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DNA C-VALUES OF 20 INVASIVE ALIEN SPECIES AND 3 NATIVE SPECIES IN SOUTH CHINA

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Abstract - Cultivated fields and forests in South China are experiencing serious damage due to invasive alien plants. We investigated the relation between DNA C-values and invasiveness. The DNA C-values of 23 species ranged from 0.39 pg to 3.37 pg. Herbs, perennials and native species had higher mean DNA C-values than shrubs, annuals and invasive alien species. DNA C-values decreased with increasing invasiveness. *Paederia scandens*, a harmful native species, has the lowest DNA C-value among the perennials, indicating that native species with low nuclear content may also possess an invasive potential.

Key words: China; DNA C-value; flow cytometry; invasiveness; South China

INTRODUCTION

Invasive species have had a very negative impact on biodiversity and economy, worldwide (Mack et al., 2000; Škraba et al.,, 2013). China is a large country with rich biodiversity, but its environment is especially vulnerable to invasive species (Xie et al., 2001). Many invasive alien species have been introduced to China (Ding et al., 2006; Liu et al., 2006; Weber and Li, 2008). Clonality, life form, geographic origin, regional distribution and degree of invasion of alien plants in China were reviewed recently (Liu et al., 2005; Huang et al., 2009; Yue et al., 2011; Lin et al., 2012).

The DNA C-value has been considered to be related to invasiveness (Rejmánek, 1996). In a large number of investigations covering many species in many families, it has been shown that naturalized alien species have smaller genomes than those that do not naturalize (Kubešová et al., 2010). Therefore, the DNA C-value possibly correlates with the invasive potential of angiosperms (Darling and Blum 2007; Chen et al., 2010; Kubešová et al., 2010). DNA C-values of many invasive species in different areas have been measured using flow cytometry with different sample treatment methods (Fu et al., 2007; Chen et al., 2010; Kubešová et al., 2010).

In order to understand the relation between invasion and nuclear DNA content, and to evaluate the invasiveness of alien species in South China as well, the DNA C-values of 23 common species, including 20 invasive alien species with different invasion degrees, and 3 related native species, were measured.

MATERIALS AND METHODS

Twenty invasive alien species and 3 native species listed in Table 1 were collected from Guangdong Academy of Agricultural Sciences in Guangzhou

(23°15´N, 113°35´E). *Arabidopsis thaliana* (L.) Heynh. seedlings were grown in a growth chamber. The DNA content was measured using *A. thaliana* as an internal standard (Bennett et al., 2003; Bennett and Leitch 2005a; Praça-Fontes et al., 2011a).

Flow cytometry

Young leaves of all species were chopped with 2 mL buffer on ice with a single-edged razor blade in a sterile Petri dish. Otto buffers were used for *A. thaliana* (Praça-Fontes et al., 2011b), and Arumuganathan and Earle (1991) buffers were used for other species. Buffer containing released nuclei was filtered through a nylon filter with a 37-μm mesh diameter.

Nuclei were pelleted by centrifugation at 10 000 rpm for 10 min at 4°C. The nuclei were resuspended in 0.5 mL Arumuganathan and Earle buffer and 100 μL of 1 mg mL^{-1} DNase-free RNase A (KeyGEN Biotech^R). The nuclear suspensions were incubated for 30 min at 37°C, followed by staining in 400 μL of 130 mg mL^{-1} propidium iodide (PI, KeyGEN Biotech^R) in the dark for 30 min.

Nuclear suspensions of samples and *A. thaliana* were mixed. At least 10 000 nuclei from a single sample or mixtures were analyzed using an Accuri C6 flow cytometer (Accuri, Ann Arbor, MI). Analysis was based on light-scatter and fluorescence signals produced at 488 nm. CFlow software was used for data analysis (Galbraith 2009). The above experiments were repeated at least five times.

Chromosome number

The DNA C-values of *Ipomoea triloba* L. and *Pharbitis nil* (L.) Choisy were lower than in a previous report (Ozias-Akins and Jarret, 1994). This was possibly caused by differences in methods or changes in sample ploidy. In order to understand the reason for the low DNA C-values of *I. triloba* and *P. nil*, chromosome numbers were determined to see whether their ploidy changed or not. For this, tips of *I. triloba* and *P. nil* were fixed in acetic alcohol (1:3 v/v) (de Campos et al., 2011) at 8:00 to 8:30 a.m. for 2 h and then hydrolyzed at 60°C in 1 M HCl for 4 min. Finally, chromosomes were stained with 1% carbol fuchsin. The chromosomes were examined under a NIKON microscope at 100 x magnification and photographs of the chromosomes were taken.

Statistical analysis

The 2C genome size of *A. thaliana* used as internal standard was 0.32 pg as reported by Bennett et al. (2003). Statistical differences of DNA C-values among species were obtained by analysis of variance (ANOVA) and Scott Knott test (p <0.05).

Chromosome numbers were determined and ploidy analysis of *I. triloba* and *P. nil* carried out according to the methods of Srisuwan et al. (2006), Yang et al. (2009) and Padma et al. (2011).

RESULTS AND DISCUSSION

The DNA 1C-values of the 20 invasive alien species and the 3 native species varied from 0.39 pg in *Pilea microphylla* (L.) Liebm. to 3.37 pg in *Peperomia pellucida* (L.) Kunth (Table 1). Comparisons between single G_0/G_1 peaks of samples and two G_0/G_1 simultaneous peaks of the internal standard and samples showed that the mean G_0/G_1 peak channel value of samples decreased slightly as *A. thaliana* was used as an internal standard (Fig. 1). The DNA 1C-values of samples were approximately 0.1 to 0.3 pg lower than the values reported by others (Fu and Feng, 2007; Kubešová et al., 2010).

Compared with the results of Ozias-Akins and Jarret (1994), the DNA 1C-values of *I. triloba* and *P. nil* (0.75 to 0.85 and 1.15 pg, respectively in Ozias-Akins and Jarret (1994)) were lower in this experiment (0.48 and 0.71 pg, respectively), while there were no changes in chromosome numbers compared with previous reports (Lopez-Lavalle and Orjeda, 2002; Yang et al., 2009; Padma et al., 2011). As can be seen in Fig. 2, the genomes were diploid.

A low coefficient of variation (CV) is a necessary FCM parameter to ensure the accuracy of DNA C-val-

Table 1. List of 23 species in South China and their DNA 1C-values, life forms, geographic origins and invasion degree

Species	1C value (pg)[a]	Life forms	Geographic origins	Invasion degree reported by distinct researchers		
				Liu et al. (2006)[b]	Wang et al. (2008)[c]	Yue et al. (2011)[d]
Alternanthera philoxeroides (Mart.) Griseb.	2.14±0.06	Perennial	America	+ + +	+ + +	+ + +
Amaranthus viridis L.	0.55±0.01	Annual	Africa	+ +	+ +	+ + +
Bidens pilosa L.	1.46±0.01	Annual	America	+ + +	+ + +	+ + +
Bidens alba (L.) var. radiata	2.01±0.05	Annual	America	+ + +		+ + +
Celosia argentea L.	2.81±0.05	Annual	India		+ +	+ +
Conyza canadensis (L.) Cronq.	0.47±0.03	Annual	America	+ +	+ +	+ + +
Conyza sumatrensis (Retz.) Walker	1.84±0.05	Perennial	America	+	+	+ + +
Eupatorium catarium Veldkamp	0.79±0.02	Annual	America	+ +	+ + +	+ + +
Ipomoea cairica (L.) Sweet	0.70±0.02	Perennial	America	+	+ + +	+ + +
Ipomoea digitata L.	1.58±0.03	Perennial	China			
Ipomoea triloba L.	0.48±0.01	Annual	Asia			+ +
Mikania micrantha Kunth	1.59±0.02	Perennial	America	+ + +	+ + +	+ +
Mimosa pudica Linn.	0.85±0.01	Shrub	America	+ + +	+ +	+ +
Oxalis corymbosa DC.	1.01±0.02	Perennial	America	+ +	+ +	+ +
Paederia scandens (Lour.) Merr.	0.43±0.02	Perennial	China			
Peperomia pellucida (L.) Kunth	3.37±0.05	Annual	America	+ +	+	+
Pharbitis nil (L.) Choisy	0.71±0.03	Annual	America	+	+	+ +
Pilea microphylla (L.) Liebm.	0.39±0.03	Annual	America	+	+ +	+ +
Scoparia dulcis L.	0.74±0.02	Annual	America	+	+ +	+ + +
Solanum torvum Swartz	1.38±0.02	Shrub	America	+	+	+ +
Sonchus arvensis L.	1.38±0.05	Perennial	Europe			+ +
Wedelia chinensis (Osbeck.) Merr.	2.85±0.04	Perennial	China or Africa	+		
Wedelia trilobata L.	2.90±0.06	Perennial	America	+ + +	+ + +	+ + +

In order to understand different definitions by distinct researchers without confusion, notations of invasion degree were unified. + + + is the most serious invasion degree, + + is the medium invasion degree, + is the lowest invasion degree. [a] The 2C genome size of *A. thaliana* used as internal standard was 0.32 pg reported by Bennett et al. (2003). The nuclei of samples and internal standard were stained by PI. At least 10,000 nuclei were analyzed using a Accuri C6 flow cytometer. Analysis was based on light-scatter and fluorescence signals produced at 488 nm. [b] The invasiveness decreases from group I, group II to group III, which was defined by Liu et al. (2006). Group I, group II and group III were converted to + + +, + + and + here.
[c] The invasion degree was defined by Wang et al. (2008). + + + is the highest damaged degree, + + is the medium damaged degree, and + is the lowest damaged degree.
[d] The invasion degree was defined by Yue et al. (2011). The invasiveness decreases from III, II to I. III, II and I were converted to + + +, + + and + here.

ues (Galbraith, 2009). CVs below 5% are considered adequate for FCM assessments in plants. The CVs of the G_0/G_1 peaks of our 23 samples varied from 1.57% to 4.24%, showing reliable nuclear DNA contents. Otto's buffer was considered to be suitable for *A. thaliana* based upon the low CVs (<5%) (Praça-Fontes et al., 2011b). Arumuganathan and Earle buffer, which provides for lower CVs compared to other buffers, was favored for other samples (Doležel and Bartoš, 2005). The Accuri C6 flow cytometer also provided an excellent measurement platform with low CVs (Bai et al., 2012), and it was recommended for routine analysis of plant nuclear DNA contents, ploidy, or investigations of other issues requiring C-value determination (Galbraith, 2009).

Both plant and animal nuclei have been used as internal standards for measuring the plant DNA C-value. Animal standards were excluded for use of calibration in plant measurement by some researchers,

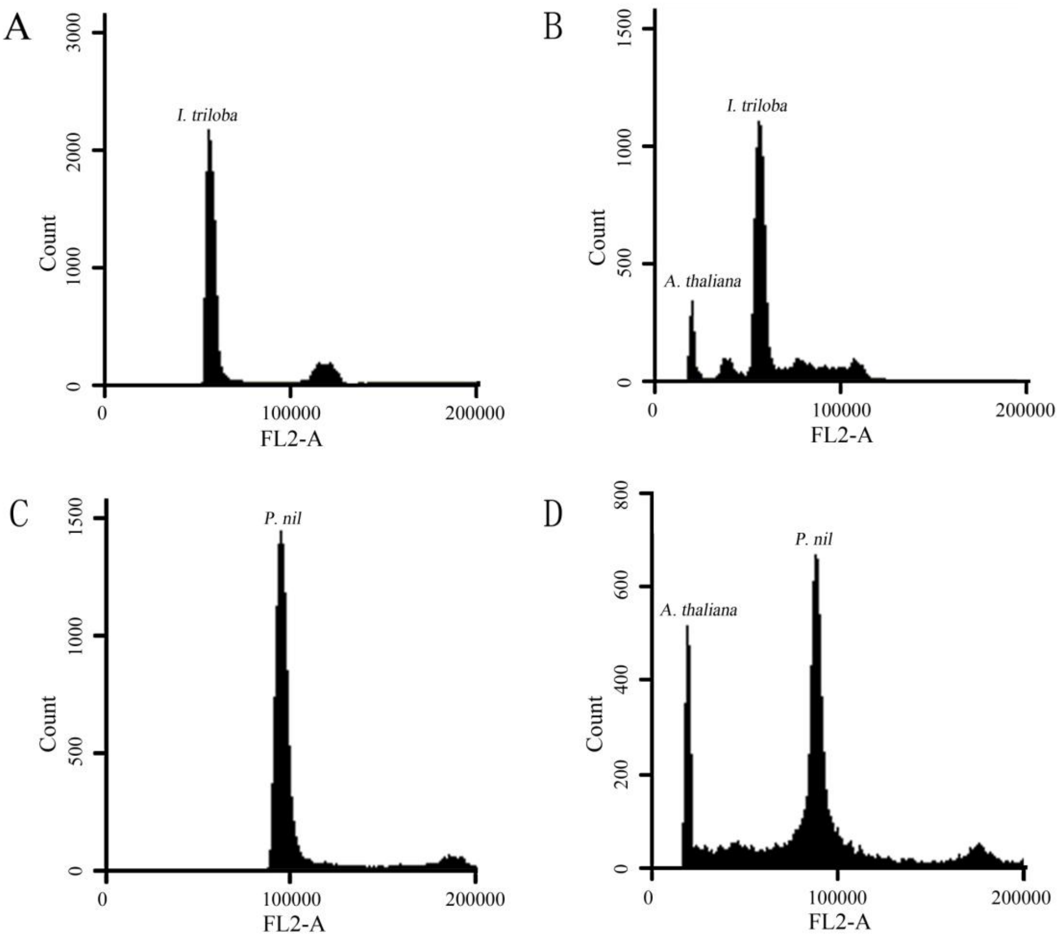

Fig. 1. Flow cytometry histograms. *A. thaliana* was used as an internal standard. The nuclei of samples were stained by PI. At least 10,000 nuclei were analyzed based on light-scatter and fluorescence signals produced at 488 nm. **A** *I. triloba* without internal standard, **B** *I. triloba* and internal standard (*A. thaliana*), **C** *P. nil* without internal standard, **D** *P. nil* and internal standard (*A. thaliana*). FL2-A is intensity of fluorescence measured through a 585/40 nm band-pass filter.

and *A. thaliana* should be used as a "gold" internal standard for plants (Bennett et al., 2003; Bennett and Leitch, 2005a; Doležel and Greilhuber, 2010; Praça-Fontes et al., 2011b). The DNA 1C-value of most samples was close to the reported value measured by using either chicken erythrocytes or plant species as internal standards (Fu and Feng, 2007; Kubešová et al., 2010), indicating that *A. thaliana* was suitable as a reference standard for plant DNA quantification.

Chen et al. (2010) compared the DNA 1C-values and basic genome sizes of 3 676 angiosperms. The results showed that the two values in herbs and perennials were significantly higher than those in trees and non-perennials, respectively, and DNA C-values also had significant effects on plant invasiveness. Comparing the DNA C-values of 29 species, including 6 native species from the same genus of invasive samples reported by Fu and Feng (2007), the same results as Chen et al. (2010) were obtained in this experiment (Table 2). Mean DNA 1C-values of herbs, native species and perennials were higher than in shrubs, invasive alien species and annuals, respectively, indicating that plants with a low nuclear content may commonly hold high invasive potential (Darling and Blum, 2007; Chen et al., 2010). However, DNA C-

Table 2. Mean, minimum and maximum of DNA 1C-values of different life forms and invasiveness

Classification	Groups	Mean (pg)	Min. (pg)	Max. (pg)
Life forms	Annual	1.25	0.39	3.37
	Perennial	1.64	0.43	2.90
	Shrub	1.11	0.85	1.38
Invasiveness	Invasive alien species	1.38	0.39	2.90
	Non-invasive native species[a]	2.51	0.43	4.70

DNA 1C-values of samples and reported native species were divided into different groups according to their ife forms and invasiveness. [a] Non-invasive native species includes six associated native species reported by Fu et al. (2007). The reported six native species were *Eupatorium chinense* L., *Bidens biternata* (Lour.) Merr., *Bidens bipinnata* L., *Alternanthera sessilis* (L.) DC., *Peperomia heyneana* Miq. Syst. Pip. and *Oxalis corniculata* L.. DNA C-values of these species were 3.769, 4.703, 3.885, 2.136, 1.760 and 1.480 pg.

Table 3. Mean, minimum and maximum of 1C-values of three invasion groups

Invasion degree	References								
	Liu et al.(2006)			Wang et al. (2008)			Yue et al. (2011)		
	Mean (pg)	Min. (pg)	Max. (pg)	Mean (pg)	Min. (pg)	Max. (pg)	Mean (pg)	Min. (pg)	Max. (pg)
+ + +	1.83	0.85	2.90	1.60	0.70	2.90	1.36	0.47	2.90
+ +	1.24	0.47	3.37	0.97	0.39	2.81	1.18	0.39	2.81
+	1.23	0.39	2.85	1.82	0.71	3.37			

In order to understand different definitions by distinct researchers without confusion, notations of invasion degree were unified. + + + is the most serious invasion degree, + + is the medium invasion degree, + is the lowest invasion degree. 20 invasive samples were divided into three invasion degrees according to Liu et al. (2006), Wang et al. (2008) and Yue et al. (2011).

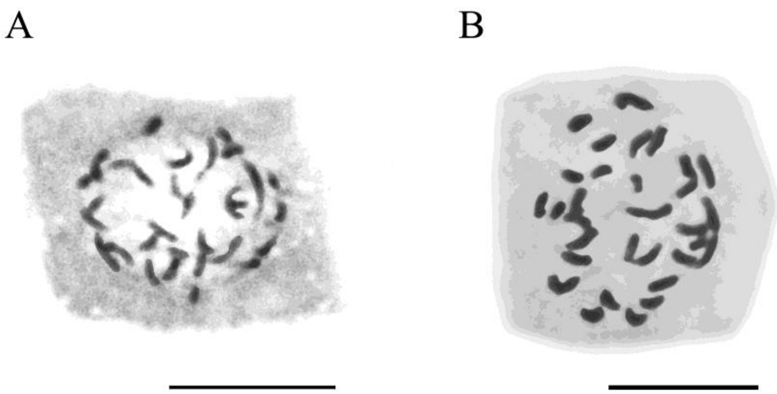

Fig. 2. Chromosomes of **A** *I. triloba*, **B** *P. nil.* Root tips of two species were fixed in acetic alcohol and then hydrolyzed at 60°C in 1 M HCl for 4 min. Chromosomes were stained with 1% carbol fuchsin. Chromosomes were counted in a NIKON microscope at 100 times magnification and photographs of the chromosomes were taken. Bar=10 μm

values were higher as the invasion degree of invasive species increased (Table 3). This indicated that DNA C-values possibly correlate with the invasiveness, but they should not be used for accurate evaluation of invasion degrees. The genus *Ipomoea* had lower DNA content than most other invasive species. *Ipomoea cairica* (L.) Sweet had the second lowest DNA C-value among perennials, next to the native species *Paederia scandens* (Lour.) Merr. Coincidentally, *I. cairica* is one of the worst invasive weeds in South China and it grows so fast that it occupies living spaces of other species quickly and considerably affects the ecology

(Lin and Liu, 2008). *P. scandens* is also considered a harmful native plant due to its ecological damage (Ye et al., 2011). It is possible that plants with low nuclear content may hold invasive potential whether they are alien species or not.

Kubešová et al. (2010) compared genome size values for some species with those extracted from the database of Bennett and Leitch (2005b). The result showed that about one third of the species had differences below 10%, which was in the acceptable range suggested by Doležel et al. 1998, but four species differed more than 1.5-fold. It should be noted that the difference mostly depends on the methodology used. Srisuwan et al. (2006) found that polyploidization could be followed by decreasing the number of 18S rDNA loci in a higher ploidy level and provided evidence for major genomic rearrangements and diploidization in polyploid *Ipomoea batatas* (L.) Lam. Genetic diversity may provide the necessary information for understanding patterns of weed invasion (Hufbauer 2004; Sterling et al., 2004; Goolsby et al., 2006; Mangolin et al., 2012). Ozias-Akins and Jarret (1994) stained nuclei by DAPI and measured DNA C-values with EPICS 753 (Coulter Corp., Hialeah, Fla.), and their results showed that the DNA 1C values of *I. triloba* and *P. nil* were 0.27 to 0.44 pg higher than the results in this experiment and there were no changes in samples' ploidy. Besides the factor of different methodologies, the variation, irrespective of ploidy differences, has often been attributed to a repetitive DNA sequence family in the ribosomal DNA intergenic spacer region (Ozias-Akins and Jarret, 1994; Dhillon and Ishiki, 1999). During the adaptation process to new environments (Stewart et al., 2009; Gaungoo et al., 2010; Lavergne et al., 2010), genes expression in invasive species changed, causing the loss of some DNA sequences simultaneously.

In conclusion, considering ours and the results of others, the invasive potential correlates negatively with DNA C-value. Invasive species in general have lower nuclear contents than non-invasive species. It should be noted that native species with low nuclear contents might also possess an invasive potential.

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