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ORIGINAL RESEARCH PAPER

Hormonal regulation of the growth of leaves and inflorescence stalk in *Muscari armeniacum* Leichtl.

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Abstract

It is known that chilling of *Muscari* bulbs is necessary for the growth of the inflorescence stalk and flowering, but not for the growth of leaves. Gibberellic acid (GA) accelerated stem growth and flowering in chilled *Muscari* bulbs. In the present experiment it was shown that in unchilled derooted *Muscari* bulbs the growth of leaves, but not the growth of the inflorescence stalk, was observed when bulbs were stored in water, GA at a concentration of 50 and 100 mg/L, benzyladenine (BA) at a concentration of 25 and 50 mg/L, or a mixture of GA+BA (50+25 mg/L), but abscisic acid (ABA) at a concentration of 10 mg/L greatly inhibited the growth of leaves. In chilled derooted *Muscari* bulbs the growth of leaves and inflorescence stalk was observed when bulbs were stored in water or GA, but BA and GA+BA treatments totally inhibited the growth of the inflorescence stalk without an effect on the growth of leaves. These results clearly showed that the growth of leaves and inflorescence stalk in *Muscari* bulbs are controlled by plant growth regulators in different ways. ABA totally inhibited the growth of leaves and inflorescence stalk in chilled derooted *Muscari* bulbs. It was shown that after the excision of the inflorescence bud in cultivated chilled *Muscari* bulbs, the inflorescence stalk died, but application of indole-3-acetic acid (IAA) 0.5% in the place of the removed inflorescence bud induced the growth of the inflorescence stalk. IAA applied under the inflorescence bud inhibited the development of flowers (flower-bud blasting) and induced the growth of the inflorescence stalk below the treatment site. These results are discussed with reference to hormonal regulation of stem (stalk) growth in tulip, narcissus, hyacinth, and *Hippeastrum*.

Keywords

Muscari armeniacum; grape hyacinth; inflorescence stalk; leaves; growth; growth regulators

Introduction

In early fall, *Muscari* bulbs with formed inflorescences, leaves and root primordia are planted in the soil where rooting and growth of the leaves a few centimeters above the soil level take place before wintertime. The flowering and further growth of leaves occur in the spring after chilling. Thus, it is interesting that in *Muscari* the growth of leaves starts without the chilling of bulbs; however, chilling is necessary for the growth and flowering of the inflorescence stalk. Saniewski [1] showed that in unchilled *Muscari* bulbs planted in a greenhouse at high temperature, strong growth of leaves took place without the growth of the inflorescence stalk. Thus, chilling is necessary for the growth of the inflorescence stalk and flowering. It should be mentioned that the growth of leaves in unchilled *Muscari* bulbs is greater than of the leaves in chilled

naturally growing *Muscari* [1]. It has been found [1] that gibberellic acid applied as a lanolin paste around the basal plate of *Muscari* at the beginning of July accelerated the flowering of naturally chilled bulbs, but did not break the dormancy of unchilled bulbs. Gibberellic acid (GA) strongly stimulated the growth of leaves and inflorescence stalk in chilled bulbs of *Muscari* in early spring, but the final length of these organs was similar to that of the control plants [2]. Hanks and Jones [3] have also documented the fact that gibberellic treatment interacted with the duration of chilling, and that GA strongly accelerated flowering and growth of the inflorescence stalk and leaves in partially chilled bulbs of *Muscari armeniacum*.

The anatomical structure of *Muscari armeniacum* Leichtl. (grape hyacinth) bulbs is similar to the structure of hyacinth (*Hyacinthus orientalis* L.) bulbs, but their growth patterns are different. *Muscari* bulbs do not require chilling for the growth of leaves, but low temperature treatment is necessary for inflorescence stalk growth and flowering, whereas in hyacinth bulbs low temperature treatment is necessary for the growth of leaves and for inflorescence stalk growth and flowering of the plants [4].

In the present study, we determined the effects of GA, benzyladenine (BA), indole-3-acetic acid (IAA), and abscisic acid (ABA) on the growth of leaves and the inflorescence stalk growth in unchilled and chilled derooted *Muscari armeniacum* bulbs.

Material and methods

Grape hyacinth (*Muscari armeniacum* Leichtl.) bulbs, 4–5 cm in circumference, with formed inflorescence stalk, leaves and root primordia, were used in the experiments. IAA, GA, BA, a mixture of GA+BA, and ABA under different concentrations were applied in these experiments. Two experiments were conducted.

Experiment A

The effect of plant growth regulators (GA, BA, GA+BA, ABA) on the growth of leaves and inflorescence stalk in unchilled and chilled *Muscari* bulbs was tested. Unchilled bulbs were stored at 20°C in a gravitationally ventilated place until treatment at the end of October, while chilled bulbs were dry-cooled at 5°C in darkness at humidity 80%, from the beginning of September until the beginning of January (16 weeks).

All the root primordia in both unchilled (October 22) and chilled (January 6) bulbs were removed, and the bulbs were kept in water (control), and aqueous solutions of GA (50 and 100 mg/L), BA (25 and 50 mg/L), a mixture of GA+BA (50+25 mg/L), and ABA (10 mg/L), at a temperature of 18–20°C in natural light conditions. During the experiment, the length of leaves was measured on the basis of morphological observations of leaf growth. Every 2 days, the newly appeared roots were excised. In every treatment, 20 bulbs were used, and the experiment was repeated twice.

Experiment B

The effect of plant growth regulators (IAA 0.5%, 2,4-D 0.2%, and GA 1.0%) was tested on the growth of the inflorescence stalk and leaves when applied in the place of the removed inflorescence stalk and under the inflorescence bud in chilled *Muscari* bulbs. *Muscari* bulbs were dry-cooled at 5°C from the middle of October until the end of February (18 weeks). In the middle of February (18 weeks), the bulbs were planted individually in pots and cultivated in a greenhouse at a temperature of 17–20°C in natural light conditions. When the length of the inflorescence stalk was about 4.0 cm (23 days after planting), the inflorescence bud was removed and the place of the removed inflorescence bud was treated with lanolin only (control), IAA 0.5%, 2,4-D, and GA 1.0% in a lanolin paste, and then in one part of the treated plants the leaves were left intact, while in another part the leaves were removed at the beginning of the experiment; newly-appeared leaves were excised every 2 days.

In another version of this experiment, the only difference was that IAA, 2,4-D, and GA were applied under the inflorescence bud 15 days after the planting of bulbs.

During the experiment, morphological observations were made and the length of the leaves and inflorescence stalk was measured. In every treatment, 10 bulbs were used, and the experiment was repeated twice.

The data were subjected to analysis of variance and Duncan's test was used to estimate the difference between means at $p \leq 0.05$.

Results

In the present experiment, it was shown that in unchilled derooted *Muscari* bulbs the growth of leaves, but no growth of the inflorescence stalk, was observed when bulbs were stored in water (Fig. 1a,b). GA and the mixture of GA+BA, applied in the same way, slightly inhibited the growth of leaves until 27 days after treatment, but at the end of the experiment it was not affected by these regulators (Fig. 1a,b). BA substantially stimulated the growth of leaves after 27 days of treatment, but at the end of the experiment it was similar to that of the control plants (Fig. 1a,b). By contrast, ABA greatly inhibited the growth of leaves in the experiment (Fig. 1a,b). None of the applied plant growth regulators induced inflorescence stalk growth.

In the chilled derooted *Muscari* bulbs, the growth of leaves and inflorescence stalk was observed when the bulbs were stored in water (Fig. 2a–c), while GA partially inhibited the growth of leaves without having an effect on the growth of the inflorescence stalk. By contrast, treatment of derooted bulbs with BA and the mixture of BA+GA totally inhibited the growth of the inflorescence stalk without affecting the growth of leaves (Fig. 2a–c). ABA totally inhibited the growth of leaves and inflorescence stalk (Fig. 2a–c).

It was shown that after the excision of the inflorescence bud in cultivated chilled *Muscari* bulbs, in intact plants or with the leaves removed, the inflorescence stalk died, but the application of IAA in the place of the removed inflorescence bud induced the growth of the inflorescence stalk (Fig. 3a–d). 2,4-D, applied in the same way as IAA, slightly stimulated growth but increased the thickening of the inflorescence stalk (Fig. 3a–d). GA slightly stimulated the growth of the inflorescence stalk when applied in the place of the removed inflorescence bud, but the stalk was thin (Fig. 3a–d). It should be mentioned that treatment of the inflorescence stalk with IAA, 2,4-D, and GA, after the removal of the inflorescence bud, had no effect on the growth of leaves and their length was about 18.0 cm in all the treatments at the end of the experiment (Fig. 3a).

When IAA was applied under the inflorescence bud of *Muscari* plants with intact leaves, the inflorescence bud died, but induction of the growth of the inflorescence stalk was observed (Fig. 4a,b). 2,4-D treatment around the inflorescence bud of *Muscari* also caused malformations in the inflorescence bud and thickening of the inflorescence stalk (Fig. 4a,b). GA applied around the inflorescence bud of *Muscari* did not affect the growth

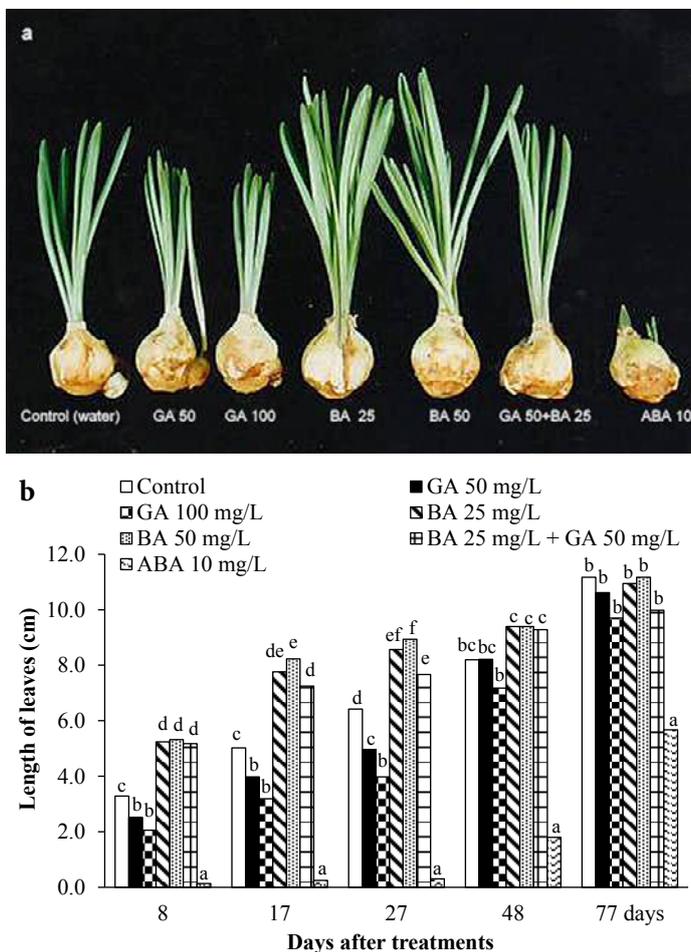


Fig. 1 The effect of plant growth regulators on leaf growth in unchilled *Muscari* bulbs; derooted bulbs were kept in water and solutions of GA 50 and 100 mg/L, BA 25 and 50 mg/L, GA 50+BA 25 mg/L, and ABA 10 mg/L – treatments performed on October 22 (experiment A). Values are calculated separately for each day of the treatment. Means followed by the same letter are not significantly different at $p \leq 0.05$ according to Duncan's test. **a** Picture of the experiment taken on November 29 (5 weeks after treatment). **b** The growth of leaves after treatments.

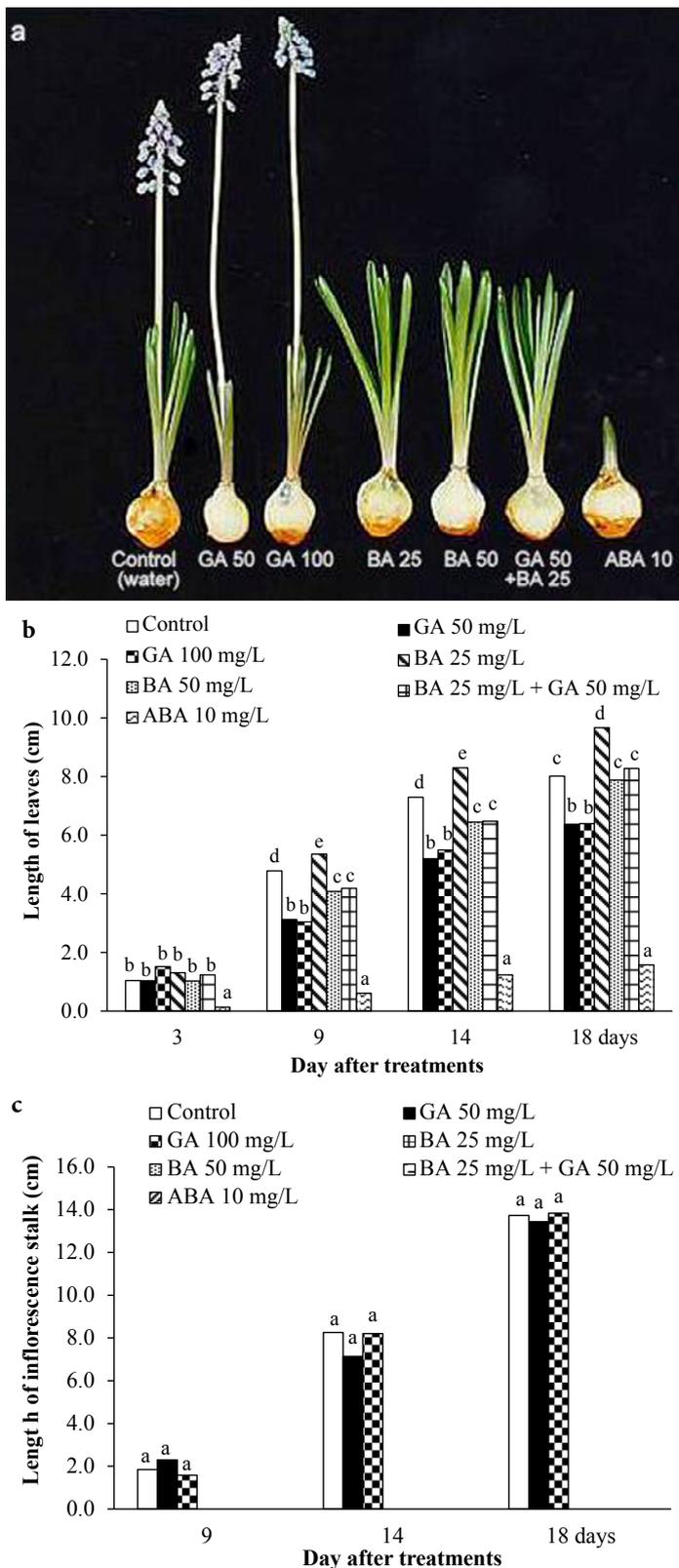


Fig. 2 The effect of plant growth regulators on leaf and inflorescence stalk growth in chilled *Muscari* bulbs; derooted bulbs were kept in water and solutions of GA, BA, GA+BA, and ABA – treatments were performed on January 6 (experiment A). Values are calculated separately for each day of the treatment. Means followed by the same letter are not significantly different at $p \leq 0.05$ according to Duncan's test. **a** Picture of the experiment taken on January 24 (2.5 weeks after treatment). **b** The growth of leaves after hormone application. **c** The growth of the inflorescence stalk after treatments.

of the inflorescence bud or the stalk (Fig. 4a,b). The growth of leaves after treating *Muscari* bulbs with IAA, 2,4-D, and GA around the inflorescence bud was similar (Fig. 4a); their length was about 14.0 cm in all the treatments at the end of the experiment.

Discussion

In unchilled *Muscari* bulbs planted in a greenhouse at high temperature, strong growth of leaves took place without the growth of the inflorescence stalk [1]. None of the applied plant regulators induced inflorescence stalk growth in unchilled tulip bulbs.

It is interesting that benzyladenine almost totally inhibited the inflorescence stalk growth in chilled derooted *Muscari* bulbs. These results show that the growth of leaves and the growth of the inflorescence stalk in *Muscari* are controlled by plant growth regulators in different ways, but the mechanism of this phenomenon is unknown.

Benzyladenine applied in a lanolin paste around the basal plate of *Muscari comosum* and *Muscari armeniacum* greatly stimulated the formation of new bulblets around the basal plate [5], whereas gibberellic acid and auxins inhibited bulblet differentiation in intact bulbs of *Muscari* [6].

Cytokinins have an inhibitory effect on auxin- and gibberellin-promoted elongation of the stem in many plants ([7] and references therein). Vanderhoef et al. [7] and Victor and Vanderhoef [8] have shown that the cytokinins – isopentyladenine, kinetin, zeatin, and benzyladenine, inhibited hypocotyl elongation induced by auxin in hypocotyl segments excised from 3-day-old soybean seedlings and promoted radial enlargement. Shibaoka [9] documented the fact that IAA-induced elongation of light-grown epicotyl segments of azuki bean (*Azuki angularis*) was inhibited by kinetin, but stem thickening increased.

ABA almost totally inhibited the growth of leaves in unchilled *Muscari* bulbs, and the growth of leaves and inflorescence stalk in chilled bulbs. The inhibitory effect of ABA on the growth of leaf and stem explants in tulips in vitro was documented by Gabryszewska and Saniewski [10] and Saniewski and Gabryszewska [11].

IAA is the main factor responsible for the inflorescence stalk elongation in *Muscari*, and the auxin is produced in flower buds. The leaves and gynoecium provide auxins which control the elongation of the stem in tulip [12–15]. Excision of the flower bud and all leaves in the early stages of tulip growth results in almost total inhibition of stem growth, and this inhibition is almost completely

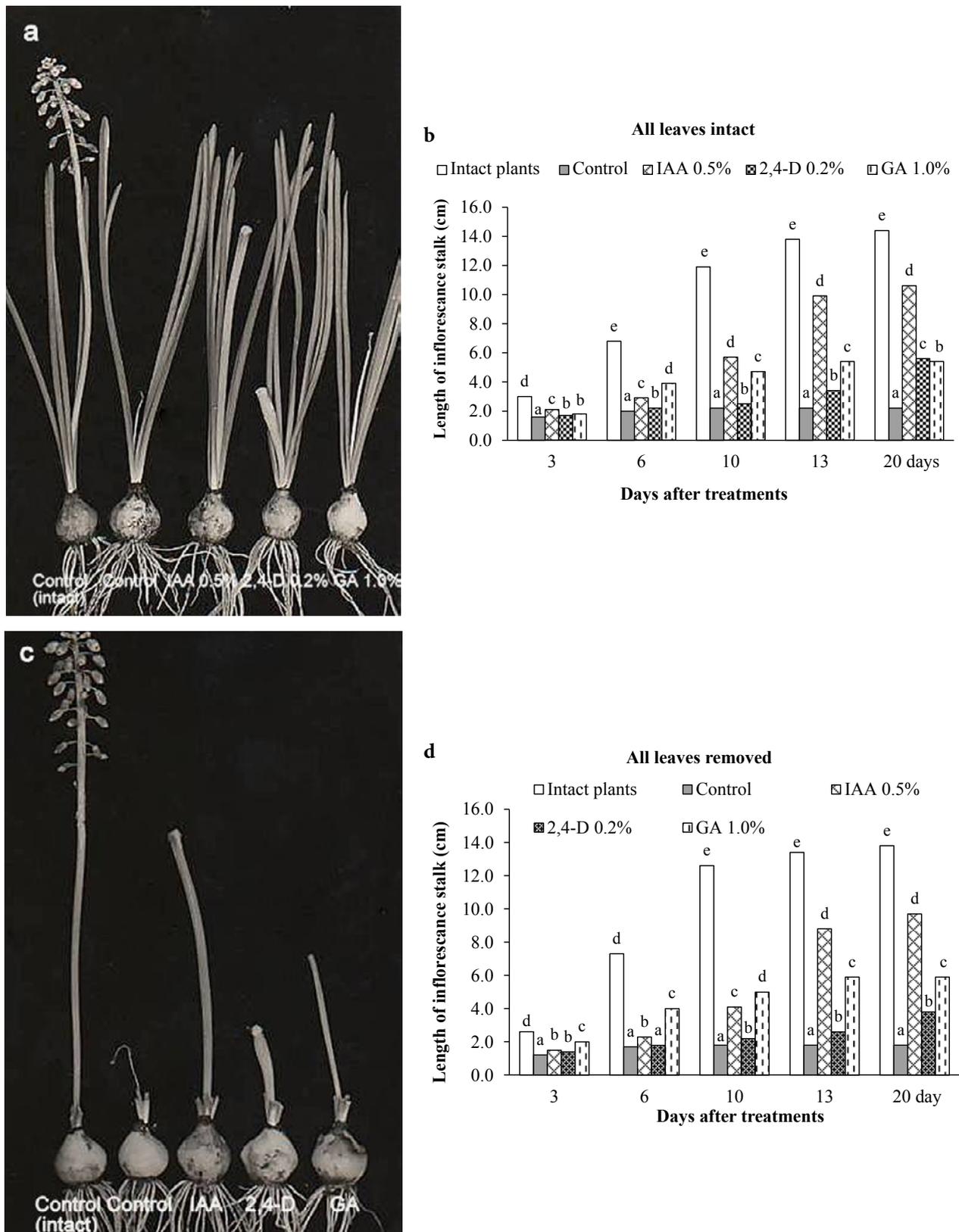


Fig. 3 The effect of plant growth regulators on the growth of the inflorescence stalk and leaves in chilled *Muscari* bulbs planted in pots and cultured in a greenhouse; plant growth regulators in a lanolin paste were applied in the place of the removed inflorescence bud – treatments performed on March 10 (experiment B). Values are calculated separately for each day of the treatment. Means followed by the same letter are not significantly different at $p \leq 0.05$ according to Duncan's test. **a** Picture of the experiment taken on March 25 (2 weeks after treatments); all leaves remained intact over the duration of the experiment. **b** The growth of the inflorescence stalk; all leaves intact over the duration of the experiment (see Fig. 3a). **c** Picture of the experiment taken on March 25 (2 weeks after treatments); all leaves were removed continuously over the duration of the experiment. **d** The growth of the inflorescence stalk; all leaves were removed continuously during the experiment (see Fig. 3c).

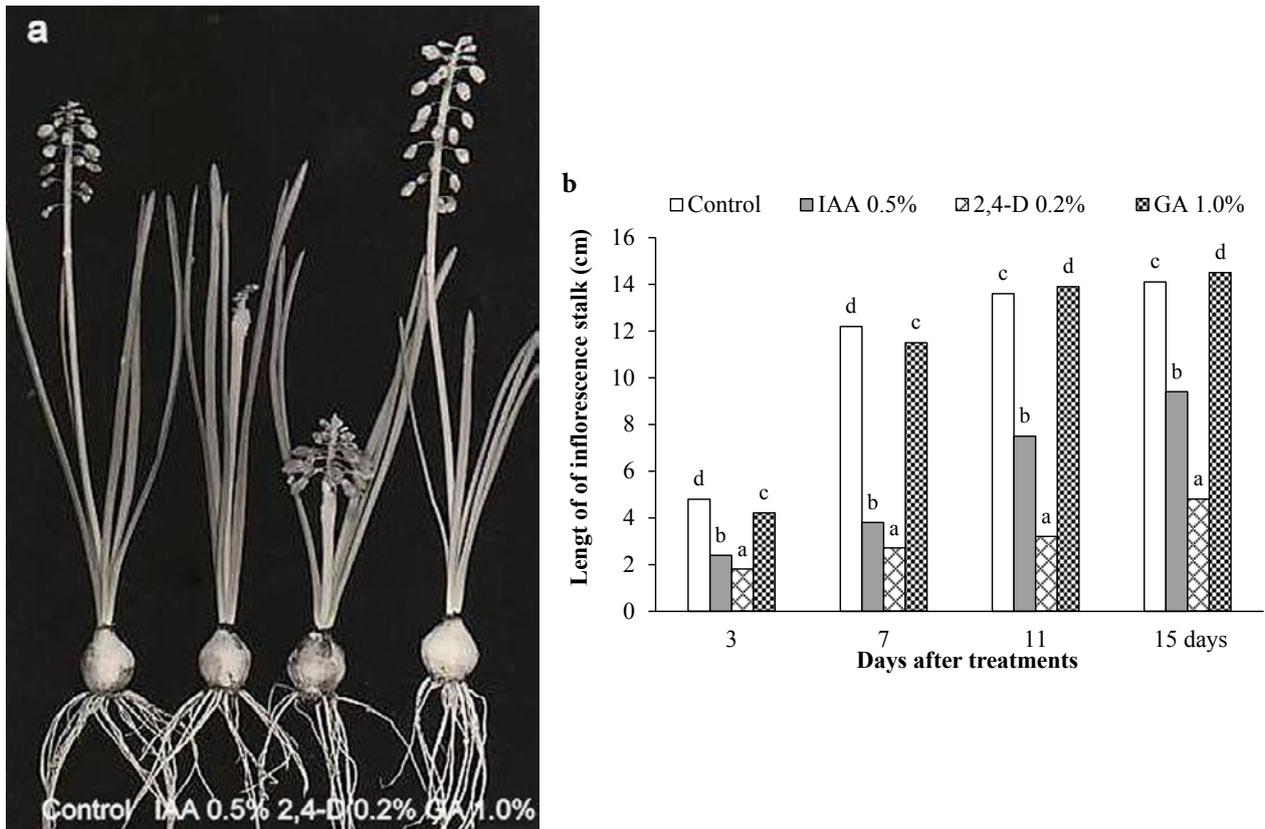


Fig. 4 The effect of plant growth regulators on inflorescence stalk and leaf growth in chilled *Muscari* bulbs planted in pots and cultivated in greenhouses; plant growth regulators as a lanolin paste were applied around the inflorescence bud – treatments performed on March 2 (experiment B). Values are calculated separately for each day of the treatment. Means followed by the same letter are not significantly different $p \leq 0.05$ according to Duncan's test. **a** Picture of the experiment taken on March 17 (2 weeks after treatments); all leaves remained intact over the duration of the experiment. **b** The growth of the inflorescence stalk (see Fig. 4a).

recovered by the exogenous application of auxin to the place where the flower bud has been removed [14,15]. It has also been found that auxin induced the growth of stem segments excised from the growing shoot of cooled tulip bulbs and in stem segments excised from cooled and uncooled tulip bulbs [16–18]. Also the growth of the stem in *Narcissus* [13], the inflorescence stalk in *Hyacinthus orientalis* [19], and the scape in *Hippeastrum* [20] are hormonally controlled by auxin.

Ethylene or sources of ethylene (2-chloroethylphosphonic acid – ethephon) applied to intact tulip plants cause many disorders, including flower bud blasting [21–26]. Consequently, auxin production by and transportation from the gynoecium will be decreased and ultimately stop. Also, application of IAA or NAA below the flower bud causes blasting in tulips but stimulates the growth of the stem below the treatment site [27]. It is well documented that IAA stimulates ethylene production in many plant organs by inducing the synthesis of 1-aminocyclopropane-1-carboxylic acid (ACC) [28]. In case of *Muscari* flower bud blasting caused by exogenously applied IAA is connected with ethylene induced by the auxin.

Conclusions

- In unchilled and chilled derooted *Muscari armeniacum* bulbs, the growth of leaves was observed when bulbs were stored in water, GA, BA, and their mixture. ABA greatly inhibited the growth of leaves. All these treatments did not break dormancy of the inflorescence stalk in unchilled derooted *Muscari* bulbs.
- In chilled derooted *Muscari* bulbs, the inflorescence stalk growth and flowering were observed if bulbs were stored in water and GA, but treatments with BA, GA+BA, and ABA totally inhibited inflorescence stalk growth.

- Application of IAA in the place of the removed inflorescence bud induced the growth of the inflorescence stalk in naturally growing plants.
- The mechanism of hormonal control of the growth of leaves and inflorescence stalk in *Muscari* differs.

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Hormonalna regulacja wzrostu pędu kwiatostanowego i liści szafirka (*Muscari armeniacum* Leichtl.)

Streszczenie

Wczesną jesienią cebule szafirków z uformowanym pękiem kwiatostanowym, liśćmi i primordiami korzeni są wysadzone do gleby, gdzie następuje ukorzenianie i wzrost liści długości kilku centymetrów nad ziemią jeszcze przed przechłodzeniem. Kwitnienie następuje wczesną wiosną po przechłodzeniu. Z cebul szafirków bez przechłodzenia wysadzanych do ogrzewanej szklarni wyrastają nienaturalnie długie liście, w porównaniu z cebulami przechłodzonymi, ale nie następuje wzrost pędu kwiatostanowego. Przechłodzenie cebul szafirków jest konieczne do wzrostu pędu kwiatostanowego, ale nie liści. Kwas giberelinowy (GA) podany w paście lanolinowej wokół piętki cebul szafirków przyspiesza kwitnienie i wzrost liści u cebul przechłodzonych, ale nie przerywa spoczynku pędu kwiatostanowego u cebul nieprzechłodzonych.

Obecne badania wykazały, że nieprzechłodzone cebule szafirków trzymane w roztworze z benzyloadeniną (BA) w stężeniu 25 i 50 mg/L, po usunięciu zaczątków korzeni, reagowały stymulacją wzrostu liści, a kwas abscysynowy (ABA) powodował całkowite zahamowanie wzrostu liści, natomiast podanie GA pozostało bez wpływu na wzrost liści. W przypadku cebul szafirków przechłodzonych w 5°C (bez ukorzeniania) i po obcięciu zaczątków korzeni, moczenie cebul w roztworze BA spowodowało całkowite zahamowanie wzrostu pędu kwiatostanowego bez wpływu na wzrost liści, natomiast w przypadku traktowania GA następował wzrost pędu kwiatostanowego i liści, podobnie jak w kontroli (przechowywanie w wodzie). ABA hamował prawie całkowicie wzrost liści i pędu.

Usunięcie pąka kwiatostanowego we wczesnym etapie wzrostu liści i pędu u szafirków powodowało całkowite zahamowanie wzrostu pędu, a nałożenie auksyny (IAA) w miejscu usuniętego pąka przywracało naturalny wzrost pędu. Natomiast podanie IAA pod pękiem kwiatostanowym we wczesnym etapie wzrostu pędu powodowało zamieranie wszystkich pąków kwiatowych, najprawdopodobniej na skutek stymulującego działania IAA na tworzenie się etylenu.