

Review

Plant Growth Regulators for the Cultivation and Vase Life of Geophyte Flowers and Leaves

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Abstract: Geophytes are a very important group among ornamental plants, for which more and more plant growth regulators (PGRs) are being used to improve the plant quality, flowering intensity, and vase life of flowers and leaves. PGRs constitute a large group of naturally occurring or synthetically produced organic chemical compounds. There are many factors that influence the efficiency of PGRs, and the method of their application plays a key role in determining their success. In the case of geophytes, the most common method of application is spraying and soaking the storage organs before planting. This article presents information on the application of PGRs to different species of geophytes, both at the cultivation stage and during the post-harvest treatment of flowers and leaves.

Keywords: PGRs; storage organs; ornamental plants; cultivation; post-harvest longevity

1. Introduction

Geophytes are herbaceous terrestrial plants that usually go through a state of dormancy, during which they “go to sleep” and form underground storage organs in the form of bulbs, corms, tubers, or rhizomes (Figure 1) [1]. These organs enable the plants to survive periods of drought and other environmental stresses by protecting the regenerating buds underground and providing stored nutrients. Geophytes have a wide geographic range but are particularly diverse in Mediterranean ecosystems [2–5]. Among geophytes, there are both monocotyledonous and dicotyledonous species [6–9]. Regardless of the storage organ, the species that belong to geophytes (Figure 2) are commonly referred to as bulbous plants [10].

Geophytes occupy a very important position in floriculture. They are grown to be used as cut flowers and potted plants for interior ornamentation. They have also valued plants for gardens and landscaped areas. Thanks to forcing, it is possible to produce flowering geophytes in containers or to use them to grow cut flowers all year round. Many species are used for culinary, medicinal, and industrial purposes. The leaves, flowers, and underground organs are edible as a fresh, dried, frozen, or sugar-preserved product. Some species are used as spices, for medicinal purposes, or as a source of essential oils for the pharmaceutical industry. Out of approximately 800 types of geophytes, seven accounts for 90% of bulb production, including *Tulipa*, *Lilium*, and *Narcissus*. In the case of the remaining 10%, the assortment of species introduced to the global flower market is constantly increasing [11].

As in the case of other ornamental plants, plant growth regulators (PGRs) are more and more often used in this group to improve the quality of plants, the intensity of flowering, and the post-harvest longevity of flowers and leaves. PGRs are organic substances that are naturally produced by tall plants, controlling growth in a place distant from the place of their production. They are active in trace amounts or as synthetic products administered exogenously [12,13].



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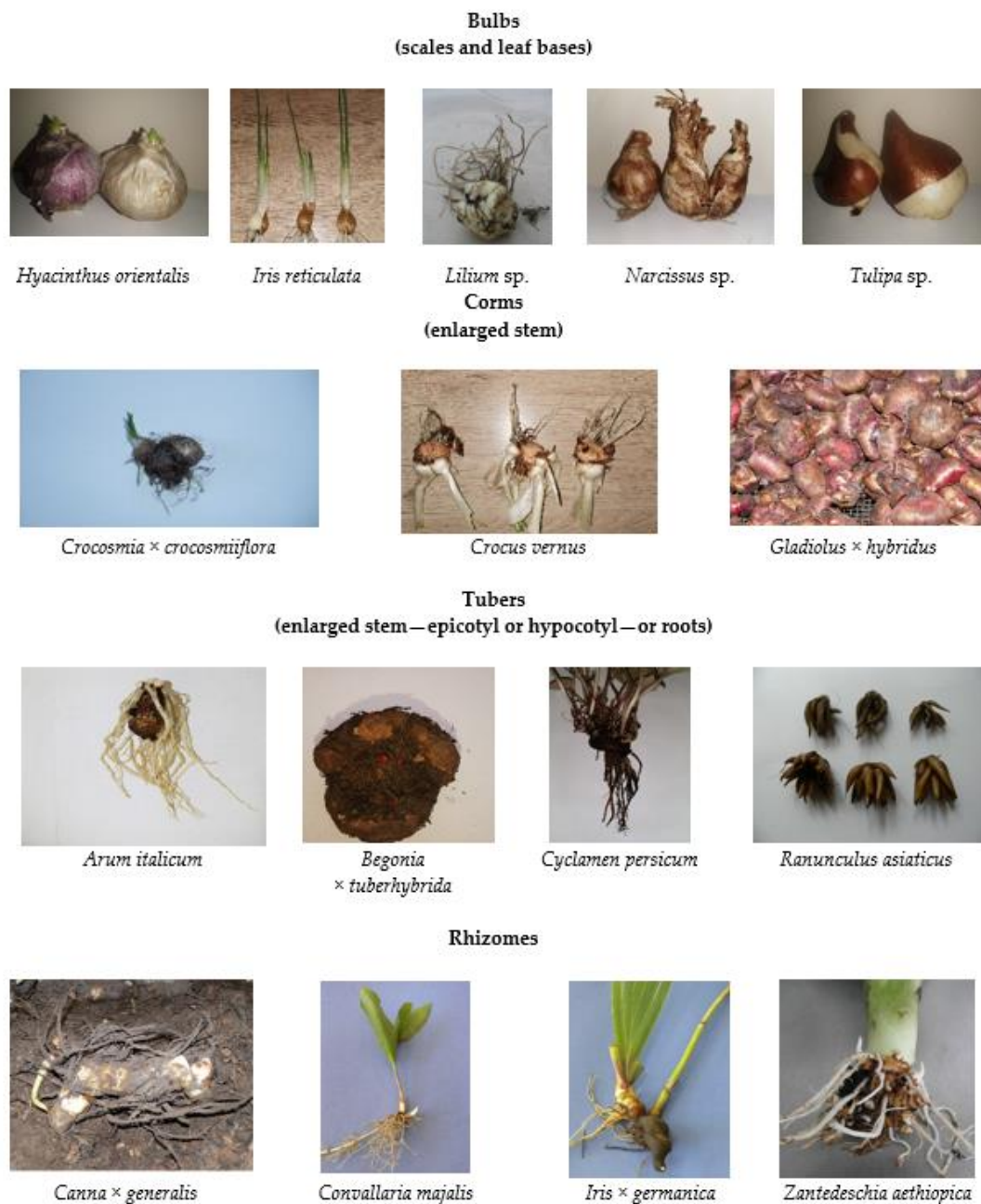


Figure 1. Storage organs in geophytes.

The most important PGRs include auxins, gibberellins (GAs), cytokinins (CKs), ethylene, and growth retardants. The effects of PGRs in plants depend on various factors, which play an important role in achieving the expected results. These factors include the method of application, the timing of application, the concentration of the PGRs, the plant species, and the environmental conditions in which the plants are grown [14]. The intensity of application is also considered an important factor influencing the effectiveness of PGRs, as some plants respond well to a single application while multiple applications are beneficial for others [15]. Other complementary factors may include the chemical properties of the solution that contains the PGRs, in particular the pH, which plays a crucial role in the absorption of the PGRs by plants [13]. Various methods are used for the application of PGRs, including foliar applications [16], drenching [17], pre-plant sowing [18], seed priming [19], pasting [20], capillary string [21] and injection [22]. In the case of ornamental plants, includ-

ing geophytes, leaf spraying [13], soaking storage organs [23–34], and spraying them [35] are the most popular methods of application.

Research is being conducted worldwide to determine the effects of PGRs on ornamental plants from different groups. In this paper, the results obtained for geophytes are presented, where PGRs were applied at the cultivation stage and in the post-harvest period for the treatment of flowers and leaves.



Figure 2. The different species of geophytes.

2. Plant Growth Regulators (PGRs) Used in Geophytes

2.1. Gibberellins (GAs)

Among the PGRs, the most numerous are gibberellins (GAs), which were discovered and isolated by Japanese researchers from the fungus *Giberella fujikuroi*, which belongs to Ascomycetes. This pathogen infects rice seedlings, causing their excessive elongation. The plants growing from such seedlings are thinner and more fragile. The disease was named *bakanae*—“crazy seedling”. In 1926, Kurosawa observed that, in sterile extracts from cultures of *Giberella fujikuroi* (the perfect sexually reproducing stage) and *Fusarium moniliforme* (the imperfect conidial stage), there is a compound that causes excessive elongation of the internodes of rice. In 1935, Yabuta, Hayashi, and Sumiki isolated chemical compounds

from the metabolic products of the fungus, which they named GAs [36,37]. The research on GAs was interrupted by World War II. It continued in the early 1950s.

GAs are acids with a structure based on a giban ring. They are denoted by the symbol GA followed by the appropriate sequence number. GAs are formed in the youngest parts of plants [38]. They are translocated by the xylem and phloem [39]. GAs interrupt hereditary plant dwarfism [40]. Under their influence, shoots elongate, and plants flower more abundantly [33]. When GAs is applied, plant dormancy can be interrupted [41], seed germination can be improved [42], flowering can be changed [31], and flower and leaf vase life can be improved [33], as GAs inhibit chlorophyll and protein degradation in leaves [43,44]. Gibberellic acid (GA₃) is the most commonly used GA [40].

2.1.1. Mechanism of GA Action

Through the use of biochemical, genetic, and molecular research techniques, the mechanism of GA signal perception and transduction in plants has been elucidated. In the first step, the GA signal is received by GA-insensitive dwarf 1 (GID1) located in the cytoplasm and nucleus. In the *Oryza sativa* genome, a single GID1 gene was identified, while in the *Arabidopsis thaliana* genome, three were discovered—GID1a, GID1b, and GID1c—with partially overlapping functions. The binding of bioactive GAs to the GID1 receptor promotes interactions between GID1 and the DELLA domain present in DELLA proteins, which are the main repressors of the GA pathway. The rapid degradation of DELLA proteins involving ubiquitin-protein ligases is a universal mode of GA function. Gas in a non-dissociated form can penetrate into the cell, as the cell membrane does not provide a barrier to limit their diffusion. An increase in the concentration of bioactive Gas in cells results in the formation of the GA–GID1 complex. Interactions between these proteins occur through hydrophilic (direct hydrogen bonds or indirect via water molecules), hydrophobic, and van der Waals interactions. This allows one of the DELLA proteins to attach via the highly conserved N-terminal DELLA and TVHYNP motifs. Eventually, a polyubiquitin chain is attached to the DELLA proteins, which is the signal for their degradation in proteasomes. The entire cycle of events leads to the release of specific transcription factors that activate or inhibit target genes [45].

2.1.2. The Effect of Gas on Flowering and Quality of Geophytes

As in the case of other species of ornamental plants, the most commonly used GA in geophytes is GA₃ (Table 1).

Table 1. The effect of PGRs on flowering and quality of geophytes and on the vase life of flowers and leaves.

Species	PGR	Effect	Source
<i>Alstroemeria aurantiaca</i>	GA ₃	better vase life of leaves	[46–48]
<i>Amaryllis belladonna</i>	GA ₃	earlier flowering, larger flowers, more leaves, better vase life of flowers	[49]
‘Zephyranthes’	GA ₃	longer flowering shoots, earlier flowering, more chlorophyll, and carotenoids	[50–52]
<i>Anemone coronaria</i>	BA	no effect on flowering intensity, shorter flower stalks, smaller flowers	[53]
<i>Arum italicum</i>	GA ₃	better vase life of leaves	[53]
	BA		[54]
<i>Convallaria majalis</i>	[Gib][Ach]	better vase life of leaves	[55]
<i>Crocsmia × crocosmiflora</i>	GA ₃	more kaempferol, quercetin, quercetin 3-O-glucoside, kaempferol 3-O-rhamnosylglucoside and β-carotene	[56]
<i>Cyklamen persicum</i>	GA ₃	longer flower stalks, earlier flowering, more flowers	[57–59]
<i>Freesia reflacta</i>	GA	taller plants, more leaves, more inflorescences shoots	[60]
	BA	longer inflorescences, larger leaves	[61]

Table 1. Cont.

Species	PGR	Effect	Source
<i>Gladiolus hybridus</i> <i>Gladiolus grandiflorus</i>	GA ₃	more adventitious corms; shorter spikes and fewer flowers on a short day, but longer spikes and more flowers on a long day earlier and better flowering shorter inflorescence shoots but longer flower clusters and more flowers more adventitious corms	[16,31,62–64] [65] [16]
<i>Gladiolus</i> sp.	IAA NAA		[32] [66,67]
<i>Hemerocallis</i> × <i>hybrida</i>	MemT MemTR [Chol][Gib] [Q-C ₂][Gib] [Gib][Ach]	better vase life of leaves	[68]
<i>Hippeastrum</i> × <i>hybridum</i>	GA ₃	better vase life of leaves	[69]
<i>Hyacinthus orientalis</i>	GA ₃	intensive growth of leaves, inhibition of the formation of adventitious bulbs	[70,71]
<i>Iris</i> × <i>hollandica</i>	GA ₃	no impact	[72]
<i>Lilium</i> sp.	GA ₃	better vase life of leaves	[73]
<i>Muscari armeniacum</i>	GA ₃	longer leaves and inflorescence stalks	[74]
<i>Tulipa</i> sp.	GA ₃	longer flower shoots	[75,76]
× <i>Amarine tubergenii</i> ‘Zwanenburg’	GA ₃	more leaves, more bulb weight, more daughter bulbs, better carbon dioxide (CO ₂) assimilation, more sugars and proteins, earlier flowering, better flowering more inflorescences	[77] [78,79]
<i>Zantedeschia aethiopica</i>	BA GA ₃ + BA		
<i>Zantedeschia</i> with colorful spathes	GA ₃ BA GA ₃ + BA BA GA ₃ MemT MemTR	better vase life of leaves later flowering, more inflorescences better vase life of flowers better vase life of leaves	[80] [23,25,27,35,81–85] [44] [43,44,86,87]

The beneficial effects of GA₃ have been used in the field cultivation of *Anemone coronaria*, inter alia. Piskornik and Piskornik [50] showed that, in the case of that species, the effect of GA₃ depends not only on the concentration but also on the timing of application, which the authors explained by the different thermal conditions prevailing after the application of this PGR. According to the authors, with respect to that species, the use of GA₃ at a concentration of 100 mg·dm^{−3} effectively improves the quality of flowers expressed by the weight and length of flowering shoots. Later studies by Janowska et al. [51] indicated that GA₃ is also worth using in *Anemone coronaria* when grown while covered. According to the authors, in the case of the ‘Sylphide’ cultivar, the use of GA₃ at 50–150 mg·dm^{−3} speeds up flowering by 11–16 days and stimulates the elongation of flowering shoots (Figure 3).

However, when GA₃ is applied at concentrations of 100 or 150 mg·dm^{−3}, the flower yield doubles. Furthermore, according to a study by Janowska et al. [52], GA₃ in this cultivar stimulates the formation of chlorophyll and carotenoids and the accumulation of sugars in the leaves. GA₃ is also useful in the cultivation of *Cyclamen persicum*. Spraying the leaves with GA₃ at a concentration of 10 or 50 mg·dm^{−3} not only initiates the growth of flower stalks but also significantly accelerates flowering and increases the number of flowers [57–59]. GA₃ is used in the cultivation of *Zantedeschia* with colorful spathes

cultivars. The results of the tests carried out indicated a differential response of the cultivars, which was closely related to the concentrations of GA₃ used. In *Zantedeschia*, the intensity of flowering depends not only on the cultivar but also on the size of the rhizomes and the length of their storage [88]. However, the size of the rhizomes is not correlated with intensive flowering, as even from the largest ones, without the use of GA₃, a very good yield of flowers was not obtained. The research conducted showed that GA₃ could be used at concentrations from 25 to 500 mg·dm⁻³ [23,81–84,89–92]. However, too high a concentration of GA₃ causes inflorescence deformation [84,89]. The use of GA₃ in colored *Zantedeschia* cultivars delays flowering but also prolongs it [23,84]. In addition to soaking rhizomes in water–GA₃ solutions, the spraying of leaves and rhizomes is used [25,35]. Such methods protect *Zantedeschia* from *Pectobacterium carotovorum* subsp. *carotovorum* [93]. Jerzy and Janowska [94] conducted a study in which they evaluated the subsequent effect of GA₃ used at the in vitro propagation stage on the flowering and quality of two *Zantedeschia* cultivars. GA₃ was applied at the final stage of in vitro plant micropropagation [95] by introducing it at 50 mg·dm⁻³ into pre-sterilized rooting medium. Prior sterilization of the medium was necessary because the GA₃ activity in the autoclave could be drastically reduced to as low as 10% [96]. In regenerated plants from GA₃-treated cuttings, the authors [94] observed an altered leaf shape and a reduced rhizome size and weight. In contrast, Andrzejak and Janowska [33] demonstrated that in *Z. albomaculata* ‘Albomaculata’, GA₃ could be replaced by mycorrhiza. The addition of arbuscular mycorrhizal fungi (AMF) stimulated flowering in this cultivar, probably because AMF produces PGRs, including GAs [93,97].



Figure 3. *Anemone coronaria* ‘Sylphide’: from the left, a control plant and plants grown from tubers soaked in GA₃ at a concentration of 50 mg·dm⁻³, 100 mg·dm⁻³, and 150 mg·dm⁻³.

Attempts were made to improve the quality of *Iris* × *hollandica* with GA₃. In the cultivars Wedgewood and ‘Prof. Blaauw’, however, no large effect of GA₃ on flower shoot elongation was found [72]. In *Tulipa* sp., on the other hand, GA₃ was shown to have a stimulating effect on flower shoot elongation [23,75], the inhibition of flower aging, and earlier flowering [98].

However, the use of GAs does not always have the desired effect. For example, in *Hyacinthus orientalis*, there was an inhibitory effect of GA₃ on the formation of adventitious bulbs in hollowed-out parent bulbs, while at the same time, there was very intensive leaf growth [70,71]. However, soaking *Gladiolus* corms in GA₃ at 100 or 500 mg·dm⁻³ had a beneficial effect on the number of adventitious corms. GA₃ also stimulated photosynthetic intensity as the chlorophyll levels increased. Moreover, plants grown under short-day conditions with GA₃ flowered; however, the forming spikes were shorter and had fewer flowers than control plants grown under natural day-length conditions. Consequently, short days and low light levels are limiting factors for GAs [62]. Janowska et al. [31] reported, however, that in *G. hybridus* ‘Black Velvet’, GA₃ at a concentration of 100–600 mg·dm⁻³ inhibited inflorescence shoot elongation but stimulated spike elongation. Moreover, it had a beneficial effect on the uptake of calcium (Ca) and manganese (Mn). Sajid et al. [61] reported that spraying *G. grandiflorus* leaves with GA₃ at a concentration of 25, 50, or 100 mg·dm⁻³ stimulated inflorescence shoot growth. The longest inflorescence stems were recorded by the authors for the treatment in which GA₃ was applied at a concentration of 100 mg·dm⁻³. Moreover, GA₃ at 50 or 100 mg·dm⁻³ stimulated spike elongation and flower development. Shoot and inflorescence elongation after GA₃ application in *Gladiolus* ‘H.B.Pitt’ was reported by Sable et al. [64]. The authors further reported that, in this cultivar, GA₃ at 100–200 mg·dm⁻³ stimulated flower development, and at 200 mg·dm⁻³, it caused significant inflorescence elongation. The beneficial effect of GA₃ on the shoot length, inflorescence development, and flower development in *Gladiolus* ‘White Prosperity’ was reported by Sajjad et al. [16]. On the other hand, in *Muscari armeniacum*, GA₃ not only accelerated flowering but also stimulated inflorescence stalk and leaf growth in partially and fully cooled bulbs [74]. GA₃ was also used for *Freesia reflecta*. Żurawik and Placek [60] reported that, in three *Freesia* cultivars from the Easy Pot group, soaking corms in a GA₃ solution with a concentration of 10, 20, 40, 80, or 160 mg·dm⁻³ for 24 h stimulated inflorescence shoot elongation and leaf development, but reduced flower diameter. The application of GA₃ increased the weight of offspring corms. The highest effect among the concentrations assessed was recorded at 160 mg·dm⁻³. In contrast, the GA₃ used in the experiment had no effect on the number of new corms obtained. An interesting study was conducted by Janowska et al. [56]. This study assessed the effect of GA₃ on the content of biologically active substances in the corms of *Crocodymia* × *crocodymiflora* ‘Lucifer’. Four groups of biologically active substances with antioxidant properties were extracted from *C. × crocodymiflora* ‘Lucifer’ corms: saponins (medicagenic acid, medicagenic acid 3-O-triglucoside, and polygalic acid), phenolic acids (caffeic acid, *p*-coumaric acid, and gallic acid), flavonoids (kaempferol, kaempferol 3-O-rhamnosylglucoside, quercetin, and quercetin 3-O-glucoside) and carotenoids (crocin and β-carotene). The corms of the ‘Lucifer’ cultivar proved to be a rich source of antioxidants. After treatment with GA₃, the antioxidative activity increased in proportion to the concentration of GA₃ used in the experiment. GA₃ increased the content of medicagenic acid, polygalic acid, caffeic acid, *p*-coumaric acid, gallic acid, kaempferol, quercetin, quercetin 3-O-glucoside, kaempferol 3-O-rhamnosylglucoside, and β-carotene without affecting the content of medicagenic acid 3-O-triglucoside and crocin.

2.2. Cytokinins (CKs)

Naturally occurring cytokinins (CKs) are derivatives of the adenine purine base, with an alkyl chain or aryl group attached to the amino group. In plants, CKs with aliphatic substituents are common, especially zeatin and dihydrozeatin. CKs with an aromatic benzyl substituent are less common. They are responsible for cell division and differentiation [96]. In horticulture, they are especially used to extend the vase life of cut flowers and florists’ greens [26–28]. CKs are produced by a variety of creative tissues, but the main sites of their synthesis include the apical meristems of the root system, young fruits and seeds during intensive growth, and callus tissue [99].

2.2.1. Mechanism of CK Action

CKs play a key role in different phases of plant growth and development. The underlying molecular mechanisms of their biosynthesis and signal transduction have recently been elucidated [100]. To date, several CK-binding proteins—CKI1, CRE1, and AHK2/3/4—have been identified as the most likely receptors for these PGRs, and the genes encoding them are known. A common feature of the receptors is that these proteins have catalytic histidine kinase activity. The proposed CK signal transduction pathway resembles the bacterial two-component response system and is based on the transfer of a phosphate group between protein components. AHP proteins mediate CK signal transduction to the cell nucleus. Genes encoding ARR proteins, or so-called response regulators, act as early response genes, the induction of which generates typical plant cell responses to CKs. CK-binding proteins are located primarily on the thylakoid membranes of plant cells and in the microsomal fraction. When CKs bind to a specific protein, a specific physiological response of the cell is initiated [100–102]. Research on CKs is closely linked to the development of in vitro cultures. In the 1950s, a compound that strongly stimulated cell division was isolated from immature maize kernels. It was given the name zeatin [103,104]. Benzyladenine (BA), which is a synthetic CK, is widely used in floriculture [105]. BA is used primarily as an ingredient in media for the in vitro propagation of plants. In recent years, it has also been used for the cultivation of ornamental plants in the ground and under covers [38]. BA can be applied as a solution to soak storage organs or spray leaves. It should be noted that BA added to water does not dissolve in it but forms a suspension. Therefore, it should be first dissolved in a small amount of ethanol (C_2H_6O), and only then should water be added [106].

2.2.2. The Effect of CKs on Flowering and Quality of Geophytes

In horticultural practice, CKs are used to a small extent (Table 1). However, ongoing research indicates that CKs in certain species have a beneficial effect on flowering intensity, as shown by Luria et al. [78] in *Z. aethiopica* following the application of BA at $350\text{ mg}\cdot\text{dm}^{-3}$. In *Zantedeschia* with colorful spathes, BA also effectively increases the intensity of flowering. An application of BA at 350 or $600\text{ mg}\cdot\text{dm}^{-3}$ in a solution for soaking the rhizomes improves the flowering of the cultivars ‘Black Magic’, ‘Mango’, and ‘Albomaculata’ [27,85]. Janowska and Stanecki [27] further showed that BA slightly delayed the flowering time of these cultivars. However, the authors noted that the application of BA at the lowest concentration in the cultivars ‘Mango’ and ‘Albomaculata’ resulted in earlier flowering of the plants. This is partially supported by the research of Tjia and Funnell [107], who achieved earlier flowering by soaking *Z. elliptica* rhizomes in BA at $50\text{--}100\text{ mg}\cdot\text{dm}^{-3}$. In contrast, Ngamau [79] obtained no yield increase in *Z. aethiopica* ‘Green Goddess’ after a BA application. There was also no increase in the yield of *A. coronaria* ‘Sylphide’ after the application of BA at $50\text{--}150\text{ mg}\cdot\text{dm}^{-3}$ in a solution for soaking the tubers (Figure 4) [51].

CKs can affect flower quality traits expressed in terms of the stalk length and the flower size and weight, as well as leaf development, with either positive or negative effects. In *F. reflata*, BA at a concentration of $50\text{ mg}\cdot\text{dm}^{-3}$ causes plants to grow vigorously and have the longest inflorescences and the largest leaf area [61]. On the other hand, in colored *Zantedeschia*, BA inhibits the growth of the inflorescence stalks, with the response to the concentrations used depending on the cultivar. In addition, BA affects the formation of longer spathes in the cultivar ‘Albomaculata’, while in the cultivars ‘Black Magic’ and ‘Mango’, it results in the growth of flowers with a smaller weight [27,85]. However, as reported by Janowska and Stanecki [86], BA at $100\text{--}600\text{ mg}\cdot\text{dm}^{-3}$ in the ‘Mango’ cultivar and at $350\text{--}600\text{ mg}\cdot\text{dm}^{-3}$ in the ‘Albomaculata’ cultivar inhibited leaf development but had a positive effect on leaf quality, for which a higher greening index and a higher protein and sugar content were recorded. The formation of shorter flower stalks following a BA application was reported by Janowska et al. [51] in *A. coronaria* ‘Sylphide’, in which, additionally, the smallest flowers developed in plants whose tubers were soaked in BA at $50\text{ mg}\cdot\text{dm}^{-3}$. Sajjad et al. [16] reported that BA had a beneficial effect on the inflorescence shoot length

in *Gladiolus* 'White Prosperity', while Sajjad et al. [63] reported a similar phenomenon for *G. grandiflorus*. In contrast, Janowska et al. [32] reported that BA at 100–600 mg·dm^{−3} inhibited the inflorescence shoot elongation of *G. hybridus* 'Black Velvet', but stimulated inflorescence elongation and flower development. Moreover, BA at 100–600 mg·dm^{−3} in the 'Black Velvet' cultivar stimulated Ca uptake without affecting the uptake of the other macronutrients Mn, zinc (Zn) (600 mg·dm^{−3}), and copper (Cu) (100–600 mg·dm^{−3}), but it inhibited the boron (B) uptake.



Figure 4. *Anemone coronaria* 'Sylphide': from the left, a control plant and plants are grown from tubers soaked in BA at 50 mg·dm^{−3}, 100 mg·dm^{−3}, and 150 mg·dm^{−3}.

2.3. Effect of a Mixture of CKs and GAs on Flowering and Plant Quality of Geophytes

In the West, ready-made preparations containing PGRs of various compositions are often used in floricultural production. These include Promalin (100 mg·dm^{−3} GA₄₊₇ + 100 mg·dm^{−3} BA) [108,109]. Unfortunately, this preparation is expensive due to the costly synthesis of GA₄₊₇. Therefore, e.g., in nursery production, it is replaced by the cheaper GA₃- and BA-containing Arbolin [110]. However, it should be mentioned that these preparations are not registered in Poland, and consequently, combined PGRs from different groups are used in studies (Table 1). Janowska and Stanecki [28] found that based on studies evaluating the effect of the combined application of GA₃ and BA on the flowering of *Zantedeschia* with colorful spathes, soaking the rhizomes in a mixture of those PGRs increased the inflorescence yield in the cultivars 'Black Magic' and 'Albomaculata,' which confirmed an earlier study by Funnell et al. [83], who found an increase in the cut inflorescence yield of up to 469% in *Zantedeschia* 'Galaxy' after treatment with Promalin compared to control plants. In this cultivar, GA₃ also caused an increase in yield, but only by half as much. Similarly, in *Z. aethiopica* 'Green Goddess,' the cut flower yield increased after the application of the BA + GA₃ mixture [79]. According to Janowska and Stanecki [26], in the *Zantedeschia* with colorful spathes cultivar, the application of the BA + GA₃ mixture influenced the growth of inflorescences with shorter stalks from the rhizomes. On the contrary, Ngamau [79] claimed that slightly longer stalks were obtained in *Z. aethiopica* 'Green Goddess' after an application of BA + GA₃; however, these differences were not statistically significant. Interesting results

were obtained by Janowska et al. [29]. The authors evaluated the effect of a mixture of BA and GA₃ on the number and size of stomata in the epidermis of *Zantedeschia* leaves. They found that in the cultivar ‘Albomaculata’, after an application of the BA + GA₃ mixture (100 + 100 or 350 + 350 mg·dm⁻³), the stomata in the upper leaf epidermis were larger, and their number decreased. In the lower epidermis, the BA + GA₃ at the concentrations used affected the formation of larger stomata, with their abundance decreasing when the mixture was applied at concentrations of 350 + 350 mg·dm⁻³.

2.4. Auxins

Auxins are synthesized in shoot and root apices. The natural auxin is indole acetic acid (IAA). Synthetic auxins include indole butyric acid (IBA), naphthalene acetic acid (NAA), methyl ester of naphthalene acetic acid (MENA), 2-methyl-4-chlorophenoxyacetic acid (MCPA), 2,3,5-triiodobenzoic acid (TIBA), 2,4-dichlorophenoxyacetic acid (2,4-D) and 2,4,5-trichlorophenoxyacetic acid (2,4,5-T). Natural auxins can be in the form of free auxins, which move freely or diffuse readily from plant tissues, or bound auxins, which are only released from plant tissues after hydrolysis, autolysis, or enzymolysis. Auxins promote growth at low concentrations, while they inhibit growth at high concentrations. [111]. The rooting of cuttings is the most important role played by auxins [112]. IBA [113] and IAA [114] are most commonly used for this purpose. Auxins influence the formation of primary, secondary, and adventitious roots [115]. They are used for the rooting of many ornamental plant species from different groups [116–120]. The stimulation of the rooting of cuttings involves reducing the number of days required for rooting [117], increasing the percentage of rooting, and increasing the length, number, and weight of roots [118].

Effect of Auxins on Flowering and Quality of Geophytes

Apart from rooting cuttings, auxins are rarely used in the cultivation of ornamental plants. However, a few studies have shown that interesting results can be obtained in geophytes treated with auxins (Table 1). According to Sharma et al. [121], auxins in *Gladiolus* ‘Friendship’ NAA (100 mg·dm⁻³) had a positive effect on corm size and weight. In *Tulipa gesneriana* ‘Cassini’, a similar effect was obtained when IAA was applied, but at a very high concentration of 5000 mg·dm⁻³ [64]. Later studies by Kumar et al. [122] on two *Gladiolus* cultivars, ‘Iyotsna’ and ‘Shabnum’, did not confirm the beneficial effect of NAA on corm size. On the other hand, Sudhan and Kumar [67] reported that in *G. grandiflorus* ‘White Friendship’, an NAA application increased not only the number and weight of corms but also the plant height, leaf number, length, width, and spike length.

3. Vase Life of Geophyte Flowers

PGRs are used to extend the post-harvest shelf life of horticultural products: vegetables [123,124], cut flowers [70,125], and florists’ greens [80]. Flowers and florists’ greens are delicate and not very durable products, and their lifespans vary from a few to several days according to the type, species, and cultivar. They have a large external surface area from which water evaporates, and they have no protection against water loss. For post-harvest longevity, the cutting stage is very important. Some flowers, such as those of *Iris*, *Narcissus*, and *Tulipa*, need to be harvested at the closed but colored bud stage. Other flowers, such as *Zantedeschia*, should be cut in full bloom. The vase life of flowers and florists’ greens is largely determined by their water balance, which is influenced by the following factors: water uptake and conduction, transpiration, the ability of cells to retain water (which determines turgor), and competition for water under stress conditions. A negative water balance, indicative of a decrease in the fresh matter, occurs when the water losses due to transpiration are greater than the water uptake [71,126–129]. Extending the vase life of flowers and florists’ greens should start at the stage of the producer, whose task it is to carry out conditioning [130,131]. This treatment can be carried out at both low and high temperatures, following the principle that the lower the temperature, the longer the conditioning. Various compounds, chemicals, PGRs, and ready-made formulations available

on the market are used for conditioning. After harvesting, however, flowers and florists' greens cannot be treated equally. In the case of flowers, sugar is often added to water, and in geophytes, this often does not work. Examples of species for which sugar cannot be added to water include *Cyclamen*, *Z. aethiopica*, and *Narcissus* [128,132]. In addition to sugar, hydroxyquinoline esters such as sulfate (8HQS) and citrate (8HQC) are often added to the cut flower medium. They inhibit microbial growth, lower the pH of the solution, and chelate some metal ions, which prevents the formation of physiological blockages and causes closure of the stomata [71,126]. For geophytes, the efficacy of a medium containing sugar and hydroxyquinoline esters was demonstrated in *Hippeastrum* × *chmielei* [133], *H. × hybridum* [134], *H. vittatum* [135], *Alstroemeria aurantiaca* [48] and *Z. albomaculata* 'Albomaculata' [43], among others. Sometimes, PGRs are used to extend the vase life of cut geophyte flowers. Janowska et al. [44] found that BA at 50–150 mg·dm^{−3} extended the post-harvest longevity of *Z. albomaculata* 'Albomaculata' inflorescences by 7–14 days.

4. Vase Life of Geophyte Leaves

Aging leaves lose turgor, lose color or dry out. Enzymes appear in the cells that destroy cell walls [136]. In cells, proteins [137,138] and chlorophyll [68,69,139] break down, but free radicals are formed, which are structures that destroy cell components [140]. In response to free radicals, reactive oxygen species (ROS) are formed, which inhibit the aging process [141–147]. The most important ROS is hydrogen peroxide (H₂O₂). Large amounts of it indicate oxidative stress [148].

As the aging processes of florists' greens are different from those of cut flowers, standard nutrient solutions are usually not very effective for them [80]. In contrast, numerous studies have shown that, in florists' greens, the extension of post-harvest longevity is caused by CKs and GAs (Table 1), which effectively inhibit chlorophyll and protein degradation. However, the response to PGRs among geophytes is closely species-related [86]. Skutnik et al. [80] reported a beneficial effect of GA₃ on the vase life of the leaves of *Z. aethiopica*. The authors reported as much as a six-fold increase in the vase life of the leaves following the application of this PGR, with concomitant inhibition of chlorophyll degradation. A similar response was reported in *Zantedeschia* leaves with colorful spathes [43,44,86,87]. In *H. × hybridum*, on the other hand, this PGR caused as much as an eight-fold increase in post-harvest leaf longevity [69]. The beneficial effect of this regulator is also used in practice in *Alstroemeria aurantiaca* [46–48] and *Lilium* sp. [73], for which it effectively prevents leaf yellowing, as it inhibits chlorophyll breakdown. *Arum italicum* leaves also respond positively to GA₃ [53]. In this species, Janowska and Schroeter-Zakrzewska [54] further showed that BA was also effective.

In addition to GA₃ and BA, other regulators from the CK group are also used to extend the vase life of florists' greens. In a study by Janowska et al. [44], topolins (Ts) were used to extend the leaf vase life of *Z. albomaculata* 'Albomaculata'. Meta-methoxytopolin (MemT) and its riboside (MemTR) were found to affect the post-harvest longevity and leaf quality of the cultivar under study. Recent studies have shown that MemTR at 50 and 100 mg·dm^{−3} also extends the leaf vase life of *Hemerocallis* × *hybrida* 'Agata' [68].

New regulators used for the post-harvest treatment of leaves are quaternary ammonium salts with selected organic cations and GA₃ anions (2-hydroxyethyl)dimethylethylammonium gibberellinate ([Chol][Gib]), acetylcholine gibberellinate ([Gib][Ach]), 1-ethyl quinine gibberellinate ([Q-C₂][Gib]) and 1-dodecyl acetylcholine gibberellinate ([Q-C₁₂][Gib]) [55,68]. The few studies to date suggest that these compounds extend the vase life of the leaves of *Convallaria majalis* (Figure 5) [55] and *H. × hybrida* 'Agata' [68].



Figure 5. *Convallaria majalis* leaves. From the left: control leaves; leaves conditioned in GA₃ (100 mg·dm^{−3}) and conditioned in [Gib][Ach] (100 mg·dm^{−3}).

5. Conclusions

As in the case of other ornamental plants, plant growth regulators (PGRs) are more and more often used in the geophyte group to improve the quality of plants, the intensity of flowering, and the vase life of flowers and leaves. In the case of geophytes, the most common method of application is spraying and soaking the storage organs before planting. In geophytes, gibberellic acid (GA₃) and benzyladenine (BA) are the most commonly used, although scientists tend to focus most of their attention on GA₃, as this regulator significantly increases the flowering intensity in many species, which is important for horticultural practice. In addition, PGRs have an impact on early flowering. After their application, plants start flowering earlier or later. PGRs also affect plant quality as expressed in plant height, length of flower or inflorescence stems, flower size, number of leaves, and yield of storage organs (bulbs, tubers, corms). PGRs also stimulate the uptake of macro- and micronutrients so that the use of mineral fertilizers can be reduced. GAs and CKs have a strong effect on the vase life, particularly on leaves, with the response of individual species depending on the regulator used and its concentration. Further research in geophytes is necessary as the response to PGRs depends not only on the species but also on the cultivar. Therefore, a uniform formula cannot be given for all cultivated species. Furthermore, it is worth focusing not only on the use of known and popular PGRs and the introduction of new, often equally effective regulators into the research, as evidenced by studies with topolins (Ts) and ionic liquids. It is worth concentrating future research efforts on determining changes in the content of biologically active compounds in geophytes after the application of PGRs, as many species contain very valuable substances with diverse uses.

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