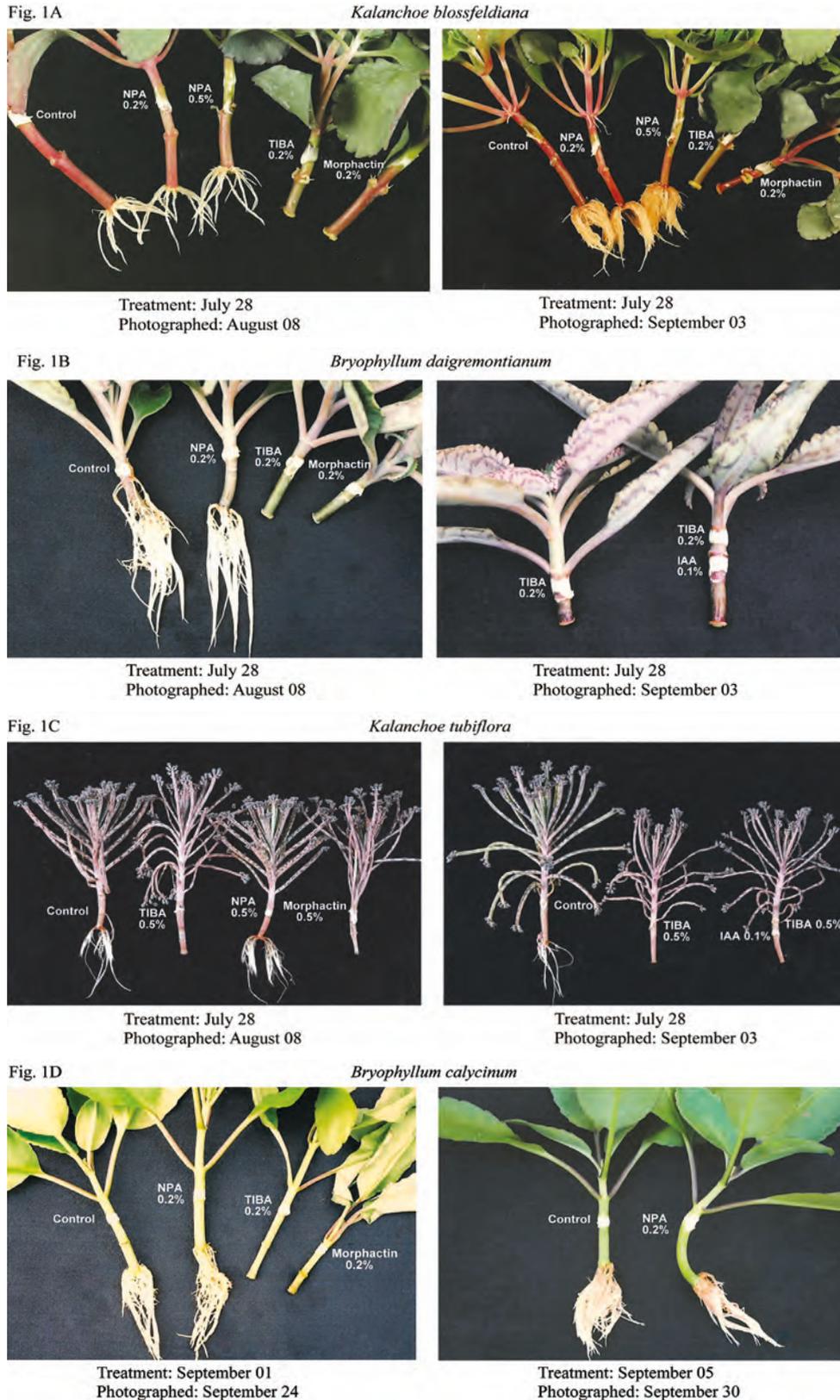


Fig. 1. The effect of TIBA, morphactin IT 3456 and NPA on rooting in some Crassulaceae species, (A) *Kalanchoe blossfeldiana*, (B) *Bryophyllum daigremontianum*, (C) *Kalanchoe tubiflora* and (D) *Bryophyllum calycinum*. TIBA, NPA and morphactin were used at concentrations of 0.2 and 0.5% (w/w) in lanolin paste and applied as a ring around the stem under the shoot with leaves.

TIBA and morphactin completely inhibited root formation but NPA did not.

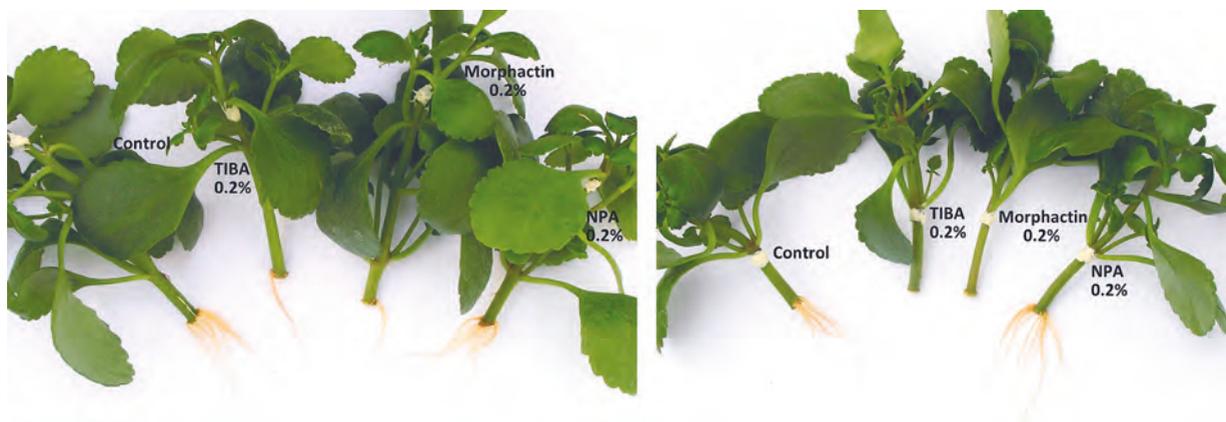


Fig. 2. The effect of TIBA, morphactin IT 3456 and NPA on rooting of cuttings of *Kalanchoe blossfeldiana*; treatments made on September 19, photographed on October 15

left – treatments around the stem as a ring under the shoot with leaves

right – treatments around the stem as a ring near the apex with leaves present below the treatment

Table 1

The effect of TIBA, NPA and morphactin IT 3456 applied in lanolin paste around the stem below leaves on root formation in cuttings of some Crassulaceae species. Measurements of number of roots were made 10 days after treatment

Species	Date of treatment	Average number of roots/plant						
		Control	TIBA		NPA		Morphactin	
			0.2%	0.5%	0.2%	0.5%	0.2%	0.5%
<i>K. blossfeldiana</i>	July 28	11	0	0	10	10	0	0
<i>B. daigremontianum</i>	July 28	9	0	-	10	-	0	-
<i>K. tubiflora</i>	July 28	11	0	0	8	8	0	0
<i>B. calycinum</i>	Sept. 01	13	0	-	12	-	0	-

Table 2

The effect of TIBA, morphactin IT 3456 and NPA applied in lanolin paste around the stem below the leaves and when applied near the top of the stem with leaves present below the treatment on root formation in cuttings of *Kalanchoe blossfeldiana*; treatments made on September 19, measurements of number of roots on October 15

Treatment around the stem as a ring	Number of roots/plant			
	Control	TIBA 0.2%	NPA 0.2%	Morphactin 0.2%
below leaves	12	0	11	0
near the top stem, leaves present below the treatment	10	3	10	2

DISCUSSION

The results of this study gave rise to an important question why NPA does not inhibit rooting in cuttings of some Crassulaceae plants. Similar observations have been reported in epiphyllous plantlets of *Bryophyllum marnierianum* [14] but the mode of actions of NPA has not been clear yet. NPA has been well known as a potent inhibitor of auxin polar trans-

port. Other chemicals, TIBA and morphactin IT 3456, have a similar function as that of NPA: they substantially inhibit rooting. NPA has been known to inhibit auxin polar transport in dicotyledons and monocotyledons by inhibiting active auxin secretion [16]. NPA inhibited auxin transport by specifically binding to the auxin efflux carrier [17]. The endogenous auxin, IAA, did not compete with NPA for the binding site [18] but the NPA-binding site was important for auxin

transport [19]. These results indicate that NPA inhibits IAA transport by specific binding to the so-called NPA receptors, thereby blocking the carrier- and/or facilitator-mediated efflux of IAA [20]. A h k a m i et al. [21], using NPA as an auxin transport blocker, showed that spontaneous root formation in leafy cuttings of *Petunia hybrida* is dependent on auxin homeostasis induced by auxin polar transport in the rooting zone. R i n c o n et al. [22] also compared the effects of auxin transport inhibitors, TIBA and NPA, on rhizogenesis and mycorrhizal establishment of spruce (*Picea abies*) seedlings inoculated with *Laccaria bicolor*. The ectomycorrhizal fungus *Laccaria bicolor*, which can synthesize IAA in pure culture, stimulated lateral root formation on spruce seedlings and the colonization of the top-root cortex by the fungus. Exogenously applied IAA also stimulated lateral root formation in spruce seedlings but to a lesser degree than *Laccaria bicolor*. It was shown that TIBA completely inhibited the stimulatory effect of *Laccaria bicolor* on lateral root formation on spruce seedlings, but NPA inhibited it only partially. T h e i n and M i c h a l k e [23] also showed that bisulfite interacted with the binding sites of NPA, and its inhibition was non-competitive. Bisulfite at 2 or 3×10^{-5} M reduced NPA binding to 50% of the control for membrane-bound and solubilized binding sites, respectively. Bisulfite has also been known to inhibit flavoprotein oxidases and a few other enzymes such as ribulose-1,5-diphosphate carboxylase, catalase, and peroxidases (cited by T h e i n and M i c h a l k e [23]). Judging from these observations together with the results in this study, TIBA, morphactin and NPA might interact with different proteins, respectively, and specifically interfere with facilitators of auxin polar transport. In addition, NPA might not be able to abolish or disturb such auxin homeostasis in some Crassulaceae species.

NPA has been reported to be a potent inhibitor of light-grown hypocotyl elongation, whereas in the dark it has no significant effect on hypocotyl growth of sunflower (*Helianthus annuus*) and marrow (*Cucurbita pepo*) seedlings [24] as well as *Arabidopsis thaliana* seedlings [25–27]. M u r p h y and T a i z [26,27] demonstrated that NPA is hydrolyzed by NPA amidase at the root-hypocotyl transition zone and other regions of *Arabidopsis thaliana* seedlings to α -naphthylamine (α NA), and then α NA combines to form 1,1'-azonaphthylene (ANA), which aggregates to yield an insoluble precipitate. The enzyme producing α NA from NPA is mostly likely arylamidase [26]. NPA amidase activity was detected in plasma membrane-enriched fractions obtained from *Arabidopsis* seedlings. The NPA-induced growth inhibition of *Arabidopsis thaliana* seedlings was strongly promoted by blue light [26,27]. J e n s e n et al. [25] and M u r p h y and T a i z [26,27] showed

that blue light wavelengths were also the most effective for the NPA-staining reaction caused by the degradation of NPA and the formation of α NA and ANA by NPA amidase and that the NPA amidase activity was inhibited by phloretin, genestein, curcumin, quercetin, bestatin and EDTA. It is possible that the amidase responsible for the NPA staining reaction either binds NPA or regulates NPA binding. The lack of inhibition of root formation in some Crassulaceae species might be caused by the lack of NPA degradation by NPA amidase to other constituents as described above.

CONCLUSIONS

1. Auxin polar transport inhibitors, 2,3,5-triiodobenzoic acid (TIBA) and methyl 2-chloro-9-hydroxyfluorene-9-carboxylate (morphactin IT 3456), completely inhibited root formation in cuttings of *Bryophyllum daigremontianum*, *B. calycinum*, *Kalanchoe blossfeldiana* and *K. tubiflora* (Crassulaceae), but 1-*N*-naphthylphthalamic acid (NPA) did not affect rooting of these species when these inhibitors were applied as a lanolin paste at a concentration of 0.2% around the stem below the leaves.
2. The application of TIBA, NPA and morphactin IT 3456 in *B. calycinum* and *K. blossfeldiana* around the stem near the top of the stem with leaves present below the treatments caused TIBA and morphactin IT 3456 to inhibit root formation only partially and again NPA did not affect root formation (the experiment was not performed on *B. daigremontianum* and *K. tubiflora*).
3. Based on these results, it is concluded that endogenous auxin transport from leaves is required for root formation in cuttings of some species of Crassulaceae, and the process is totally inhibited by TIBA and morphactin IT 3456 but not by NPA.
4. To clarify the differential mode of action of NPA in rooting of cuttings in some Crassulaceae plants compared to that of TIBA and morphactin IT 3456, further intensive studies focusing on the molecular aspects of the mode of action of NPA will be required in the near future.

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Authors' contributions

The following declarations about authors' contributions to the research have been made: designing

the experiments: MS, JU; field work: JG, EW-L, JU; writing of the manuscript: MS, KM, JU.

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Zróźnicowany wpływ inhibitorów polarnego transportu auksyny na ukorzenie niektórych gatunków z rodziny Crassulaceae

Streszczenie

Badano wpływ inhibitorów polarnego transportu auksyny, kwasu 2,3,5-trójjodobenzoowego (TIBA), kwasu 1-*N*-naftyloftalamowego (NPA) i morfaktyny,

kwasu metylo 2-chloro-9-hydroksy-fluoreno-karboksyowego (IT 3456), na tworzenie korzeni w sadzonkach niektórych gatunków Crassulaceae, *Brophyllum daigremontianum*, *B. calycinum*, *Kalanchoe blossfeldiana* i *K. tubiflora*. Sadzonki tych gatunków łatwo się ukorzeniają w wodzie bez dodatkowego traktowania. Stwierdzono, że TIBA i morfaktyna całkowicie hamują tworzenie się korzeni, kiedy inhibitory były zastosowane w paście lanolinowej na łodydze poniżej liści. Kiedy TIBA i morfaktynę u *B. calycinum* i *K. blossfeldiana* podano wokół łodygi przy wierzchołku, a liście na łodydze były poniżej traktowania, korzenie tworzyły się ale w mniejszym stopniu niż w roślinach nietraktowanych. Otrzymane wyniki sugerują, że endogenna auksyna jest niezbędna dla tworzenia się korzeni w sadzonkach roślin z rodziny Crassulaceae. Zróźnicowane działanie NPA w porównaniu z TIBA i morfaktyną na ukorzenie jest dyskutowane z różnym wpływem oddziaływania NPA na polarny transport auksyny.

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