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SENESCENCE OF CUT LEAVES OF *Zantedeschia aethiopica* AND *Z. elliottiana*. PART II. FREE AMINO ACIDS ACCUMULATION IN RELATION TO SOLUBLE PROTEIN CONTENT

Julita Rabiza-Świder, Ewa Skutnik, Mariusz Wachowicz, Aleksandra J. Łukaszewska

Warsaw Agricultural University

Abstract. Proteolysis and free amino acid accumulation occur during leaf senescence. As senescence is under control of plant hormones leaves of *Zantedeschia aethiopica* Spr. and *Zantedeschia elliottiana* Engl., two species grown for the florists' green, were pulse treated 24 hours with solutions of benzyladenine or gibberellic acid (0.1 mmol·dm^{-3} and 0.25 mmol·dm^{-3}, respectively) in order to delay senescence and to prolong their vase life. GA_3 but not BA retarded proteolysis in both species. A standard preservative solution used to prolong the longevity of cut (8-HQC + 2% S; 8-hydroxyquinoline citrate + 2% sucrose) accelerated proteolysis in the *Z. aethiopica* leaves but had no effect on leaves of *Z. elliottiana*. Soluble protein losses were accompanied by elevated levels of free amino acids, however, range of these increases did not correspond to decreases in protein contents. A massive accumulation of free amino acids occurred in the sugar-fed leaves of both species. Growth regulators somewhat limited free amino acid accumulation in leaves held in the preservative, BA being more effective in *Z. elliottiana* while GA_3 in *Z. aethiopica*.

Key words: Benzyladenine, gibberellic acid, free amino acids, proteolysis, cut leaves, senescence, *Zantedeschia aethiopica*, *Zantedeschia elliottiana*

INTRODUCTION

Senescence is the last step of plant life cycle. During this step, degradation of cell constituents occurs. One of the characteristics of senescence is the loss of proteins that permits a remobilization of nitrogen reserves [Huffaker 1990]. A decrease in the soluble protein level in detached leaves was evident two days after leaf detachment in rice [Chen et al. 1997] and in wheat [Peeters and Van Laere 1992] – two model plants.

Corresponding author – Adres do korespondencji: Julita Rabiza-Świder, Ewa Skutnik, Mariusz Wachowicz, Aleksandra J. Łukaszewska, Department of Ornamental Plants, Warsaw Agricultural University (SGGW), ul. Nowoursynowska 159, 02-787 Warszawa

A breakdown of leaf proteins results in a rapid concomitant increase in the free amino acid content [Peeters and Van Laere 1992; Gilbert et al. 1998] but independent amino acid synthesis also occurs. For example, under water stress conditions 75% of proline is synthesized *de novo* [Fukutoku and Yamada 1984].

So far, few reports on proteolysis during senescence of ornamental plants used as florists' green have been published [Skutnik et al. 1999; Skutnik et al. 2003]. In this paper we report on the differences in protein loss during senescence of two *Zantedeschia* species widely used as the florists' green and on the effects of benzyladenine, gibberellic acid and a standard preservative solution on proteolysis and on the accumulation of free amino acids.

MATERIAL AND METHODS

Plants of *Zantedeschia aethiopica* Spr. and *Zantedeschia elliottiana* Engl. were grown in the greenhouses of the Department of Ornamental Plants of the Warsaw Agricultural University, Warsaw, Poland. Mature, healthy, undamaged leaves were harvested in the morning, graded for uniformity, treated with growth regulators (BA or GA_3) and placed in vases with water or a preservative containing 8-hydroxyquinoline citrate (8HQC 200 mg·dm^{-3}) and sucrose (S 20 g·dm^{-3}). The vases were placed under controlled conditions: temperature 20^{o}C, relative humidity 60 %, 12 hrs photoperiod with light intensity of 35 μmol·m^{-2}·s^{-1} PAR. Growth regulators were applied as pulse conditioning: leaves were placed for 24 hrs in aqueous solutions containing 0.25 mmol·dm^{-3} GA_3 or 0.10 mmol·dm^{-3} BA. Leaves untreated with growth regulators and placed directly into water or preservative served as controls. Samples were collected on day 6 and 10 for the short-lasting *Z. elliottiana* and on day 6, 10 and 16 for the *Z. aethiopica*, the species with a longer longevity. Tissue from three leaves was pooled on each sampling date. Three samples were weighted for the analyses of soluble protein and free amino acid contents, and three replications of each extract were made, creating nine readings per data point. At the same time, three samples were tested for dry weight - the material was dried at 105ºC until a constant weight was achieved.

The soluble protein and free amino acid contents were determined according to Lowry et. al. [1951] and Rosen [1957], respectively, calculated from previously plotted standard curves, and expressed in mg of albumin bovine serum or μmol leucine, respectively, per gram of dry leaf weight (DW).

The results were statistically evaluated with ANOVA 2 and the means were compared using Duncan's test at probability level P = 0.95%.

RESULTS AND DISCUSSION

The levels of soluble protein and free amino acids in senescing cut leaves of *Z. aethiopica* and *Z. elliottiana* held in water

Proteolysis and free amino acids accumulation are common phenomena related to senescence [Huffaker 1990]. In the detached leaves of both species under study, the soluble protein content was decreasing; slowly during the first days of the experiment (to 94% and 88% in *Z. aethiopica* and *Z. elliottiana*, respectively, on day 6) and accelerating toward the end of leaf life span. The levels of soluble proteins at the end of the experiment (the 16th day for *Z. aethiopica* and the day 10th for *Z. elliottiana*) dropped to 49 and 61% of the initial level on day "0" (tab. 1, tab. 2). In the first six days, the contents of free amino acids increased three-fold in both species. Later on, clear differences between the species were present. In *Z. aethiopica*, free amino acids increased dramatically, almost nine-fold relative to the initial value, while in *Z. elliottiana* a marked decrease was observed, with the final content being only 28% higher than at the beginning of vase life (tab. 3, tab. 4).

Table 1. The soluble protein content ($mg \cdot g^{-1}$DW) in senescing cut leaves of *Zantedeschia aethiopica* Spr. treated with BA or GA_3, placed into distilled water or preservatives; initial value: 77.1 $mg \cdot g^{-1}$DW (100%)

Tabela 1. Zawartość białek rozpuszczalnych ($mg \cdot g^{-1}$s.m.) w trakcie starzenia się ciętych liści *Zantedeschia aethiopica* Spr. traktowanych BA i GA_3, przeniesionych do wody destylowanej lub pożywki standardowej; zawartość początkowa: 77,1 $mg \cdot g^{-1}$ s.m. (100%)

Treatment Traktowanie ($mmol \cdot dm^{-3}$)	Soluble protein content ($mg \cdot g^{-1}$ DW) on day: Zawartość białek rozpuszczalnych ($mg \cdot g^{-1}$ s.m.) w dniu:			Mean for a treatment $LSD_{0.05}$ = 5.12 Średnia dla traktowania $NIR_{0,05}$ = 5,12
	6.	10.	16.	
H_2O	72.7 (94%)	38.4 (50%)	37.6 (49%)	49.60 ab[1]
8-HQC + 2%S	71.5 (93%)	37.9 (49%)	31.2 (40%)	46.87 a
BA 0.1; 24h → H_2O	73.7 (96%)	75.6 (98%)	52.3 (68%)	67.20 c
BA 0.1; 24h → 8-HQC + 2%S	63.2 (82%)	59.4 (77%)	37.1 (48%)	53.26 b
GA_3 0.25; 24h → H_2O	73.7 (96%)	75.3 (98%)	62.9 (82%)	70.63 c
GA_3 0.25; 24h → 8-HQC + 2%S	72.5 (94%)	77.0 (100%)	52.6 (68%)	67.39 c
Mean for a term $LSD_{0.05}$ = 3.62 Średnia dla terminu $NIR_{0,05}$ =3,62	71.23 c	60.60 b	45.62 a	

[1]Means followed by the same letter do not differ significantly at α = 0.05 (Duncan's test); to compare the means within the table: $LSD_{0.05}$ = 8.86.

[1]Wartości oznaczone tą samą literą nie różnią się istotnie przy α = 0,05 (test Duncana); dla porównania wartości wewnątrz tabeli: $NIR_{0,05}$ = 8,86.

Proteolysis and free amino acids accumulation in cut flowers usually occur concomitantly [Paulin 1971]. This was also observed in cut leaves of *Z. aethiopica* but the range of changes in free amino acids was much greater than that in soluble proteins. Therefore, proteolysis could not be the only process that contributed to the free amino acid accumulation. An increased level of free amino acids (especially of asparagine and proline) was found in the phloem sap of *Medicago sativa* L. in response to a water deficit [Girousse et al. 1996]. Water deficit also affects the vase life of cut flowers even though they are held in water. Generally, the water balance of cut flowers is impaired due to vascular blockage and reduced water uptake [Halevy and Mayak 1981]. The same may well be true for cut leaves. Amino acid accumulation suggests that they may play a role in the osmotic adjustment, at the same time serving also as available sources of carbon and nitrogen [Gilbert et al. 1998].

The effects of the preservative on the soluble protein and free amino acid contents in cut leaves of *Z. aethiopica* and *Z. elliottiana*

A standard preservative solution containing 2% sucrose and 200 mg·dm^{-3} citrate or sulphate of 8-hydroxyquinoline (8-HQC or 8-HQS) is often used to prolong a vase life of many species of cut flowers. It has antibacterial properties and provides respirational substrate [Halevy and Mayak 1981]. Paulin [1971] showed that preservative solution (8-HQS + 4% S) delayed proteolysis and free amino acids accumulation in cut flowers. However, earlier experiments showed that this solution also had a deleterious effect on

Table 2. The soluble protein content (mg·g^{-1}DW) in senescing cut leaves of *Zantedeschia elliottiana* Engl. treated with BA or GA_3, placed into water or preservatives; initial value: 132.3 mg·g^{-1}DW (100%)

Tabela 2. Zawartość białek rozpuszczalnych (mg·g^{-1}s.m.) w trakcie starzenia się ciętych liści *Zantedeschia elliottiana* Engl. traktowanych BA i GA_3, przeniesionych do wody destylowanej lub pożywki standardowej; zawartość początkowa: 132,3 mg·g^{-1} s.m. (100%)

Treatment Traktowanie (mmol·dm^{-3})	Soluble protein content (mg·g^{-1}DW) on day: Zawartość białek rozpuszczalnych (mg·g^{-1} s.m.) w dniu:		Mean for a treatment $LSD_{0.05}$ = 7.69 Średnia dla traktowania $NIR_{0,05}$ = 7,69
	6.	10.	
H_2O	116.7 (88%)	80.9 (61%)	98.8 ab[1]
8-HQC + 2%S	119.8 (91%)	95.9 (72%)	107.8 c
BA 0.1; 24h → H_2O	109.0 (82%)	103.8 (78%)	106.4 bc
BA 0.1; 24h → 8-HQC + 2%S	108.2 (82%)	84.3 (64%)	96.3 a
GA_3 0.25; 24h → H_2O	140.5 (106%)	140.4 (106%)	140.5 d
GA_3 0.25; 24h → 8-HQC + 2%S	142.9 (108%)	123.8 (94%)	133.4 d
Mean for a term $LSD_{0.05}$ = 4.44 Średnia dla terminu $NIR_{0,05}$ = 4,44	122.9 b	104.9 a	

[1] Explanations as in table 1; to compare the means within the table: $LSD_{0.05}$ = 10.88.
[1] Objaśnienia jak w tabeli 1; dla porównania wartości wewnątrz tabeli: $NIR_{0,05}$ = 10,88.

cut leaves. It dramatically reduced the vase life of *Z. aethiopica* [Skutnik et al. 2001] and decreased chlorophyll contents in senescing leaves of *Z. aethiopica* and *Z. elliottiana* [Skutnik et al., this issue]. In this experiment, the preservative delayed proteolysis only in the leaves of *Z. elliottiana* (tab. 2) and in *Z. aethiopica* it did not significantly affect soluble proteins relative to the water control (tab. 1). On the contrary, placing leaves of both species into the preservative solution resulted in accumulation of free amino acids, more dramatic in *Z. aethiopica*: over 20-fold increase relative to the level at the start of the experiment and a nearly three-fold increase relative to controls (tab. 3). Similarly as in the case of water control, the scale of increases in the free amino acid contents in the sugar-fed leaves did not correspond to the changes in soluble proteins.

The effects of BA and GA_3 on the soluble protein and free amino acid contents in cut leaves of *Z. aethiopica* and *Z. elliottiana*

In many plant species, certain hormones may delay senescence. Delayed leaf senescence was observed in rice, where a BA-treatment extended proteolysis [Chen et al. 1997]. Senescence-retarding effects of cytokinin was also noted in transgenic tobacco with autoregulated synthesis of cytokinin activated at the onset of senescence [Wingler et al. 1998, Jordi et al. 2000]. Gibberellins are not as effective as cytokinins but in some species they have beneficial effect on the postharvest longevity of cut leaves [Skutnik et al. 2001]. Our earlier experiments have shown that an application of gibberellic acid to cut leaves of *Z. aethiopica* prolonged their postharvest life, retarded chlorophyll loss and reduced the electrical conductivity of cell sap from leaves [Skutnik et al. 2001]. Also in *Z. elliottiana*, chlorophyll was preserved in senescing leaves after a pulse conditioning with GA_3 [Skutnik et al., this issue]. In this experiment, a beneficial effect of GA_3 application was confirmed on the leaves of *Z. aethiopica* and *Z. elliottiana*. Gibberellic acid delayed proteolysis in *Z. aethiopica* where the protein loss was only 18% in 16 days of the experiment (tab. 1). The result was even better in *Z. elliottiana*, where soluble proteins were left intact until the last day of the leaf senescence (tab. 2). Cytokinin was less effective than GA_3 in delaying proteolysis but again *Z. elliottiana*, responded better to the treatment maintaining 78% of the initial protein content on the last day of the experiment (tab. 2) while *Z. aethiopica* maintained the 68% of its proteins (tab. 1). In both species, the gibberellic acid maintained the soluble proteins at higher levels in leaves placed into the preservative than did benzyladenine. The combination of the BA-treatment and the preservative maintained the proteolysis at a level similar to the control.

Table 3. The free amino acid content (μmol(leucine)·g^{-1}DW) in senescing cut leaves of *Zantedeschia aethiopica* Spr. treated with BA or GA_3, placed into water or preservatives; initial value: 185.9 μmol(leucine)·g^{-1}DW (100%)

Tabela 3. Zawartość wolnych aminokwasów (μmol(leucyny)·g^{-1}s.m.) w trakcie starzenia się ciętych liści *Zantedeschia aethiopica* Spr. traktowanych BA i GA_3, przeniesionych do wody destylowanej lub pożywki standardowej; zawartość początkowa: 185,9 μmol(leucyny)·g^{-1} s.m. (100%)

Treatment Traktowanie (mmol·dm^{-3})	Free amino acid content (μmol(leucine)·g^{-1}DW) on day Zawartość wolnych aminokwasów (μmol(leucyny)·g^{-1} s.m.) w dniu			Mean for a treatment $LSD_{0.05}$ = 94.79 Średnia dla traktowania $NIR_{0,05}$ = 94,79
	6.	10.	16.	
H_2O	558.3 (300%)	1148.9 (618%)	1625.6 (874%)	1110.93 b[1]
8-HQC + 2%S	1251.5 (673%)	1975.2 (1063%)	4602.4 (2476%)	2609.70 e
BA 0.1; 24h → H_2O	314.5 (169%)	301.1 (162%)	1600.3 (861%)	738.62 a
BA 0.1; 24h → 8-HQC + 2%S	1042.8 (561%)	2035.3 (1095%)	3591.2 (1992%)	2223.09 d
GA_3 0.25; 24h → H_2O	291.4 (157%)	304.9 (164%)	1466.6 (789%)	687.63 a
GA_3 0.25; 24h → 8-HQC + 2%S	970.8 (522%)	1502.7 (808%)	3350.4 (1802%)	1941.27 c
Mean for a term $LSD_{0.05}$ = 67.02 Średnia dla terminu $NIR_{0,05}$ = 67,02	738.21 a	1211.34 b	2706.07 c	

[1]Explanations as in table 1; to compare the means within the table: $LSD_{0.05}$ = 164.17.

[1]Objaśnienia jak w tabeli 1; dla porównania wartości wewnątrz tabeli: $NIR_{0,05}$ = 164,17.

Table 4. The free amino acid content (μmol(leucine)·g^{-1}DW) in senescing cut leaves of *Zantedeschia elliottiana* Engl. treated with BA or GA_3, placed into water or preservatives; initial value: 646.5 μmol(leucine)·g^{-1}DW (100%)

Tabela 4. Zawartość wolnych aminokwasów (μmol(leucyny)·g^{-1}s.m.) w trakcie starzenia się ciętych liści *Zantedeschia elliottiana* Engl. traktowanych BA i GA_3, przeniesionych do wody destylowanej lub pożywki standardowej; zawartość początkowa: 646,5 μmol(leucyny)·g^{-1} s.m. (100%)

Treatment Traktowanie (mmol·dm^{-3})	Free amino acid content (μmol(leucine)·g^{-1}DW) on day: Zawartość wolnych aminokwasów (μmol(leucyny)·g^{-1} s.m.) w dniu:		Mean for a treatment $LSD_{0.05}$ = 155.68 Średnia dla traktowania $NIR_{0,05}$ = 155,68
	6.	10.	
H_2O	2015.6 (312%)	826.8 (128%)	1421.2 a[1]
8-HQC + 2%S	2664.8 (412%)	2269.2 (351%)	2467.0 b
BA 0.1; 24h → H_2O	1588.6 (246%)	1404.8 (217%)	1496.7 a
BA 0.1; 24h → 8-HQC + 2%S	2167.1 (335%)	968.2 (150%)	1567.7 a
GA_3 0.25; 24h → H_2O	1419.8 (220%)	1666.6 (258%)	1543.2 a
GA_3 0.25; 24h → 8-HQC + 2%S	2199.8 (340%)	2435.1 (377%)	2317.5 b
Mean for a term $LSD_{0.05}$ = 89.88 Średnia dla terminu $NIR_{0,05}$ = 89,88	2009.3 b	1595.1 a	

[1]Explanations as in table 1; to compare the means within the table: $LSD_{0.05}$ = 220.17.
[1]Objaśnienia jak w tabeli 1; dla porównania wartości wewnątrz tabeli: $NIR_{0,05}$ = 220,17.

Generally, both growth regulators reduced the amino acid accumulation in *Z. aethiopica* though at the last day of experiment the contents of free amino acids in the hormone treated and untreated leaves, kept in water, were comparable. GA_3 was more effective than BA in case of the sugar-fed leaves (tab. 3). On the contrary, statistical analysis did not reveal a significant effect of growth regulators on the free amino acids accumulation in *Z. elliottiana* leaves kept in water. However, on the last day of the experiment the BA pretreated leaves of this species had significantly less amino acids than those conditioned with GA_3 (tab. 4).

A comparison of such senescence-related processes as proteolysis and free amino acid accumulation suggests more differences between the two *Zantedeschia* species in this study than in case of the chlorophyll degradation study [Skutnik et al., this issue]. At the end of the leaf senescence the soluble protein level was higher in *Z. elliottiana* than in *Z. aethiopica* while the free amino acid content increased by 28% in the former species and by several hundred percent in the latter. The negative effect of the sugar-containing flower preservative, as shown by the accumulation of free amino acids, was weakened by GA_3 in *Z. aethiopica* while in *Z. elliottiana* BA was more effective. However, in both species it was gibberellic acid that better preserved soluble proteins than did cytokinin. Studies aiming to elucidate the role of the sugar-containing preservative and growth regulators in controlling senescence in detached leaves of the two *Zantedeschia* species are under way.

CONCLUSIONS

1. Senescence of detached leaves of *Z. aethiopica* and *Z. elliottiana* is accompanied by decreases in the soluble protein contents and increases in free amino acids, however, the scale of these changes is different in the two species, and the free amino acid accumulation cannot be attributed solely to proteolysis.

2. Placing leaves into preservative solutions results in a massive accumulation of free amino acids in both species.

3. GA_3 is more effective than BA in decreasing losses of soluble proteins in leaves of the *Zantedeschia* species studied.

4. In the sugar-fed leaves, benzyladenine more effectively limited the free amino acid accumulation in *Z elliottiana* while GA_3 did so in *Z. aethiopica*.

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STARZENIE CIĘTYCH LIŚCI *Zantedeschia aethiopica* I *Z. elliottiana*. CZĘŚĆ II. AKUMULACJA WOLNYCH AMINOKWASÓW A ZAWARTOŚĆ BIAŁEK ROZPUSZCZALNYCH

Streszczenie. W trakcie postępującego starzenia się ciętych liści dochodzi do proteolizy oraz akumulacji wolnych aminokwasów w ich tkankach. Wiadomym jest, iż starzenie się, jak i inne procesy fizjologiczne, kontrolowane są przez regulatory wzrostu, dlatego też cięte liście dwóch gatunków znajdujących zastosowanie jako zieleń cięta (*Zantedeschia aethiopica* Spr. i *Zantedeschia elliottiana* Engl.) poddano 24-godzinnemu kondycjonowaniu w roztworach benzyloadeniny (0,1 mmol $\cdot dm^{-3}$) oraz kwasu giberelinowego (0,25 mmol$\cdot dm^{-3}$), by opóźnić ich starzenie się i przedłużyć pozbiorczą trwałość. W przypadku obu gatunków jedynie GA_3 skutecznie opóźnił rozkład białek rozpuszczalnych. Pożywka standardowa (8-HQC + 2% S; cytrynian 8-hydroksychinoliny + 2% sacharoza), stosowana w celu przedłużenia trwałości ciętych kwiatów, przyspieszyła proteolizę w przypadku liści *Z. aethiopica*, jednak nie miała równie niekorzystnego wpływu w przypadku liści *Z. elliottiana*. Spadkowi zawartości białek rozpuszczalnych towarzyszyła akumulacja wolnych aminokwasów, jednak zakres obu zjawisk nie był porównywalny. W przypadku obu gatunków największą akumulację wolnych aminokwasów stwierdzono w liściach wstawionych do roztworów zawierających sacharozę. Kondycjonowanie w roztworach obu regulatorów wzrostu ograniczyło wzrost zawartości wolnych aminokwasów w liściach przełożonych do pożywki standardowej, przy czym benzyloadenina okazała się skuteczniejsza w przypadku *Z. elliottiana* a GA_3 – *Z. aethiopica*.

Słowa kluczowe: benzyloadenina, kwas giberelinowy, wolne aminokwasy, proteoliza, zieleń cięta, starzenie, *Zantedeschia aethiopica*, *Zantedeschia elliottiana*

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