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Review

Genotype diversity assessment of common snowdrop (*Galanthus nivalis* L.) based on chlorophyll and carotenoids partitioning among different plant organs

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Summary

Common snowdrop (*Galanthus nivalis* L.) is a very important and typical feature of the Slovenian landscape. People eagerly await early spring to collect these plants for decorating their homes. Snowdrop collecting has always been a very popular activity among children. Morphological characterisation of snowdrops has shown that genotypes can be arranged into separate groups based on different flower characteristics. For this experiment, they were arranged into four groups: genotypes with green perianth (GP), genotypes with green streaks in the perianth (GSP), genotypes with yellowish perianth (YP) and normal white perianth genotypes (WP). Detailed pigment analysis showed that the concentrations of chlorophylls a and b were generally 0.2 and 0.5 µg mm^{-2}, respectively; significantly higher in plant spathes than in plant green leaves. GP genotypes contained significantly more chlorophyll, both a and b, in their leaves than WP genotypes. On the other hand, WP plants contained as much chlorophyll a and b in their spathes as GP plants.

Keywords
green leaves, petals, spathe, vase life

Significance of this study

What is already known on this subject?

- A strong variability is noticed in the population of snowdrops on natural sites. Many of these differences remain stable over generations.

What are the new findings?

- The present work serves for characterisation of these differences among various snowdrop groups.

What is the expected impact on horticulture?

- Observed differences are a very important basis for the future work with snowdrops regarding selection, biotechnology, etc. These differences induce an interest for this plant species for potential use in floral industry.

Introduction

The natural distribution of common snowdrop (*Galanthus nivalis* L.) in Europe extends from the Pyrenees in the west to the Ukraine in the east; it extends north up to Paris and south to the European part of Turkey. The naturally present variability of flower colours, based on differently spaced and shaped green sections in the perianth in this plant species, has been already observed for centuries. It was even initially thought that the *Galanthus* genus includes several species, although it was later well documented that all these differences actually originate in the strong variability of the *Galanthus nivalis* species. Two different species were later described, *Galanthus reginae-olgae* Hort., which can be found on the Peloponnese and *Galanthus cilicus* Baker, deriving from southern Turkey (Becket, 1988; Davis, 1999; Bishop et al., 2001; Jovanović et al., 2018).

Bavcon (2007, 2008, 2014) well documented that the variability among plants in the species *Galanthus nivalis* is based on very different characteristics: flower shape and size, number of flowers of a plant as a whole, shape of outer perianth segments, shape of inner perianth segments, number of outer and inner perianth segments, colour of outer perianth segments, colour pattern of inner perianth segments and shape and colour of ovary. The colour pattern of the outer and inner perianth segments and the colour of the ovary, are certainly the most important parameters from the point of view of the ornamental flower industry (Bishop et al., 2001; Bishop, 2013; Grimshaw, 2013). It has also been documented in particular that the different flower parts of plants with different colour patterns have different ecological functions. Plants with green elements in the perianth segments, for example, are often naturally present in areas with wet soils near rivers and also in areas with deeper water sources. They are less susceptible to winter frost and they also begin to grow later in spring. It has even been observed that if the outer green perianth segments are damaged due to frost injury, the inner perianth segments often remain undamaged (Bavcon, 2007, 2008, 2014).

The colour patterns of flowers are created by plant pigments. Based on their involvement in photosynthesis, they can be divided into photosynthetically active and non-photosynthetically active pigments. The main role in the photosynthetically active pigment group belongs to chlorophyll but carotenoids are also essential components of the photosynthetic apparatus. Both chlorophyll and carotenoids, like other pigment compounds, are also responsible for the colour development of a plant part. Chlorophyll absorbs light in both the red and blue parts of the spectrum, reflecting only green light, carotenoids reflect only yellow and orange (Glover, 2014; Taiz et al., 2015). The question of why petals sometimes contain chlorophyll and, conversely, why leaves

or stems, like petals, sometimes remain without chlorophyll development, is more complex. This pattern, the absence of chlorophyll development in flowers, is a very important evolutionary result, which enables the majority of plants to be recognised by pollinators against a background of leaves when the flowers are ready to be pollinated (Ohmiya et al., 2014; Nikolić, 2017).

This question is additionally interesting because many plants contain chloroplasts in petals in their early developmental stages but, thereafter, as the maturation state of petals increases, the chloroplast content decreases and fully open flowers contain only trace amounts of chloroplasts (Pyke and Page, 1998; Bavcon, 2014). Correlated with the decreased chlorophyll content in chloroplasts during flower bud development, increased anthocyanin accumulation has been reported (Schmitzer et al., 2009, 2010). The explanation of this may have recently been provided. Ohmiya et al. (2017) showed in a comparison of some chrysanthemum mutants with green petals with non-green chrysanthemums that the green ones lost the ability to degrade chloroplasts due to lost or reduced activity of factors that suppress chloroplast biosynthesis.

This explanation is also supported by studies with variegated types of plants in which a blockage was present in all plant types with more or less yellowish or whitish leaves during chlorophyll biosynthesis precursor (Li et al., 2017; Chen et al., 2018).

Snowdrop species can be potentially very interesting for such studies because there are individuals in this plant group with very different levels of green coloured perianth. Studies on the biochemical mechanism leading to such differences in the flower colours of snowdrops are lacking. The aim of our study was to ascertain what role the differences play in plants with different intensity levels of green perianth compared with plants of whiter or fully white perianth. We focused on differences in chlorophylls a and b and carotenoids in different plant organs: the perianth, green leaves and spathe.

Materials and methods

Plant material

The snowdrop plants used in this study were collected *in situ* throughout Slovenia. The collection of different genotypes was started in 2000 (Bavcon, 2003, 2008, 2014; Bavcon and Marinček, 2004) but plants used in this study were collected 2012 and 2013. The collected genotypes were classified into eight groups (Bavcon, 2008, 2014), according to flower shape, marbling type and size, and the number of flowers on a plant as a whole.

For research purposes in this study, we rearranged the plants from the eight main groups into the following subgroups: plants with nearly green perianth (GP), plants with green streaks in the perianth (GSP), plants with yellowish perianth (YP) and plants with fully white perianth (WP) (Figure 1).

The snowdrop collecting season started at the beginning of first snowdrop flowering, i.e., in the middle of December, and continued until May. As soon as bigger populations of common snowdrops appeared in late winter, the localities



Figure 1. Common snowdrop (*Galanthus nivalis* L.) with different marbled perianth: A. plants with ordinary white perianth; B. plants with green perianth; C. and D. plants with perianth of different streakiness level.

were systematically observed. Notes of specific features of the plants were made.

The plants were then dug up and transferred in plastic bags from the original site to the University Botanic Garden in Ljubljana, where they were planted in 10×10 cm pots. Plants were shaded using a shade cloth and they were not given extra protection during the winter.

At the end of the following winter, when the plants started to flower again, each pot was examined, observations were recorded, and a comparison made to the original description of the plant. This comparison determined which plant features on the snowdrops stayed unchanged from the previous year. Feature stability was checked over two to three years.

For pigment measurements, different plant parts were sampled during flowering time in March 2015. We collected parts of the perianth, spathe and green leaves. Two replicates were used for each plant part at each plant. The sampled material was stored in plastic bags and immediately (10 min by car) transported to the laboratory facility in a cooling bag. The material was frozen at -20°C.

Pigment identification

The contents of chlorophyll a and b and total carotenoids were evaluated according to the method of Wellburn (1994). From the frozen material, 4 mm leaf discs were cut out. They were transferred into 1.5 mL plastic microtubes in which they were mashed with 0.5 mL dimethyl sulphoxide (DMSO) and crystals of magnesium hydroxide carbonate. Samples were left in a water bath (65°C) in the dark for 2 h. Samples were cooled to room temperature, decanted into vessels and absorption was measured on a Lambda Bio spectrometer (Perkin Elmer, Waltham, MA) at 649 nm (chlorophyll b) and 665 nm (chlorophyll a). The concentrations of photosynthetic pigments in extracts were determined by Wellburn (1994).

Statistical evaluation

The experiment was set as a single factor experiment, with a group of genotypes (the degree of intensity of the green coloration of the perianth) as the factor. For all measurements (chlorophyll and carotenoid content), two well-developed organ parts (perianth, spathe or green leaf) from one plant (one genotype) were used as replicates and end values were average values from these replicates. One-way analysis of variance (ANOVA) was performed for statistical analysis. Statistically significant differences were tested with the Duncan test at a 0.95 confidence level.

Results

Chlorophylls and carotenoids partitioning in different plant organs

All snowdrops contained the majority of chlorophyll in the green leaves and spathe; the perianth of all snowdrops only contained chlorophyll in traces. The concentrations of both chlorophyll a and b were higher in the plant spathe than in green leaves and, in this plant organ, reached values between 0.2 and 0.5 μg mm^{-2}, while the values in green leaves ranged between 0.17 and 0.42 μg mm^{-2} (Figure 2). Both green leaves and spathe contained more chlorophyll a than chlorophyll b. A comparison of plants with different green marbling of the perianth showed that concentrations of chlorophyll a in both green leaves and spathe were significantly higher in GP plants. There was the same difference in leaves of plants with perianth marbling in all other studied patterns, but in the case of the spathe, only against YP plants. It should be stressed that WP plants contained as much chlorophyll a and b in their spathe as GP plants. If green leaves and spathe contained more chlorophyll a than chlorophyll b, then the plant perianth contained more chlorophyll b than the a-form. The concentrations of the b-form ranged between 0.071 and nearly 0.1 μg mm^{-2}, whereas the concentrations of the a-form were between 0.04 and 0.085 μg mm^{-2} (Figure 2). Among the different plant organs, the spathe tended to accumulate the highest values of carotenoids and the perianth the lowest. GP genotypes contained statistical higher carotenoid values in their spathe than did YP and WP genotypes (Table 1).

Genotype differences based on chlorophyll and carotenoid contents

Generally, GP genotypes contained higher concentrations of both chlorophylls in their leaves and WP genotypes the

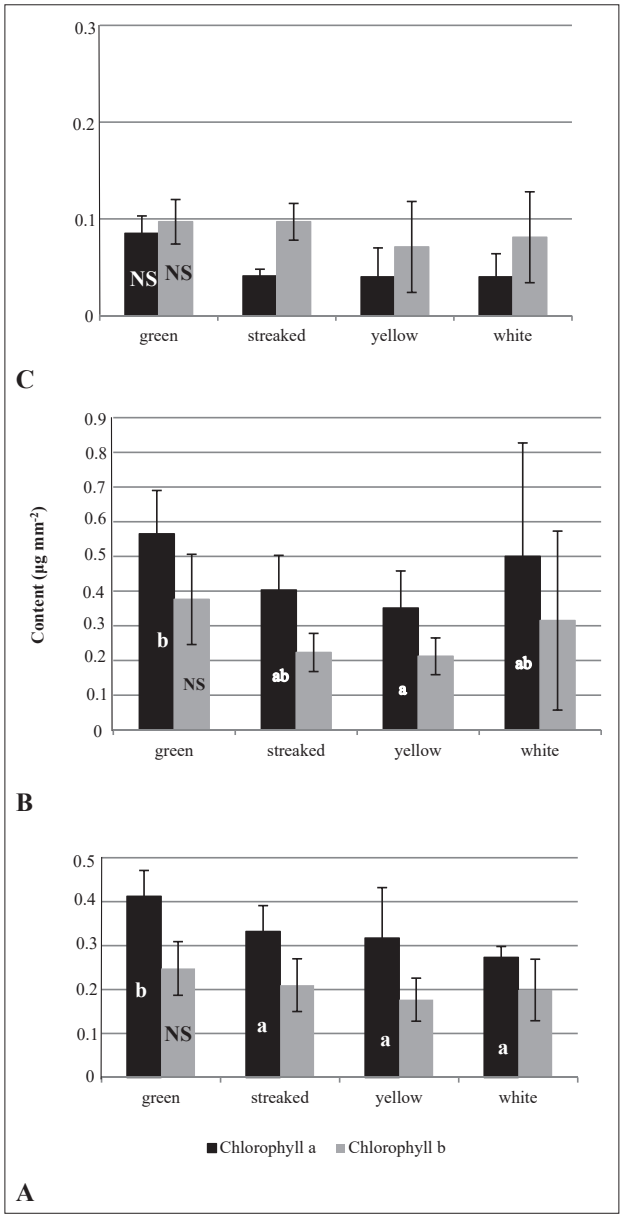


Figure 2. Organ partitioning of chlorophyll a and b in snowdrops (*Galanthus nivalis* L.) with different petal marbling in 2015 (A = leaves; B = spathe; C = perianth). Mean values ± standard deviation are presented. Different letters assign statistical differences at P ≤ 0.05 (Duncan), NS = not significant.

lowest concentrations. The difference was statistically significant, as already mentioned. There were also differences in chlorophyll and carotenoid contents among genotypes of a specific colour pattern. Genotypes with collection numbers 2703, 3405 and 3439 from the GP group, 3454 and 3466 from the GSP group, 2706 and 2716 from the YP group and 2702 from the WP group, showed slightly higher chlorophyll (especially chlorophyll a) values but these differences were not statistically significant (Figure 3). Genotypes 3405, 3454, 2706 and 2702 also tended to contain higher concentrations of carotenoids but the differences were not significant (Table 2). In the spathe, genotypes 2116 and 2703 from the GP group of genotypes slightly stand out from the other genotypes in terms of higher chlorophyll and carotenoid (also genotype 2730) values but the differences were not signifi-

Table 1. Carotenoid concentrations in different organs of snowdrop (*Galanthus nivalis* L.) in relation to different genotype groups of different marbled perianth. Mean values ± standard deviation are shown. Different letters assign statistical differences at $P \leq 0.05$ (Duncan) for each perianth colour group individually; NS = not significant.

Organ	Perianth marbling type	Content (µg mm^{-2})
Leaves	Green	0.092 ± 0.010 NS
	Streaked	0.079 ± 0.020 NS
	Yellow	0.072 ± 0.030 NS
	White	0.063 ± 0.003 NS
Spathe	Green	0.032 ± 0.032 NS
	Streaked	0.119 ± 0.026 NS
	Yellow	0.108 ± 0.028 NS
	White	0.143 ± 0.063 NS
Perianth	Green	0.022 ± 0.004 b
	Streaked	0.016 ± 0.004 ab
	Yellow	0.011 ± 0.005 a
	White	0.011 ± 0.004 a

Table 2. Carotenoid concentrations in green leaves of snowdrop (*Galanthus nivalis* L.) in relation to different genotypes. Mean values ± standard deviation are shown; NS = not significant at $P \leq 0.05$ (Duncan) for each perianth colour group individually.

Perianth marbling type	Genotype	Content (µg mm^{-2})
Green	2116	0.080 ± 0.004 NS
	2703	0.098 ± 0.019 NS
	2714	0.077 ± 0.001 NS
	2730	0.075 ± 0.006 NS
	3405	0.116 ± 0.014 NS
	3413	0.100 ± 0.019 NS
	3434	0.093 ± 0.015 NS
	3439	0.097 ± 0.004 NS
Streaked	2686	0.062 ± 0.020 NS
	3314	0.064 ±0.038 NS
	3454	0.097 ± 0.031 NS
	3366	0.091 ± 0.009 NS
Yellow	2706	0.082 ± 0.036 NS
	2716	0.074 ± - NS
	3396	0.056 ± 0.023 NS
	3421	0.076 ± 0.039 NS
	2730-A	0.070 ± 0.015 NS
White	2702	0.079 ± 0.004 NS
	3325	0.047 ± 0.002 NS

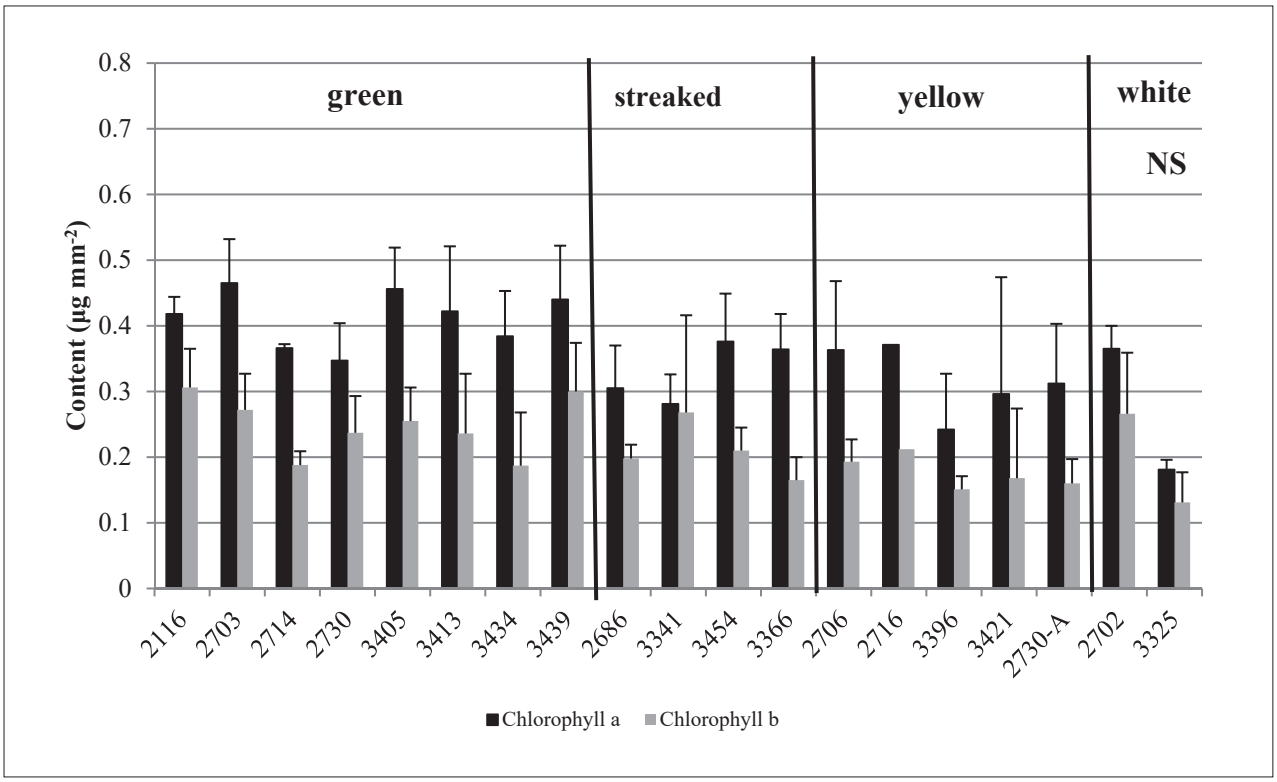


Figure 3. Chlorophyll a and b concentrations in green leaves of snowdrop (*Galanthus nivalis* L.) in relation to different genotypes with different marbled perianth. Mean values ± standard deviation are shown; NS = no statistical differences were present at $P \leq 0.05$ (Duncan) for each perianth colouring group individually.

cant. Genotype 2686 from the GSP group of genotypes, 2706 and 2730-A from the YP group and 2702 from the WP group also showed slightly higher chlorophyll and carotenoid (also genotype 3314 from the GSP group) values but, here too, the differences were not significant (Figure 4; Table 3). Genotypes 3405 and 3413 from the GP group showed significantly higher chlorophyll and carotenoid (genotype 2116 also) values in the perianth itself than did other genotypes in the same group, and significantly the lowest values were measured in the perianth of plants of genotype 2703 and also carotenoids in 2714. Differences in chlorophyll values in other marbling groups were not significant (Figure 5; Table 4).

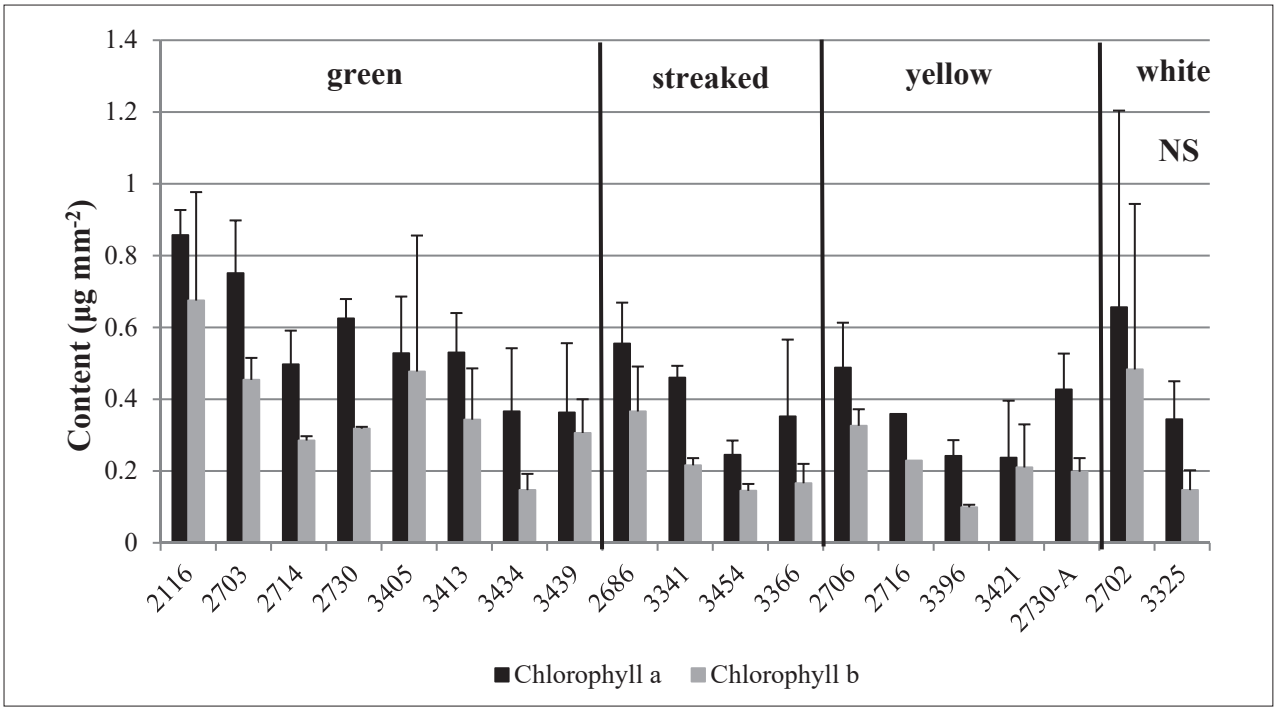


Figure 4. Chlorophyll a and b concentrations in spathe of snowdrop (*Galanthus nivalis* L.) in relation to different genotypes with different marbled perianth. Mean values ± standard deviation are shown; NS = no statistical differences were present at P ≤ 0.05 (Duncan) for each perianth colouring group individually.

Table 3. Carotenoid concentrations in spathe of snowdrop (*Galanthus nivalis* L.) in relation to different genotypes. Mean values ± standard deviation are shown; NS = not significant at P ≤ 0.05 (Duncan) for each perianth colour group individually.

Perianth marbling type	Genotype	Content (µg mm^{-2})
Green	2116	0.144 ± 0.042 NS
	2703	0.160 ± 0.043 NS
	2714	0.141 ± 0.004 NS
	2730	0.175 ± 0.015 NS
	3405	0.116 ± 0.020 NS
	3413	0.141 ± 0.031 NS
	3434	0.120 ± 0.056 NS
	3439	0.087 ± 0.045 NS
Streaked	2686	0.123 ± 0.005 NS
	3314	0.155 ± 0.031 NS
	3454	0.079 ± 0.005 NS
	3366	0.117 ± 0.064 NS
Yellow	2706	0.138 ± 0.012 NS
	2716	0.114 ± - NS
	3396	0.088 ± 0.013 NS
	3421	0.087 ± 0.056 NS
	2730-A	0.115 ± 0.029 NS
White	2702	0.159 ± 0.090 NS
	3325	0.126 ± 0.035 NS

Table 4. Carotenoid concentrations in perianth of snowdrop (*Galanthus nivalis* L.) in relation to different genotypes. Mean values ± standard deviation are shown. Different letters assign statistical differences at P ≤ 0.05 (Duncan) for each perianth colour group individually; NS = not significant.

Perianth marbling type	Genotype	Content (µg mm^{-2})
Green	2116	0.030 ± 0.006 cd
	2703	0.012 ± 0.002 a
	2714	0.013 ± 0.002 a
	2730	0.015 ± 0.001 ab
	3405	0.035 ± 0.010 d
	3413	0.029 ± 0.002 cd
	3434	0.022 ± 0.006 bc
	3439	0.020 ± 0.004 ab
Streaked	2686	0.011 ± 0.001 NS
	3314	0.013 ± 0.002 NS
	3454	0.024 ± 0.013 NS
	3366	0.017 ± 0.001 NS
Yellow	2706	0.008 ± 0.005 NS
	2716	0.007 ± - NS
	3396	0.018 ± 0.001 NS
	3421	0.012 ± 0.011 NS
	2730-A	0.008 ± 0.001 NS
White	2702	0.008 ± 0 NS
	3325	0.013 ± 0.008 NS

Discussion

Petals of all snowdrop groups (green, streaked, yellow and white) contained much lower levels of both chlorophylls than did the spathe and green leaves. This is probably the result of a lower expression level of chlorophyll biosynthesis genes in petals than in green leaves or spathe, as already reported for other plant species (Ohmiya et al., 2017). The reason for the stronger green colouration of the spathe is also probably a result of snowdrop developing parts each year. When snowdrop flowers grow out of the ground, the spathe is the first part of the flower to be exposed to the sun's irradiation and also later, when the flowers begin to open, the spathe covers the developing flower and is therefore exposed to the sun at the most direct angle. The development of chloroplasts, with chlorophyll formation, is therefore particularly affected in the spathe.

Chlorophyll concentrations in different snowdrop organs showed that GP or GSP plants tended to contain higher chlorophyll levels in their perianth, but the differences were not significant. This may be an interesting fact, especially because several studies have shown in various plants (chrysanthemum, carnation) that plants with green petals also have higher expression levels of genes responsible for chlorophyll synthesis and, at the same time, the degradation level was low in plants with green petals (Ohmiya et al., 2014, 2017). The absence of significant differences in our experiment were probably caused by the environmental conditions (temperatures, irradiance, etc.), which also affect chlorophyll biosynthesis, in addition to the described changes at the genetic level. It must be considered in relation to environmental conditions that both irradiance and temperature are different at the perianth surface to that in the surrounding air. Furthermore, the colour of the perianth is very important for the temperature on the perianth surface. A white perianth is generally cooler than a green or yellowish perianth, as already reported, and so the chlorophyll degradation process in our white snowdrops was probably not so intensive (Rejšková et al., 2010).

However, the GP plants in our experiment showed significantly stronger accumulation of chlorophyll a in their green leaves, and also in the spathe, than did YP plants. The perianth is an important photosynthetic plant organ in evolutionary terms; it is even assumed to have derived from the leaves (Glover, 2014). However, the perianth later, during evolution, lost the possibility of forming chloroplasts with chlorophyll, as shown by Pyke and Page (1998). These authors also explained that in a genus such as *Cheiranthus* spp., which is known for coloured petals, leucoplast differentiation is a default pathway and that the appearance of the mutation resulting in the loss of this function is necessary for chloroplasts to be formed again in such petals. Such a mutation is also probably the real explanation for the GP plants in our experiment, resulting in chlorophyll formation in their perianth so that photosynthesis can also take place in the perianth of these plants. The photosynthesis occurring in the perianth consequently caused stronger chlorophyll formation in the leaves of these plants, too. The main reason for this genetic based abnormality is that the pattern of the green perianth is very stable through following generations. Plants derived from the original GP plants (their clones) retained this pattern. The perianth's evolutionary history, as shown by Pyke and Page (1998), is also probably why WP snowdrops developed a spathe with the same chlorophyll concentration in it as GP plants. These plants probably have to compensate for the very low level of photosynthesis in the perianth with higher photosynthesis in other organs, such as the spathe.

Based on the findings of Ohmiya et al. (2017), who reported that chlorophylls present in different plant organs are present in different tissues in these organs (in leaves they are present only in mesophyll cells, whereas in green petals they are present in both mesophyll and epidermal cells), we performed a comparison of chlorophylls separately for specific organs. Different genotypes were then compared with regard to chlorophyll level in these organs. Such a detailed analysis of different genotypes in the separate perianth co-

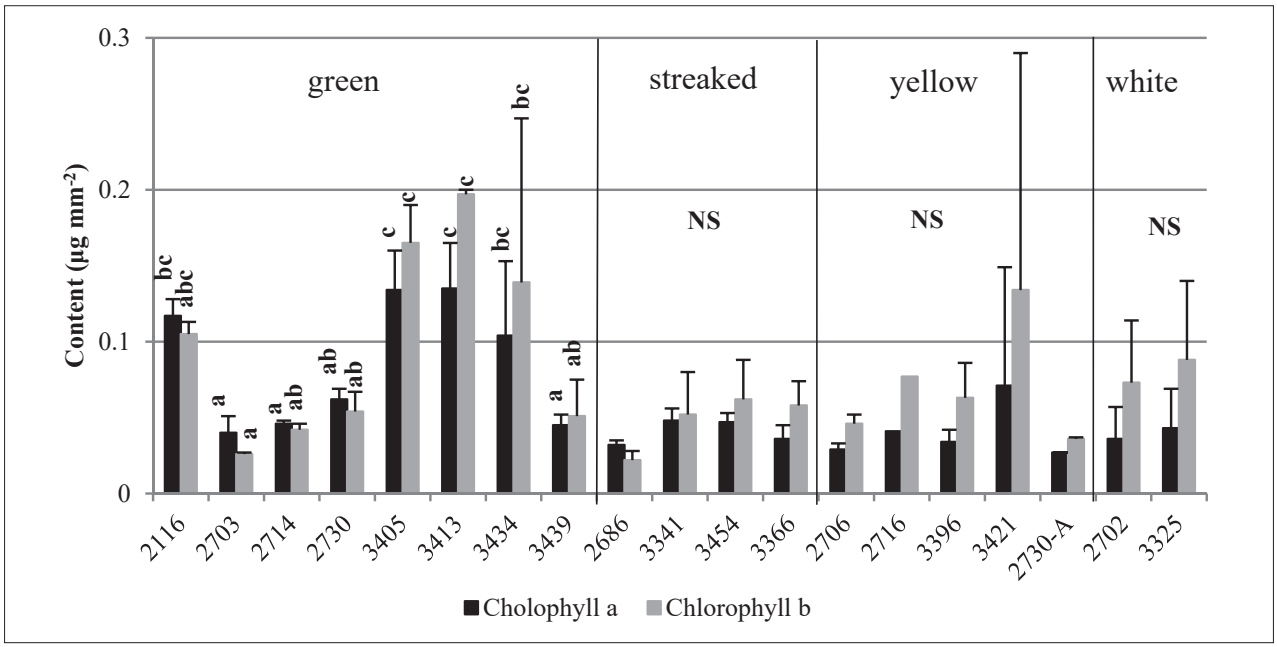


Figure 5. Chlorophyll a and b concentrations in perianth of snowdrop (*Galanthus nivalis* L.) in relation to different genotypes with different marbled perianth. Mean values ± standard deviation are shown. Different letters assign statistical differences at $P \leq 0.05$ (Duncan) for each perianth colour group individually; NS = not significant.

louration groups showed differences in levels of accumulation of chlorophyll in different plant organs. These differences were significant among genotypes in the GP group when chlorophyll was measured in the perianth. Genotypes with higher chlorophyll levels in the perianth also had significantly higher carotenoid levels in the perianth. Carotenoids accumulated significantly in tissues with higher potential for photosynthesis, so these pigments are also very important for the process of photosynthesis, as previously described by Glover (2014). On the other hand, genotypes with significantly higher levels of chlorophyll a in the perianth tended to have lower levels of chlorophyll (especially chlorophyll a) in other organs, especially in the spathe. This could again be explained by the specific level of photosynthesis, as reported by Chen et al. (2017). When this level cannot be reached with a specific organ due to lower chlorophyll levels in this organ, then the photosynthesis level to compensate the lack of photosynthesis has to be driven by another organ.

Specific differences in the amount of pigment, especially in the perianth, among different genotypes may also be very interesting in relation to the vase life of snowdrop plants of these genotypes. Wang et al. (2017) reported that higher levels of photosynthetic pigment in the perianth of plants may extend the vase life of flowers due to the role of carotenoids, which can balance the oxidation metabolism of various substances, including chlorophylls a and b. The slowdown of oxidation processes can consequently delay the ageing process of flower parts, which can prolong the vase life of flowers. This can also be observed in *in vivo* conditions, where GP snowdrops blossom longer than obviously WP plants. The genotypes of snowdrop with higher levels of these pigments may thus be very interesting due to the potential ability to extend the vase life of their flowers.

Conclusions

The variability of snowdrops in Slovenia is fascinating and comprehensive. Different genotypes differed not only based on their morphological characteristics but also in terms of different pigment accumulation. Chlorophyll partitioning among different plant organs is based on the ability of this organ to drive photosynthesis. The role of carotenoids is also very important with regard to the quality of a plant's vase life and thus in relation to the potential involvement of snowdrop plants in the ornamental flower industry.

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