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RESEARCH NOTES

Genome Size and Ploidy Level of Commercial *Eustoma grandiflorum* (Raf.) Shinners

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ABSTRACT

***Eustoma grandiflorum* is considered as the 'next rose' in floriculture, ranking top-ten in cut flowers. In this study, we investigated the ploidy level and genome size of 28 commercial cultivars of *E. grandiflorum* through flow cytometry. The analysis of each cultivar showed that only one cultivar was tetraploid, whereas the rest were diploids. By comparing with a standard reference genome of *Solanum lycopersicum*, the genome size (1C) of *E. grandiflorum* cultivars ranged from 1.26 to 2.64 Gb, which was in line with their ploidy levels and previous data. Although a large number of plant phenotypic diversities were observed in the experimental cultivars, the genome size displayed little difference in diploids, indicating that the monoploid DNA amount of *E. grandiflorum* is relatively conserved during artificial selection. It is possible to sequence the genome of *E. grandiflorum* using the latest sequencing techniques, which could provide a solid foundation for molecular biology research and molecular breeding for *E. grandiflorum*.**

Keywords: Genomics, Germplasm, Lisianthus, Nuclear DNA amount, Polyploidy.

INTRODUCTION

Eustoma grandiflorum (Raf.) Shinners belongs to the family of Gentianaceae and is native to the warm regions of southern United States, northern Mexico, and the northern parts of South America (Marques *et al*., 2018). Lisianthus, the common name of *E. grandiflorum*, is a relatively new floral crop to the floricultural market and is widely used as cut flowers (Hankins and Mullins, 2019). In the past 30 years, Lisianthus went from a practically anonymous plant to one of the top-ten cut flower crops in the world, now considered as the 'next rose' and creates a miracle in floricultural breeding (Fang *et al*., 2018). The wild type of *E. grandiflorum* is a diploid species with the ability both for selfing and cross-pollination. The commercial cultivars are almost F_1 hybrids in floricultural market and are commonly propagated by seed (Jafari *et al*., 2017).

E. grandiflorum is economically and culturally important around the world, with rising interests of all aspects in this floricultural crop and leading to a parallel increase in scientific literature. However, it is also an 'orphan plant' in floriculture research, still lacking the research interest of other ornamental cut flowers such as roses or lilies. Limited research has been done regarding the inheritance of ornamental traits and its regulation genes in *E. grandiflorum*, such as the characterization of several MADS-box

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genes involved in floral development (Chuang *et al*., 2018; Nakano *et al*., 2011). However, the functional analysis of the abovementioned genes were still studied in the transformed *Arabidopsis* plants, while the genetic transformation of *E. grandiflorum* was well studied in the late 20th century (Deroles *et al*., 1993; Giovannini *et al*., 1996; Handa *et al*., 1995; Ledger *et al*., 1997; Semeria *et al*., 1996). This may be due to lack of genomic information leading to research obstacles in *E. grandiflorum*. In addition, two independent studies have measured the nuclear DNA content (2C value) of *E. grandiflorum*, which is 3.26 pg to 3.53 pg for diploid and 6.33 pg for tetraploid (Lindsay *et al*., 1994; Yumbla-Orbes *et al*., 2020).

In this study, the genome size and ploidy level of 28 commercial cultivars were investigated to provide a basic genomic information for *E. grandiflorum*.

MATERIALS AND METHODS

Plant Materials

In this study, we selected 28 commercial cultivars of *E. grandiflorum* to analyze the ploidy level and genome size. These cultivars represent the most popular commercial cultivars in the floricultural market with different flower colors and shapes. The youngest three terminal leaves of each cultivar were measured. The cultivars were planted by SAKATA® (Japan) and the plant seedlings were obtained from Yunnan Dianxi Flower Co., Ltd. (Yunnan Province, China). All seedlings were planted separately in a greenhouse (without heating) under natural conditions at the experimental farm of Yunnan Academy of Agricultural Sciences (Yunnan Province, China).

Ploidy Level and Genome Size Determination

Ploidy analysis and genome size determination of each cultivar was conducted by a flow cytometer (BD FACScalibur, BD Bioscience, USA), equipped with a 488 nm and a 635 nm laser, together with a chromosome ploidy analysis software of BD FACStation. Briefly, the leaf sample from one individual plant (typically 20 mg) was placed in the center of a plastic culture dish

(Guangzhou JetBio-Filtration Co., Ltd., TCD000090) with 1 mL ice-cold nuclei isolation buffer (45 mM $MgCl_2 \cdot 6H_2O$, 20 mM MOPS, 30 mM Sodium citrate, 1% (W/V) PVP 40, 0.2% (v/v) Tritonx-100, 10 mM Na_2EDTA, pH= 7.0). Then, the tissue was chopped immediately in the buffer with a new sharp razor blade, and the homogenate was mixed by pipetting up and down for several times (avoiding air bubbles). The homogenate was then filtered through a 42-mm nylon mesh into a labeled sample tube to isolate nuclei from leaf debris, and stained with 25 µL DNA fluorochrome PI (propidium iodide, 50 mg mL^{-1}). The mixture solution with stained nuclei of the standard and the sample were measured through flow cytometer with at least 10,000 nuclei. The Coefficient of Variation (CV) of both sample and reference for every measurement was controlled within 5%. One sample per cultivar was analysed to determine the ploidy level and genome size by comparing with a standard reference of *Solanum lycopersicum* (derived from the 'Heinz 1706' inbred line, genome size (1C) was 0.88 Gb) (Consortium, 2012) based on the method of Arumuganathan and Earle (1991). Calculation of Genome Size (GS) of each sample was performed by the following formulas: GS= (Sample fluorescence intensity/Reference fluorescence intensity)×0.88 Gb.

One-way ANOVA with Tukey's HSD post-hoc test was used to compare the mean of genome size in different series of *E. grandiflorum* diploid cultivars at the 5% significance level.

Plant Phenotype Measurement

The phenotype of 28 commercial cultivars were measured, including the plant height

and flower diameter. The data of plant height was obtained from five individual plants in the same planting time. The flower diameter was measured from the full open stage flower with five replicates. The relationship between these phenotypic measures and the genome size of cultivars was tested using linear regression analyses. Data analysis and statistics were performed by Microsoft Excel 2016 and Data Processing System (Tang and Zhang, 2013).

RESULTS AND DISCUSSION

The genome size and ploidy level of 28 commercial *E. grandiflorum* cultivars were measured and analyzed (Figures 1, 2; Table 1). The genome size (1C) of diploids ranged from 1.26 to 1.52 Gb, displaying some variation among the genome size in diploid cultivars. We then compared the genome size between different series of cultivars (i.e. Aube, Corell, Celeb, Reina, etc.). For instance, Reina cultivars displayed the highest genome size (1.51±0.00 Gb, n= 2), while Celeb varieties showed the lowest values (1.41±0.02 Gb, n= 5), but we found no significant differences between diploid series (Figure 3). Moreover, these cultivars displayed diverse phenotypes with different flower color, flower type, and plant height. To test the relationship between phenotypic traits and genome sizes in *E. grandiflorum*, we carried out linear regression analyses of genome size with plant height and flower diameter in diploid cultivars. Although there was a tendency for a positive relationship between genome size and plant height, as well as between genome size and flower diameter, the regression analysis revealed no significant relationship among these variables (Figure 4).

Previously, the terms of DNA diploid or tetraploid were used to describe the results of flow cytometry without measuring the number of chromosomes (Lindsay *et al*., 1994). In this study, we compared the nuclear DNA content of 28 commercial cultivars by flow cytometry with the previous study. In the 28 commercial cultivars, the ploidy level of most tested cultivars was diploid, except for cultivar 'Corelli 899', which was a tetraploid. However, no difference in plant height and flower size were observed between tetraploid 'Corelli 899' and the other 27 diploid cultivars, indicating that the phenotypic characteristics of tetraploid cultivar was within the range of variability of diploid cultivars. Further, the genome size (1C) of 'Corelli 899' was 2.64 Gb, which was approximately twice that of diploid cultivars (1.44±0.06 Gb, n= 27). This was consistent with the results of ploidy level, i.e. doubled chromosomes with doubled genome size. Previously, it was reported that the genome size (1C value) of diploid was about 1.56 Gb, and that of tetraploid was 3.09 Gb in *E. grandiflorum* (Lindsay *et al*., 1994; Yumbla-Orbes *et al*., 2020), which was in line with our results. In all, the variation of genome size displayed small differences, indicating the genome of *E. grandiflorum* was conserved during the artificial breeding process.

In plants, the genome of *E. grandiflorum* is not small, since the genome of model plant *Arabidopsis thaliana* is only 0.13 Gb (Cheng *et al*., 2017). However, if compared with daylilies (Hemerocallis) or tulips (Tulipa), the genome size of *E. grandiflorum* is relatively small. For example, the nuclear DNA content of two cultivars in *Hemerocallis×hybrida* were detected from 7.84 to 16.98 Gb (Podwyszyńska *et al*., 2015), while the genome sizes (2C) of species in the genus of Tulipa ranged from 32.29 to 67.48 Gb (Zonneveld, 2009). Recently, with the improvement of genomic sequencing technology and assemble quality, more and more floricultural plant genomes have been determined, such as *Nymphaea colorata* (409 Mb) (Zhang, L. *et al*., 2020), *Phalaenopsis aphrodite* (1.03 Gb) (Chao *et al*., 2018), *Helianthus annuus* (3.60 Gb) (Badouin *et al*., 2017) and *Dendrobium catenatum* (1.11 Gb) (Zhang, G.-Q. *et al*., 2016). Therefore, the genome of *E. grandiflorum* can be well sequenced by applying the latest sequencing techniques.

Figure 1. The 28 commercial cultivars of *E. grandiflorum* used in this study**.** The number corresponds to the cultivar in Table 1. Bars= 1 cm.

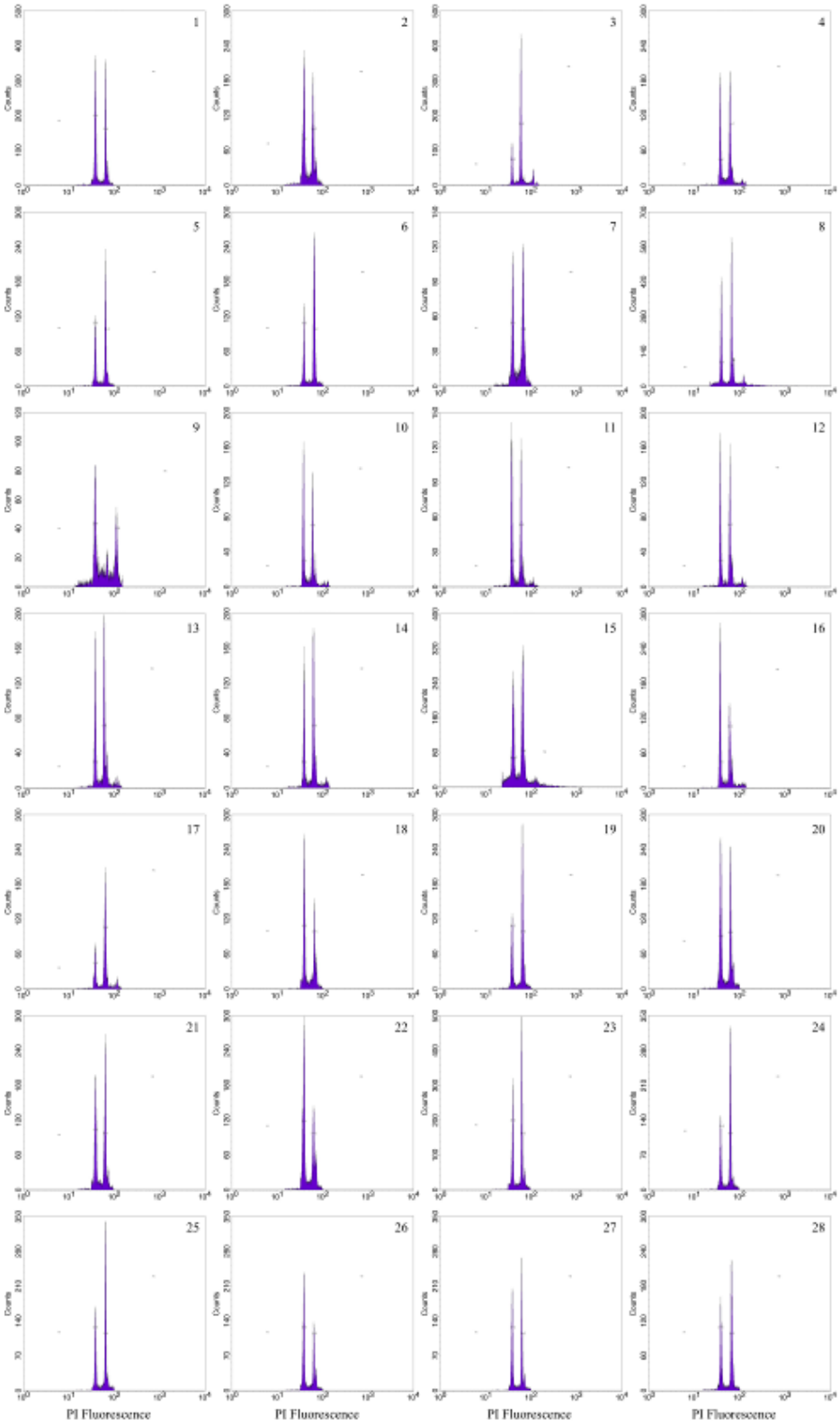

Figure 2. Representative flow cytometry histograms with DNA content of the 28 commercial *E. grandiflorum* cultivars used in this study. The number corresponds to the cultivar in Table 1. The DNA content values are described in accompanying table.

Table 1. Genome size, ploidy level and plant phenotype of *E. grandiflorum* commercial cultivars.

No	Cultivar name	Flower color	Reference fluorescence intensity	Sample fluorescence intensity	Reference CV[a] (%)	Sample CV[a] (%)	Genome size (1C)	Ploidy level	Plant height (cm)	Flower diameter (cm)
1	Aube 297	Deep lavender	37.68	63.40	3.31	4.36	1.48 Gb	Diploid	51.6 ± 4.04	9.4 ± 0.42
2	Aube 406	Red	38.28	60.50	3.89	4.05	1.39 Gb	Diploid	43.8 ± 3.56	9.8 ± 0.27
3	Arosa 324	Champagne	37.51	57.95	3.39	3.03	1.36 Gb	Diploid	55.8 ± 3.35	7.8 ± 0.27
4	Arosa 945	Blue flash	37.21	61.38	3.62	4.62	1.45 Gb	Diploid	52.8 ± 1.92	9.8 ± 0.27
5	Corelli 753	Blue	37.50	63.91	3.57	4.20	1.50 Gb	Diploid	68.2 ± 3.83	11.0 ± 0.35
6	Corelli 754	Light lavender	37.63	64.00	3.44	3.75	1.50 Gb	Diploid	61.2 ± 1.30	8.6 ± 0.42
7	Corelli 755	Yellow	38.23	65.73	3.81	4.56	1.51 Gb	Diploid	56.4 ± 5.32	9.7 ± 0.45
8	Corelli 756	Salmon pink	38.05	54.41	3.21	3.64	1.26 Gb	Diploid	56.8 ± 2.39	9.3 ± 0.45
9	Corelli 899	Deep pink	37.28	111.89	4.53	4.29	2.64 Gb	Tetraploid	57.8 ± 3.56	9.3 ± 0.45
10	Celeb 348	Garnet	36.88	58.48	3.66	3.62	1.40 Gb	Diploid	71.2 ± 2.59	10.2 ± 0.57
11	Celeb 301	Turn red	36.97	58.39	3.50	3.36	1.39 Gb	Diploid	42.8 ± 1.92	7.7 ± 0.57
12	Celeb II	Green	37.34	59.83	3.42	3.51	1.41 Gb	Diploid	59.2 ± 3.03	9.1 ± 0.55
13	Celeb 116	Pink	37.29	59.23	3.54	3.23	1.40 Gb	Diploid	58.4 ± 1.52	5.4 ± 0.42
14	Celeb 304	Lilac	37.89	62.38	4.11	3.96	1.45 Gb	Diploid	68.8 ± 2.59	8.4 ± 0.42
15	Croma III	White	39.32	64.99	4.22	4.62	1.45 Gb	Diploid	66.6 ± 3.97	5.7 ± 0.45
16	F16-776	Spiral pink	36.83	59.45	3.40	59.45	1.42 Gb	Diploid	48.0 ± 2.35	10.3 ± 0.45
17	F15-352	Pink	37.25	62.07	4.10	3.91	1.47 Gb	Diploid	58.8 ± 2.39	9.7 ± 0.45
18	Reina II	Deep lavender	38.38	66.08	3.38	4.83	1.52 Gb	Diploid	57.4 ± 3.71	7.6 ± 0.65
19	Reina III	Pink flash	37.39	64.15	3.86	4.18	1.51 Gb	Diploid	70.8 ± 3.83	9.7 ± 0.45
20	Rosita 440	Pink	37.67	62.08	3.89	3.52	1.45 Gb	Diploid	64.2 ± 3.11	5.7 ± 0.45
21	Rosita 484	Pure white	37.88	61.41	3.98	3.57	1.43 Gb	Diploid	74.8 ± 2.17	7.7 ± 0.45
22	Rosita 199	Color pink	37.43	61.63	4.01	4.16	1.45 Gb	Diploid	64.2 ± 3.03	6.4 ± 0.42
23	Rosita 593	Pure white	38.14	61.96	3.47	3.60	1.43 Gb	Diploid	64.4 ± 2.70	8.7 ± 0.45
24	Rosita 619	Blue picotee	38.16	61.60	3.75	3.06	1.42 Gb	Diploid	66.4 ± 3.51	7.5 ± 0.50
25	Rosita 203	Pink picotee	37.83	63.14	3.45	3.15	1.47 Gb	Diploid	64.0 ± 4.06	7.2 ± 0.27
26	Voyage 738	Pure white	37.34	63.15	3.50	4.45	1.49 Gb	Diploid	62.8 ± 2.59	9.8 ± 0.27
27	Voyage 782	Green	37.42	62.02	3.50	3.87	1.46 Gb	Diploid	58.6 ± 3.71	10.1 ± 0.55
28	Voyage 928	Champagne	38.14	65.69	3.77	4.00	1.52 Gb	Diploid	68.0 ± 4.47	11.0 ± 0.35

[a] CV: Refers to Coefficient of Cariation.

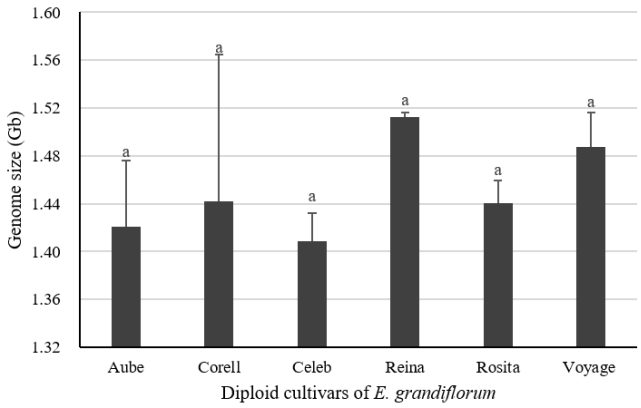

Figure 3. Comparison of genome size in different series of *E. grandiflorum* diploid cultivars**.** Data represent mean values of genome size in each diploid cultivar series. Small letters denote non-significant differences of genome size among different cultivar series.

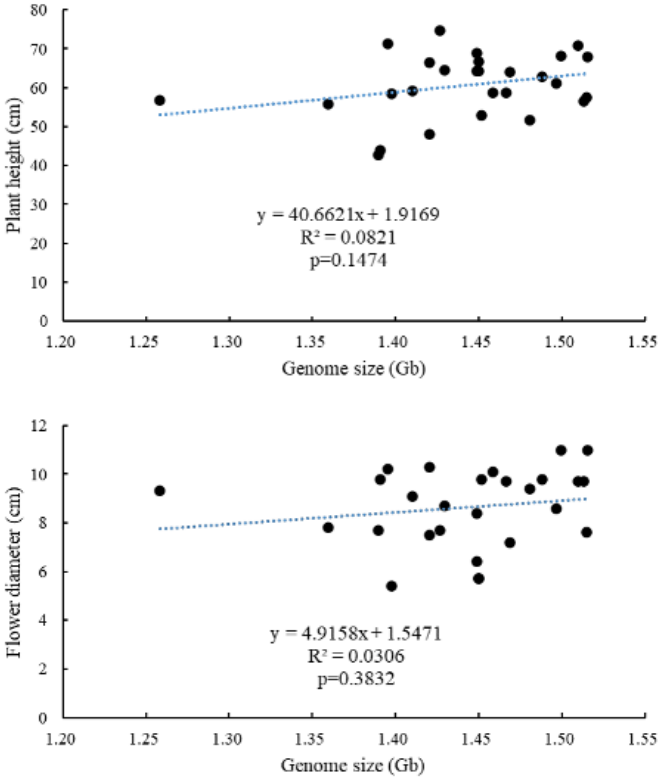

Figure 4. Results of linear regression analyses between phenotypic traits and genome sizes in diploid cultivars of *E. grandiflorum*. Statistical significance was analyzed under 5% significance level ($p < 0.05$).

CONCLUSIONS

In conclusion, this study assessed the ploidy level and genome size of commercial cultivars in *E. grandiflorum*. Flow cytometer analysis of leaf samples showed that only one selected cultivar was tetraploid, whereas the rest of 27 cultivars were diploids. The average genome size (1C) of diploid plants was about 1.44 Gb, whereas the tetraploid was almost doubled to 2.64 Gb. Moreover,

there was no correlation between genome size and plant phenotypes in diploid cultivars, and no difference in the genome size of each diploid cultivar series. In additional, our data are consistent with previous independent studies on the genome size of *E. grandiflorum*, indicating that the *E. grandiflorum* genome is relatively conserved during breeding and selection, although large diversity in plant phenotype was achieved.

Whole-genome sequencing is at the cutting edge of life sciences in the new millennium. Recently, using PacBio Sequel Ⅱ platform and the CCS (Circular Consensus Sequencing) sequencing strategy, the sequencing of medium-sized genomes, like *E. grandiflorum*, has become cheap and effective. Genome sequence of *E. grandiflorum* is crucial and essential for further in-depth research of *E. grandiflorum* in the era of molecular biology and genomics. With the development of new biotechnology, such as gene editing, many characteristics of *E. grandiflorum* that did not exist in model plants are now an advantage for studying specific traits and the involved regulation mechanism. For instance, several homolog genes involving in vernalization have been identified and characterized in *E. grandiflorum*. These findings suggested that flowering regulation by vernalization in *Eustoma* differs from the paradigm developed for *Arabidopsis* (Nakano *et al*., 2011). However, the vernalization mechanism is still unclear in *Eustoma*. In addition, *E. grandiflorum* harbours rich flower colours, especially the special blue petals are a potential model for studying the regulation mechanism of blue flowers. A recent study reported that a new flavonol triglycoside has been isolated from the flower of *E. grandiflorum*, as well as eight known flavonols (Abe *et al*., 2016). More importantly, a new efficient floral-dipping transformation of post-anthesis technique has been established that provides an easier way to conduct the transformation and gene edition in *E. grandiflorum* (Fang *et al*., 2018). However, the genomic information of *E. grandiflorum* are prerequisites for all future studies. Therefore, it is necessary to sequence the genome of *E. grandiflorum*, which could provide a breakthrough for the molecular researches, as well as the plant breeding via biotechnology.

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اندازه ژنوم و سطح پلوئیدی *Eustoma grandiflorum* (Raf.) Shinners تجاری

ف. لی، ی. چنگ، ر. یو، و س. یانگ

چکیده

امروزه، گیاه *Eustoma grandiflorum* در گلکاری به عنوان "رُز بعدی" در نظر گرفته می شود و در رتبه دهم گل‌های شاخه‌بریده قرار دارد. در این پژوهش، سطح پلوئیدی و اندازه ژنوم ۲۸ رقم تجاری *E. grandiflorum* از طریق فلوسایتومتری بررسی شد. تجزیه و تحلیل هر رقم نشان داد که تنها یک رقم تتراپلوئید و بقیه دیپلوئید بودند. با مقایسه با ژنوم مرجع استاندارد *Solanum lycopersicum*، اندازه ژنوم (1C) ارقام *E. grandiflorum* از ۱.۲۶ Gb تا ۲.۶۴ Gb متغیر بود که با سطوح پلوئیدی و داده های قبلی آنها مطابقت داشت. اگرچه تنوع زیادی در فنوتیپی گیاهی در ارقام آزمایش مشاهده شد، اندازه ژنوم تفاوت کمی در دیپلوئیدها نشان داد، که نشان می‌دهد مقدار DNA مونوپلوئید *E. grandiflorum* در طول انتخاب مصنوعی نسبتاً حفظ می‌شود. به این ترتیب، تعیین توالی ژنوم *E. grandiflorum* با استفاده از آخرین تکنیک های توالی یابی، که می تواند پایه ای محکم برای تحقیقات زیست شناسی مولکولی و اصلاح ژنتیکی مولکولی برای *E. grandiflorum* فراهم کند، امکان پذیر است.