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Variation in morphophysiological characters of fruits of *Trigonobalanus doichangensis* (Fagaceae) according to individual trees, populations and years

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Abstract *Trigonobalanus doichangensis* is recognized as a rare and endangered plant of China. The morphological and physiological traits of fruits were investigated in one population over 2 years (2006–2007) and in four populations during 2007 in order to facilitate ex-situ conservation and eventual reforestation through planting of propagules. The results indicated that morphological traits including fruit length, fruit width and 1,000-fruit weight showed significant variation among individual trees within populations ($P < 0.01$), however, not among populations. And each of them had significant positive correlation with each other ($P < 0.01$). Seed abortion occurred, and there was significant variation in percentage of fruit fill among populations and among individual trees within populations, whereas, percentage of fruit fill showed no correlation with the morphological traits. As for fruit germination, germination percentage, germination index and vigor index presented significant variation among populations and among individual trees within populations. The three germination-related indices had significant positive correlations with each other ($r \geq 0.9$, $P < 0.01$) and with percentage of fruit fill ($r > 0.86$, $P < 0.01$), however, possessing weak correlations with morphological traits. It was also found that each of the traits mentioned above showed significant variation among individual trees within years, however, not between years. In addition, more than 48% of the variation occurred among individual trees both within populations and within years in all the fruit characters. We suggest that collecting fruits from various individuals at each of populations will be the preferred strategy to conserve the most genetic diversity of the species.

Keywords Population variation · Seed abortion · Seed germination · Seed mass

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Introduction

The fagaceous genus *Trigonobalanus* Forman shows many ancestral features of the family (Forman 1964; Crepet and Nixon 1989; Nixon and Crepet 1989) and was probably widely distributed (perhaps over the whole northern hemisphere) during the tertiary period or even before (Zhou 1992). The broadly circumscribed genus *Trigonobalanus* includes only three species, *T. verticillata*, *T. excelsa* and *T. doichangensis* (Sun et al. 2007). The latter species is most closely related to the genus *Quercus* L. (Zhou 1992) and thus its study is of greatest interest in terms of phylogeny of Fagaceae, continental drift theory, and global environmental changes (Sun et al. 2006). However, due to habitat degradation, over exploitation and reproductive barriers, it is restricted to some five locations scattered in north Thailand, south and southwest Yunnan Province, China. The species has been seriously threatened and is being pushed to the verge of extinction (Sun et al. 2006). It was listed as a national rare and endangered plant in 1984 and has also been proposed as a second-ranked plant for national protection in China (Anon. 1999). Therefore, it is urgent that practical conservation and tree improvement measures be undertaken to preserve genetic diversity of *T. doichangensis*.

Fruits (nuts) of *T. doichangensis* are both of the dispersal unit and germination unit. Propagation from fruits is preferable to vegetative reproduction as it will provide the greatest genetic diversity and will be least detrimental to the extant populations. *T. doichangensis* bears female flowers with one ovary. Each ovary has six ovules but only one has the potential to develop into a seed with an embryo. Some ovaries however, have only aborted ovules and the fruits are either empty or lignified. Sun et al. (2006) reported that the germination percentage of *T. doichangensis* was low and considerable seed abortion occurred in the species. According to our preliminary observations of consecutive years, fully-formed nuts collected at the same time differ obviously in color (dark and light), and dark-colored fruits have significantly higher rate of well-developed seeds (unpublished report). Thus, only the dark-colored fruits were used in the present experiments.

In a previous work (unpublished report), we studied the extent of genetic variation in fruit and seedling traits of *T. doichangensis* at population level, based on a mixture of the two kinds of fruits. An understanding of the differences in fruit traits at different levels, as well as in different years should provide reference points for ex-situ conservation and tree improvement. The specific objectives of the present study were as follows: (1) to determine variation of morphological and physiological traits of pre-sorted fruits among individual trees, populations and years; (2) to look for possible correlations between various fruit characters.

Materials and methods

Fruit collection

Fruits, known botanically as nuts, or popularly as acorns, of *Trigonobalanus doichangensis* were collected from four populations located in the south and southwest Yunnan Province, China. The geographic locations and climatic conditions of these populations are shown in Table 1. The Cangyuan population was sampled in 2006 and 2007, and the other populations were sampled in 2007. Depending on the fruit bearing specimens, we randomly selected 12 trees in Cangyuan population, 11 trees in Lancang population, and we only found four and three fruiting trees in Menglian and Ximeng populations, respectively. The fruits were pooled by individual tree and brought back within 5 days to the laboratory at Kunming Botanic Garden, (KBG) (latitude of 25°01′N, longitude of 102°41′E and elevation of 1,900 m), where fruit processing, measurement and germination experiments were conducted. Dark-colored fruits were used in all the experiments mentioned below unless otherwise stated.

Assessment of morphological traits of fruits

To evaluate the variability in fruit morphological characters, fruit length, width, and 1,000-fruit weight were quantified. The length and width of fruits were measured individually using a digital micro caliper. Three replicates of 50 fruits per tree were randomly selected for measuring. For weight determination, four replicates of 100 fruits per tree were weighed and then the 1,000-fruit weight was calculated.

Test of fruit fill and germination

For each parent tree and fruit year, three replicates of 100 fruits were randomly selected and dissected with a scalpel. The percentage of fruit fill (i.e. fruits containing seeds) was calculated for each parent tree.

Variation in germination of *T. doichangensis* fruits was investigated at KBG. Three replicates of 100 fruits per tree were randomly sampled and placed on top of two-layers of filter papers, previously moistened with distilled water in Petri dishes. The Petri dishes were placed in a germination chamber at constant temperature of 25°C under a 12-h light photoperiod. The germination conditions were chosen

Table 1 Geographic locations and climatic conditions of fruit collection sites

Sites	Latitude (°N)	Longitude (°E)	Altitude (m)	Mean annual rainfall (mm)	Mean annual temperature (°C)
Menglian	22.30	99.53	1,020	1363.3	27.4
Lancang	22.43	99.80	1,450	1626.5	27.3
Cangyuan	23.32	99.98	1,730	1741.1	24.9
Ximeng	22.60	99.63	1,040	2739.0	19.6

according to Zhou et al. (2003). The filter papers were kept moist, and germinating fruits were counted every day until no further germination was observed. Fruits were considered germinated when the radicle protruded 2 mm. At the end of the germination test, the fresh weight of seedlings was measured with an electronic balance, and germination index and vigor index were calculated. In addition, the ungerminated fruits were dissected and then tested for viability with 0.1% 2,3,5-triphenyl tetrazolium chloride (TTC). If an embryo was found and turned red, the seed was judged to be viable and lack of germination was due to seed dormancy.

Germination index and vigor index reflecting the state of seed vigor were calculated as follows:

Germination index (GI)

$$\mathrm{GI} = \sum (Gt/Dt)$$

Gt, number of seeds germinating on the tth day of incubation; Dt, number (t) of days of incubation.

Vigor index (VI)

$$\mathrm{VI} = \mathrm{GI} \times S$$

S, the average fresh weight of seedlings on the eleventh day of incubation (g).

Statistical analysis

Statistical analyses were performed using SPSS 11.0. Nested analysis of variance (Nested ANOVA) and restricted maximum likelihood (REML) estimation of variance components were used in the general linear model (GLM) to test the differences and variance of morphological and physiological characters of fruits between years, populations and individual trees. Correlation among fruit characters was determined by Pearson's product–moment test, based on individual trees. Arcsine transformation was used for percentage data before statistical analysis. The $P \leq 0.01$ significance level was used for all studies.

Results

Morphological characters of fruits

The morphological characters of fruits are shown in Table 2. Variation of length, width and 1,000-fruit weight was significant among individual trees both within populations and years, but these measures were not significant when the several populations and the 2 years were compared ($P < 0.01$). More than 50% of the variation occurred among individual trees both within populations and within years, in the three traits mentioned above (Tables 3, 4).

Fruit fill and germination

Significant variation of percentage of fruit fill was observed among populations and among individual trees within populations, each of which contributed roughly equally to the overall variation. In Cangyuan population, up to 95.75% of the total variation occurred among plants within years (Table 5).

Fruits began to germinate after 3 days of incubation, with a peak after 5–6 days, followed by occasional germination thereafter. The fruits that did not germinate were found to be empty or contain non-viable seeds, according to the result of TTC test, no dormancy was observed.

The results of fruit germination are shown in Table 2. Fruit germination percentage, germination index and vigor index exhibited significant variation among populations, among individual trees within populations and within years, however, not between years (Tables 3, 4). Analyses of variance showed that more than 60% of the total variation was attributed to variation among individual trees both within populations and within years in the germination-related indices (Tables 3, 4).

Table 2 Comparative descriptive statistics for mother plant differences in fruit characters of *Trigonobalanus doichangensis*

Trait	Mean	Standard deviation	Minimum value	Maximum value
FL (mm)	5.36	0.35	4.57	5.93
FW (mm)	3.73	0.4	2.86	4.36
W (g)	13.2	1.92	8.6	16.43
G (%)	25.84	11.48	0	46.91
GI	4.41	3.16	0	10.22
VI	0.12	0.09	0	0.33
EP (%)	33.11	15.57	6.54	57.24

FL, fruit length; FW, fruit width; W, 1,000-fruit weight; G, germination percentage; GI, germination index; VI, vigor index; EP, percentage of fruit fill

Table 3 Results of nested ANOVA for the variation in fruit morphological traits and fruit germination among populations and among plants within populations, with the percentage of variation accounted for by each source of variation

Source of variation	df	MS	*F*	*P*	Percent of total
Fruit length					
Population	3	0.389	1.159	0.344	0
Plant (population)	26	0.335	15.361	0	82.81
Error	60	0.02183			17.19
Fruit width					
Population	3	1.147	3.467	0.031	20.12
Plant (population)	26	0.331	10.051	0	59.76
Error	60	0.03291			20.12
1,000-fruit weight					
Population	3	18.64	1.298	0.296	6.64
Plant (population)	26	14.361	129.638	0	90.47
Error	90	0.111			2.89
Germination percentage					
Population	3	1284.032	4.586	0.01	28.42
Plant (population)	26	280.003	28.066	0	64.36
Error	60	9.977			7.22
Germination index					
Population	3	103.193	5.045	0.007	29.22
Plant (population)	26	20.453	26.094	0	63.12
Error	60	0.784			7.66
Vigor index					
Population	3	7.71E-02	5.181	0.006	25
Plant (population)	26	1.49E-02	21.447	0	62.5
Error	60	6.94E-04			12.5

Correlation of fruit characters

Table 6 showed that fruit length, width and 1,000-fruit weight had significant correlations with each other, and all of them had weak correlations ($r < 0.4$, $P < 0.01$) with percentage of fruit fill and germination-related indices. However, percentage of fruit fill and each of the germination-related indices possessed significant positive correlations ($r > 0.8$, $P < 0.01$) with each other.

Table 4 Results of nested ANOVA for the variation in fruit morphological traits and fruit germination between years and among plants within years, with the percentage of variation accounted for by each source of variation

Source of variation	df	MS	*F*	*P*	Percent of total
Fruit length					
Year	1	0.745	3.411	0.08	15.09
Plant (year)	20	0.218	8.247	0	60.38
Error	44	0.0265			24.53
Fruit width					
Year	1	0.557	2.436	0.134	8.70
Plant (year)	20	0.229	5.14	0	53.04
Error	44	0.0445			38.26
1,000-fruit weight					
Year	1	0.124	0.014	0.908	0
Plant (year)	20	9.078	42.923	0	90.91
Error	66	0.211			9.09
Germination percentage					
Year	1	199.133	0.691	0.416	0
Plant (year)	20	288.033	25.983	0	89.13
Error	44	11.085			10.87
Germination index					
Year	1	36.804	1.902	0.183	6.88
Plant (year)	20	19.35	16.83	0	78.28
Error	44	1.15			14.84

Table 5 Variance and distribution of variance in percentage of fruit fill in *Trigonobalanus doichangensis*

Source of variation	df	MS	*F*	*P*	Percent of total
Population	3	3869.513	10.477	0.000	48.83
Plant (population)	26	369.319	60.781	0.000	48.71
Error	60	6.076			2.46
Year	1	105.198	0.261	0.615	0
Plant (year)	20	403.234	71.054	0.000	95.75
Error	44	5.675			4.25

Discussion

Seed size is one of the more important characters related to the adaptive capabilities of plants (Hendrix et al. 1991; Turnbull et al. 1999; Geritz 1995). And in general, the seed size of a given species is less variable than the number of seeds or other reproductive traits (Silvertown and Charlesworth 2001). However, variability in seed size within species has been reported for many plants. Significant variation in seed mass occurred at various levels such as among populations (Jacquemyn et al. 2002; Vaughton and Ramsey 1998; Loha et al. 2006; Mamo et al. 2006), among individuals (Eriksson 1999; Howe and Richter 1982) and among the individual fruits of a single specimen (Obeso 1993; Mendez 1997). The seed size may be influenced by maternal effect (Roach and Wulff 1987; Schwaegerle and Levin 1990; Dawsn and Ehleringer 1991), phenology (Ågren 1989), interaction among parent plants, among offspring (seeds) and among parent/offspring (Ganger 1997; Niesenbaum 1999; Uma Shaanker et al. 1988). In addition, seed size variation can also result from low or variable selection pressure, resource availability, the effect of position on plants and other physiological factors (Stearns 1992; Herrera 1990). As the dispersal and germination units, fruits of *T. doichangensis* presented significant variation in fruit length, width and 1,000-fruit weight among individual trees. In addition, the most variation in fruit size occurred among individual trees within populations. This might be due to maternal effects of genetic or physiological traits.

According to Sun et al. (2006), considerable seed abortion occurred in *T. doichangensis* and the percentage of well developed fruits was less than 10%. The seedlessness of seemingly well-developed fruits may be attributed to absence of pollination and fertilization (Zimmerman and Pyke 1988; Whelan and Goldingay 1989), resource limitation (Zimmerman and Pyke 1988), intra-fruit sibling rivalry (Uma Shaanker et al. 1988; Mohan Raju et al. 1996) and other factors. Batches of fruits from the same tree can be divided into dark-colored and light-colored propagules, and percentage of seed abortion between the two kinds of fruits differed significantly (unpublished report). The variation in seed abortion between the two kinds of fruits may result from phenology. In addition, the difference of fruit fill percentage between the present study and previous report (<10%) (Sun et al. 2006) may be due to sampling strategy and year effect. Therefore, sampling strategy must be taken into consideration when determining sample size of fruit collection for conservation or reforestation. As for dark-colored fruits, most of the variation in percentage of fruit fill occurred among populations and among individual trees within

Table 6 Pearson's product–moment correlation coefficient between fruit characters, based on individual trees in the four populations of China

	FL	FW	W	G	GI	VI	EP
FL	1	0.498**	0.729**	−0.054	−0.048	0.096	0.067
FW		1	0.677**	0.174	0.185	0.308	0.252
W			1	0.281	0.253	0.358	0.358
G				1	0.958**	0.900**	0.914**
GI					1	0.959**	0.899**
VI						1	0.862**
EP							1

** Correlation is significant at the 0.01 level

FL, fruit length; FW, fruit width; W, 1,000-fruit weight; G, germination percentage; GI, germination index; VI, vigor index; EP, percentage of fruit fill

populations. The variation may be related to differences in geo-climate of populations, resource availability, reproductive phenology, and the proportion of male and female flowers. McLemore (1975), Silen and Osterhaus (1979) and Noland et al. (2006) reported genetic variation in percentage of empty seeds among individual trees for several species. Relevant study should also be conducted to begin to understand the large amount of variation of fecundity among individual trees of *T. doichangensis*. It was observed that there was no apparent correlation between percentage of fruit fill and fruit morphological traits. Therefore, it is not possible to sort out fruits filled with seeds according to the fruit morphological characters.

Germination percentage, germination index and vigor index were used to evaluate the quality of fruits. As for each of the three germination-related indices, most of the variation occurred among individual trees within populations. The variation might originate from maternal factors as well as minor environmental conditions. Wulff (1995) and Gutterman (2000) reported that maternal factors, such as position of the seed in the fruit/tree and the age of the mother plant markedly influence the germinability of seeds. It was observed that germination percentage, germination index and vigor index had weak correlations with fruit morphological traits. Therefore, it could be concluded that the fruit size of *T. doichangensis* does not relate to its fruit germination capacity. Selecting fruits on the basis of mass is not an appropriate way to enhance germination for reforestation projects. These results have been confirmed by our current experiments on germination of four different sized fruits. The germination of both of the heaviest and lightest fruits were poorer (mean = 18.04%) than that of those from the two intermediate categories (mean = 27.25%) (unpublished report). Concerning the relationship between seed mass and germination, published results have been rather inconsistent, although the majority of the studies report positive effects of seed mass on germination (Shaukat et al. 1999; Gómez 2004; Khan 2004; Vera 1997; Milberg et al. 1996). Paz et al. (1999) reported that the effects of seed mass on germination were specific to species and habitat. As to *T. doichangensis*, fruit morphological traits might be adapted to dispersal, dormancy and other functions. Germination index and vigor index could reflect seed vigor, and seed vigor is considered to be a more reliable index for predicting plant growth rate and crop production than a simple assessment of capability to germinate (Perry 1978). Vigor index that reflects the combined result of germination initiation and seedling growth showed no correlation with fruit mass. However, fresh weight of seedlings showed significant positive correlation (data not shown) with fruit mass in *T. doichangensis*. Similar results have been reported that larger seeds conferred an advantage in terms of greater seedling growth (Leishman 1999; Cordazzo 2002). This may be related to large reserves of nutritive substances.

Various species showed great fluctuations in their fruiting crop across years (Herrera 1998; Osada 2005), and endogenous nutrition and hormones of fruiting trees differed between high-yield and low-yield years (Sha et al. 2007; Qi et al. 2006).

Therefore, morphophysiological characters of fruits/seeds may be influenced by fruiting crop. Our preliminary observations reveal that there are high-yield and low-yield years in *T. doichangensis*. The percentage of fruit fill, germination percentage and germination index showed no significant variation between the 2 years. However, these results were based on only one population. In order to fully understand the year effect, further study should be conducted for more years, based on the whole population.

Conclusion

The percentage of well-developed seeds of dark-colored fruits is significantly higher than that of light-colored fruits (unpublished report). In the present study, only dark-colored fruits were used. Results provide evidence that fruit-related parameters differ significantly among individual trees, each of which accounting for more than 48% of the total variation. For bulk fruit collection, either for ex-situ conservation or reforestation, collection should be made from various individuals, especially from different populations, as there is some variation in fruit traits among populations. Fruit morphological traits did not show significant correlations with percentage of fruit fill and germination-related indices, therefore, it is futile to collect fruits according to fruit size. Although there was no apparent significant variation between the 2 years in the tested parameters, further study should be conducted on a larger sample. In addition, selecting and analyzing additional individuals from each population in future study should be considered to get more precise data.

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