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ORIGINAL RESEARCH PAPER

# Differential effects of *N*-1-naphthylphthalamic acid (NPA) and 2,3,5-triiodobenzoic acid (TIBA) on auxin control of swelling of the shoots of *Bryophyllum calycinum* Salisb.

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## Abstract
The effects of *N*-1-naphthylphthalamic acid (NPA) and 2,3,5-triiodobenzoic acid (TIBA) on the swelling of the stem in intact and decapitated plants of *Bryophyllum calycinum* in relation to the interaction with auxin, indole-3-acetic acid (IAA), are described. NPA induced conspicuous local internode swelling only in the area of its application in intact plants and in the decapitated internode in the case of simultaneous application of IAA on the top of the internode. By contrast, TIBA applied to an internode of intact plants induced swelling along the entire internode above the treatment area, and similar results were obtained in the decapitated internode when TIBA was applied in the middle of the internode and IAA was applied onto the top of the internode. The differential effect of NPA and TIBA on stem swelling in *B. calycinum* is discussed in relation to their differential mode of action on auxin transport.

## Keywords
polar auxin transport; *Bryophyllum calycinum*; indole-3-acetic acid; *N*-1-naphthylphthalamic acid (NPA); 2,3,5-triiodobenzoic acid (TIBA); stem; swelling

## Introduction

One major plant hormone, auxin, plays a crucial role in controlling various physiological phenomena in plant growth and development such as cell elongation, apical dominance, and tropism. Auxin is mainly synthesized in the apical part of the shoot and young leaves and is transported basipetally from cell to cell through a combination of membrane diffusion and carrier-mediated transport. This polar auxin transport is well documented [1]. The molecular aspects of polar auxin transport have recently been studied intensively and it is considered to be controlled by the efflux carriers and/or facilitators, PIN-FORMED (PIN) and ATP-binding cassette subfamily B (ABCB proteins), and the influx carriers and/or facilitators, AUXIN RESISTANT1/LIKE AUXIN RESISTANT (AUX1/LAX), located on the plasma membrane [2–5].

It is also well known that polar auxin transport is almost completely inhibited by several compounds such as *N*-1-naphthylphthalamic acid (NPA), 2,3,5-triiodobenzoic acid (TIBA) and methyl 2-chloro-9-hydroxyfluorene-9-carboxylate (morphactin IT 3456). Among them, NPA has been shown to inhibit this transport in both dicotyledonous and monocotyledonous plants by inhibiting active auxin secretion [6]. NPA has also

been reported to inhibit polar auxin transport through its binding to a specific site, the so-called NPA receptor in plant cells [7], indicating that the NPA-binding site is important for polar auxin transport [8]. TIBA and morphactins are also well known for many years to inhibit polar auxin transport in plants and to induce abnormalities in leaf and/or shoot growth. There are numerous reports of these compounds relevant to these aspects [9–22].

Our effort to determine the physiological effects of polar auxin transport inhibitors has been productive, resulting in novel findings for the rooting of cuttings of crassulacean plants. TIBA and morphactin IT 3456 completely inhibited root formation in the cuttings of *Bryophyllum calycinum* Salisb., *B. daigremontianum* Hamet & Perrier, *B. tubiflora* (L.f.) Ker Gawler, and *Kalanchoë blossfeldiana* Poelln. (Crassulaceae), but NPA did not, when these inhibitors were applied around the stem below the leaves. This suggests that TIBA, morphactin IT 3456, and NPA interact with different proteins, and that they interfere with the facilitators of polar auxin transport [23]. A series of our studies on the physiological effects of the inhibitors of polar auxin transport have lead to an additional finding on the swelling of the stem in intact and decapitated plants of *B. calycinum* [3,4]. This paper reports the differential effects of NPA and TIBA on internode swelling in *B. calycinum* and the mode of action of these compounds is discussed in relation to that of auxin.

## Material and methods

Three- to 5-month-old plants of *B. calycinum* propagated from epiphyllous buds arising in the marginal notches of excised leaves were used for our experiments. The plants were grown under natural light and temperature conditions in a glasshouse. Treatments with NPA and TIBA at concentrations of 0.2 or 0.5% in lanolin paste, respectively, and with IAA at a concentration of 0.1% in lanolin paste, were applied to plants as described below. Treatment with lanolin only served as a control.

### Experiment 1

NPA at a concentration of 0.2% was applied around the middle of an internode, in two places on one internode, or on one side of an internode in two neighboring internodes in actively growing intact plants of *B. calycinum* as shown in Fig. 1 and Fig. 2. TIBA at a concentration of 0.5% was applied in the middle or lower part of an internode in actively growing plants as shown in Fig. 3.

### Experiment 2

Naturally grown *B. calycinum* plants were decapitated below a node and the top of the decapitated internode was smeared with lanolin only or 0.1% IAA, and 0.2% NPA or 0.5% TIBA was applied in the middle of the decapitated internode, as shown in Fig. 4.

All of the treatments in Experiments 1 and 2 were repeated three to five times with at least eight plants per treatment.

## Results

### Effect of NPA and TIBA on internode growth in intact *B. calycinum* plants

NPA applied at a concentration of 0.2% in lanolin paste to the middle of an actively growing internode of intact *B. calycinum* induced pronounced local swelling of the stem in and near the area of treatment (Fig. 1a,b). The degree of swelling in the upper side of the treatment was much larger than that in the lower side. When NPA was applied in

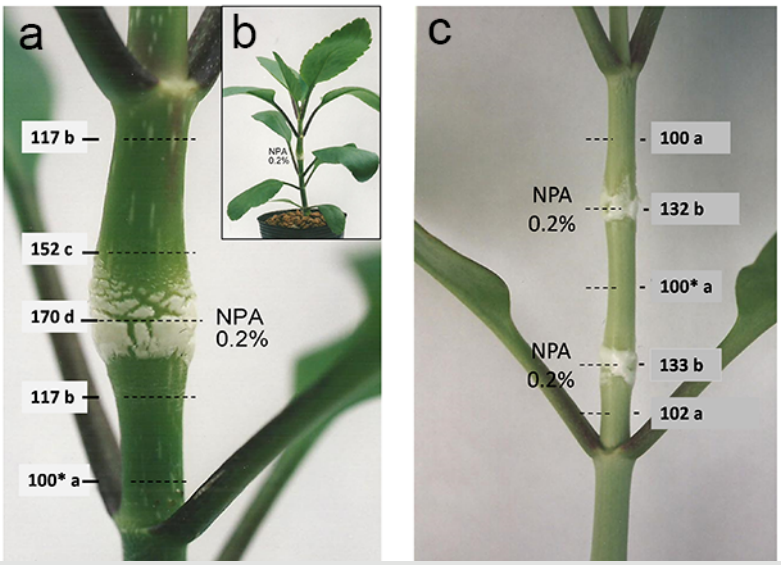


**Fig. 1** The effect of 0.2% NPA on internode swelling in intact *B. calycinum*. **a,b** Treatment around the middle of an internode; views of the treated internode (**a**) and the entire plant (**b**); pronounced swelling can be seen in the area of treatment. Treatments applied on July 9 and photographed after 5 days. **c** NPA was applied in two places of one internode; swelling in the areas of treatment can be seen. Treatments applied on November 11 and photographed after 7 days. Values in the photograph indicate relative diameter (%) of internode against non-treated area (*). Means followed by the same letter are not significantly different at the $p = 0.05$ level according to Duncan's test.

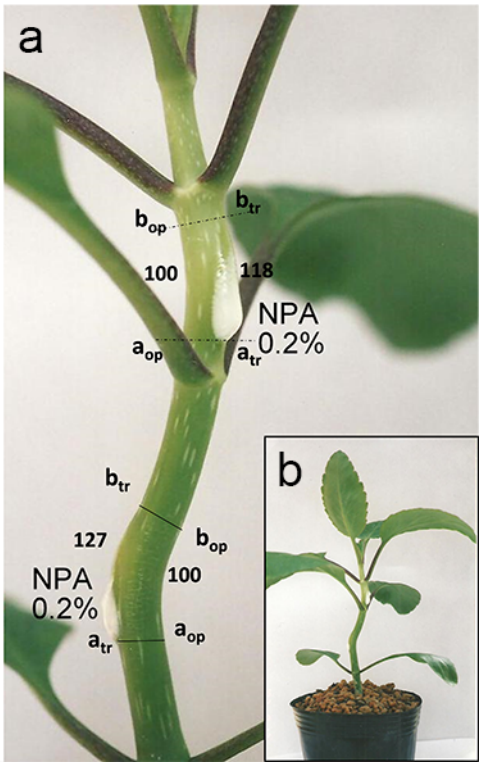


**Fig. 2** The effect of 0.2% NPA applied on one side in two internodes on internode swelling in intact *B. calycinum*. **a,b** Treatment on one side in two internodes; views of the treated internodes (**a**) and the entire plant (**b**). Swelling and bending can be seen in the areas of treatment. Treatments applied on November 11 and photographed after 7 days. Values in the photograph indicate relative length of treated side to opposite side ($a_{tr} \sim b_{tr}$ / $a_{op} \sim b_{op}$; %) of the internode.

two places of a growing internode of intact plants, the local swelling of the stem was observed in each of the treated areas (Fig. 1c), whereas the degree of swelling was smaller than that induced by the application of NPA in one place of a growing internode.

In the case of NPA applied to one side of a growing internode of *B. calycinum*, stem swelling was observed only on the treated side, resulting in slight bending of the internode in the opposite direction to the treated side (Fig. 2). The treated side was ca. 30% longer than the opposite side. Thus, NPA application to one side of a growing internode caused differential growth, resulting in bending of the internode.

TIBA applied at a concentration of 0.5% in the same way as NPA to an actively growing internode of intact *B. calycinum* induced pronounced swelling of the stem only above the application area. In contrast to NPA, the swelling induced by TIBA was observed in the treated internode for a long distance away from the area of treatment and, to a smaller degree, in the next internode (Fig. 3).

## Effect of NPA and TIBA on internode growth in decapitated *B. calycinum* plants in the presence or absence of IAA application

In the decapitated stems of *B. calycinum*, the application of 0.2% NPA or 0.5% TIBA in the middle of the internode did not induce swelling of the internode (Fig. 4a,c,e). 0.1% IAA applied alone onto the top of the decapitated stem did not induce swelling either (Fig. 4b). However, when IAA was applied onto the decapitated internode and NPA in the middle of that internode, local swelling was observed in the area of treatment (Fig. 4d). When TIBA was applied in the middle of the last internode of a decapitated stem of *B. calycinum* and IAA in the area of decapitation, stem swelling in that internode was observed above the TIBA treatment area up to the top of the internode (Fig. 4f, Tab. 1).

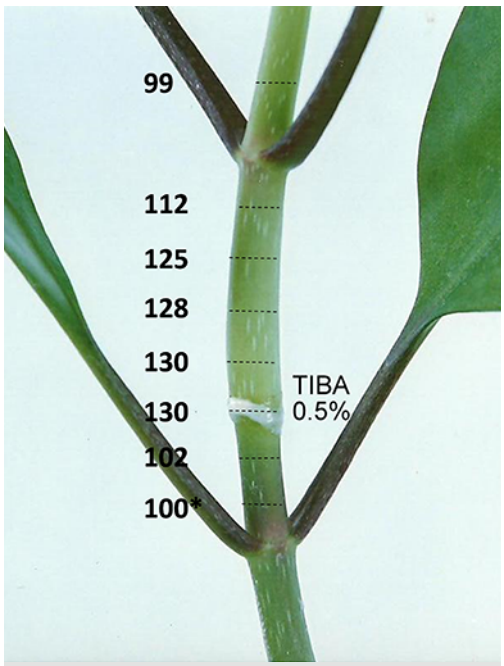


**Fig. 3** The effect of 0.5% TIBA on internode thickening in intact *B. calycinum*; thickening along the entire internode above the area of treatment can be seen. Treatment applied on July 9 and photographed after 5 days.

In all experiments with both intact and decapitated plants in which IAA was applied in the area of decapitation, responses of all plants in a particular treatment were very similar. These results suggest that IAA moved from the shoot apex interacts with locally supplied polar auxin transport inhibitors NPA and TIBA, causing swelling of actively growing internodes of *B. calycinum*.

## Discussion

As described in "Introduction", we have recently reported the novel physiological findings of NPA, TIBA, and morphactin IT 3456 in the rooting of cuttings in several Crassulaceae. TIBA and morphactin IT 3456 completely inhibited root formation in the cuttings of *B. calycinum*, *B. daigremontianum*, *B. tubiflora*, and *K. blossfeldiana*, but NPA did not, when these inhibitors were applied around the stem below the leaves [23]. In the present study, NPA substantially induced conspicuous local swelling in the stem of intact and decapitated plants of *B. calycinum* when IAA was additionally applied on the top of decapitated internode, suggesting that the local interaction of NPA with endogenous auxin is necessary for swelling.

We suggest that the local swelling of the stem in intact *B. calycinum* plants induced by NPA is caused by local interaction of NPA with endogenous auxin, but the interaction is not connected with inhibition of the polar auxin transport and the accumulation of auxin in

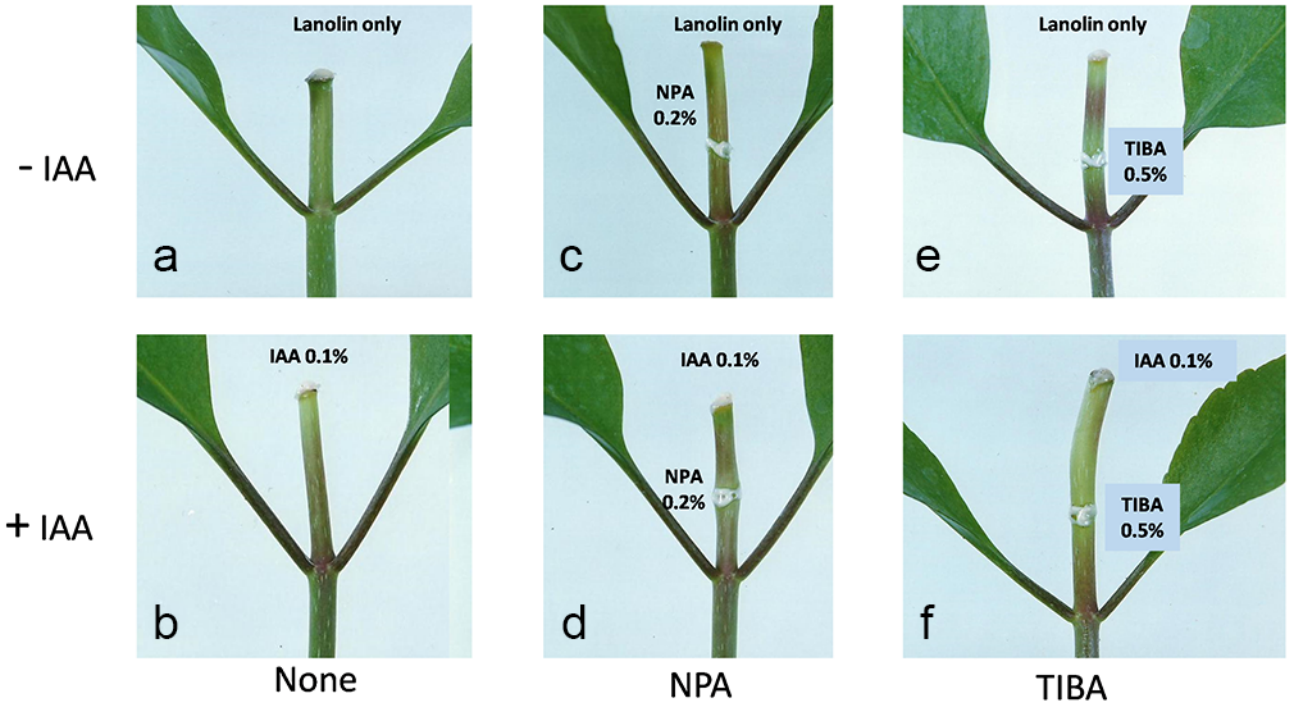


**Fig. 4** The effect of NPA (0.2%), TIBA (0.5%), and IAA (0.1%) applied to the last internode of decapitated shoots of *B. calycinum* on the swelling of the treated internodes; treatments were applied on August 12 and pictures were taken after 12 days. **a** In control plants, lanolin only was applied in the area of decapitation and in the middle of the last internode. Lanolin applied in the middle of the internode was removed before taking the photograph. **b** IAA was applied in the area of decapitation. Lanolin applied in the middle of the last internode was removed before taking the photograph. **c** Lanolin was applied in the area of decapitation and NPA in the middle of the last internode. **d** IAA applied in the area of decapitation and NPA in the middle of the last internode; local swelling can be seen in the area of treatment with NPA. **e** Lanolin was applied in the area of decapitation and TIBA in the middle of the last internode. **f** IAA was applied in the area of decapitation and TIBA in the middle of the last internode; swelling along the entire internode can be seen above the area of treatment with TIBA.

**Tab. 1** The effect of NPA, TIBA, and IAA applied in lanolin paste on stem swelling in decapitated shoots of *B. calycinum*.

| Treatments (area of internode) | Diameter of internode (mm) | | |
|---|---|---|---|
| | middle of internode | 1.5 cm above middle | 1.5 cm below middle |
| Control (lanolin on top and middle) | 5.36 [a] (97) | 5.18 [a] (93) | 5.55 [a] (100) |
| Lanolin (top) and NPA 0.2% (middle) | 5.46 [a] (96) | 5.26 [a] (93) | 5.67 [a] (100) |
| Lanolin (top) and TIBA 0.5% (middle) | 5.80 [a] (102) | 5.37 [a] (95) | 5.66 [a] (100) |
| IAA 0.1% (top) and lanolin (middle) | 5.19 [a] (98) | 4.92 [a] (93) | 5.28 [a] (100) |
| IAA 0.1% (top) and NPA 0.2% (middle) | 6.71 [b] (119) | 5.17 [a] (91) | 5.66 [a] (100) |
| IAA 0.1% (top) and TIBA 0.5% (middle) | 5.92 [ab] (106) | 6.44 [b] (116) | 5.57 [a] (100) |

Means in a row followed by the same letter are not significantly different at the $p = 0.05$ level according to Duncan's test. The values in the parentheses show the diameter of the treated part expressed as a percentage of the diameter of the internode measured at 1.5 cm below the middle of the internode.

the swelling area. In consequence, stimulation of cell division and/or cell elongation and/or cell enlargement takes place, so that pronounced swelling is finally observed. The fact that NPA applied in two places on one internode of an intact *B. calycinum* plant induced local swelling in each area of treatment also suggests that NPA did not inhibit the polar transport of endogenous auxin. When NPA was applied on one side of an internode in intact plants, the swelling and bending was observed only in the area of treatment, indicating that the bending was not connected with eventual auxin activity of NPA.

NPA applied in the middle of an internode after decapitation of the upper part of *B. calycinum* (removal of the source of auxin) did not induce swelling of the stem, but when additional IAA was applied onto the decapitated end of the stalk, local swelling in the area of the NPA treatment was observed. Again, this is additional evidence that the swelling induced by NPA in the stem of intact *B. calycinum* plants is caused by interaction with endogenous auxin only in the area of NPA application, but the mechanisms of the interaction are unknown. These results also suggest that NPA itself is not transported in the tissues or organs of *B. calycinum*. It is also probably the same effect in other species of Crassulaceae in not inhibiting basipetal polar transport of auxin. NPA, in contrast to TIBA and morphactin, did not inhibit rooting in cuttings of a few species of Crassulaceae [23].

The powerful polar auxin transport inhibitors, NPA, TIBA, and morphactin IT 3456 have shown various effects on plant growth and development. As described in the "Introduction", these compounds have been considered to affect plant growth and development at the molecular level, by interference with the auxin efflux carriers and/or facilitators of PINs and ABCB proteins located on plasma membrane, but the detailed mechanism still remains unclear [24]. NPA has already been shown to bind to the NPA receptors, which are important in polar auxin transport in plant cells [7,8]. Katekar and Giessler [20], however, reported that NPA inhibited polar auxin transport by specifically binding to the auxin efflux carrier, strongly suggesting that the NPA-binding site is controversial. IAA itself does not compete with NPA for the binding site [25]. Thein and Michalke [26] showed that bisulfite interacted with binding sites of NPA by non-competitive inhibition.

It seems that the swelling induced by NPA in *B. calycinum* is not caused by ethylene produced by local accumulation of endogenous or exogenous auxin. It should be noted that NPA did not stimulate ethylene production in the internodes of intact and decapitated plants of *B. calycinum*, and application of 1-aminocyclopropano-1-carboxylic acid stimulated ethylene production but did not induce swelling in the plant (data not shown). It was previously found that the application of NPA or TIBA failed to induce ethylene in the roots of *Pisum sativum* [27] or the roots of *Arabidopsis thaliana* [24]. Further studies on the mechanism of the induction of swelling by NPA in the stem of *B. calycinum* are in progress.

In contrast to NPA, TIBA applied to the basal part of an internode of intact plants of *B. calycinum* induced swelling along the entire internode above the treatment area. TIBA applied in the middle of the last internode of the decapitated plants did not induce any swelling. However, additional application of IAA onto the area of decapitation caused swelling of the internode above the area treated with TIBA. These results suggest that TIBA inhibits polar auxin transport and was itself transported acropetally in the shoots of *B. calycinum*. However, Thomson et al. [28] have suggested that TIBA was transported basipetally in corn coleoptiles. TIBA has been reported to compete for the same binding sites as that of IAA [28–30]. In addition, TIBA is transported in a polar basipetal manner, but NPA is not [28].

The binding site of morphactin is also controversial. Morphactin has been shown to bind to the NPA receptor, suggesting that it inhibits polar auxin (IAA) transport by the same mechanism as NPA. Morphactin has also been reported to translocate basipetally as well as acropetally through both sieve tubes and xylem elements [31,32]. This strongly suggests that morphactin moves faster than TIBA and NPA in plant tissues. Morphactin IT 3456 and NPA are very effective inhibitors of the basipetal transport of NAA in hypocotyl sections of *Helianthus annuus* and *Cucurbita pepo* seedlings [22].

We reported here the fact that the differential effect of NPA and TIBA on stem swelling in *B. calycinum* is clearly related to their differential mode of action on auxin transport. It is possible that NPA did not inhibit polar auxin transport in plants with crassulacean acid metabolism (CAM). It is known that TIBA completely inhibits root development on plantlets formed on leaves excised from intact *B. marnierianum*, but NPA does not [33]. NPA did not affect the formation of vegetative structures at bracteoles which are formed after removal of flower buds in *Agave tequilana* (CAM plant) [34]. Molecular mechanisms of NPA and TIBA inducing stem swelling and an anatomical survey of swollen internodes in *B. calycinum* will be studied in detail in the near future.

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## Zróżnicowany wpływ kwasu 1-*N*-naftyloftalamowego (NPA) i kwasu 2,3,5-trójjodobenzoesowego (TIBA) w relacji do auksyny na grubienie pędu *Bryophyllum calycinum*

### Streszczenie

W pracy przedstawiono zróżnicowany wpływ kwasu 1-*N*-naftyloftalamowego (NPA) i kwasu 2,3,5-trójjodobenzoesowego (TIBA) na grubienie łodygi w całych i dekapitowanych roślinach *B. calycinum* w relacji do interakcji z auksyną, kwasem indolilo-3-octowym (IAA). NPA silnie indukował miejscowe grubienie łodygi tylko w miejscu jego traktowania w roślinach całych i w dekapitowanych międzywęźlach w przypadku jednoczesnego podania IAA na wierzchołek międzywęźla. Z drugiej strony, TIBA podany na środek międzywęźla całych roślin indukował grubienie łodygi wzdłuż całego międzywęźla powyżej miejsca traktowania i podobne wyniki otrzymano w międzywęźlach dekapitowanych kiedy TIBA podano na środek międzywęźla i jednocześnie IAA nałożono na wierzchołek dekapitowanego międzywęźla. Zróżnicowany wpływ NPA i TIBA na grubienie łodygi *B. calycinum* jest dyskutowany w relacji z ich zróżnicowanym mechanizmem działania na transport auksyny.

 