根尖分生组织细胞核大小：
一个可能用于植物入侵性评估的新指标

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摘　要：植物的入侵性与 DNA C-值之间存在统计学上的负相关关系。在这种关系中，细胞和细胞核大小可能起关键作用，因此我们推测分生组织细胞核大小在评估植物或至少某些分类群的入侵性方面有潜在的应用价值。本研究以豌豆属（*Vicia*）5 种入侵能力不同的植物为材料，观察了它们的分生组织染色体、细胞核和细胞大小以及有丝分裂速率，同时测定了种子产量、单位种子干重产生的幼苗生物量（近似于幼苗相对生长速率）和生活史的长短。结果显示根尖分生区细胞核较小的植物细胞较小，细胞分裂速率快，单位种子干重产生的幼苗生物量高，种子小而数量多，生活史短。这些结果表明 5 种豌豆属植物中分生组织细胞核较小的倾向于具有较高的入侵性，其原因主要是：（1）能够产生小而多的种子；（2）具有较高的有丝分裂速率、相对较快的幼苗生长速率和短的生活史。分生组织细胞核大小影响植物入侵性与 DNA C-值的作用是一致的，在植物入侵性评估模型中，分生组织细胞核大小在评估植物入侵性方面可能具有潜在的应用价值，而且其测定方便、费用低廉。但是，这一指标的应用范围和条件需要进一步筛选。

关键词：分生组织；细胞学指标；入侵性；种子产量；世代时间

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Root Meristematic Karyon Size：Possible New Index in the Evaluation of Plant Invasiveness

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Abstract：Many reports have found a statistically negative correlation between DNA C-value and plant invasiveness，with meristematic karyon size playing a key role in this correlation according to previous research. We hypothesized that meristematic karyon size could be applied as an evaluation index of plant invasiveness for at least some taxa. To test this hypothesis，we examined the sizes of karyons，cells，and mitosis rates of five *Vicia* species with different invasiveness and DNA C-values，and also investigated their seed production，seedling weight/dry seed weight（similar to relative seedling growth rate），and their life spans. Results showed that plants with smaller meristematic karyons were prone to have smaller chromosomes，karyons，cells，and seeds，quicker mitosis，higher relative seedling growth rate，shorter generation time，and produce more and smaller seeds. Furthermore，among the five *Vicia* species，plants with smaller meristematic karyons exhibited higher invasiveness，which may be explained by two aspects：（1）smaller seeds with much higher seed production；and（2）higher rates of cell division and seedling growth with shorter

generation times. The effects of meristematic karyon size on plant invasiveness coincided with that of the DNA C-value. Therefore, for plant invasiveness evaluation models, meristematic karyon size has potential value in invasiveness assessment due to its convenience and lower expense, though more work is needed to determine its application scope and methodology.

Key words：Meristematic tissues；Cytological indices；Invasiveness；Seed production；Generation time

Plant invasion poses serious challenges in the world today. Though many different indices, including secondary chemistry[1], species traits, DNA C-value and genome size[2,3] and gene expression[4], have been suggested to evaluate plant invasiveness, we still have no general tool to predict which plants are potential invaders. Therefore, it is important to determine which indices are clearly and broadly correlated with plant invasiveness.

Weed plants are mainly distributed in human-disturbed environments and are not purposely cultivated[5]. Weeds exhibit many traits that allow them to invade into human-disturbed ecosystems easily. Studies have shown that invasiveness is similar to weediness[6,7]. For example, invasive North and South American species naturalized in France (274 species) could be divided into agricultural weeds and environmental weeds according to their habitats in France[8]. Sutherland (2004) studied plant invasiveness by observing the trait differences between weeds and non-weeds in North America [9].

Generally speaking, weed species have higher invasiveness[5,8], and the success of many important weeds may be associated with several traits correlated with a low DNA C-value (amount of DNA in the unreplicated gametic nucleus). These traits include establishing, developing, and reproducing quickly with many small seeds[10,11]. There are many reports on the potential of DNA C-values to evaluate plant invasiveness[10,12–14]. DNA C-values and genome size both have significant effects on plant invasiveness, especially in herbs, dicots, monocots, perennials, non-pe-

rennials, diploids, polyploids, and the Compositae and Poaceae families, but not significant in trees or the Fabaceae family [3], though there are some exceptions in some taxa[15].

With lower DNA C-values, plants generally have smaller karyons and cells[16–20]. This tendency makes plants more highly invasive due to：1) smaller seeds and higher seed production；and 2) shorter new cell reproduction time, which may accelerate growth rate and shorten life span[12,13,21]. According to this hypothesis, the relationship between DNA C-values and plant invasiveness is linked to karyon and cell size. In other words, karyon and cell size play a key role in the mechanism of how the DNA C-value affects plant invasiveness. This begs the question of why karyon and cell size is not used to evaluate plant invasiveness in lieu of, or at least as a supplement to, DNA C-values.

Moreover, DNA C-values of plants are mainly determined by flow cytometry[12,22]. However, the values gained from different measuring strategies, with different dyes and instruments, can vary[23,24]. In addition, flow cytometers are expensive and the measuring process is time-consuming. Conversely, the karyon size of meristematic cells is relatively stable and much more convenient to determine.

Therefore, testing and comparing the correlation between DNA C-values and invasiveness is important, and experiments on the relationship between karyon size and plant invasiveness using related species are needed. We found five *Vicia* species to be ideal materials. *Vicia sativa* L., *V. tetrasperma* (L.) Schreber, and *V. hirsuta*

(L.) S. F. Gray are three widely occurring weed species in China, as well as in many other countries[25,26], and their DNA C-values (pg) are 1. 90, 3. 25, and 4. 25, respectively[27]. *Vicia tenuifolia* Roth. is not clearly invasive[25,26], and its DNA C-value is 8. 0 pg[27]. *Vicia faba* L. is a highly domesticated and globally cultivated crop species[25,26], and its DNA C-value is 11. 90 pg[27]. Their ranks of invasiveness (or weediness) are reversed with their DNA C-values.

By examining meristematic karyon size, cell size, seed production, relative seedling growth, and life spans of the five *Vicia* species, then analyzing the relationship of their invasiveness with these indices, we investigated the feasibility of whether meristematic karyon size, in lieu of DNA C-values, could be applied as an index in the assessment of plant invasiveness.

1　Materials and Methods

1. 1　Seed collection and seed weight

In April 2007, seeds of *V. sativa*, *V. tetrasperma*, *V. hirsuta*, and *V. faba* were collected from a suburb of Jinhua City, Zhejiang, China (29°07′06″N, 119°37′47″E, alt. 45.9 m) and *V. tenuifolia* seeds were collected in August 2006 in Shihezi, Xinjiang, China(44°20′50″N, 85°58′57″E, alt. 400 m). All seeds were air-dried and stored in paper bags at room temperature in the laboratory at Zhejiang Normal University. One hundred mature seeds with five replicates for each species were selected to determine seed weight. The values were changed into 1000-seed weights.

1. 2　Projected areas of meristematic karyon, cells, and mitosis rate

Seeds were placed into a 9 cm Petri dish with five pieces of filter paper and 9 mL of deionized water. The seeds were not submerged but imbibed on moistened paper. The dish was sealed with Parafilm and then placed in a growth chamber with constant temperature until seeds germinated to form roots. The incubating temperature was set to a constant 25℃, with a 12 h light/12 h dark regime.

Root tips (1. 5–2. 0 cm for *V. faba* and 0. 8–1. 2 cm for the other species) were treated for 24 h at 4℃ and fixed in 3∶1 (absolute ethanol∶acetic acid) for 24 h. The samples were then stained with Carbol fuchsin for 30 – 40 min after 8 min of hydrolysis in 1∶1 (95% ethanol∶38% HCl). Temporary slides for determining chromosome, karyon and cell sizes were prepared using the conventional squashing method. The micrographs were taken under a 100× oil lens using a Motic digital microscope DMB1-223 (Motic Ltd. Corp., Xiamen, China). Five hundred cells and karyons in mitotic interphase for each species were used to determine the projected areas of cells and karyons.

The five *Vicia* species are annual or biennial plants, and the temperature in their growth periods mostly varies from 10℃ to 30℃. For comparison of the relative seedling growth rates (seedling dry weight / dry weight of seed) of the five species under different temperatures, their seedlings were cultivated for three days at 10℃, 15℃, 20℃, 25℃, and 30℃, respectively. Chromosome slides from these seedlings were then prepared. For each treatment, 10 slides prepared with clear and dispersive meristematic cells were used to take micrographs under a 40× lens. To determine the mitosis rate (number of cells under prophase, metaphase, and anaphase / total meristematic cells), 10 successive graphs were taken for each slide using a Motic digital microscope DMB1–223.

The average mitosis rate of each species from 10℃ to 30℃ was calculated, and its relationship with karyon size was also analyzed.

1. 3　Seedling growth rate

Seedling growth rates of the five *Vicia* spe-

cies were compared. To destroy the epidermis and thus overcome dormancy, their seeds were soaked in vitriol oil for 18 min and rinsed with deionized water before the experiment. All seeds were soaked in deionized water for 4 h before germination. After rinsing, seeds were placed in Petri dishes with moist filter paper. Each dish was sealed with Parafilm and placed in a growth chamber at 15℃, with a 12 h light/12 h dark cycle.

Immediately after germination, 35 seedlings per treatment per species were selected and placed into new Petri dishes for continued growth in a growth chamber. Each species had five treatments with cultivating temperatures of 10℃, 15℃, 20℃, 25℃, and 30℃, respectively. Vaporized water in each Petri dish was replenished as needed. Two weeks later, the 30 largest seedlings for each treatment were dried to a constant weight at 80℃ and then weighed.

1.4 Life span and seed production

Field plots were established in December 2007 in the suburb of Jinhua, Zhejiang Province, China (29°07′06″N, 119°37′47″ E). Five 1 m^2 plots were cleared of the surface 5 cm of soil, and replaced with water-washed sand to remove soil vegetation as well as for better fertilization. Each plot received an initial application of 50 g/m^2 of Fusheng's Special Fertilizer (15-15-15) (Fusheng Fertilizer Co., Ltd, Tianjing, China). On December 16, 2007, 15 seedlings per species germinated in the growth chamber were cultivated

20 cm apart. Thereafter, all plants were watered as needed and fertilized every 30 days. The lowest and highest temperatures were recorded each day.

On March 16, 2008, five seedlings of each species with the lowest biosize were removed. For each plant individual, the first dates of flowering and production of mature fruits were recorded, and shedding seeds were collected and stored. In May 2008, plants for which about half of the seeds had matured were uprooted and washed. Seed production of each individual was counted. All plant individuals were dried to a constant weight at 80℃ and weighed.

1.5 Data analysis

Data were presented as means ± standard errors (SE). A one-way analysis of variance (ANOVA) using SPSS 15.0 statistical software was employed to test differences. Least significant difference (LSD) was used when the variances were homogeneous; otherwise, Dunnett's T3 test was used. Regression analyses were performed using SPSS 15.0 software.

2 Results

2.1 Projected areas of meristematic karyons and cells, and seed weight

The meristematic karyons and cells in the root tip and seeds of *V. faba* were significantly larger, followed by *V. tenuifolia*, *V. sativa*, *V. hirsuta* and *V. tetrasperma* (Table 1).

Regression analyses with a linear model (Ta-

Table 1 Projected areas of total chromosomes, karyons and cells, and seed weights of the five *Vicia* species

Species	Karyon projected area (μm^2)	Cell projected area (μm^2)	Chromosome projected area (μm^2)	Seed weight (g)	DNA 1C-value * (pg)
V. sativa	89.47 ± 1.67 c	338.29 ± 4.98 c	55.41 ± 3.90 c	13.48 ± 0.03 c	1.90
V. tetrasperma	48.87 ± 0.82 e	220.52 ± 2.90 e	67.50 ± 6.23 d	3.81 ± 0.06 e	3.25
V. hirsuta	70.98 ± 1.22 d	267.57 ± 3.37 d	104.44 ± 4.34 b	4.89 ± 0.03 d	4.25
V. tenuifolia	124.00 ± 1.86 b	500.94 ± 6.47 b	113.65 ± 4.22 b	22.83 ± 0.05 b	8.00
V. faba	225.59 ± 2.85 a	724.14 ± 11.93 a	184.12 ± 10.68 a	1269.12 ± 4.82 a	11.90
★ Regression with karyon project area		R^2 = 0.976 P = 0.002	R^2 = 0.8095 P = 0.038	R^2 = 0.852 P = 0.025	R^2 = 0.837 P = 0.029

Notes: Same letter within a column indicates no difference among species at $P < 0.05$ level. ＊: NA C-values cited from Bennett and Leitch (1995)[27]. ★: Cell projected area, chromosome projected area, 1000-seed weight and DNA 1C-value are regressed with karyon project area using a linear model, respectively.

ble 1) showed that the meristematic karyon projected area was significantly correlated with meristematic cell projected area, chromosome projected area, seed weight, and DNA 1C-value. Additionally, the correlation between DNA 1C-value and meristematic cell projected area was significant, while that between DNA 1C-value and seed weight was not significant.

2.2 Mitosis rate

The relationship of the average mitosis rate with meristematic karyon size is shown in Fig. 1. With the increase in meristematic karyon size, the mitosis rate decreased linearly ($P < 0.2$).
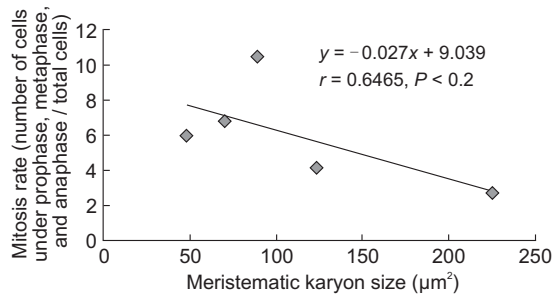

$y = -0.027x + 9.039$
$r = 0.6465, P < 0.2$

Fig. 1　Relationship between average mitosis rate and meristematic karyon projected area of the five *Vicia* species

2.3 Seedling growth rate

After two weeks cultivation, the ranks of seedling dry weight of the five *Vicia* species (Table 2) were similar to that of their seed weights, especially for the treatments at temperatures higher than 15℃. The absolute seedling growth rate (namely, absolute seedling dry weight) of *V. faba*, which had the largest 1000-seed weight, was the highest, while those of *V. tetrasperma* and *V. hirsuta* with smaller 1000-seed weights were lower.

Nevertheless, the situation on seeding dry weight / seed weight (similar to relative seedling growth rate), which reflects competitive ability of a species, was different from absolute seedling growth rate. For example, with the smallest 1000-seed weight, *V. tetrasperma* grew quicker than *V. hirsuta* under all temperatures except 20℃. We further analyzed the relationship of relative seedling weight with karyon size among the five species. Interestingly, the relative seedling weight was significantly negatively related with karyon projected area (Fig. 2).

2.4 Life span and seed production

By May 18, 2008, all cultivated plants were uprooted except *V. tenuifolia* (it maintained strong vegetative growth but did not flower during the experiments). In the 154 days of cultivation (from December 16, 2007), the mean temperature was 11.72℃, with a lowest temperature of −2℃ and highest temperature of 34℃.

The dry weight of *V. faba* individuals was the highest, followed by *V. sativa*, *V. hirsuta*, and *V. tetrasperma* (Table 3). The juvenile period (period from emergence to flowering) of *V. faba* (about 96 d) was the shortest. However, its generation time (period from emergence to first matured fruit) was the longest. With the increase in karyon size (x), their generation time (y) extended, following: $y = 0.088x + 127.7$ ($r = 0.9731, P < 0.01$) (Fig. 3). The seed number per *V. faba* individual was about 16, which was significantly lower than those of *V. sativa*, *V. Tetrasperma*, and *V. hirsuta* (Table 3).

Regression analyses showed that with increa-

Table 2　Seedling dry weights of the five *Vicia* species after cultivation at different temperatures for 14 days (mg)

Species	10℃	15℃	20℃	25℃	30℃
V. sativa	2.20 ± 0.06 b	4.00 ± 0.06 b	4.66 ± 0.07 b	3.83 ± 0.06 b	2.46 ± 0.05 b
V. tetrasperma	1.26 ± 0.02 c	1.95 ± 0.04 e	2.09 ± 0.04 d	2.21 ± 0.05 d	1.99 ± 0.04 d
V. hirsuta	0.71 ± 0.03 e	1.72 ± 0.03 d	2.10 ± 0.03 d	1.90 ± 0.04 e	1.56 ± 0.04 e
V. tenuifolia	1.12 ± 0.02 d	2.20 ± 0.06 c	3.14 ± 0.05 c	3.21 ± 0.04 c	2.25 ± 0.03 c
V. faba	45.36 ± 0.61 a	69.02 ± 1.64 a	138.95 ± 1.88 a	112.71 ± 2.48 a	90.25 ± 2.57 a

Note：Same letter within a column indicates no difference at the 0.05 level of significance.
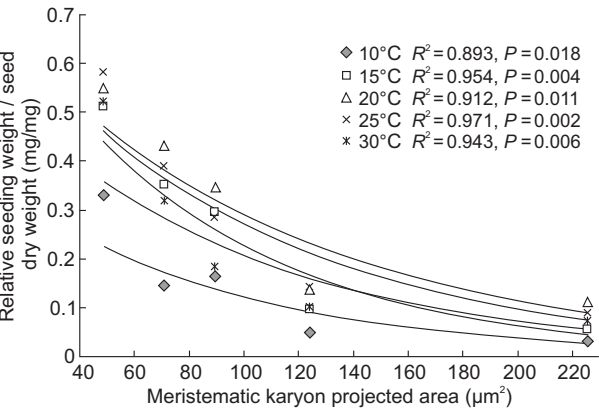
Regressions are drawn using the Power model, and relative R^2 and P values are shown.

Fig. 2　Relationship between relative seedling weight (seedling dry weight / seed weight) and meristematic karyon projected area of the five *Vicia* species

sing karyon projected area (x), seed number per individual (Y1) decreased following Y1 = −1. 8049x + 437. 79 (R^2 = 0. 8989, P = 0. 05), and seed number per dry weight of an individual (Y2) decreased following Y2 = 1044. 6 × e^{−0. 0331x} (R^2 = 0. 9973, P = 0. 001) (Fig. 4).

3　Discussion

　　Exploring effective assessment models to e-valuate plant invasiveness deserves more atten-tion. Because plant invaders have many similar at-tributes, a robust assessment model needs to in-clude many essential and practical indices. Our results imply that, in lieu of DNA C-value, meris-tematic karyon size may be an effective index for evaluating plant invasiveness.

　　The species with smaller DNA C-values, such as *V. tetrasperma* and *V. sativa*, tended to have small meristematic karyons and cells (Table 1),

higher mitosis (Fig. 1) and relative seedling growth rates (Fig. 2), developed more quickly with shorter life spans (Table 3, Fig. 3) and pro-duced more and smaller seeds (Fig. 4).

　　There is a maximum limit to the mass of DNA for species that can complete development in a given time. In any environment where a plant must complete its life-cycle in a given time in or-der to survive, all reproducing species are cer-tain to have a very low DNA C-value[33]. There-fore, short life-cycles, which are related to small meristematic karyons, are vital for inva-sive species.

　　Most plant invaders are considered to be largely opportunistic, capable of exploiting chan-ging environmental conditions and human or na-tural disturbances[28,29]. Invasive plants first colo-nize and then persist in their new environments, and later become abundant and dominant com-ponents of the plant community[30]. Producing many small seeds greatly contributes to the ability of plant invaders to overcome the difficulties of long-distance distribution and population estab-lishment. Furthermore, the ability to quickly grow and develop enables plant species to swiftly uti-lize environmental resources and space.

　　Based on these attributes, plants with small meristematic karyons may out-grow and out-re-produce native species in new habitats, particu-larly for annuals and biennials. It can be conclu-ded, therefore, that similar to the effect of the DNA C-value, lower meristematic karyon size benefits plant invasiveness.

Table 3　Life spans, seed production, and dry weights of the four *Vicia* species

Species	DW (g)	PF (d)	PM (d)	Seed production (seed number/individual)
V. sativa	7.7 ± 0.8 b	106.7 ± 0.5 a	133.5 ± 0.9 b	347.0 ± 30.5 a
V. tetrasperma	1.5 ± 0.1 d	106.4 ± 0.6 a	133.9 ± 0.8 b	312.0 ± 28.9 a
V. hirsuta	2.5 ± 0.2 c	105.6 ± 0.5 a	133.9 ± 0.8 b	290.4 ± 38.9 a
V. faba	27.6 ± 2.9 a	94.4 ± 0.3 b	148.2 ± 0.2 a	16.8 ± 1.9 b

Notes: Same letter within a column indicates no difference among species at the 0.05 level. DW = dry weight of the plant individual; PF = period from emergence to flowering; PM = period from emergence to generation of a mature legume. *V. tenuifolia* maintained strong vegetative growth, but did not flower during the experiments.

$y = 0.088x + 127.7$
$r = 0.9731, P < 0.01$
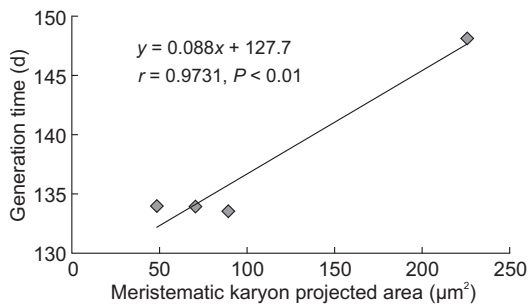
Regressions are drawn using the linear model, and relative r and P values are shown.

Fig. 3　Relationship between generation time and meristematic karyon projected area of the five *Vicia* species

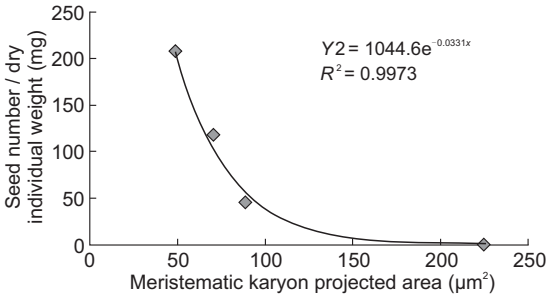$Y2 = 1044.6e^{-0.0331x}$
$R^2 = 0.9973$

Fig. 4　Relationship between seed number per dry individual weight and meristematic karyon projected area of the *Vicia* species

Applying the squashing method to prepare temporary slides for observation of karyon and cell sizes is a conventional practice. Although the sizes of karyons or cells may be affected by the squashing force, in the present study more than 500 cells were observed in each treatment, and thus the cytological differences among different species were believable.

No single index can be applied to predict all invasion phenomena. In current plant invasion risk assessment systems, such as the Australian exotic plant risk assessment system[31] and the Chinese alien plant invasive risk assessment systems[32], many indices have been applied to form an integrated risk value to evaluate the invasiveness of a focal plant. The objective of the present work was to find new indices to improve or enrich the risk assessment index system, not to replace existing evaluation indices. This study showed that plants with small DNA C-values sta-

tistically had smaller apical meristem karyons and cells, high mitosis rates, smaller seeds with higher relative seedling growth rates, had shorter life cycles, and thus tended to be more highly invasive. Compared with DNA C-values, the root meristem karyon size is relatively easily determined. Therefore, karyon size is suggested as a new index in the assessment of plant invasiveness in lieu of DNA C-value.

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