



Family selection and evaluation of *Larix gmelinii* var. *principis-rupprechtii* (Mayr.) Pilger based on stem analysis data at multiple sites

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Abstract *Larix gmelinii* var. *principis-rupprechtii* (Mayr.) Pilger is an important native tree species in North China with advantages of fast growth, straight trunk, and good wood properties. The multi-year and multi-site breeding research of families of the species has not been reported previously. Based on diameter at breast height (DBH), height and volume of 25 families on four experimental sites, we calculated variance components, genetic parameters, juvenile and mature trait correlations and made genotype main effect plus genotype × environment interaction effect (GGE) biplot based on the breeding values estimated using the method of best linear unbiased prediction (BLUP). Compared with height, DBH and volume had higher heritability and larger variation coefficients, making them the more suitable traits for family selection and evaluation. Based on these, GGE biplots containing 20 combinations of site × age were drawn

using data at 13 to 17 years when the interactions between family and location were strong. Test sites classifications based on DBH, and volume were inconsistent, with two categories for DBH and one for volume. The Guyuan site was the most suitable with strong discriminating ability, high representativeness and stability among tree ages. Integrating the ranking results of DBH and volume, families 66, 76, 82 and 111 were high-yielding and stable, families 78 and 96 were high-yielding with above average stability, families 72 and 79 were high-yielding with below average stability, whereas stability of family 100 was inconsistent between DBH and volume. Early selection based on DBH was convenient and reliable, and can be made at seven years. This study provides support for the selection of *Larix gmelinii* var. *principis-rupprechtii* families in Hebei province and an example for the application of stem analysis data from multiple sites in tree breeding.

Conghui Zheng and Jianfeng Dai have been contributed equally to this paper.

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Introduction

Larix gmelinii var. *principis-rupprechtii* (Mayr.) Pilger is an important native tree species in mountainous regions of North China, and can be used as a large diameter timber species or as pulp for paper making. It has broad development and application prospects. Provenance or family selection is the foundation of tree breeding and is of significance for providing suitable germplasm for specific areas (Pan et al. 2018). Regional trials or multi-site trials can be used to study genotype by environment

(G × E) interactions. By analyzing the adaptability and genetic stability of each germplasm, suitable material for an individual site or for multi-sites can be selected (Lin 2019; Zheng et al. 2019). Based on multi-year observations of trial stands, genetic parameters for growth traits can be estimated. They are critical for designing optimal breeding strategies and for shortening the breeding cycle. In the past, provenance or family tests were often based on single year and single-site experiments, single year and multi-site experiments, or multi-year and single site experiments, and have been reported for species such as *Pinus elliottii* Engelmann (Zhang et al. 2017), *L. kaempferi* (Lamb.) Carrière (Pan et al. 2018), *L. gmelinii* var. *principis-rupprechtii* (Zheng et al. 2019), *L. olgensis* Henry (Zhang et al. 2020), *Cunninghamia lanceolata* (Wu et al. 2019) and *P. tabuliformis* Carrière (Li et al. 2015). Multi-year and multi-site tests can make more accurate and reliable assessments of provenance or family and site, the G × E interactions, and the identification of early age selection (Xu and Li 2015). Presently, most multi-site and multi-year studies have focused on agricultural crops (Badu-Apraku et al. 2013; Kivuva et al. 2014; Laurie and Booyse 2015; Laurie et al. 2015; Dia et al. 2016). For tree species, due to their long growth cycle, there have been only a few studies about G × E interaction or early selection based on multi-site and multi-year experiments (Bian et al. 2014; Diao et al. 2016). Such studies based on multi-site and multi-year tests have not been reported for *L. gmelinii* var. *principis-rupprechtii*.

In order to decide the appropriate breeding strategies, four trial plantations of 25 *L. gmelinii* var. *principis-rupprechtii* families were established in Hebei province. The study objectives were to: (1) describe variations in genetic parameters for growth traits with age; (2) determine the most appropriate age for early selection; (3) select families with high yield and good cross-sites stability; and, (4) select sites with high discriminating ability, strong representativeness, and good cross-age stability. These findings help in promoting the genetic improvement of *L. gmelinii* var. *principis-rupprechtii*.

Materials and methods

Sample plots and data collection

Four family trials of *L. gmelinii* var. *principis-rupprechtii* were carried out in 2003 at four sites in Hebei province: Zhazi, Weichang (CZ); Mayinggou, Chicheng (CC); Liutiaogou, Guyuan (GY); and Yudaokou, Weichang (YDK). The environmental conditions are detailed in Table 1. A randomized complete block design of 25 half-sib families was used in each trial with 10-tree plots and three replicates. In 2019, one average tree from each family was felled to obtain stem analysis data, i.e., growth data of 300 trees at 5–17 years of age, including inside-bark diameter at breast height (DBH), tree height, and inside-bark stem volume.

Statistical analysis

Family models of each trait (DBH, height and volume) for multiple sites are listed in Naranjo et al. (2012) and Ling et al. (2021) (Eq. 1). They were mixed linear models based on individual ages. The ASReml 4.0 package of R software was used (Gilmour et al. 2016).

$$Y_{ijkl} = \mu + S_i + R_{i(j)} + F_k + SF_{ik} + e_{ijkl} \quad (1)$$

where, Y_{ijkl} is observed value of family k in block j at site i ; μ is the overall mean; S_i is the fixed effect of the i th site; $R_{i(j)}$ is the fixed effect of the j th block within the i th site; F_k is the random effect of the k th family; SF_{ik} is the random interaction effect of the i th site and the k th family; and e_{ijkl} is the random residual effect.

Based on the above-mentioned family models, the family variance components (V_f), the family × site variance components ($V_{f \times l}$), and the ratio of $V_{f \times l}$ to V_f ($V_{f \times l}/V_f$) of DBH, height and volume were estimated and analyzed for each age. Significance of variance was tested using the likelihood ratio test (Diao et al. 2016; Lai et al. 2017). Individual-tree heritability (h_i^2), family heritability (h_f^2) and variation coefficients at phenotypic, environmental, and genetic levels (PCV , ECV and GCV) of each trait were calculated with Eqs. 2–6 (Ren et al. 2010; Li et al. 2015;

Table 1 Environmental conditions for each test site

Code	Site	Elevation (m)	Slope direction	Average annual temperature (°C)	Annual average rainfall (mm)	Soil type	Annual frost-free period (d)
CZ	Zhazi, Weichang	1300	Semi-shady	4.7	450	Mountain brown soil	110
CC	Mayinggou, Chicheng	1360–1490	Shady	2.1	407	Mountain leached cinnamon soil	97
GY	Liutiaogou, Guyuan	1800	Semi-shady	1.4	400	Chestnut soil	98
YDK	Yudaokou, Weichang	1530	Gentle-slope land	0.5	460	Meadow soil	79

Pan et al. 2018), followed by analyzing their trends with tree age.

$$h_i^2 = 4\sigma_f^2 / (\sigma_e^2 + \sigma_f^2) \quad (2)$$

$$h_f^2 = \sigma_f^2 / (\sigma_e^2 / r + \sigma_f^2) \quad (3)$$

$$PCV = SD_P / \bar{X} \quad (4)$$

$$ECV = SD_E / \bar{X} \quad (5)$$

$$GCV = SD_G / \bar{X} \quad (6)$$

where, h_i^2 is individual-tree heritability, h_f^2 family heritability, σ_f^2 variance component of family, σ_e^2 variance component of environment, r the number of repetitions, PCV phenotypic variation coefficient (%), ECV environmental variation coefficient (%), GCV genetic variation coefficient (%), SD_P phenotypic standard deviation, SD_E environmental standard deviation, SD_G genetic standard deviation, and \bar{X} the mean of the measured trait.

Wricke (1962) eco valence (E_i) and the main genotype effect plus genotype \times environment interaction effect (GGE) biplot were used to evaluate the stability of families. For traits with higher heritability and variation coefficient, E_i values for each family were calculated. A family with lower E_i is stable. The breeding values of families for traits with higher heritability and higher variation coefficient were then estimated using the best linear unbiased prediction (BLUP) at ages with greater values of $V_{f \times e} / V_f$ (i.e., stronger G \times E interaction according to Lin et al. 2013). The BLUP data obtained by adding the breeding values and the overall means were used in GGE biplot analysis done by the R software package, GGEBiplotGUI (Yan 2010). To evaluate the yield and stability of families under different environments (i.e., groups of site \times age) and the discriminating ability, representativeness and between age stability of the sites, three views of GGE biplots for each trait were analyzed; they were: a “Which-Win-Where” view showing grouping of environments and the best family for each environment, a “Discriminating Ability vs. Representativeness” view showing discriminating ability and representativeness of environments, and a “Mean vs. Stability” view showing mean and stability of families.

Genetic (R_G) and phenotypic correlations (R_P) between growth traits (i.e., DBH, height and volume) at early ages and volume at age 17 were calculated with Eqs. 7–8 (Wu et al. 2019). Efficiency of early selection (E) was estimated with Eq. 9 (Wu et al. 2007). Based on the R_G , R_P and E ,

the appropriate early selection traits and selection age can be determined.

$$R_G = Cov_{G12} / \sqrt{\sigma_{G1}^2 \times \sigma_{G2}^2} \quad (7)$$

$$R_P = Cov_{P12} / \sqrt{\sigma_{P1}^2 \times \sigma_{P2}^2} \quad (8)$$

$$E = (i_E \times R_G \times h_E) / (i_L \times h_L) \quad (9)$$

where, R_G is genetic correlation, Cov_{G12} is the genetic covariance between traits (DBH, height or volume) in early years with the volume at age 17, σ_{G1}^2 genetic variance for traits in early years, σ_{G2}^2 is genetic variance for the volume at age 17, R_P is phenotypic correlation, Cov_{P12} is the phenotypic covariance between traits in early years with the volume at age 17, σ_{P1}^2 is phenotypic variance for traits in early years, σ_{P2}^2 is phenotypic variance for the volume at age 17, E is efficiency of early selection, i_E and i_L are the selection intensity in the early and late ages ($i_E = i_L$ in this calculation), and h_E and h_L are the square root of the heritability in the early and late ages.

Results

Estimates of variance components for DBH, height and volume at each age

The p value of site effect and the estimates of variance components for DBH, height and volume at each individual age are shown in Table 2. Site was significant for all the traits for ages between 5 and 17 years ($p < 0.001$). For DBH, the family effect was significant at most ages ($p < 0.05$), except for a marginal significance at age 14 ($p = 0.058$), and the family \times site interaction was significant ($p < 0.05$) after age 13. For height, the family \times site interaction was significant ($p < 0.05$) at most ages except for age 6, and the family effect was not significant from age 5 to 17 ($p > 0.1$). For volume, the family effect was significant ($p < 0.05$) after age 6, and the family \times site interaction was significant ($p < 0.05$) after age 11.

The ratios of $V_{f \times e} / V_f$ (i.e., $V_{f \times e} / V_f$) for DBH and volume were larger for ages 13–17, indicating the stronger G \times E interactions for DBH and volume at these ages compared with other ages (Fig. 1). The $V_{f \times e} / V_f$ for height changed from 3.67 to 1.778 811, which was much larger than the values for DBH and volume (Fig. 1).

Heritability and variation coefficient for each trait

The family heritability for DBH, volume and height varied from 0.40 to 0.55, 0.29 to 0.54 and 0.00 to 0.33, respectively, and the corresponding individual-tree heritability

Table 2 Estimates of variance components for various traits at each individual age

Age	Trait	<i>p</i> value of site	Family variance components (V_f)	Family \times site variance components ($V_{f \times i}$)	Residual variance components (V_e)
17	DBH	<2e-16 ***	0.100**	0.163***	0.528
	Volume	<2e-16 ***	7.691e-06**	1.343e-05***	4.207e-05
	Height	<2e-16 ***	0.029	0.104***	0.389
16	DBH	<2e-16 ***	0.087*	0.155***	0.498
	Volume	<2e-16 ***	5.682e-06*	1.101e-05***	3.396e-05
	Height	<2e-16 ***	0.010	0.101**	0.396
15	DBH	<2e-16 ***	0.061*	0.138***	0.493
	Volume	<2e-16 ***	3.791e-06*	8.464e-06***	2.689e-05
	Height	<2e-16 ***	0.001	0.096**	0.440
14	DBH	<2e-16 ***	0.047	0.113**	0.508
	Volume	<2e-16 ***	2.582e-06*	5.804e-06***	1.995e-05
	Height	<2e-16 ***	3.012e-07	8.833e-02**	4.994e-01
13	DBH	<2e-16 ***	0.053*	0.083*	0.534
	Volume	<2e-16 ***	2.172e-06*	3.727e-06**	1.542e-05
	Height	<2e-16 ***	4.794e-08	8.527e-02**	4.737e-01
12	DBH	<2e-16 ***	0.053*	0.063	0.563
	Volume	<2e-16 ***	1.594e-06*	2.133e-06*	1.170e-05
	Height	<2e-16 ***	5.649e-08	9.502e-02**	4.657e-01
11	DBH	<2e-16 ***	0.062*	0.049	0.589
	Volume	<2.2e-16***	1.091e-06**	1.119e-06*	7.608e-06
	Height	<2e-16 ***	5.455e-08	9.489e-02**	4.453e-01
10	DBH	<2e-16 ***	0.071**	0.016	0.642
	Volume	<2e-16 ***	5.620e-07**	4.140e-07	4.652e-06
	Height	<2e-16 ***	6.370e-08	6.582e-02*	3.982e-01
9	DBH	<2e-16 ***	0.058*	0.005	0.652
	Volume	<2e-16 ***	2.036e-07*	8.935e-08	2.041e-06
	Height	<2e-16 ***	9.641e-08	1.080e-01***	3.849e-01
8	DBH	<2e-16 ***	0.052*	0.008	0.578
	Volume	<2e-16 ***	6.584e-08*	2.841e-09	8.241e-07
	Height	<2e-16 ***	9.228e-08	8.639e-02**	4.119e-01
7	DBH	<2e-16 ***	2.582e-02*	2.149e-08	3.974e-01
	Volume	<2e-16 ***	1.76487e-08*	1.148e-14	2.408e-07
	Height	<2e-16 ***	2.288e-07	6.082e-02*	4.225e-01
6	DBH	<2e-16 ***	1.055e-02*	8.675e-08	1.672e-01
	Volume	2e-16 ***	3.510e-09*	3.077e-14	5.259e-08
	Height	<2e-16 ***	4.527e-08	2.842e-02	4.473e-01
5	DBH	1e-12 ***	3.146e-03*	2.849e-08	5.287e-02
	Volume	4e-11 ***	3.347e-10	6.209e-15	1.006e-08
	Height	<2e-16 ***	8.560e-08	5.266e-02**	3.058e-01

Degrees of freedom=3 for site. *** $p < 0.001$, ** $p < 0.01$, and * $p < 0.05$; the same applies to the tables below

estimates varied from 0.22 to 0.51, 0.13 to 0.49 and 0.00 to 0.22, respectively (Fig. 2). Family heritability was higher than the individual tree heritability estimates for all traits. The family and individual tree heritability estimates of DBH and volume were greater than those of height.

The phenotypic variation coefficients for DBH, volume and height varied from 9.0% to 65.8%, 19.6% to 85.0% and

7.6% to 25.9%, respectively. The corresponding environmental variation coefficients varied from 8.4% to 63.9%, 18.4% to 83.6% and 7.4% to 25.9%, respectively. The corresponding genetic variation coefficients varied from 2.6% to 15.6%, 6.8% to 17.4% and 0.01% to 1.8%, respectively (Fig. 3). The three types of variation coefficients for each trait decreased with age and gradually stabilized. For all

traits, the phenotypic variation coefficients had the largest values, followed by the environmental variation coefficients, and genetic variation coefficients were smallest. For each type of variation coefficients, volume had the highest variation coefficients, followed by DBH and height.

Selection and evaluation of families and sites

Given the higher heritability and higher variation coefficients of DBH and volume compared to height (Figs. 2 and 3), the ecovalences (E_i) of DBH and volume at age 17 for

Fig. 1 Age trends of V_{pf}/V_f values

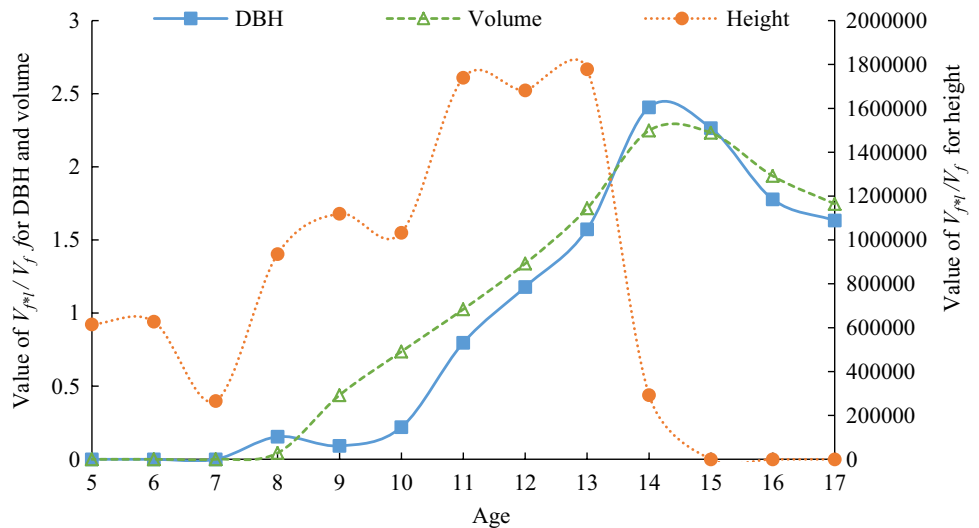


Fig. 2 The effects of tree age on individual tree and family heritability estimates for DBH, height and volume

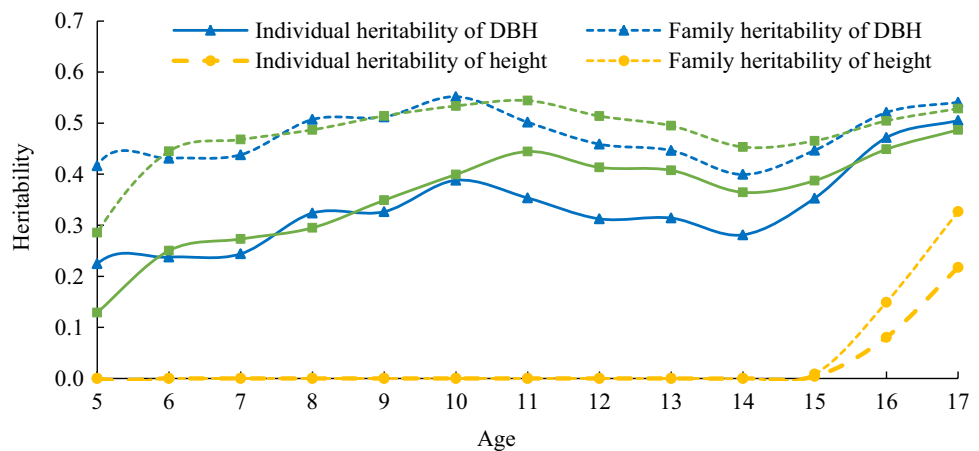
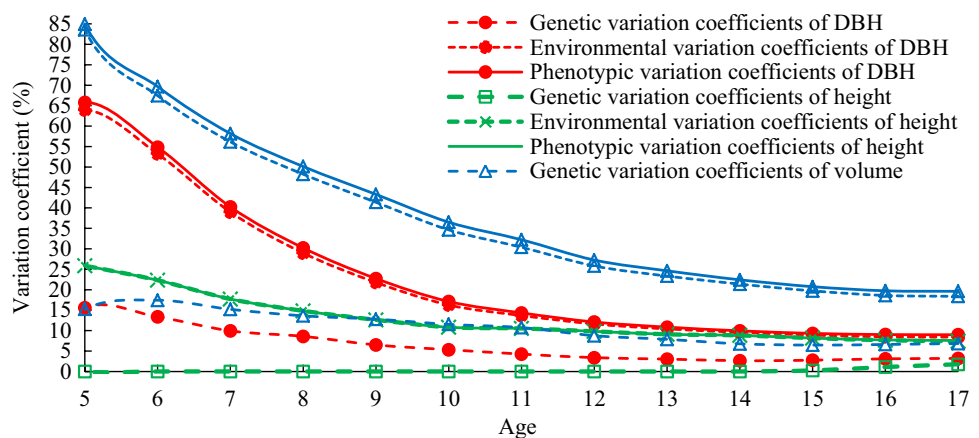


Fig. 3 Age trends of genetic, environmental, and phenotypic variation coefficients for DBH, height and volume



each family were calculated and ranked in order to evaluate the genetic stability of each family (Table 3). Among the top 12 families with high stability, the mean DBH values of families 66, 68, 82, 76, 111, 96 and 78 were higher than the mean DBH of all the other families at all sites (9.9 cm); similarly, the mean volumes of the above-mentioned families (except for family 68) were higher than the mean volume of all the other families at all sites (0.04 m³). Hence, families 66, 68, 82, 76, 111, 96 and 78 were preliminarily judged as high yielding and with above average stability. Family 100 ranked 13th among 25 families, with a mean DBH greater than 9.9 cm and a mean volume equal to 0.04 m³. Therefore, family 100 could be considered as a high yielding and moderately stable family. Among the 12 families ranked after family 100, the mean DBH values of families 42, 72, 79, 77 and 56 were greater than 9.9 cm, and the mean volume of families 72 and 79 was greater than (or equal to) 0.04 m³. Therefore, families 72 and 79 could also be judged as high yielding and with below average stability.

For DBH and volume, GGE biplots containing 20 environment combinations (i.e., site × age. Sites = CZ, CC, GY and YDK; ages = 13, 14, 15, 16 and 17) were made based on DBH and the volume BLUP data.

For DBH, the interaction between families and environment is shown in Fig. 4a. The biplot was divided into seven sectors in polygon view, and the vertex families had the best performance in each sector. The 5 site × age combinations of site YDK were in the same group, with family 78 as a possible candidate, and the 15 site × age combinations of sites CZ, CC and GY belonged to the other group, with family 111 performing best. The grouping results of the sites were consistent across ages. Discriminating ability and representativeness of each site × age combination are shown in Fig. 5a. The solid line with an arrow represents the average environment axis (AEA), and the length of the dotted line between the site × age combination and the origin represents the discriminating ability of an environment combination. The angle between the environment combination vector and the AEA indicates the representativeness of environment combination. The smaller angle means the stronger representativeness (Ling et al. 2021). The first two principal components accounted for 76.5% of total G × E interaction. Site CZ had the highest representativeness, followed by sites GY and CC, and site YDK had the lowest representativeness. The representativeness of the sites was consistent across ages.

Table 3 Ecovalence (E_i) of DBH and volume at age 17 for each family

Family	DBH			volume			Mean of E_i order	Rank of Stability
	Mean (cm)	E_i	E_i order	Mean (m ³)	E_i	E_i order		
86	9.7	0.08	1	0.039	0.5e-5	1	1.0	1
66	10.0	0.14	2	0.041	1.3e-5	2	2.0	2
46	9.5	0.18	4	0.038	1.9e-5	4	4.0	3
68	9.9	0.31	5	0.040	3.5e-5	8	6.5	4
87	9.6	0.49	10	0.038	1.3e-5	3	6.5	5
82	10.3	0.45	8	0.043	2.9e-5	6	7.0	6
50	9.6	0.31	6	0.039	4.4e-5	10	8.0	7
76	10.3	0.45	9	0.045	3.0e-5	7	8.0	8
116	9.3	0.43	7	0.035	4.6e-5	11	9.0	9
111	10.9	0.15	3	0.052	9.8e-5	17	10.0	10
96	10.1	0.61	12	0.044	4.1e-5	9	10.5	11
78	10.9	0.59	11	0.049	8.0e-5	14	12.5	12
100	10.1	0.90	15	0.041	5.3e-5	12	13.5	13
52	9.8	0.79	14	0.038	8.6e-5	16	15.0	14
35	9.4	3.11	25	0.038	2.4e-5	5	15.0	15
49	9.7	0.64	13	0.040	1.2e-4	18	15.5	16
42	10.0	1.08	16	0.040	8.6 e-5	15	15.5	17
72	10.1	1.41	20	0.042	6.0 e-5	13	16.5	18
79	9.9	1.17	17	0.041	1.4e-4	20	18.5	19
59	9.2	1.24	18	0.035	1.3e-4	19	18.5	20
77	10.2	1.95	22	0.040	1.4e-4	21	21.5	21
56	10.1	1.29	19	0.040	2.4e-4	25	22.0	22
1	9.5	1.77	21	0.040	1.5e-4	23	22.0	23
53	9.6	2.80	24	0.038	1.4e-4	22	23.0	24
97	9.7	2.37	23	0.038	1.9e-4	24	23.5	25

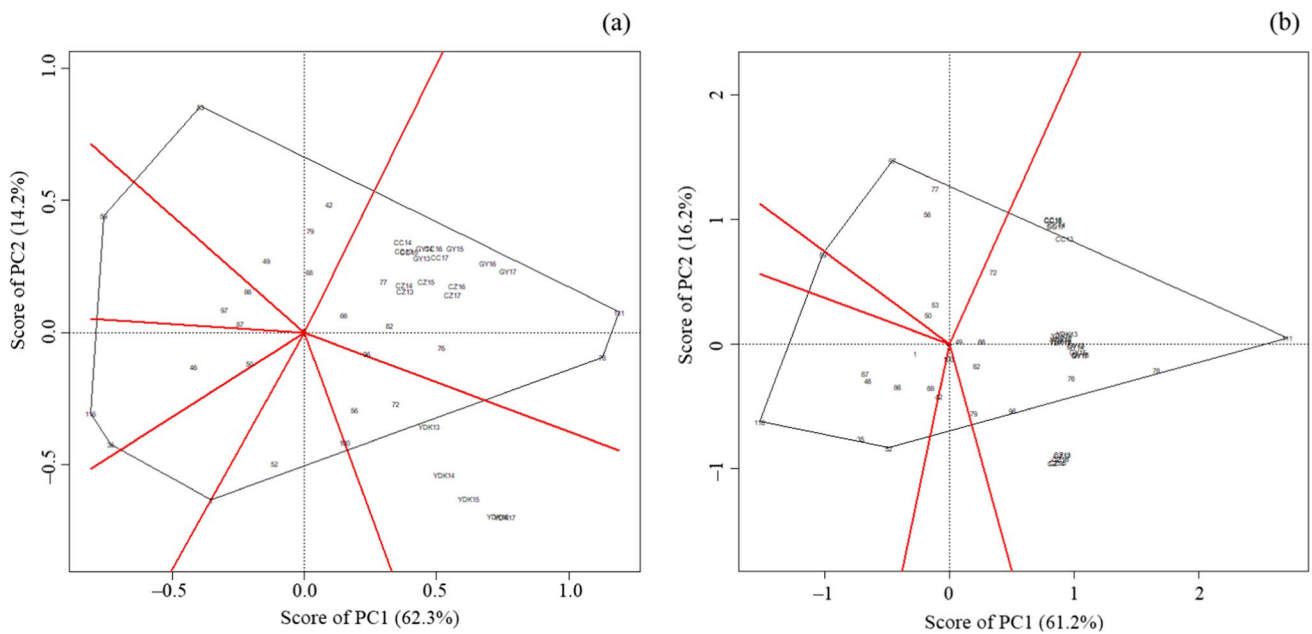


Fig. 4 Site groupings and the best family for each site; **a**= DBH (Scaled=0, Centered=G+GE, SVP=Symmetrical); **b** volume (Scaled=Std Deviation, Centered=G+GE, SVP=Symmetrical)

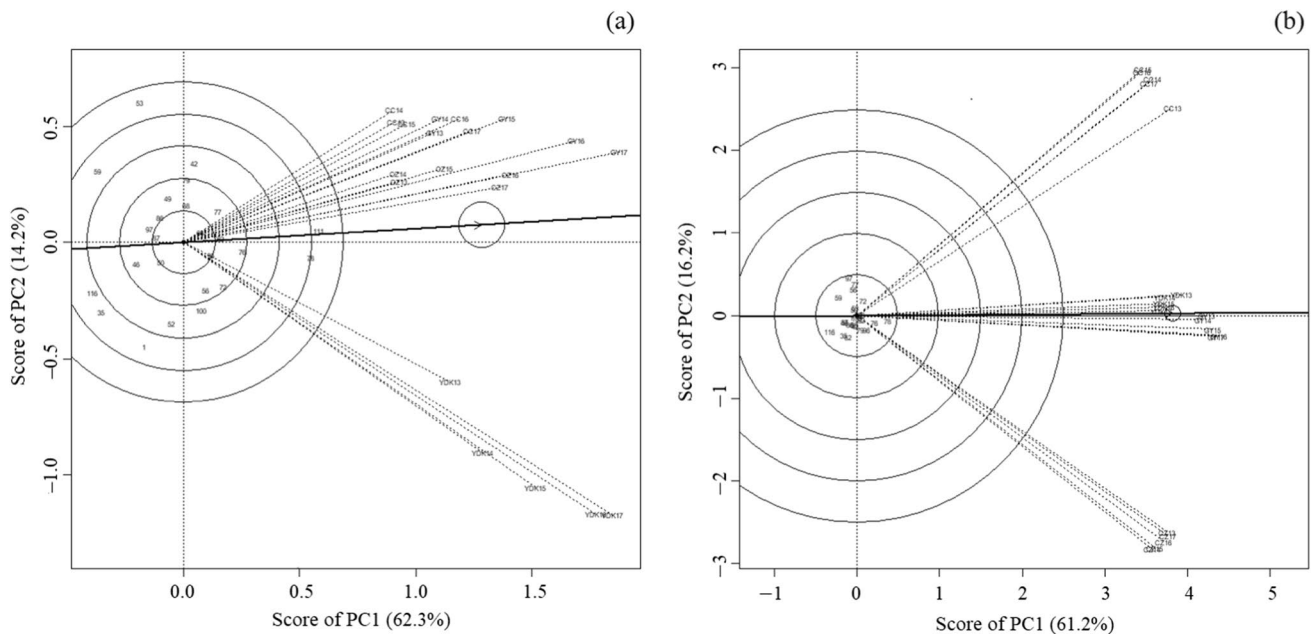


Fig. 5 Discriminating ability and representativeness of the sites; **a** DBH (Scaled=0, Centered=G+GE, SVP=Column Metric Preserving); **b** volume (Scaled=Std Deviation, Centered=G+GE, SVP=Column Metric Preserving)

At ages 15, 16 and 17, site YDK had the highest discriminating ability, followed by sites GY and CZ, and site CC had the lowest discriminating ability. At ages 13 and 14, site YDK had the highest discriminating ability, followed by sites GY and CC, and site CZ had the lowest discriminating ability. For sites YDK, GY and CC, they had the highest

discriminating ability at age 17, followed by ages 16, 15 and 14, and they had the lowest discriminating ability at age 13. For site CZ, it had the highest discriminating ability at age 16, followed by ages 17, 15 and 14, and it had the lowest discriminating ability at age 13. Overall, site GY had the large discriminating ability, high representativeness

and good cross-age stability, thus was the most suitable site to effectively select the high-yielding and stable families (Fig. 5a).

Yield performance and stability of the families are shown in Fig. 6a. The solid line with an arrow represents the average environment axis (AEA). The vertical solid line to the AEA through the origin denotes the overall mean DBH. The DBH of the families on the left of the vertical solid line was lower than the overall mean, whereas the DBH of the families on the right of the solid line was higher than the overall mean. The vertical dotted lines to the AEA represent the average DBH and the stability of the DBH of each family across all environment combinations. The longer the vertical dotted line, the less stable the family (Ling et al. 2021). Families 111, 76, 82, 96, 66, and 77 were high-yielding and highly stable; families 78, 56 and 68 were high-yielding with above average stability; families 72 and 79 were high-yielding with below average stability; and families 42 and 100 were high-yielding and unstable (Fig. 6a).

For volume, the 20 site \times age combinations of four sites were in the same group, with family 111 performing the best, followed by family 78. The grouping results of the sites were basically consistent across ages (Fig. 4b). The first two principal components accounted for 77.4% of total $G \times E$ interaction. Site GY had the highest representativeness, followed by site YDK, and sites CC and CZ had the lower representativeness. The representativeness of the sites was roughly consistent across ages (Fig. 5b). Overall, site GY had high representativeness and good cross-age stability,

thus was the optimum test site. Families 111, 78, 82, 76, 100, 66 and 49 were high-yielding and highly stable, and families 96, 72 and 79 were high-yielding and had average stability (Fig. 6b).

Early selection of families

The genetic correlations (R_G) between DBH in early ages and volume at age 17 (v_{17}) started to be significantly positive from age 6 ($p < 0.05$) and varied from 0.76 to 0.99 (Table 4). The R_G between the volume at early ages and the v_{17} began to be significantly positive from age 5 ($p < 0.05$) and varied from 0.90 to 0.99 (Table 4). For height, only the R_G between the height at a few ages (9, 12, 16 and 17) and the v_{17} were significant ($p < 0.05$). The phenotypic correlations (R_P) between the traits at early ages and the v_{17} started to be significantly ($p < 0.01$) positive (0.31–0.82) from age 5 for DBH, age 3 ($p < 0.01$) for height (0.21–0.62) and age 5 ($p < 0.05$) for volume (0.35–0.99) (Table 4). The R_G and R_P between the traits at early ages and the v_{17} gradually increased with age. From age 7, most of the R_G and R_P between the traits in early ages and the v_{17} exceeded 0.5 (Table 4). The early selection efficiencies (E) of height were lower than those of DBH and volume at all ages (Fig. 7). The E of DBH and volume increased quickly from ages 5 to 7, and after age 7 were kept in the narrow ranges of 0.82 to 0.99 and 0.88 to 0.99, respectively, i.e., the E exceeded the critical value of early selection (0.8) (Zhang et al. 2013) from age 7. Hence, the appropriate early selection age of

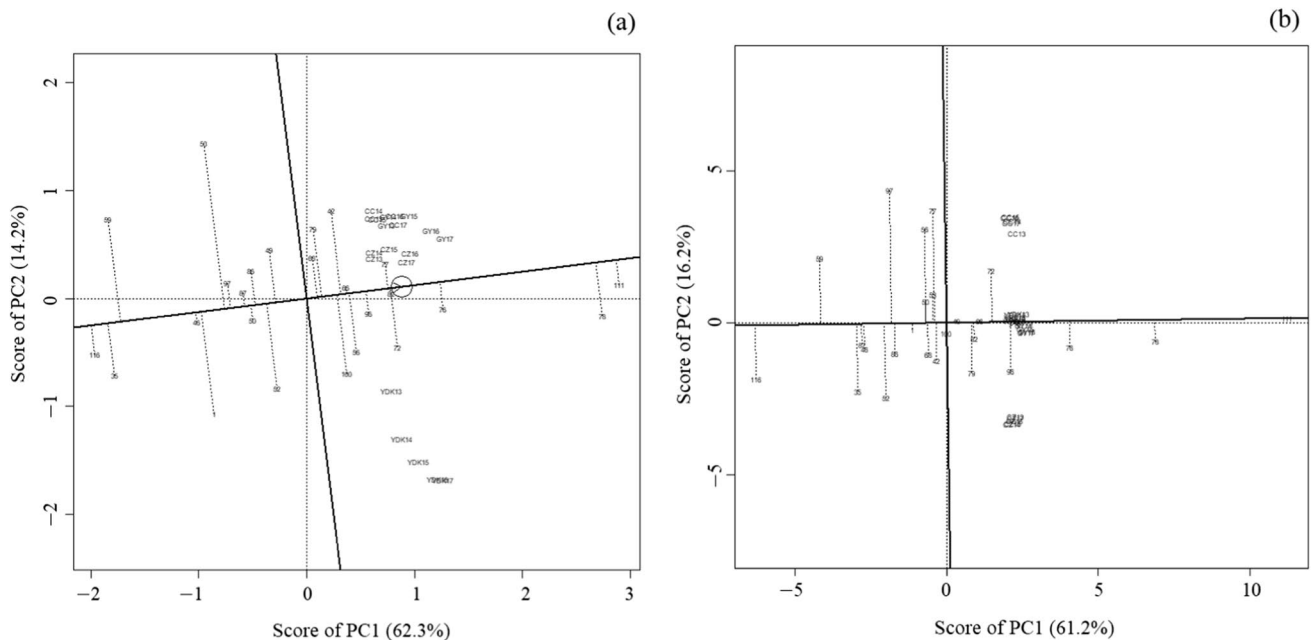


Fig. 6 Mean and stability of the families; **a** DBH (Scaled=0, Centered=G+GE, SVP=Row Metric Preserving); **b** volume (Scaled=Std Deviation, Centered=G+GE, SVP=Row Metric Preserving)

Table 4 Correlation estimates (\pm standard errors) between traits (DBH, height and volume) at early ages and volume at age 17 (v_{17})

Age	DBH- v_{17}		Height- v_{17}		Volume- v_{17}	
	$R_G \pm SE$	$R_P \pm SE$	$R_G \pm SE$	$R_P \pm SE$	$R_G \pm SE$	$R_P \pm SE$
1	–	–	0.95 \pm 1.18	0.09 \pm 0.06	–	–
2	–	–	0.65 \pm 1.73	0.09 \pm 0.06	–	–
3	–	–	0.70 \pm 0.45	0.21 \pm 0.06***	–	–
4	–	–	0.72 \pm 0.42	0.28 \pm 0.05***	–	–
5	0.62 \pm 0.32	0.31 \pm 0.06***	0.96 \pm 1.50	0.30 \pm 0.05***	0.90 \pm 0.33*	0.35 \pm 0.05***
6	0.76 \pm 0.23*	0.44 \pm 0.05***	0.99 \pm 0.96	0.40 \pm 0.05***	0.91 \pm 0.18**	0.49 \pm 0.05***
7	0.91 \pm 0.17**	0.52 \pm 0.04***	0.77 \pm 0.76	0.43 \pm 0.05***	0.93 \pm 0.14**	0.57 \pm 0.04***
8	0.86 \pm 0.15**	0.57 \pm 0.04***	0.99 \pm 0.90	0.48 \pm 0.05***	0.95 \pm 0.12***	0.63 \pm 0.04***
9	0.87 \pm 0.13**	0.60 \pm 0.04***	0.98 \pm 0.31**	0.49 \pm 0.05***	0.95 \pm 0.08***	0.68 \pm 0.03***
10	0.87 \pm 0.11***	0.66 \pm 0.04***	0.99 \pm 0.84	0.49 \pm 0.05***	0.95 \pm 0.07***	0.74 \pm 0.03***
11	0.91 \pm 0.09***	0.69 \pm 0.03***	0.99 \pm 1.00	0.50 \pm 0.05***	0.94 \pm 0.06***	0.79 \pm 0.02***
12	0.98 \pm 0.07***	0.72 \pm 0.03***	0.99 \pm 0.52*	0.51 \pm 0.04***	0.93 \pm 0.05***	0.83 \pm 0.02***
13	0.99 \pm 0.06***	0.75 \pm 0.03***	0.95 \pm 1.15	0.50 \pm 0.05***	0.95 \pm 0.04***	0.87 \pm 0.02***
14	0.99 \pm 0.05***	0.78 \pm 0.02***	0.75 \pm 0.64	0.55 \pm 0.04***	0.97 \pm 0.03***	0.91 \pm 0.01***
15	0.99 \pm 0.04***	0.81 \pm 0.02***	0.69 \pm 0.31	0.60 \pm 0.04***	0.99 \pm 0.01***	0.96 \pm 0.01***
16	0.99 \pm 0.03***	0.82 \pm 0.02***	0.68 \pm 0.23*	0.62 \pm 0.04***	0.99 \pm 0.01***	0.99 \pm 0.01***
17	0.99 \pm 0.03***	0.82 \pm 0.02***	0.71 \pm 0.18**	0.62 \pm 0.04***	0.99 \pm 0.01***	0.99 \pm 0.01***

R_G =Genetic correlation, R_P =Phenotypic correlation, and SE =Standard error

Larix gmelinii var. *principis-rupprechtii* was seven years for DBH and volume.

Discussion

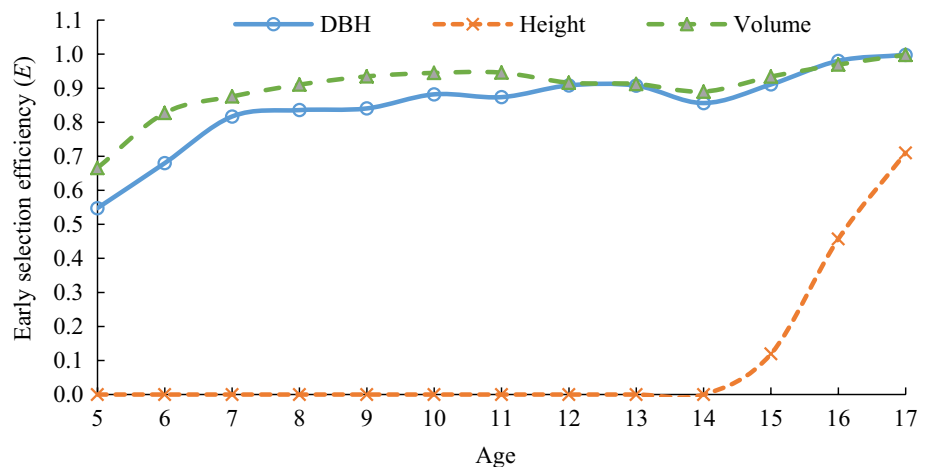
Traits used for family evaluation

Traits with higher heritability can be more stably passed on to the next generation and are less affected by the environment. Traits with larger variation coefficients are more suitable for family evaluation. Based on traits with high variation and high heritability and using multi-age and multi-site data, effective analysis can be carried out at ages when the

family \times location interactions are intense in order to select high-yielding stable families across multiple sites and ages, to select the most suitable site for family selection, and to propose a suitable family selection strategy for different sites.

DBH and volume of the families evaluated at four sites had moderate heritability values from 0.43 to 0.55 after age 6, similar to those of DBH (0.45) and volume (0.43) for half-sib families according to Xing et al. (2019), and also close to the heritability ranges of DBH (0.49 to 0.58) and volume (0.55 to 0.65) for *L. kaempferi* (Lamb.) Carr. (Diao et al. 2016). Family heritability values were higher than those of the individual trees for DBH, volume and height, which is consistent with Diao et al. (2016) and Lai et al. (2017) and

Fig. 7 Early selection efficiency (E) of each trait at different ages



indicates that higher genetic gains may be achieved with family selection in *L. gmelinii* var. *principis-rupprechtii*. The fact that the genetic, environmental, and phenotypic variation coefficients for each trait decreased with age and gradually remained stable, is consistent with reports on *C. lanceolata* and *L. kaempferi* (Sun et al. 2004; Diao et al. 2016; Wu et al. 2019), but in contrast with another study on *L. kaempferi* (Pan et al. 2018). For all traits, the phenotypic variation coefficients had the largest values, followed by the environmental variation coefficients and genetic variation coefficients, indicating that the environmental impacts on the three traits were greater than the genetic impacts.

Heritability at each age was lower for height than DBH and volume, which agrees with Yin et al. (2019) but in contrast with Diao et al. (2016) and Lai et al. (2017). Because the three variation coefficients of volume and DBH were higher than those of height at each age indicates that volume and DBH were more sensitive to environmental influences and showed greater variation among families. This is supported by studies by Sun et al. (2004), Diao et al. (2016) and Yin et al. (2019). Therefore, volume and DBH had higher, more stable genetic characteristics, greater variation, and higher selection potential than height in this study. Hence, volume and DBH were the suitable traits for family selection of *L. gmelinii* var. *principis-rupprechtii*, consistent with research results on *P. massoniana* Lamb. and *L. kaempferi* (Yang et al. 2010; Bai et al. 2012; Pan et al. 2018). As volume is a function of DBH and height, and particularly dependent on diameter, DBH should be the most suitable and convenient trait for family evaluation.

It should be noted that the heritability and genetic variation coefficients of height were close to zero over many years, and V_{ps}/V_f ratios were higher for height than for those of DBH and volume (Figs. 1, 2, 3), which is related to the insignificant effects of from age 5 to 17 for height ($p > 0.1$) (Table 2). The 25 families in this study were second-generation superior half-sib families, which may account for the insignificant family effects on height. In addition, the growth data at different ages in this study were obtained by analyzing the stems of harvested trees, and only one average tree of each family was felled in each replicate. This might have affected the accuracy of the results to some extent. In future research, it will be important to increase the number of harvested trees in each plot to obtain more stem analysis data, or to measure growth data yearly in the field, which could reduce the environmental impact and improve the accuracy of genetic parameter estimation.

Different breeding goals require different evaluation and selection methods. Given that *L. gmelinii* var. *principis-rupprechtii* is an important timber species, growth traits are key considerations in breeding. Volume and DBH traits were used to evaluate the families, and a relatively ideal selection effect was achieved. In addition, form and wood

properties are also important aspects in breeding of the species. In order to achieve the maximum possible gain in all traits simultaneously, multi-trait selection based on selection index can be used (Carreras et al. 2017). Therefore, more precise selection based on various traits should be done in the future.

Early selection

When volume at rotation age is the target trait, some studies indicate that height was the best early selection trait due to its higher heritability, larger juvenile-to-mature correlation, and lower effect due to spacing compared to other traits (Balocchi et al. 1993). In contrast, some research showed that DBH was the more efficient early selection trait (Ma et al. 2000; Sun et al. 2004), and other studies suggested that selection based on both height and DBH was most reliable in early selection (Lai et al. 2014; Diao et al. 2016). In this study, volume at age 17 (v_{17}) was the target trait, and the results indicate that DBH was the more effective early selection trait than height and volume. Compared to total height, DBH at various ages had higher heritability, stronger correlation with v_{17} , and larger early selection efficiency. Moreover, DBH is more easily measured than height. These results agree with the findings of Ma et al. (2000) and Sun et al. (2004). Similarly, to the heritability of height, the fact that the early selection efficiency of height was close to zero before age 14 was also due to the insignificant family effect of height. These results were obtained under the assumption that the stand density of the four sites was similar. In addition, because the growth data of young and middle-aged stands were used to determine early selection age and no data on older plantations were available, more accurate estimates incorporating data from mature stands should be done in future.

Similar studies have been carried out on larch. Considering 15 years as the mature age for pulpwood for *L. kaempferi*, Sun et al. (2004) found that age 6 was the most suitable early family selection age for DBH. Diao et al. (2016) considered that the optimum selection age for this species in Hubei and Liaoning was 5 years for DBH and four for height. Lai et al. (2014) suggested that the optimum selection age for *L. kaempferi* was 5 years for DBH. Based on data of 13-year-old hybrid larch, Miao et al. (2018) indicated that 6 years was the optimum age for DBH. Zhang et al. (1996) studied a 30-year-old *L. olgensis* plantation and considered that 10 years was the most suitable selection age. The present study notes that early selection of *L. gmelinii* var. *principis-rupprechtii* can be carried out at age 7, which is close to the results of the above studies. From age 7, the genetic correlation between DBH at an early age, and volume at age 17 was high (above 0.86, Table 4), indicating that early-to-late correlation of growth traits was controlled

mainly by genetic factors, further supporting the effectiveness of early selection (Ma et al. 2000; Sun et al. 2004). With the increase in age, phenotypic and genetic correlations generally gradually increased, indicating that the effect of early selection increased with age, which is consistent with the results of Wu et al. (2019).

Cross-site analysis

Both single-site and cross-site analyses can be carried out in multi-site family trials to reveal age-related trends in genetic parameters. The linear mixed model with the family effect and family \times block interaction effect as random effects and with the block effect as a fixed effect, is usually used for single-site analysis. The same model with the additional factors of site (fixed effect) and family \times site interaction (random effect) is used for cross-site analysis (Diao et al. 2016; Yin et al. 2019; Ling et al. 2021). Both analyses were carried out in this study, and the results show that the genetic parameters of growth traits from cross-site analyses were more stable and reliable than those from single-site analyses. This is consistent with the findings by Weng et al. (2007). Therefore, all the results presented in this study were based on the multi-site analysis model with a view to developing more reliable strategies for tree breeding and early selection.

Conclusion

Based on the stem analysis data of 25 half-sib families of *L. gmelinii* var. *principis-rupprechtii* 5–17 years of age at four test sites, the variance components, genetic parameters, and correlations between growth traits at early ages and volume at age 17 were calculated, and genotype main effect plus genotype-environmental interaction effect (GGE) biplots based on best linear unbiased prediction data drawn. DBH was determined to be the best trait for *L. gmelinii* var. *principis-rupprechtii* early selection, and the optimum time was 7 years. Volume and DBH were more suitable traits than height for family selection. The first two principal components in genotype \times environment biplots accounted for 76.5% and 77.4% of the total interaction for DBH and volume, respectively. Site GY was the most suitable site because of its stronger discriminating ability, representativeness and stability across all ages. Families 66, 76, 82 and 111 were high-yielding and highly stable, families 78 and 96 were high-yielding and above average stability, and families 72 and 79 were high-yielding and below average stability. This study can support decision-making for the selection of *L. gmelinii* var. *principis-rupprechtii* in northern Hebei and provides an example for the application of multi-year and multi-site data in tree breeding.

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