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The Influence of Altitude and Latitude on Breeding of *Amomum tsaoko* (Zingiberaceae)

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Abstract

Objective: To explore the effect of altitude and latitude on breeding of *Amomum tsaoko* Crevost et Lemaire, a flexistylous ginger, which fruit is used as common materia medica and a food condiment. Methods: The 7 populations were selected randomly from the three floristic zones of Yunnan. Adult plants and infructescences were chosen randomly to gain flower number and fructification percentage per inflorescence, and seed number per fruit. All date was analyzed by SPSS (13.0 version). Results: As *A. tsaoko* was distributed (or transplanted) from a habitat at lower latitude and/or altitude to a site of higher latitude and/or altitude, the flower number per inflorescence increased, on the contrary, the fructification percentage per inflorescence decreased. The competition for reproductive resource was beneficial to increase flower number and seed production. Conclusions: The habitats in south of the tropic of cancer were favorable to the reproduction of *A. tsaoko*, which reproductive costs were lower and harvest was higher. Increasing flower number per inflorescence may be a strategy to promote the plant to distribute into alpine habitats for both female and male reproductive success.

Keywords

***Amomum tsaoko*; Flower Number per Inflorescence; Reproduction; Trade-Off; Floral Longevity**

1. Introduction

Amomum tsaoko Crevost et Lemaire is a flexistylous ginger cultivated in China for collection fruit as common materia medica [1] and a food condiment. The plant distributed in Yunnan province, Southwest China [2], but now its wild (or natural) population is almost extinct in Yunnan, and it is cultivated as an economic plant at many areas in the province.

In the course of cultivation of the plant, how did environmental factors influence on its reproduction? And

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how did the plant adapt to the environmental changes? Because flower, fruit and seed are reproductive organs of plant, so their quantitative change would reflect the reproduction conditions of a population, and reproductive resource status of the plant [3-6]. Therefore, we studied the reproduction conditions of the 7 populations of *A. tsaoko* in different areas, and address the following questions: 1) how did latitude and altitude influence on the flower number and fructification percentage per inflorescence, seed number per fruit? 2) How is the reproductive competition among the flower number and fructification percentage per inflorescence, seed number per fruit? 3) How does the flowering strategy of the plant change to adapt to alpine habitats? 4) How is the site chosen for cultivation of the plant?

2. Material and Method

2.1. Research Species

A. tsaoko is a perennial herb of Zingiberaceae, usually 2 - 3 m in height. Inflorescence consists of a densely flowered spike that arises from rhizomes. Distinct characters of the plant from the other *Amomum* species are a showy yellow labellum with two red nectar guides, anther appendage, crimson and leathery ligule. Flowering occurs from April to June, and by September-December capsules are ripe [2].

2.2. Study Sites and Field Observation

Yunnan province was broken into five floristic zones [7]. Our preliminary investigation showed that *A. tsaoko* was growing in the three floristic zones: 1) the south and southwest, 2) the southeast, 3) the west and northwest. In each floristic zone, 2 or 3 populations were chosen to test the effect of altitude and latitude on breeding of the plant (**Table 1**). In each population, we selected adult plants at random, and ripe infructescences were sampled randomly from each individual in August-October. These infructescences were subjected to observations. We got both the number of mature fruits (excluding immature ones which maybe fell off early after anthesis) and scars of flowers in an infructescence (*i.e*. the number of flowers in a ripe inflorescence), and also got number of seeds in each fruit.

2.3. Statistical Analyses

Per infructescence, fructification percentage was the proportion of mature fruit number to total flower number. Date on fructification percentage, flower number per inflorescence and seed number per fruit, as well as altitude and latitude of the 7 populations were checked by Homogeneity of variance test, and compared by one-way analysis of variance (ANOVA) test. Student Newman Keuls Test (S-N-K test) was used for multiple comparisons among pairs of means. Correlation was tested by Partial Correlate and Stepwise. For statistical tests, the SPSS statistical program package (13.0 version) was used.

3. Results

3.1. Comparison of Flower Number and Fructification Percentage per Inflorescence, Seed Number per Fruit among the 7 Populations

Flower number per inflorescence was 87.49 ± 21.25 (Mean ± SD, range from 9 to 143), and fructification percentage per inflorescence was 19.06 ± 11.07 (range from 1.57 to 54.93) % (**Table 2**). For flower number and fructification percentage per inflorescence, greatly significant differences were detected among the 7 populations and among the plant individuals (**Table 3**).

Seed number per fruit was 33.03 ± 12. 63 (range from 1 to 82) (**Table 4**), with greatly significant difference among the populations ($df = 6$, $F = 6.945$, $P = 0.000 < 0.01$ = and the plant individuals ($df = 94$, $F = 33.839$, $P = 0.000 < 0.01$). By S-N-K test of seed number per fruit, the 7 populations were divided into 4 subsets (**Table 5**).

3.2. The Influences of Altitude and Latitude on Flower Number and Fructification Percentage per Inflorescence, Seed Number per Fruit

By controlling the influence of populations, significant negative correlation was detected between flower num-

Table 1. Information of the seven populations of *A. tsaoko*.

Population	Site	Altitude (m)	Latitude	Floristic zones*	Geographical location**	Individual	Inflorescence	Fruit
1	Maguan	1524	22˚51.631′N	2	S	16	76	934
2	Lvchun	2043	22˚53.837′N	1	S	18	81	1587
3	Baoshan	2070	24˚50.289′N	3	N	15	68	1203
4	Jinping	1662	22˚51.783′N	2	S	14	57	1021
5	Jinghong	1581	21˚29.675′N	1	S	14	54	925
6	Xichou	1670	23˚22.326′N	2	S	14	56	906
7	Gongshan	1425	27˚32.952′N	3	N	10	42	702
			Total			101	434	7278

*1: the south and southwest, 2: the southeast, 3: the west and northwest; **S: South of the tropic of cancer (23˚26′N), N: North of the tropic cancer.

Table 2. Descriptives of the inflorescences from the seven populations.

Character	Population	N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Minimum	Maximum
						Lower Bound	Upper Bound		
Flower number per inflorescence	1	76	78.7765	20.4062	2.2134	74.3750	83.1780	25	127
	2	81	86.8108	17.5232	1.6632	83.5147	90.1069	37	135
	3	68	90.7576	21.7663	1.8945	87.0098	94.5054	9	135
	4	57	99.0909	19.5495	4.1680	90.4232	107.7587	45	128
	5	54	79.9189	20.2558	3.3300	73.1653	86.6726	40	132
	6	56	91.5000	29.9403	8.0019	74.2130	108.7870	21	143
	7	42	100.1071	19.6060	3.7052	92.5047	107.7096	59	133
	Total	434	87.4895	21.2532	1.0261	85.4727	89.5064	9	143
Fructification percentage per inflorescence (%)	1	76	14.8449	7.8376	0.8501	13.1544	16.5355	2.25	40.30
	2	81	29.5911	8.8956	0.8443	27.9178	31.2643	2.70	54.93
	3	68	13.7125	9.0146	0.7846	12.1603	15.2647	1.57	54.00
	4	57	11.4114	6.0866	1.2977	8.7127	14.1100	2.70	24.44
	5	54	24.7500	11.0672	1.8194	21.0600	28.4400	1.94	45.57
	6	56	17.2143	6.1791	1.6514	13.6466	20.7820	9.00	29.00
	7	42	14.7129	7.6587	1.4474	11.7431	17.6826	5.00	36.00
	Total	434	19.0588	11.0684	0.5344	18.0085	20.1092	1.57	54.93

Table 3. Tests of between-subjects effects on flower number and fructification percentage per inflorescence.

Source	Type I Sum of Squares		df	Mean Square		F		Sig.
	Flower number	Fructification percentage		Flower number	Fructification percentage	Flower number	Fructification percentage	
Corrected Model	95563.700[a]	33625.699[b]	100	955.637	336.257	3.206	5.864	0.000
Intercept	3283743.797	155829.605	1	3283743.797	155829.605	11017.076	2717.516	0.000
Population	17678.427	20656.897	6	2946.404	3442.816	9.885	60.039	0.000
Individual	77885.274	12968.802	94	828.567	137.966	2.780	2.406	0.000
Error	97763.502	18808.393	333	298.059	57.343			
Total	3477071.000	208263.697	434					
Corrected Total	193327.203	52434.092	433					

[a]R Squared = 0.494 (Adjusted R Squared = 0.340); [b]R Squared = 0.641 (Adjusted R Squared = 0.532).

Table 4. Descriptives of seed number per fruit from the seven populations.

Population	N	Mean	Std. Deviation	Std. Error	95% Confidence Interval for Mean		Minimum	Maximum
					Lower Bound	Upper Bound		
1	934	25.4366	11.6900	0.3695	24.7115	26.1616	1	60
2	1587	37.3830	11.7928	0.2130	36.9654	37.8007	4	81
3	1203	29.7468	11.3402	0.2851	29.1876	30.3060	3	64
4	1021	30.7009	12.4354	0.8129	29.0992	32.3025	8	64
5	925	31.5542	12.7687	0.4506	30.6697	32.4387	4	74
6	906	35.3711	11.7017	0.8401	33.7141	37.0281	5	82
7	702	34.8195	12.6819	0.6349	33.5714	36.0677	5	72
Total	7278	33.0280	12.6339	0.1481	32.7376	33.3183	1	82

Table 5. Multiple comparisons of seed number per fruit among the seven populations (S-N-K, $\alpha = 0.05$).

Population	N	Subset			
		1	2	3	4
1	934	25.4366			
3	1203		29.7933		
4	1021		30.7009		
5	925		31.5542		
7	702			34.8195	
6	906			35.3711	
2	1587				37.3830
Sig.		1.000	0.062	0.479	1.000

ber and fructification percentage per inflorescence ($df = 426$, $R = -0.261$, $P = 0.000$); and significant correlations also existed between flower number per inflorescence and seed number per fruit ($df = 426$, $R = 0.132$, $P = 0.006$), as well as between fructification percentage per inflorescence and seed number per fruit ($df = 426$, $R = 0.278$, $P = 0.000$).

By Stepwise, the equation ($y = 16.251 + 2.393x_3 + 0.008x_2$) was the optimal regression model of flower number per inflorescence (y: flower number per inflorescence, x_2: altitude, x_3: latitude) (**Table 6**); the equation ($y = 58.209 - 0.121x_1 + 0.007x_2 - 1.770x_3$) was the optimal regression model of fructification percentage per inflorescence (y: fructification percentage per inflorescence, x_1: flower number per inflorescence, x_2: altitude, x_3: latitude) (**Table 7**); the equation ($y = -35.087 + 0.010x_2 + 0.490x_4$) was the optimal regression model of seed number per fruit (y: seed number per fruit, x_2: altitude, x_4: longitude) (**Table 8**).

3.3. The Influence of Geographical Location on Flower Number and Fructification Percentage per Inflorescence, Seed Number per Fruit

For the populations located at south of the tropic of cancer (N23˚26′), flower number and fructification percentage per inflorescence, seed number per fruit were 84.57 ± 20.51 (range from 21 to 143), 22.08 ± 11.20 (range from 1.94 to 54.93) %, 33.87 ± 12.83 (range from 1 to 82), respectively; as of the populations at north of the tropic of cancer were 91.57 ± 21.98 (range from 9 to 140), 14.10 ± 9.12 (range from 1.57 to 54.00) %, 30.81 ± 11.75 (range from 3 to 72). Greatly significant differences occurred between the two populations of different geographical location, viz. in flower number ($df = 443$, $F = 11.667$, $P = 0.001$) and fructification percentage per inflorescence ($df = 443$, $F = 62.065$, $P = 0.000$), and in seed number per fruit ($df = 7274$, $F = 85.656$, $P = 0.000$).

Table 6. Coefficients[(a)] for flower number per inflorescence.

Model		Unstandardized Coefficients		Standardized Coefficients	t	Sig.
		B	Std. Error	Beta		
1	(Constant)	31.358	14.941		2.099	0.036
	Latitude	2.350	0.626	0.176	3.755	0.000
2	(Constant)	16.251	16.672		0.975	0.330
	Latitude	2.393	0.624	0.179	3.834	0.000
	Altitude	0.008	0.004	0.094	2.014	0.045

[a]Dependent Variable: flower number per inflorescence.

Table 7. Coefficients[(a)] for fructification percentage per inflorescence.

Model		Unstandardized Coefficients		Standardized Coefficients	t	Sig.
		B	Std. Error	Beta		
1	(Constant)	68.849	7.547		9.123	0.000
	Latitude	−2.096	0.316	−0.301	−6.629	0.000
2	(Constant)	72.381	7.402		9.779	0.000
	Latitude	−1.831	0.313	−0.263	−5.842	0.000
	Flower number per inflorescence	−0.113	0.023	−0.216	−4.804	0.000
3	(Constant)	58.209	8.123		7.166	0.000
	Latitude	−1.770	0.309	−0.254	−5.732	0.000
	Flower number per inflorescence	−0.121	0.023	−0.233	-5.237	0.000
	Altitude	0.007	0.002	0.172	3.939	0.000

[a]Dependent Variable: fructification percentage per inflorescence.

Table 8. Coefficients[(a)] for seed number per fruit.

Model		Unstandardized Coefficients		Standardized Coefficients	t	Sig.
		B	Std. Error	Beta		
1	(Constant)	16.225	1.131		14.339	0.000
	Altitude	0.009	0.001	0.173	14.987	0.000
2	(Constant)	−35.087	8.089		−4.338	0.000
	Altitude	0.010	0.001	0.189	16.052	0.000
	Longitude	0.490	0.076	0.076	6.406	0.000

[a]Dependent Variable: seed number per fruit.

4. Discussion

4.1. Correlations among Flower Number per Inflorescence, Fruit and Seed Production in *A. tsaoko*

Previous studies on fruiting character of *A. tsaoko* showed that the fruit abortion occurred after initiation because of environmental factors (e.g. humility) [8]. Therefore, in this study, the fructification percentage per inflorescence reflected the plant final reproductive success, which combined both fruit set and fruit abortion. By the optimal regression equations and ANOVA analysis, there was a trade-off between flower number and fructification percentage per inflorescence, and significantly positive correlation between flower number per inflorescence and seed number per fruit. The former relationship was a typical response found in the other plants because of limited reproduction resource [9-11]. An inflorescence was more attractive to pollinator in comparison with a single flower because the integrated flowers were more striking to insects [12,13]. Based on this, the latter relationship implied probably that the inflorescences with numerous flowers easily attracted pollinators for reproduction assurance. The results might be associated with the pollinators (*i.e.* bees) activity. Because bees didn't visit repeatedly those flowers with low reward, they were likely remembered by their pollinators [14].

Because of limited reproduction resource, a competition among reproductive organs for reproduction assurance was widespread in plants [9]. Therefore, the correlations among flower number per inflorescence, fruit and seed production likely reflected that competition of reproduction resource in *A. tsaoko*. Results from our study showed the competition for reproductive resource was beneficial to increase flower number and seed production, in contrast, such competition wasn't partial to amplifying fruit number.

4.2. The Influence of Altitude and Latitude on Flower Number per Inflorescence, Fruit and Seed Production in *A. tsaoko*

Results from this study showed that there was a strong effect of both altitude and latitude on the flower number per inflorescence and the fruit production of *A. tsaoko*. When the latitude and/or altitude of those populations were elevated, the flower number per inflorescence increased significantly, on the contrary, the fructification percentage per inflorescence decreased significantly. On contrast to altitude, the influence of latitude on both flower number and fructification percentage per inflorescence was more significant according to the value of coefficients in their optimal regression equations. We suggested that *A. tsaoko* was distributed (or transplanted) from a habitat at lower latitude and/or altitude to a site of higher latitude and/or altitude, the flower number per inflorescence increased, on the contrary, the fructification percentage per inflorescence decreased.

By its optimal regression equation, both altitude and longitude influenced significantly the seed number per fruit. Based on the comparison of their variation (altitude: 1425 - 2070 m vs. longitude: 98˚46.501′ - 104˚49.333′) in the study, we considered that altitude was the main effect on the seed number per fruit, which increased when the altitude of population elevated.

It is known that change of day length is related to latitude, and yearly temperature averages will decrease

0.8˚C as latitude increase 1˚ from south to north in the Northern Hemisphere, in addition, temperature would decrease when altitude elevates (*i.e*. 0.6˚C/100 m). The topography of Yunnan shows that the northwest is higher and the southeast lower, so from the east to the west the latitude is rising and the altitude also elevating continually. Therefore, the significant influence of both latitude and altitude on flower number per inflorescence likely reflected that lower temperature and higher temperature difference between day and night would be beneficial to increase the flower number per inflorescence. The fruit and seed production would partly depend on its pollinators. However, cooler temperatures could be a proximate cue for the ultimate factor of low pollinator availability [15]. Therefore, low pollinator activity in habitat where latitude and/or altitude elevated would lead to less fruit and seed production. The tropic of cancer is the boundary between the north temperate zone and the tropic. The populations of *A. tsaoko* growing in south of the tropic of cancer had significantly less flower number per inflorescence, and significantly higher fruit and seed production than the population in north of the tropic of cancer. Such significant differences probably demonstrated that the habitats in south of the tropic of cancer were favorable to the reproduction of *A. tsaoko*, which reproductive costs were lower and harvest was higher. These results would provide beneficial information for further study on the plant about the origin of cultivation, and for selection of cultivated site.

4.3. Flowering Strategy and Female Fitnesss

Floral longevity, the length of time a flower remains open and functional, was determined by a balance between female fitness accrual rates (pollen receipt), male fitness accrual rates (pollen dissemination), and the cost of flower maintenance [16-18]. In plant reproductive ecology floral longevity played a central role, it determined plant reproductive assurance and overall fitness [19], because it affected the number of pollinator visits, the amount and quality of pollen received and disseminated, as well as floral display size [20,21]. Floral longevity could ensure successful pollination in habitats where pollinators were few, unpredictable [17,18,20,22]. For example, long floral duration could significantly increase successful pollination and fruit set in *Kalmia latifolia* [15]. In addition, previous studies demonstrated that plants growing in alpine habitats, which typically had sparse or uncertain pollinators, had longer floral durations than plants at lower elevations with more abundant, predictable pollinators [23-27].

Floral longevity played a central role in the distribution of zingiberaceae from tropics to alpine habitats, in the course the duration of floral life had a tendency to increase for effective enhancement of both female and male fitness. Therefore, based on increasing of floral longevity, ginger was divorced from tropical habitat and distributed toward high elevation habitat [28]. For *A. tsaoko*, as a flexistylous ginger, the longevity of a single flower was only 1 d, which opened at dawn and withered at dusk. Flexistyly is a unique and "active" floral mechanism to decrease inbreeding and promote outcrossing by changing position of style [29-39]. Therefore, extension of floral longevity for a single *A. tsaoko* flower would not increase outcrossing.

Our study in Baoshan population suggested that floral longevity of *A. tsaoko* was only 1 d, and the flowers in inflorescence opened in proper order every day, *i.e*. 1 - 6 flowers per 1 d for the most inflorescences and mean 3 - 4 flowers per 1 d [40]. Cui *et al*. suggested that floral longevity of *A. tsaoko* in Yuanjiang population was only 1 d, and 3 - 5 flowers from an inflorescence opened every day [8]. Based on this, the inflorescence with more flowers had longer anthesis, meaning that the floral longevity was prolonged at the inflorescence level. In addition, an inflorescence was more attractive to pollinator than a single flower [12,13]. Therefore, increasing flower number per inflorescence may be a strategy to having greater attraction to pollinators for both female and male reproductive success. The strategy would promote the plant to distribute into those habitats with higher elevation, where its pollinator was unpredictable or sparse.

By the ANOVA analysis, both plant-intrinsic and environmental factors influenced significantly the flower number per inflorescence, fruit and seed production ($P = 0.000 < 0.01$). For the seed number per fruit, effect of the former was stronger than the latter. On the contrary, both flower number and fructification percentage per inflorescence were influenced by environmental factors more than plant-intrinsic factors. Therefore, the seed number per fruit possibly reflected that the certain plant-intrinsic trait, which might demonstrate that the plant individuals differed in reproductive resource status conditions. Such as different rate of nectar secretion among the plant individuals, and those flowers with higher rewards might receive more visits from pollinators (unpublished data), and possibly more seed number per fruit. A further study on the seed production will provide further insight into the fitness and the ecological adaptation of the plant.

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