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A novel perspective on seed yield of broad bean (*Vicia faba* L.): differences resulting from pod characteristics

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Broad bean (*Vicia faba* L.) is an important crop worldwide. An increase in seed yield would increase both the grain reserve and the profit for farmers. Previous studies on increasing broad bean seed yield have focused mainly on increases at the whole population level. Few studies have focused on the differences in plant type within populations. In this study, we classified broad bean plants into four categories based on pod type, and then evaluated the ratio of each category in field-grown broad bean populations. We analysed the seed and pod characteristics of each category, and their contributions to total seed yield. The number of seeds per pod, and the number of pods or seeds per plant differed among the four plant categories, but the seed weight was relatively uniform. There were significant differences in seed yield per plant among the four plant categories. We calculated the effects of increasing the proportion of each plant category by 10% or to 100% on seed yield, and found that seed yield could be improved by increasing the ratio of plants with the highest seed production rate. This study provides a novel perspective on estimating the seed yield of broad bean.

Broad bean (*Vicia faba* L.), an ancient crop species that originated in the Near East¹, is mainly grown in Europe, North Africa, the Middle East, and China¹. It is an important leguminous crop worldwide because of its nutrient-rich seeds. It is extensively used as a legume, a vegetable, and as fodder. In China, broad bean is widely cultivated in Sichuan, Yunnan, Guizhou, Hunan, Hubei, Jiangsu, Zhejiang, and Qinghai provinces, and the planting area and total production account for 53% and 61% of those worldwide, respectively². Therefore, increases in the seed yield of broad bean will result in greater economic profits and a larger food supply.

There have been many studies on improving the seed yield of broad bean. One of the main factors in the seed yield instability of broad bean is excessive flower and pod abortion — up to 87% of the flowers/pods are aborted³. To solve this problem, alternative plant types have been selected and developed, for example, plants with a determinate growth habit and early flowering⁴. The sowing rate and planting density can directly influence seed yield and the profitability of a crop⁵. Seed yield was shown to increase with increasing sowing rate⁵. The most important characteristics for improving the seed yield of broad bean were reported to be plant height, number of stems and pods per plant, biological yield, harvest index, 100-seed weight, and number of days to flowering and maturity⁶. Among these characteristics, the number of stems per plant, the number of pods per plant, and biological yield were those most strongly affected by environmental conditions⁷. Compared with small-seeded cultivars, large-seeded cultivars of broad bean produce higher yields⁸. In addition, better crop management, improvements in disease management, and rhizobium inoculation were shown to increase broad bean yields in Australia⁶. Most of the studies on increasing the seed yield of broad bean have focused on breeding new varieties, improving environmental conditions, and improving agricultural management on the whole population level; however, few studies have focused on the contributions of different plant types or pod types within the population to the seed yield.

We have cultivated broad bean in southwest China for a long time. In our continuing observation, we noticed that broad bean plants produce three types of full pods. These have been designated as Pod I (containing one seed), Pod II (two seeds), and Pod III (three seeds) (Figure 1A). Based on the pod types, the broad bean plants can be classified into four categories: Category I, all pods are Pod I (Figure 1B); Category II, all pods are Pod II (Figure 1C); Category III, pods are either Pod I or Pod II (Figure 1D); and Category IV, at least one Pod III is among the pods (Figure 1E). Because the four categories of plants produce different numbers of seeds, and seed

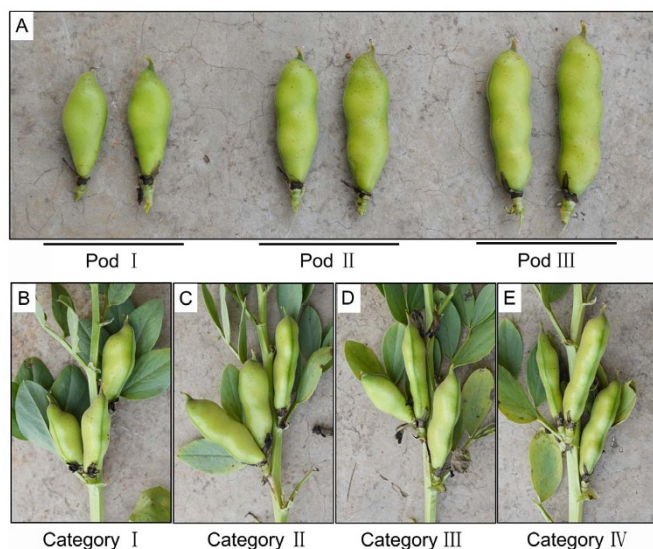


Figure 1 | Morphology of three pod types and four plant categories of broad bean. (A) Morphology of Pod I, Pod II, and Pod III. Morphology of plants in Category I (B), Category II (C), Category III (D), and Category IV (E). The photographs of the pods and plants were taken by Xiong Li.

size is relatively stable within a species⁹, we hypothesized that plants producing different numbers of seeds as a result of their pod characteristics might affect the seed yield of a broad bean population. Thus, in the present study, we investigated and analysed the proportion of plants in each category, and the seed yields of different pod types, in broad bean plants grown in a uniform field. The aim of this study was to determine whether there were differences in the number of seeds and seed yield among the three pod types and the four plant categories, and to determine the contributions of the different pod types and plant categories to seed yield. The findings of this study can provide a theoretical basis for estimating and improving the seed yield of broad bean in agricultural production.

Results

Proportions of plant categories and pod types in a field-grown broad bean population. As the plants in the various quadrats were in similar environmental conditions, we observed little variation in plant size or the timing of maturity among the four plant categories (Figure S1). Every quadrat contained plants in Categories I, II, and III, and most quadrats (all except for quadrats 2, 9, 11, and 15) also contained Category IV plants. The broad bean plants were grown at

a density of 55 plants/m², and the frequency of Categories I, II, III, and IV was 13, 28, 14, and <1 plants/m² respectively. Category III plants made up the largest proportion of plants (50.77%; Figure 2A), followed by Category I plants (22.87%; Figure 2A) and Category II plants (25.33%; Figure 2A). Only 1.03% of plants were Category IV plants (Figure 2A), indicating that this category of plants had little effect on yield. Among the three pod types, Pod I, II, and III were produced by 53.78%, 45.82%, and 0.4% of plants per unit area. These proportions were significantly different (Figure 2B), suggesting that pod type significantly contributed to seed yield.

Variations in number of pods and seeds among different plant categories. The range in the number of pods produced by each category of plants, and the mean values for the number of pods per plant are shown in Figure 3A and Table 1, respectively. Category I plants produced 1–5 pods (mean, 2.90). Category II plants produced 2–4 pods (mean, 2.22). Category III plants produced 2–4 pods (mean, 2.82). Category IV plants produced 1–4 pods (mean, 1.96). In general, therefore, Category I and III plants produced more pods than did Category II and IV plants (Table 1).

Next, we evaluated seed production by plants in each category (Figure 3B, Table 1). Category I plants produced 1–5 seeds (mean, 2.90). Category II plants produced 4, 6, or 8 seeds (mean, 4.44). Category III plants produced 3–7 seeds (mean, 4.12). Category IV plants produced 3–8 seeds (mean, 4.34). Collectively, Category I plants produced significantly fewer seeds than did Category II, III, and IV plants (Table 1). However, there was no obvious difference in the number of seeds produced among Category II, III, and IV plants (Table 1).

The mean number of seeds per pod was 1.47 for Category III plants and 2.39 for Category IV plants (Table 1). As Category I and II plants produced only 1 and 2 seeds per pod, respectively, there were significant differences in the number of seeds per pod among the four plant categories (Table 1).

Variations in seed weight among plant categories. The average weight of a single seed did not differ significantly among the four plant categories (range, 0.77–0.83 g; Table 1). This result indicated that the total seed weight per plant was mainly determined by the number of seeds produced. The seed yield per plant for Category I, II, III, and IV plants was 2.37 g, 3.63 g, 3.41 g and 3.40 g, respectively, consistent with the number of seeds produced by each category (Table 1).

Relationships between seed and pod characteristics. Correlation analyses revealed that the number of pods per plant was significantly negatively correlated with mean number of seeds per pod (Table 2). The number of seeds per plant was significantly positively correlated

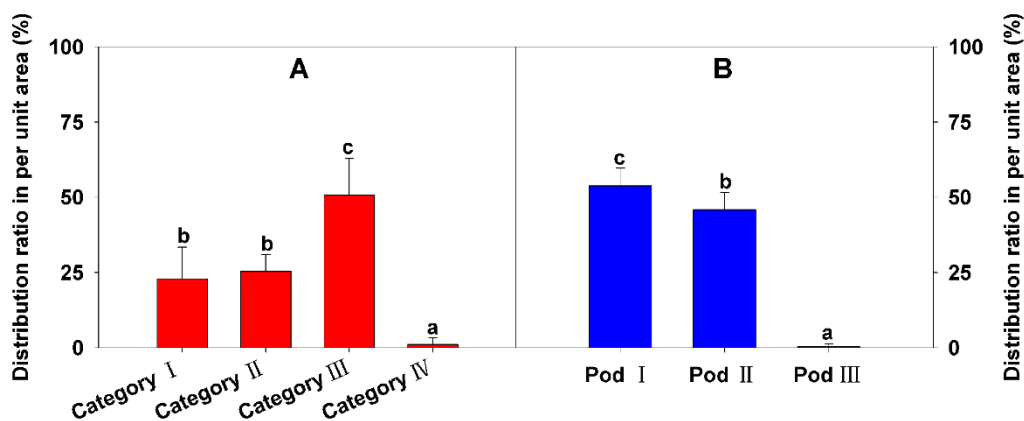


Figure 2 | Proportions of four plant categories and three pod types per unit area. (A): Proportions of four plant categories per unit area. (B): Proportions of three pod types per unit area. Data are mean \pm SE ($n=15$ quadrats). Different letters following mean values indicate significant difference (Tukey's test, $P<0.05$).

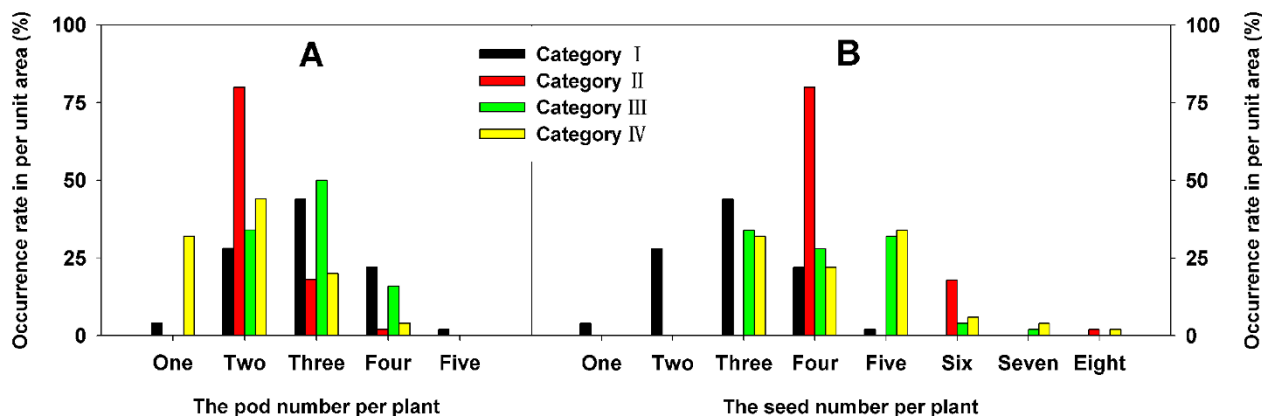


Figure 3 | Number of seeds and number of pods per plant in four plant categories. (A): Number of pods per plant in four plant categories. (B): Number of seeds per plant in four plant categories.

with seed yield per plant (Table 2) because the seed size was relatively constant among the four plant categories.

Contributions of plant categories and pod types to seed yield.

Based on the seed yield of each pod type and plant category and their proportions in the population, we calculated that plants in Categories I, II, III, and IV contributed 16.80%, 26.38%, 55.76%, and 1.07% of total seed yield, respectively (Figure 4A). Among the pod types, Pod I, II, and III contributed 44.85%, 54.61%, and 0.54% of total seed yield, respectively (Figure 4B). These results suggested that altering the proportions of the pod types or plant categories could affect seed yield.

We calculated the potential changes in seed yield resulting from changing the proportion of plants in each category within the population, while maintaining the same planting density (Table 3). A 10% increase in the proportion of Category I plants would change seed yield by -3.91% to -3.23% (Table 3); a 10% increase in Category II plants would change seed yield by 0.68% – 3.91% (Table 3); a 10% increase in Category III plants would change seed yield by -0.68% to 3.23% (Table 3); and a 10% increase in Category IV plants would change seed yield by -0.71% to 3.20% (Table 3). Similarly, we calculated the potential changes in seed yield resulting from changing the proportion of pod types within the population. A 10% increase in the proportion of Pod I would reduce seed yield by 3.62% (Table 3); a 10% increase in Pod II would increase seed yield by 3.62% (Table 3); and a 10% increase in Pod III would increase seed yield by 1.86% – 5.49% (Table 3). If the population consisted of 100% Category I, II, III, or IV plants, the seed yield would change by -26.64% , 12.45% , 5.68% , and 5.34% , respectively (Table 3); similarly, 100% of Pod I, II, and III would change seed yield by -16.82% , 19.40% , and 38.05% , respectively (Table 3).

Discussion

It is important to analyse the number of pods and the number of seeds per plant to identify factors contributing to seed yield¹⁰. The number of pods per plant is determined by the number of flowers per

plant, and the proportion of flowers that develop into mature pods¹⁰. In another study, the number of seeds per pod showed only minor variations with respect to planting density, row width, and node position. This result suggested that within a genotype, a larger proportion of the variation in the number of seeds per plant is explained by variations in the number of pods per plant¹⁰. In the present study, we observed three different types of mature pods in broad bean (Figure 1A). There were different proportions of the three pod types in the population (Figure 2B). The plants were classified into four categories based on pod type (Figure 1B–E). In the field population, all four plant categories were present and were easily distinguishable from each other (Figure 2A). Variations in the number of seeds per pod and pods per plant resulted in different numbers of seed per plant (Table 1). The plants with one seed per pod (Category I) produced lower seed outputs than did plants in the other three categories (Table 1).

A correlation analysis of the four plant categories showed that seed number per pod was negatively correlated with number of pods per plant (Table 2). Therefore, there was a trade-off between pod size and the number of pods, rather than between seed size and the number of seeds. This finding differed from those of other studies^{11–13}. Consequently, a single plant would need to reduce the number of pods to devote more resources to produce bigger pods (e.g. Pod II or III), since the plant has limited resources. Thus, under resource limitation, there are two strategies to optimize reproductive adaptability; produce more pods, or produce bigger pods. The two strategies would result in different numbers of seeds per plant or per unit area. In our study, the single seed weight was almost the same among the different plant categories. This result was consistent with those of a previous study, which reported that seed size remains relatively stable within a plant species⁹. Our results suggested that the seed yield of broad bean was mainly dependent on the number of seeds per plant or per unit area, explaining why the number of seeds per plant was significantly positively correlated with the seed yield per plant (Table 2).

Table 1 | Seed and pod characteristics of four plant categories. Data are mean \pm SE ($n = 50$ plants). Different letters within a column indicate significant difference (Tukey's test, $P < 0.05$)

Plant category	Number of pods per plant	Number of seeds per plant	Number of seeds per pod	Single seed weight (g)	Seed yield per plant (g)
I	2.90 ^b	2.90 ^a	1.00 ^a	0.82 ^a	2.37 ^a
II	2.22 ^a	4.44 ^b	2.00 ^c	0.82 ^a	3.63 ^b
III	2.82 ^b	4.12 ^b	1.47 ^b	0.83 ^a	3.41 ^b
IV	1.96 ^a	4.34 ^b	2.39 ^d	0.77 ^a	3.40 ^b


Table 2 | Correlations between pairs of pod characteristics. “*” represents significant correlation (0.05 level, bilateral)

		Number of pods per plant	Number of seeds per plant	Number of seeds per pod	Single seed weight	Seed yield per plant
Number of pods per plant	Pearson correlation	1	-.728	-.968*	.784	-.635
	Sig. (2-tailed)		.272	.032	.216	.365
Number of seeds per plant	Pearson correlation	-.728	1	.856	-.307	.990*
	Sig. (2-tailed)	.272		.144	.693	.010
Number of seeds per pod	Pearson correlation	-.968*	.856	1	-.733	.776
	Sig. (2-tailed)	.032	.144		.267	.224
Single seed weight	Pearson correlation	.784	-.307	-.733	1	-.170
	Sig. (2-tailed)	.216	.693	.267		.830
Seed yield per plant	Pearson correlation	-.635	.990*	.776	-.170	1
	Sig. (2-tailed)	.365	.010	.224	.830	

Because the seed outputs differed among the plant categories, and there were different proportions of the four categories in the field population, it should be possible to alter the seed yield per unit area by changing the proportions of different pod types and plant categories at a constant plant density. When the ratios were hypothetically increased by 10% or to 100% under the present conditions, Category I and Pod I negatively affected seed yield, while the other plant categories and pod types mainly had positive effects (Table 3). Because there was only a small proportion of Pod III and Category IV in the field (Figure 2), our analyses suggested that Pod II and Category II plants had the greatest potential to improve the seed yield of the broad bean population.

Several studies have analysed the correlations among different plant characters and seed yield^{14–23}. For example, positive and negative selection resulted in large variations in seed number per pod in white mustard²². Number of seeds per unit area is an important yield component in soybean, and the crop was able to compensate for lower numbers of pods by increasing the 100-seed weight²³. There have been many studies on the factors affecting crop yields, with the aim of improving yields as much as possible. Studies on a range of legumes have shown that there is potential to increase seed yield by increasing the number of pods at maturity, rather than increasing seed size or number of seeds per pod^{24,25}. The numbers of pods and seeds are affected by the environmental conditions during flowering and seed set^{26–29}. Optimizing the CO₂ concentration³⁰, light²⁹, or irrigation^{31,32} can increase the number of pods and seeds. Genetic factors have also been shown to regulate the number of seeds per pod^{33,34}. Whereas those studies focused on the factors contributing to the number and size of pods and seeds among populations, we focused on the contribution of different plant categories within a

population to the seed yield of broad bean. Our results show that there are several categories of broad bean plants, and differences in outputs will still exist among these categories, regardless of any strategies aimed at increasing yield. The results of this study suggest that increasing the proportion of Category II or Pod II in the population is a good strategy to increase the seed yield of broad bean populations.

To understand the basis of seed yield, it is important to consider the factors causing the differences in pod characteristics. It is likely that some differences have a genetic basis, and some are the result of physiological and environmental conditions. In soybean, the *ln* gene is a key regulator of the number of seeds per pod³⁴. The pod types of broad bean may also be under genetic control. If this is the case, then seeds from Pod II/Category II plants can be collected and used to generate a stable genotype for breeding. We observed that two or three pod types could be present on the same plant (in Category III and IV plants), which may be a result of genetic differences or environmental factors. Although there is some evidence that the number of pods per plant is under genetic control, there is a larger body of evidence that environmental conditions, including CO₂ concentration³⁰, light intensity²⁹ or irrigation^{31,32}, affect the number of pods produced after flowering and setting. Overall, our results suggested that genotype and environmental factors affect the seed yield of broad bean. To analyse the contributions of genotype and environment, seeds from various genotypes can be sown under different environmental conditions. Because environmental factors are difficult to control, the best way to improve seed yield is to select for genotypes producing Pod II that show strong tolerance to adverse environmental conditions. Our results provide a novel perspective on the seed yield of broad bean in agricultural production. Further research is required to determine which genetic and/or enviro-

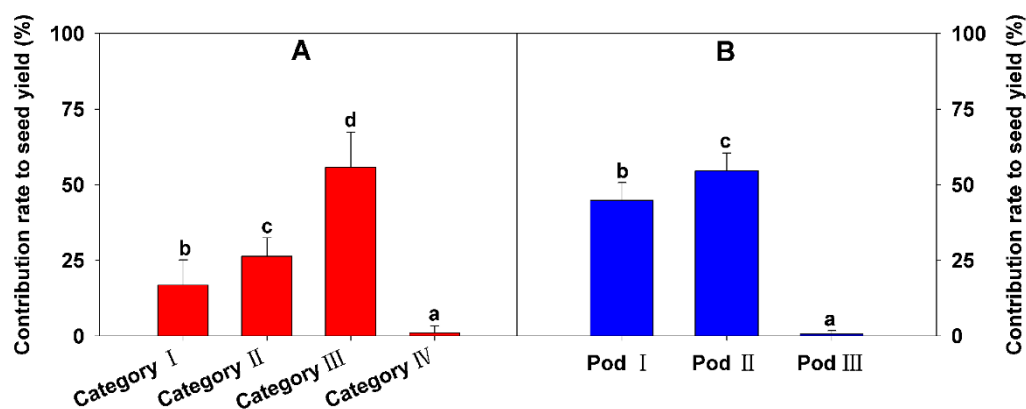


Figure 4 | Contributions of four plant categories and three pod types to seed yield per unit area. (A): Contributions of four plant categories to seed yield per unit area. (B): Contributions of three pod types to seed yield per unit area. Data are mean \pm SE ($n=15$ quadrats). Different letters following mean values indicate significant difference (Tukey's test, $P<0.05$).



Table 3 | Estimated effects of changing proportions of plant categories or pod types on seed yield. Estimates were based on increasing proportion of each category or pod type by 10% or to 100% of the total population. “–” and “+” represent seed yield decrease and increase, respectively

		Increased by 10%	Increased to 100%
Plant category	I	–3.91% to –3.23%	–26.64%
	II	+0.68% to +3.91%	+12.45%
	III	–0.68% to +3.23%	+5.68%
	IV	–0.71% to +3.20%	+5.34%
Pod type	I	–3.62%	–16.82%
	II	+3.62%	+19.40%
	III	+1.86% to +5.49%	+38.05%

Environmental factors control the distribution of plants in the four plant categories.

Methods

Evaluation of plant categories and pod types in the field. In southwest China, broad bean seeds are usually sown in October and harvested in May of the following year. Our study was conducted in April 2014, when the seeds were mature, in 40×10 m² farmland plots in Qujing, Yunnan, China. The broad bean cultivar used in this study was Kidney bean 147. The plants were grown from parental seeds that were collected from the same population; therefore, the studied population had a similar genetic background. During the growth period, no fertilizer was applied and 15 mg L⁻¹ deltamethrin solution was evenly sprayed to control aphids in mid-February during flowering. A total of 15 quadrats, each 2×2 m², were evaluated (Figure 5). In each quadrat, we recorded the number of plants in the four categories and the number of pods in each pod type. The proportions of plants in each category and pod type per unit area were calculated based on the quadrat area.

Evaluation of seed and pod production by plants in four categories. To investigate the number of seeds and pods produced by plants in the four categories, 50 plants in each category without signs of herbivore damage, abscission, or decay, were randomly selected from the field. For each plant, the numbers of pods and seeds and the numbers of each pod type were recorded.

Measurement of seed weight. After the seeds reached maturity (mid-May), the seeds of the 50 plants in each category (200 plants in total) were harvested and sun-dried to a constant weight. Three seeds from each plant, or one or two from plants producing fewer than three seeds, were selected randomly to determine seed weight. Mean seed weight values represent the single-seed weight of a plant. The total seed weight per plant was calculated from the number of seeds per plant. Mean values were calculated for each plant category.

Effects of different pod characteristics on seed yield. For each of the four plant categories, we calculated total seed yield per unit area, based on the single-plant seed yield and number of plants in each category per unit area. The total seed yield of each plant category was used to calculate the contribution of each plant category to seed yield. We calculated the potential changes in seed yield resulting from increasing the proportion of a certain plant category by 10% or to 100% under the same planting density. Likewise, we calculated the contributions of different pod types to seed yield.

Statistical analysis. Statistical analyses were performed using the Statistical Software Package for Social Science (SPSS) version 18.0. One-way ANOVA was used to test the significance of differences among samples. Differences were considered significant at $P < 0.05$.

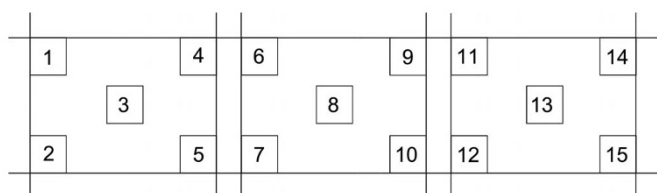


Figure 5 | Sketch map of survey quadrats in farmland. Numbers in boxes indicate quadrat number.

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Author contributions

Y.P.Y. designed the research; X.L. performed experiments; X.L. analysed data and prepared the figures and tables; X.L. and Y.P.Y. wrote the manuscript.

Additional information

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