The effect of genome size on detailed species traits within closely related species of the same habitat

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Received 18 July 2008; accepted for publication 26 March 2009

In spite of the large number of studies on genome size, studies comparing genome size and growth-related traits across a wider range of species from the same habitat, taking into account species phylogeny, are largely missing. I estimated the relationship between genome size and different seed and seedling traits in perennial herbs occurring in dry calcareous grasslands in northern Bohemia, Czech Republic. There was no relationship between genome size and plant traits in simple regression analyses, but several strong relationships emerged in analyses based on pairwise phylogenetically independent contrasts. There was a significant relationship between monoploid genome size and production of above-ground biomass, seedling establishment success and seed weight and between holoploid genome size and seed dormancy. Because the results are based on phylogenetically independent contrasts over a range of species from the same type of habitat, they allow me to conclude that these patterns were not because of species group or habitat type, but really show a correlation with genome size. In contrast to previous studies, I found a higher number of relationships with monoploid than with holoploid genome size. This may be because the traits observed in this study are directly related to plant growth and thus to life-cycle time, which is determined by monoploid genome size. © 2009 The Linnean Society of London, Botanical Journal of the Linnean Society, 2009, 160, 290–298.


INTRODUCTION

Recently, there has been an enormous increase in the number of studies estimating genome size of different taxa (Bennett, Bhandol & Leitch, 2000). It has been suggested that genome size (including both holoploid 2C and monoploid genome size 1Cx, Greilhuber et al., 2005) is one of the fundamental attributes of all living organisms that influence many different phenotypic and phenological characters at subcellular, cell, tissue and organismic level (Grime, 1998; Bennett et al., 2000; Bennett & Leitch, 2005). Many recent studies thus attempted to find adaptive consequences of genome size (e.g. Knight, Molinari & Petrov, 2005; Kron, Suda & Husband, 2007).

There is a positive correlation between genome size and cell volume and duration of meiosis (e.g. Van't Hof & Sparrow, 1963; Evans & Rees, 1971). These cellular level effects translate into effects on various biological traits (Bennett, 1987; Beaulieu et al., 2008). The most commonly studied trait, seed size, has been shown to strongly positively correlate with genome size within Pinus species (Wakamiya et al., 1993; Grotkopp et al., 2004), within species of the British flora (Thompson, 1990) and in larger sets of species (Knight et al., 2005; Beaulieu et al., 2007a; Beaulieu, Leitch & Knight, 2007b). There is a significant relationship between genome size and minimum generation time (Bennett, 1972, 1987), month of first flowering (Baranyi & Greilhuber, 1999), growth form (Ohri, 2005), minimum germination temperature (Thompson, 1990), frost resistance (Macgillivray &
EFFECT OF GENOME SIZE ON PLANT GROWTH 291

Grime, 1995) and maximum photosynthetic rate (Knight et al., 2005).

Beaulieu et al. (2007a, b) suggested that most of the studies on the relationships between species traits and genome size were carried out using a wide range of unrelated species without taking into account the phylogenetical relationships between the species (e.g. Bennett, 1972, 1987; Thompson, 1990). When taking phylogeny into account, the analyses have usually been carried out within a single genus or family (e.g. Wakamiya et al., 1993; Grotkopf et al., 2004).

Studies that compare genome size between closely related species in larger species groups and over multiple groups of species are usually concerned with evolutionary changes in genome size (e.g. Albach & Greilhuber, 2004; Bureš et al., 2004; Leitch et al., 2007). Several recent studies, however, performed phylogenetical analyses of traits such as leaf mass per unit area (LMA), photosynthetic rate and seed mass over larger species groups (e.g. Knight et al., 2005; Morgan & Westoby, 2005; Beaulieu et al., 2007a, b, 2008; Knight & Beaulieu, 2008).

The need to consider phylogenetical relationships between species is highly debated (e.g. Harvey, Read & Nee, 1995; Westoby, Leishman & Lord, 1995a, b; Silvertown & Dodd, 1996; Freckleton, Harvey & Pagel, 2002; Poock et al., 2006) and many authors have suggested that the phylogenetical and functional explanations for species traits are not mutually exclusive (see also Grime & Hodgson, 1987). It is thus useful to perform both types of analyses in each case and compare the results.

Studies investigating detailed species traits and taking phylogeny into account usually compare species based strictly on their phylogenetical relationships without considering their occurrence in different environments. This is an important issue as habitat conditions are known to be related to genome size (e.g. Levin & Funderburg, 1979) and to a large extent to species traits (e.g. Hodkinson et al., 1998; Wright & Westoby, 1999). It is thus difficult to decide if species traits are determined by genome size or by habitat type. As a result, we still have relatively limited knowledge of the relationship between genome size and life-history traits of species based on comparison of species from different groups, but taking into account both species phylogeny and habitat conditions (but see Grime, Shacklock & Band, 1985; Knight & Ackerly, 2002).

The aim of this study is to estimate the relationship between genome size and plant traits within a group of species occurring in a single habitat type. Specifically, I asked the following questions. (1) What is the relationship between genome size and plant traits related to plant reproduction and growth? (2) How does this relationship change when taking into account phylogenetical relationships between the species?

To do this, I selected 22 species-forming pairs of congeneric species occurring in dry calcareous grasslands in northern Bohemia, Czech Republic. In a previous study (Tremlová & Münzbergová, 2007), we measured traits related to reproduction and growth in these species. In this study, I estimated genome size of these species and looked at the relationship between genome size and the species traits. Because some studies (e.g. Grotkopf et al., 2004; Beaulieu et al., 2007a, b) have shown different relationships between species traits and holoploid and monoploid genome size, I tested relationships between both of these values and species traits.

MATERIAL AND METHODS

STUDY REGION AND PLANT MATERIAL

I selected 22 native perennial herbs forming pairs of closely related species (Table 1). The plant names and their authors are standardized according to The International Plant Names Index (2008). Names of the families follow the Angiosperm Phylogeny Group (2003). The species are restricted to dry calcareous grasslands in northern Bohemia, Czech Republic (Tremlová & Münzbergová, 2007). The mean annual rainfall in the study region is 453 mm. The mean temperature of the warmest month (July) is 18 °C and of the coldest month (January) is ~2 °C (Czech Hydrometeorological Institute).

FLOW CYTOMETRY

To take into account potential variation in nuclear DNA amount, I used at least six individuals from at least two populations for genome size measurements. I did the measurements on at least three different days to take into account potential variation in the functioning of the flow cytometer.

I prepared the nuclear samples from fresh leaves. In a few cases in which obtaining clear peaks from leaf material was difficult, I used flowering stems (Inula spp.). I used the procedure of Suda, Kyncl & Freiová (2003) in the analyses. Because of high variation in 2C value between species, I had to use different internal standards in different species (Table 1). For calculation of the 2C values, I compared all the internal standards with Pisum sativum L. 'Ctirad' (2C = 9.09 pg), and the 2C values for all species are thus based on the value of P. sativum. I took data on the 2C values for Cirsium acaule (L.) Scop. and Cirsium pannonicum Link from Bureš et al. (2004) and data on chromosome numbers from Kubát (2002). In cases with multiple published chromosome numbers, the chromosome numbers were estimated.
Table 1. List of species used in the study with internal standards used for measurements of nuclear DNA amount

<table>
<thead>
<tr>
<th>Pair</th>
<th>Species</th>
<th>Family</th>
<th>2C value (pg)</th>
<th>SE</th>
<th>Sample size</th>
<th>Int. stand.</th>
<th>Ploidy level</th>
<th>1Cx value (pg)</th>
<th>2n</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>Asperula cynanchica</em> L.</td>
<td>Rubiaceae Juss. (1789), nom. cons.</td>
<td>3.85 ± 0.0033</td>
<td>9</td>
<td>Z</td>
<td>4</td>
<td>0.96</td>
<td>40</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Asperula tinctoria</em> L.</td>
<td>Rubiaceae Juss. (1789), nom. cons.</td>
<td>2.38 ± 0.0017</td>
<td>9</td>
<td>Z</td>
<td>2</td>
<td>1.19</td>
<td>22</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td><em>Astragalus cicer</em> L.</td>
<td>Fabaceae Lindl. (1836), nom. cons.</td>
<td>8.34 ± 0.0021</td>
<td>9</td>
<td>Z</td>
<td>8</td>
<td>1.04</td>
<td>64</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Astragalus glycyphyllos</em> L.</td>
<td>Fabaceae Lindl. (1836), nom. cons.</td>
<td>1.61 ± 0.0019</td>
<td>9</td>
<td>S</td>
<td>2</td>
<td>0.81</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td><em>Campanula glomerata</em> L.</td>
<td>Campanulaceae Juss. (1789), nom. cons.</td>
<td>3.68 ± 0.0062</td>
<td>10</td>
<td>G</td>
<td>2</td>
<td>1.84</td>
<td>30</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Campanula rotundifolia</em> L.</td>
<td>Campanulaceae Juss. (1789), nom. cons.</td>
<td>4.66 ± 0.004</td>
<td>9</td>
<td>B</td>
<td>4</td>
<td>1.17</td>
<td>68</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td><em>Centaurea jacea</em> L.</td>
<td>Astereae Martynov (1820), nom. cons.</td>
<td>3.8 ± 0.0024</td>
<td>9</td>
<td>G</td>
<td>4</td>
<td>0.95</td>
<td>44</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Centaurea scabiosa</em> L.</td>
<td>Astereae Martynov (1820), nom. cons.</td>
<td>3.58 ± 0.0041</td>
<td>9</td>
<td>G</td>
<td>2</td>
<td>1.79</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td><em>Cirsium acaule</em> (L.) Scop.</td>
<td>Astereae Martynov (1820), nom. cons.</td>
<td>2.62 ± 0.003</td>
<td>2</td>
<td>Z</td>
<td>2</td>
<td>1.31</td>
<td>34</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Cirsium pannonicum</em> Link</td>
<td>Astereae Martynov (1820), nom. cons.</td>
<td>2.44 ± 0.004</td>
<td>2</td>
<td>Z</td>
<td>2</td>
<td>1.22</td>
<td>34</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td><em>Coronilla vaginalis</em> Lam.</td>
<td>Fabaceae Lindl. (1836), nom. cons.</td>
<td>3.28 ± 0.0029</td>
<td>9</td>
<td>Z</td>
<td>2</td>
<td>1.64</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Coronilla varia</em> L.</td>
<td>Fabaceae Lindl. (1836), nom. cons.</td>
<td>2 ± 0.0013</td>
<td>9</td>
<td>Z</td>
<td>4</td>
<td>0.5</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td><em>Inula hirta</em> L.</td>
<td>Astereae Martynov (1820), nom. cons.</td>
<td>3.73 ± 0.0174</td>
<td>9</td>
<td>Z</td>
<td>2</td>
<td>1.87</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Inula salicina</em> L.</td>
<td>Astereae Martynov (1820), nom. cons.</td>
<td>3.39 ± 0.016</td>
<td>9</td>
<td>Z</td>
<td>2</td>
<td>1.7</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td><em>Lotus corniculatus</em> L.</td>
<td>Fabaceae Lindl. (1836), nom. cons.</td>
<td>2.55 ± 0.0024</td>
<td>9</td>
<td>S</td>
<td>4</td>
<td>0.64</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Medicago falcata</em> L.</td>
<td>Fabaceae Lindl. (1836), nom. cons.</td>
<td>1.8 ± 0.0011</td>
<td>10</td>
<td>G</td>
<td>2</td>
<td>0.9</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td><em>Laserpitium latifolium</em> L.</td>
<td>Apiaceae Lindl. (1836), nom. cons.</td>
<td>5.78 ± 0.0044</td>
<td>9</td>
<td>G</td>
<td>2</td>
<td>2.89</td>
<td>22</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Peucedanum cervaria</em> Cusson ex Lapeyr.</td>
<td>Apiaceae Lindl. (1836), nom. cons.</td>
<td>4.04 ± 0.0035</td>
<td>9</td>
<td>Z</td>
<td>2</td>
<td>2.02</td>
<td>22</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td><em>Salvia pratensis</em> L.</td>
<td>Lamiaceae Martynov (1820), nom. cons.</td>
<td>0.91 ± 0.0012</td>
<td>10</td>
<td>G</td>
<td>2</td>
<td>0.46</td>
<td>18</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Salvia verticillata</em> L.</td>
<td>Lamiaceae Martynov (1820), nom. cons.</td>
<td>1.37 ± 0.0014</td>
<td>9</td>
<td>G</td>
<td>2</td>
<td>0.68</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>11</td>
<td><em>Trifolium medium</em> L.</td>
<td>Fabaceae Lindl. (1836), nom. cons.</td>
<td>8.62 ± 0.0056</td>
<td>9</td>
<td>Z</td>
<td>10</td>
<td>0.86</td>
<td>80</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Trifolium montanum</em> L.</td>
<td>Fabaceae Lindl. (1836), nom. cons.</td>
<td>2.54 ± 0.0017</td>
<td>9</td>
<td>Z</td>
<td>2</td>
<td>1.27</td>
<td>16</td>
<td></td>
</tr>
</tbody>
</table>

Values marked * come from Bureš et al. (2004). The internal standards (Int. stand.) used were: B, *Bellis perennis* L. (2C = 3.6 pg); G, *Glycine max* Merr. ‘Polanka’ (2C = 2.5 pg); S, *Solanum lycopersicum* L. ‘Stupnické polní tyčkové rané’ (2C = 1.96 pg); Z, *Zea mays* L. ‘CE-777’ (2C = 5.43 pg).

No herbaria collections were obtained within this study. All these species were, however, repeatedly documented from the region. Specimens of all these species from the region are available in collections of F. A. Novák from 1910 to 1925 and are deposited in the herbaria of the Charles University, Prague, Czech Republic (PRC).

SE, standard error.
for the purpose of this study from plants collected in the study region by V. Jarolimová (Campanula rotundifolia L., Asperula cynanchica L., Asperula tinctoria L. and Salvia verticillata L.).

Species traits

The data on species traits were collected in a previous study (Tremlová & Münzbergová, 2007); I used seed production per plant, seed weight, seed bank survival, seedling establishment success, seed dormancy and production of above-ground biomass within a single field season in this study.

I estimated seed weight by weighing five groups of ten seeds and seed production per plant by counting number of seeds in 20 randomly selected individuals in three populations of the species. I measured traits related to plant growth in an open-air common garden experiment, in Průhonice, central Bohemia, Czech Republic. The climate in the garden is comparable with the climate in the area where the species were collected. As plants grown in pots are more susceptible to drying out than plants in the field, the pots received additional water daily. In late summer (August to September) 2003, I sowed 50 seeds of a single species in 19 × 19 × 19 cm pots in a common garden in a 1 : 2 mixture of sand and garden soil. For each species, I used seeds originating from three different populations. I placed seeds from one locality into one pot; there were three replicates per population and species, giving nine pots per species.

In November 2003, I recorded germination of the seeds as a binary variable – seeds germinated in autumn or they did not (i.e. germinated just in spring). The ability to germinate in the autumn indicates that the seeds do not possess any type of dormancy. For determining seed dormancy, it is important that the seeds were sown shortly after being harvested. I refer to this variable as seed dormancy (yes/no).

In May 2004, I recorded number of plants in the pots. This number served as estimate number of seedlings that germinated, survived and established. I refer to this value as establishment success.

In November 2004, I harvested the plants, dried to constant weight and weighed. I used the weight of the largest plant per species as an estimate of growth ability of the species; in all cases there were 1–3 large plants in the pot and sometimes also many small ones. We have previously shown that size of the largest plant provides a relatively good estimate of the maximum size a plant can reach in natural conditions within 1 year (Tremlová & Münzbergová, 2007).

To estimate ability to survive in the seed bank, I buried three nylon bags per species, each containing 50 seeds, at each of two different localities in November 2003, excavated them in October 2004 and tested the excavated seeds for viability. I regularly watered the seeds with distilled water on Petri dishes, kept them in a growth chamber under a fluctuating regime (12 h light at 20 °C, 12 h dark at 10 °C) and regularly removed germinated seeds. I stimulated the seeds that did not germinate by adding Gibberellic acid and abrading by sandpaper. I tested the seeds that still did not germinate and did not decay for viability using the tetrazolium test. I counted all seeds identified as viable by any of the methods. I used the same procedure to estimate the viability of fresh seeds (proportion of viable seeds) to provide a baseline from which to estimate the decline in germination over time. The ability to form a seed bank indicates that the seed can survive given that it does not have suitable conditions for germination. It, however, does not imply it has any intrinsic dormancy (Baskin, Thompson & Baskin, 2006).

Data analyses

I used 2C values (holoploid genome size) as well as 1Cx (monoploid genome size) values in the analyses. The holoploid genome size is a value related mainly to cell volume, monoploid genome size is, in contrast, mainly related to cell cycle time (Bennett, 1987; Grotkopp et al., 2004; Beaulieu et al., 2007a, b) I tested the relationship between 2C and 1Cx value and all the species traits using linear regression, with 2C and 1Cx value taken as independent variables. The exception was presence/absence data on seed dormancy tested using logistic regression. The data on seed bank and seed germination were square root transformed and data on above-ground biomass and seed production were log transformed before the analyses to gain normality.

To take into account species phylogeny, I performed a phylogenetical independent contrast (PIC) analysis (e.g. Westoby, 2002; Tremlová & Münzbergová, 2007). In this way, I could test the relationships between 2C and 1Cx values and species traits after taking the phylogenetical relationships into account. First, I performed a pairwise PIC analysis. I also performed a full independent contrasts analysis in Phylocom (Webb, Ackerly & Kembel, 2007). To do this, I used Phylomatic (Webb & Donoghue, 2005) to create a consensus tree for the species as an input. The consensus tree provided by Phylomatic (Webb & Donoghue, 2005), is, however, not well resolved for the studied species and contains a lot of polytomies. I used probability based on sign test provided by Phylocom to assess significance of the relationship between 2C and 1Cx values and species traits. To get insights into the relationships between the single...
There was a strong negative correlation between seed weight and establishment success of the seeds in the dataset. There was also a significant positive correlation between seed weight and seed dormancy and between seed bank and seed production; no other correlations were significant (Table 2).

There were no significant relationships with genome size in the regression analyses and several strongly significant relationships were detected in the pairwise PIC analyses (Table 3). The results based on the pairwise PIC analysis showed strong negative relationship between monoploid genome size and production of above-ground biomass within 1 year (Fig. 1A) and between monoploid genome size and seed establishment success (Fig. 1B). There was also a strong positive relationship between monoploid genome size and seed weight (Fig. 1C) and between holoploid genome size and seed dormancy (Fig. 1D). No other relationships were significant (Table 3).

The relationship between holoploid genome size and seed dormancy was also marginally significant when performing the full independent contrasts analysis using Phylocom, based on consensus phylogenetical tree, but no other relationships significant in the pairwise PIC analysis, were significant. This analysis, however, showed an additional significant positive relationship between monoploid genome size and seed bank survival (not shown).

**DISCUSSION**

The results indicate no significant relationship between holoploid genome size and monoploid
genome size and species traits in regression analyses, but several strong significant relationships in pair-wise PIC analyses. These relationships were found across a number of congeneric pairs in species sharing the same habitat, thus providing the estimate of the effect of genome size without confounding effects of different habitats of the species. The results based on pair-wise PIC do not correspond to results derived using full independent contrasts based on the consensus phylogenetical tree. This may be because the within-family resolution is generally missing in the consensus tree (Webb & Donoghue, 2005), making this tree unsuitable for the purpose of this study. While the full independent contrasts approach is useful when working with large datasets for unrelated species (Webb & Donoghue, 2005), it is not suitable for the relatively small set of closely related species used here. I thus suggest that the results based on the pairwise PIC are more informative in this case.

Using the simple PIC analysis, I found three strong significant relationships with monoploid genome size and one strong significant relationship with holoploid genome size. In this study, monoploid genome size had a strong negative effect on production of above-ground biomass within 1 year. Species with larger monoploid genome sizes have longer cell cycle time (e.g. Bennett, 1987; Grotkopp et al., 2004) and my data suggest that cell cycle time has direct consequences for plant growth over one field season. This relationship also corresponds to the findings of Bennett, Leitch & Hanson (1998) who suggested that weedy species, i.e. quickly growing species, have small genome sizes. Also, Bennett (1987) demon-
strated that ephemeral species have on average smaller genome sizes than long-lived perennials. The results presented here demonstrate that the relationship between individual growth rate and monoploid genome size holds even within a single growth form, perennial herbs, from the same habitat after taking phylogeny into account.

This study also demonstrated a strong positive relationship between monoploid genome size and seed weight. A similar relationship was repeatedly demonstrated both within genera (e.g. Wakamiya et al., 1993; Grotkopp et al., 2004) and over a range of unrelated species (Thompson, 1990; Knight et al., 2005). Beaulieu et al. (2007a) demonstrated that the relationship is not linear, but, in fact, has a more complex shape. Here, I confirmed that a linear relationship could be found also over a range of species pairs from the same habitat conditions.

I also found strong significant negative relationship between monoploid genome size and seed establishment success. This relationship was in the opposite direction than the relationship between monoploid genome size and seed weight and was because of poorer germination in larger seeds. This contradicts studies indicating that larger seed size is usually associated with better germination and seedling establishment (Harper, 1977). My data, however, come from germination in a common garden, where the plants received additional water, and the advantage of being larger may not be important. Furthermore, the data come from a comparison of pairs of closely related species and I am not aware of any other study comparing germination success of seeds of different size from a group of closely related species.

I did not find a significant relationship between genome size and seed production, despite the significant relationship between genome size and seed weight and the commonly demonstrated relationship between seed size and seed production (Eriksson & Jakobsson, 1998; Moles & Westoby, 2004; Moles et al., 2004). In this dataset no relationship between seed size and seed production was, however, found. As for seed germination, this may be because most studies on the seed size/seed production trade-off did not take phylogeny into account and did not use species from the same habitat. The results based on pairwise PIC analysis showed no relationship between holoploid or monoploid genome size (1Cx and 2C value) and seed bank survival, suggesting that the ability of seeds to form a permanent seed bank cannot be predicted from these values.

Holoploid genome size was significantly correlated only with seed dormancy when using pairwise PIC analysis. This relationship was also marginally significant when using the analysis based on the Phylomol consensus tree. The data suggest that species with smaller holoploid genome sizes tend to germinate in autumn, whereas species with larger genomes are more likely to germinate in spring. The total DNA amount is known to be related to cell size, suggesting that the species with smaller cell sizes tend to show lower levels of dormancy.

Generally, monoploid genome size was a better predictor of species traits than holoploid genome size in this study. This finding corresponds to findings of Grotkopp et al. (2004) but contrast, for example, with Beaulieu et al. (2007a, b). In this study, the higher number of significant relationships with monoploid genome size may be because the monoploid genome size is related to cell cycle time and most of the traits considered in this study are directly related to plant growth.

CONCLUSIONS

This study revealed several strong significant, and many non-significant, relationships between genome size and species traits and it generally confirms previous findings on the effect of genome size on species traits, while adding information on the generality of these patterns. Several strong relationships were revealed in a pairwise PIC analysis over a range of genera from the same habitat type and it was thus possible to conclude that these patterns were not as a result of species phylogeny or habitat type but show a correlation with genome size. Importantly, the results are based on perennial herbs only and thus demonstrate the validity of the genome size/species traits relationships within this growth form.

ACKNOWLEDGEMENTS

I would like to thank to V. Jarolímová for estimating the chromosome numbers and P. Trávníček for help with cytometric analyses. This study was supported by GAAV A60050623. It was also partly supported by MSMT 0021620828 and AV0Z60050516.

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