ACTA SCIENTIARUM POLONORUM *Acta Sci. Pol., Hortorum Cultus 3(2) 2004, 57-65*

SENESCENCE OF CUT LEAVES OF *Zantedeschia aethiopica* AND *Z. elliottiana*. PART I. CHLOROPHYLL DEGRADATION

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Abstract. Chlorophyll degradation occurring during leaf senescence in under control of plant hormones. Changes in the chlorophyll content and the effects of BA (benzyladenine) and GA_3 (gibberellic acid) on this process were analyzed during senescence of cut leaves of *Zantedeschia aethiopica* Spr. and *Zantedeschia elliottiana* Engl., two species grown for the florists' green. Both growth regulators were applied as 24 h pulse treatment: 0.25 mmol·dm^{-3} and 0.1 mmol·dm^{-3} for GA_3 and BA, respectively. Gibberellic acid was more effective than benzyladenine in delaying senescence of both *Zantedeschia* species leaves by retarding chlorophyll loss. A standard preservative solution used to prolong longevity of cut flowers (8-HQC /citrate of hydroxyquinoline/ +2% S /sucrose/) radically accelerated chlorophyll loss of *Z. aethiopica* leaves but had no effect on pigment degradation in leaves of *Z. elliottiana*. However, in both species the preservative diminished the positive effect of GA_3 treatment on final chlorophyll content.

Key words: chlorophyll degradation, cut leaves, florists' green, gibberellic acid, benzyladenine, *Zantedeschia aethiopica*, *Zantedeschia elliottiana*

INTRODUCTION

Leaf senescence is an endogenously controlled degenerative process that ultimately leads to organ death. It can be age-dependent or caused by external factors [Gan and Amasino 1997]. During this process organelles are degraded gradually, starting from chloroplasts [Smart 1994]. The breakdown of chlorophyll occurs in the three consecutive steps, each catalyzed by one of three enzymes: chlorophyllase, Mg-dechelatase, and pheophorbide *a* oxygenase. The step catalyzed by pheophorbide *a* oxygenase is the most significant for yellowing of senescing leaves [Matile et al. 1996]. In some stay-green mutants the activity of this enzyme is missing [Thomas et al. 2002]. Yellowing of

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the leaves is the most obvious visible symptom of leaf senescence, however, the chlorophyll loss starts earlier than yellowing. Senescence in water-deficient plants is triggered by an early signal occurring while leaf photosynthesis is still active [Pic et al. 2002] so in most studies of leaf senescence chlorophyll content is used as a measure of senescence. Plant hormones are involved in controlling the senescence, with cytokinins [Downs et al. 1997; Skutnik et al. 1999] and gibberellins [Rabiza-Świder et al 2003] delaying, while ethylene [Hodges and Forney 2000], abscisic acid [Guak and Fuchigami 2002] and jasmonates [Rossato et al. 2002] accelerating the process. A delay of senescence, including its visual symptoms, is most important in case of the florists' green. It was found that in *Hosta* sp. a pulse treatment or a brief postharvest dip in a solution of benzyladenine (BA) can increase a vase life of leaves 5–10 times as compared to water controls, while gibberellic acid (GA_3) considerably extends a display life of cut leaves of *Zantedeschia aethiopica* and *Hippeastrum* × *hybridum* [Skutnik and Łukaszewska 2001]. Here, changes in chlorophyll contents during leaf vase life of two *Zantedeschia* species grown for the florists' green are compared and the effect of the standard preservative used to prolong vase life of cut flowers as well as that of BA and GA_3 on chlorophyll loss is shown.

MATERIAL AND METHODS

Leaves of *Zantedeschia aethiopica* and *Zantedeschia elliottiana* were grown in the greenhouses of the Department of Ornamental Plants of the Warsaw Agricultural University. Mature, healthy, undamaged leaves were harvested in the morning, graded for uniformity, treated with growth regulators and placed in vases with distilled water or preservative containing 8-hydroxyquinoline citrate (8-HQC 200 $mg \cdot dm^{-3}$) and sucrose (S 20 $g \cdot dm^{-3}$) in controlled conditions: temperature 20ºC, relative humidity 60%, 12 hrs photoperiod with light intensity of 35 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PAR and there were 20 leaves in each combination. Growth regulators were applied as pulse conditioning: leaves were placed for 24 hrs in aqueous solutions containing either 0.25 $mmol \cdot dm^{-3}$ GA_3 or 0.10 $mmol \cdot dm^{-3}$ BA. Leaves untreated with growth regulators and placed directly in water or a preservative served as controls. Samples were collected two (*Z. elliottiana*) or three times (*Z. aethiopica*) during the experiment. In the longer-lived *Z. aethiopica* chlorophyll determinations were made at day 6^{th}, 10^{th} and 16^{th} of the experiment while in the short-lasting *Z. elliottiana* on first two dates only. For a more detailed picture of changes in the chlorophyll content during leaf senescence a separate experiment was conducted with leaves held in distilled water and samples for pigment measurements were collected at shorter intervals: in *Z. aethiopica* 8 measurements were made during 19 days of the experiment while in *Z. elliottiana* – 7 measurements during 13 days. Tissue from three leaves was pooled on each sampling date. Three samples were weighted for the analyses of chlorophyll content, and three replications of each extract were made generating nine readings per data point. Independently, three samples were weighted for the measurements of dry weight: leaf tissue was dried at 105ºC until a constant weight was achieved.

The chlorophyll content was determined according to Moran and Porath [1980] and calculated from a previously plotted standard curves and expressed in $mg \cdot g^{-1}$ on dry weight (DW) basis. All results were statistically evaluated with ANOVA 1 and ANOVA 2 and the means were compared using the Duncan's test at probability level P = 95%.

RESULTS AND DISCUSSION

Chlorophyll content in senescing cut leaves of *Zantedeschia aethiopica* and *Z. elliottiana* placed into water

Leaves of *Zantedeschia aethiopica* and *Z. elliottiana* differed in their initial total chlorophyll (*a* + *b*) contents (fig. 1 and 2, tab. 3 and 4). This could be anticipated as the latter species is white-maculated. Regardless, in both *Zantedeschia* species similar changes in the chlorophyll content during senescence of cut leaves were observed. A significant decrease was already noted after 24 hours after detachment from the mother plants, and it kept progressing until the end of the experiment. Chlorophyll loss was less dramatic in the shorter-lived *Z. elliottiana*, where 24% of the total chlorophyll was still present on 13th day (fig. 2), while in leaves of the longer lasting *Z. aethiopica* 93% was lost by day 19 (fig. 1). As shown by the chlorophyll *a* : chlorophyll *b* ratio, both chlorophylls were degraded at the same rate in both species (tab. 1, Fig 1; tab. 2 and fig. 2). There was no significant change in the *a* : *b* ratio until day 13 in *Z. aethiopica* (tab. 1) and till day 8 in *Z. elliottiana* (tab. 2). In the final days of the experiment (day 19 for *Z. aethiopica* and day 13 for *Z elliottiana*), it was chlorophyll *a* that was disappearing faster which produced lower values of the *a* : *b* ratio relative to the freshly harvested leaves of both species. Different results were observed during a dark-induced senescence of barley leaves [Scheumann et al. 1999] and senescent *Triticum aestivum* L. [Lu et al. 2001] and *Phaseolus vulgaris* L. [Fang et al. 1998]. In those field-grown experiments chlorophyll *b* disappeared faster resulting in a significant increase in the chlorophyll *a* : chlorophyll *b* ratio.

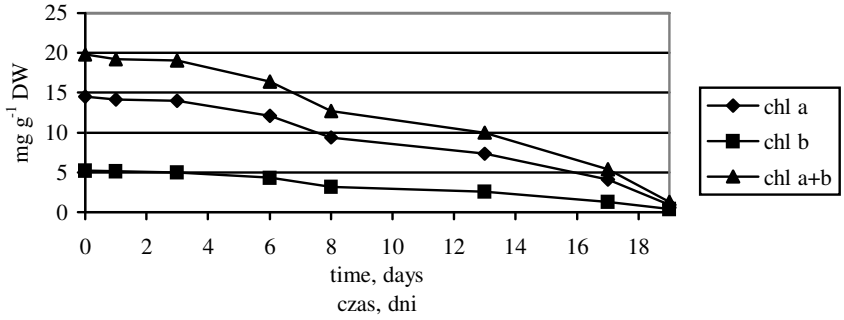

Fig. 1. The chlorophyll contents ($mg \cdot g^{-1}$ DW) in senescing cut leaves of *Zantedeschia aethiopica* Spr. placed into distilled water

Rys. 1. Zawartość chlorofilu ($mg \cdot g^{-1}$ DW) w trakcie starzenia się ciętych liści *Zantedeschia aethiopica* Spr. wstawionych do wody destylowanej

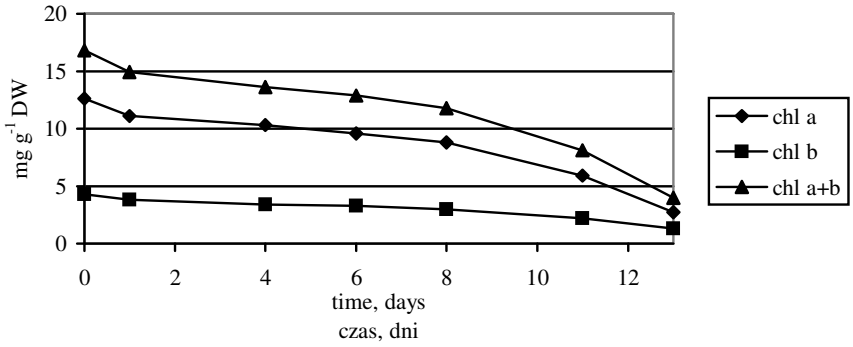

Fig. 2. The chlorophyll contents (mg·g^{-1} DW) in senescing cut leaves of *Zantedeschia elliottiana* Engl. placed into distilled water

Rys. 2. Zawartość chlorofilu (mg·g^{-1} DW) w trakcie starzenia się ciętych liści *Zantedeschia elliottiana* Engl. wstawionych do wody destylowanej

Table 1. The chlorophyll *a* : chlorophyll *b* ratio in senescing cut leaves of *Zantedeschia aethiopica* Spr.

Tabela 1. Stosunek zawartości chlorofilu *a* do chlorofilu *b* w trakcie starzenia się ciętych liści *Zantedeschia aethiopica* Spr.

Initial value Zawartość początkowa	Day – Dzień						
	1.	3.	6.	8.	13.	17.	19.
2.8 b[1]	2.8 b	2.8 b	2.8 b	2.9 bc	2.8 b	3.1 c	2.4 a

[1]Means followed by the same letter do not differ significantly at α = 0.05 (Duncan's test).

[1]Wartości oznaczone tą samą literą nie różnią się istotnie przy α = 0,05 (test Duncana).

Table 2. The chlorophyll *a* : chlorophyll *b* ratio in senescing cut leaves of *Zantedeschia elliottiana* Engl.

Tabela 2. Stosunek zawartości chlorofilu *a* do chlorofilu *b* w trakcie starzenia się ciętych liści *Zantedeschia elliottiana* Engl.

Initial value Zawartość początkowa	Day – Dzień					
	1.	4.	6.	8.	11.	13.
3.0 cd[1]	3.0 cd	3.1 d	3.0 cd	2.9 c	2.7 b	2.1 a

[1]Explanations as in table 1. – Objaśnienia jak w tabeli 1.

Table 3. The chlorophyll contents (mg·g^{-1} DW) in senescing cut leaves of *Zantedeschia aethiopica* Spr. treated with BA and GA_3, placed into water or preservative; initial value: 21.2 mg·g^{-1} DW (100%)

Tabela 3. Zawartość chlorofilu ogólnego (mg·g^{-1} s.m.) w trakcie starzenia się ciętych liści *Zantedeschia aethiopica* Spr., traktowanych BA i GA_3 wstawionych do wody destylowanej lub pożywki; zawartość początkowa: 21,2 mg·g^{-1} s.m. (100%)

Treatment Traktowanie (mmol·dm^{-3})	Chlorophyll (*a+b*) content (mg·g^{-1} DW) on day: Zawartość chlorofilu (*a+b*) (mg·g^{-1} s.m.) w dniu:			Mean for a treatment $LSD_{0.05}$ = 0.41 Średnia dla traktowania $NIR_{0,05}$ = 0,41
	6.	10.	16.	
H_2O	17.8 (84%)	17.3 (82%)	10.0 (47%)	15.06 e[1]
8-HQC + 2%S	10.4 (49%)	5.0 (24%)	2.8 (13%)	6.01 a
BA 0.1; 24h → H_2O	17.8 (84%)	17.9 (84%)	8.1 (38%)	14.58 d
BA 0.1; 24h → 8-HQC + 2%S	15.8 (75%)	13.5 (64%)	3.1 (15%)	10.80 b
GA_3 0.25; 24h → H_2O	20.0 (94%)	19.3 (91%)	19.9 (94%)	19.72 f
GA_3 0.25; 24h → 8-HQC + 2%S	19.1 (90%)	15.3 (71%)	7.0 (33%)	13.78 c
Mean for a term $LSD_{0.05}$ = 0.29 Średnia dla terminu $NIR_{0,05}$ = 0,29	16.80 c	14.70 b	8.48 a	

[1]Explanations as in table 1; to compare the means within the table: $LSD_{0.05}$ = 0.70.
[1]Objaśnienia jak w tabeli 1; dla porównania wartości wewnątrz tabeli: $NIR_{0,05}$ = 0,70.

Table 4. The chlorophyll contents (mg·g^{-1} DW) in senescing cut leaves of *Zantedeschia elliottiana* Engl. treated with BA and GA_3, placed into water or preservative; initial value: 16.8 mg·g^{-1} DW (100%)

Tabela 4. Zawartość chlorofilu ogólnego (mg·g^{-1} s.m.) w trakcie starzenia się ciętych liści *Zantedeschia elliottiana* Engl. traktowanych BA i GA_3, wstawionych do wody destylowanej lub pożywki; zawartość początkowa: 16.8 mg·g^{-1} s.m. (100%)

Treatment Traktowanie (mmol·dm^{-3})	Chlorophyll (*a+b*) content (mg·g^{-1}DW) on day: Zawartość chlorofilu (*a+b*) (mg·g^{-1} s.m.) w dniu:		Mean for a treatment $LSD_{0,05}$ = 0.41 Średnia dla traktowania $NIR_{0,05}$ = 0,41
	6.	10.	
H_2O	6.9 (41%)	5.5 (33%)	6.2 bc[1]
8-HQC + 2%S	6.6 (39%)	5.1 (30%)	5.8 b
BA 0.1; 24h → H_2O	7.9 (47%)	5.3 (32%)	6.6 c
BA 0.1; 24h → 8-HQC + 2%S	7.1 (42%)	3.1 (19%)	5.1 a
GA_3 0.25; 24h → H_2O	15.7 (94%)	16.3 (97%)	16.0 e
GA_3 0.25; 24h → 8-HQC + 2%S	12.3 (73%)	12.5 (74%)	12.4 d
Mean for a term $LSD_{0,05}$ = 0.30 Średnia dla terminu $NIR_{0,05}$ = 0,30	9.4 b	8.0 a	

[1]Explanations as in table 1; to compare the means within the table: $LSD_{0.05}$ = 0.74.
[1]Objaśnienia jak w tabeli 1; dla porównania wartości wewnątrz tabeli: $NIR_{0,05}$ = 0,74.

The effect of the preservative (8-HQC + 2% S) on the chlorophyll content in cut leaves of *Zantedeschia aethiopica* and *Zantedeschia elliottiana*

In *Z. aethiopica*, a significant reduction in the chlorophyll content was observed in the leaves of treated with a sugar-containing preservative: only 13% of the starting chlorophyll level was present on the last day of the experiment while in control leaves retained 47% (tab. 3). In contrast, in *Z. elliottiana*, the solution of 8-HQC + 2% sucrose had no such deleterious effect: changes in the chlorophyll content of leaves held in the preservative solution were similar to those observed in the controls kept in water (tab. 4).

A standard preservative solution, containing 2% sucrose and 200 $mg \cdot dm^{-3}$ citrate or sulphate of hydroxyquinoline (8-HQC or 8-HQS) is often used to prolong the vase life of many species of cut flowers. It has antibacterial properties and provides respirational substrate [Halevy and Mayak 1981]. However, the same preservative accelerated leaf yellowing in several species grown for the florists' green [Skutnik and Łukaszewska 2001]. Sugar treatment also hastened senescence of leaf discs in the model plant *Nicotiana tabacum* and sugar levels were higher in tobacco leaves that were about to senesce as compared to younger leaves [Masclaux et al. 2000]. Skutnik et al. [2001] showed that a sugar-containing preservative dramatically reduced vase life and decreases chlorophyll content in the *Z. aethiopica* leaves.

The effect of BA and GA_3 on the chlorophyll content in cut leaves of two *Zantedeschia* species

The beneficial effect of GA_3 applications on the leaves of both *Zantedeschia* species studied was observed. Following the treatment, 94–97% of the initial chlorophyll content in *Z. aethiopica* and *Z. elliottiana* leaves was still present at the end of the experiment, i.e. at day 16 or 10, respectively (tab. 3, tab. 4). Benzyladenine did not retard chlorophyll loss in either species. Furthermore, in *Z. aethiopica* the final chlorophyll content was lower in the BA treated leaves than in the controls.

In both species pretreatment with benzyladenine did not counteract the deleterious effect of the preservative solution, furthermore in *Z. elliottiana* leaves treated with BA and placed into preservative the final chlorophyll loss was greater than in untreated leaves held in the preservative solution. Gibberellic acid was more effective in counteracting the negative effect of 8-HQC + S; however chlorophyll loss in the sugar-fed leaves was more pronounced than in leaves placed in water after conditioning in the GA_3 solution.

Similarly to other developmental processes, plant senescence is controlled by hormones [Thomas and Stoddart 1980]. Cytokinins are generally identified as the most effective class of senescence-retarding growth regulators although their effect is often species- or cultivar-specific. A cytokinin treatment delays senescence in rice leaves [Chen et al. 1997] and in harvested heads of broccoli [Downs et al. 1997]. Senescence-retarding effects of cytokinin were also noted in transgenic tobacco with autoregulated synthesis of cytokinin activated at the onset of senescence [Wingler et al. 1998]. While not as effective as cytokinins, in some species gibberellins also delay senescence [Kappers et al. 1998, Skutnik et al 2001]. Earlier experiments have shown that applications of the gibberellic acid to cut leaves of *Z. aethiopica* prolongs their postharvest life by

retarding chlorophyll loss and increase in the electrical conductivity of cell sap from leaves [Skutnik et al. 2001].

In general, in cut leaves of both *Zantedeschia* species chlorophyll degradation proceeded in a similar way although the white maculated *Z. elliottiana* contains less green pigment and has a shorter vase life. Also their response to gibberellic acid was the same. However, the sugar-containing preservative did not affect a final chlorophyll content in *Z. elliottiana* while it hastened pigment degradation in *Z. aethiopica*, decreasing the positive effect of GA_3 in both species. The studies on other senescence aspects of these two *Zantedeschia* species and a role of the exogenous sugar in a holding solution are in progress.

CONCLUSIONS

1. The senescence of detached leaves of *Zantedeschia aethiopica* and *Z. elliottiana* is accompanied by progressive chlorophyll loss, less pronounced in the shorter-lived *Z. elliottiana.* In both species chlorophyll *a* and chlorophyll *b* are degraded at a similar rate, with chlorophyll *a* disappearing faster at the final days of leaf senescence.

2. *Z. aethiopica* and *Z. elliottiana* differ in their response to the preservative used to prolong the vase life of cut flowers (8-HQC + S); it accelerates chlorophyll degradation in cut leaves of *Z. aethiopica* while does not affect pigment content in senescing leaves of *Z. elliottiana*.

3. A pulse treatment with GA_3 after harvest is effective while BA is ineffective in preventing chlorophyll loss in the leaves of both *Zantedeschia* species held in water. Placing leaves into a preservative solution reduces the positive effect of gibberellic acid.

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STARZENIE CIĘTYCH LIŚCI *Zantedeschia aethiopica* I *Z. elliottiana*. CZĘŚĆ I. ROZKŁAD CHLOROFILU

Streszczenie. Degradacja chlorofilu zachodząca w trakcie starzenia się ciętych liści regulowana jest przez fitohormony. W doświadczeniach analizowano zmiany zawartości chlorofilu w trakcie starzenia się ciętych liści dwóch gatunków stosowanych jako zieleń cięta (*Zantedeschia aethiopica* Spr. i *Zantedeschia elliottiana* Engl.) i wpływ BA (benzyloadeniny) i GA_3 (kwasu giberelinowego) na ten proces. Roztwory obu regulatorów wzrostu aplikowano w formie 24-godzinnego kondycjonowania (BA – 0,1 mmol·dm^{-3}; GA_3 –

0,25 mmol·dm^{-3}). Kwas giberelinowy okazał się skuteczniejszy od benzyloadeniny w opóźnianiu rozkładu chlorofilu w przypadku obu gatunków, zwiększając tym samym ich trwałość. Pożywka standardowa, używana w celu przedłużenia pozbiorczej trwałości ciętych kwiatów, (8-HQC /cytrynian 8-hydroksychinoliny/ + 2% S /sacharoza/) istotnie przyspieszyła degradację chlorofilu w ciętych liściach *Z. aethiopica*, nie mając jednocześnie wpływu w przypadku *Z. elliottiana.* W obu jednak przypadkach pożywka osłabiła pozytywny wpływ GA_3 na końcową zawartość chlorofilu.

Słowa kluczowe: degradacja chlorofilu, zieleń cięta, kwas giberelinowy, benzyloadenina, *Zantedeschia aethiopica*, *Zantedeschia elliottiana*.

Accepted for print – Zaakceptowano do druku: 21.06.2004