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Study on Morphological Traits of Natural Populations of *Vaccinium uliginosum* at Different Altitudinal Gradients on Changbai Mountain

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Abstract: *Vaccinium uliginosum* (VU) is one of the most precious wild berry plants distributed in the Changbai Mountain region in northeast China. Eight key morphological traits of VU were analyzed to examine the variation among and within five natural populations at different altitudes, as well as their response to environmental factors. The study results showed an increasing trend of variation among populations with ascending altitudes, but the range variation within populations exhibited a decreasing trend. The diversity level among populations was found to be higher than that within populations, and the five populations of VU were classified into four groups. Except for leaf width and twig length, all other morphological traits demonstrated significant or extremely significant correlations. Generally, with increasing altitude, leaf length decreased, while plant height, clear bole height, and basal diameter decreased significantly, and similar trends were observed with moisture factors, while a significant positive correlation was found with temperature factors. Among them, the morphological traits of clear bole height and basal diameter exhibited the strongest correlation with environmental factor variations. Overall, these findings indicate extensive variation in the morphological traits of VU within and among populations at different altitudes, with clear responses to changes in environmental factors.

Keywords: bilberry; altitudinal gradient; phenotypic diversity; environmental factors; variability

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1. Introduction

Under the long-term mutual influence between plants and the environment, plants exhibit specific morphological and phenological characteristics [1]. These traits reflect the adaptability of plants to their environment and can further reveal their nutrient allocation strategies [2], as well as the survival and adaptation strategies of plants [3]. Additionally, by exploring the response characteristics of plant morphological traits to environmental gradients, we can further uncover the dominant factors driving plant community aggregation [4].

The growth conditions of plants vary significantly with altitude; generally, as the altitude increases, the average temperature gradually decreases, precipitation decreases, atmospheric pressure decreases, solar radiation intensifies, soil fertility decreases, and the growing season for plants shortens, and these changes result in a series of variations in plant morphological traits [5,6]. Studies have shown that, as the altitude increases, the morphological traits of the leaves of the Hawthorn species in the Junggar region undergo significant changes; at lower altitudes, they primarily increase leaf area and chlorophyll content to rapidly acquire the necessary resources for growth; however, at higher altitudes, they adapt to low-temperature stress and intense light radiation by increasing leaf thickness and palisade tissue thickness and reducing leaf area and chlorophyll content [7]. There are also significant differences in leaf traits such as the leaf area and length–width ratio of the *Castanopsis carlesii* species between high and low altitudes [8]. The variation in altitude is closely related to environmental factors such as temperature, precipitation, atmospheric pressure, and solar radiation, which, in turn, influence the growth and development of plants [9]. With ongoing global climate change, both the growth and distribution of plants have been significantly influenced, resulting in the increased prevalence of diseases [10] and a decline in productivity [11]. Plants at different elevations experience distinct environmental pressures and resource constraints, leading to varied adaptive strategies. Investigating changes in plant morphology facilitates the identification of threatened species and habitats, enabling the development of corresponding conservation measures. Furthermore, as global climate change progresses, plants face more intricate and unpredictable environmental conditions [12]. Studying the morphological variations of plants across diverse elevation gradients assists in predicting species' responses to future climate changes. This knowledge can guide the implementation of suitable conservation measures, ensuring the survival and reproduction of these species.

Vaccinium uliginosum is a deciduous perennial shrub in the Vaccinium genus of the Ericaceae family [13]. It is distributed in Asia, Europe, and North America, with a primary distribution in the northern part of the Greater Khingan Range and Changbai Mountain in Jilin Province, China [14,15]. Given the high edible and medicinal value of its fruits, this plant has attracted widespread attention both domestically and internationally [16–20]. However, current studies on VU mainly focus on breeding, cultivation, and the regulatory mechanisms of anthocyanins [21], and there is limited research on the response of the morphological traits of VU to environmental gradient changes under natural conditions. The population distribution of VU spans a wide range of latitudes, and its morphology is sensitive to changes in latitude, making it a good indicator of variations in climatic and environmental pressures. However, the overall quantity of VU resources is decreasing because of factors such as unsustainable harvesting practices and inappropriate picking methods [22]. Therefore, investigating the response characteristics of VU to changes in altitude in the context of global climate change is of great significance for protecting this species. In this study, we selected wild VU distributed at different altitudes on Changbai Mountain as the research object, and the leaf length, leaf width, twig length, basal diameter, plant height, clear bole height, and other indicators were measured to explore the variation in morphological traits among and within VU populations. Moreover, the correlations between each morphological trait and environmental factor were analyzed, which could provide basic data for the resource conservation of VU. This research can provide valuable insights into how VU populations are affected by climate change-induced altitudinal shifts. By understanding these response characteristics, appropriate conservation strategies can be developed to mitigate the negative impacts and ensure the long-term survival of this species.

2. Materials and Methods

2.1. Study Area

Changbai Mountain is located in the northeastern region of China, at the southeastern border of Jilin Province and North Korea, ranging from 41°23′ to 42°36′ N in latitude and 126°55′ to 129°00′ E in longitude. Given its unique natural conditions and for historical and social reasons, Changbai Mountain has become one of the most intact areas for the preservation of natural ecosystems in China, and even globally. This region experiences a temperate continental climate influenced by monsoons, characterized by long, cold winters and short, warm, and rainy summers. However, because of the high altitude of the mountain range, there is significant variation in climate with altitude, and the foothills exhibit a typical warm temperate climate, while the mountaintops display a complex and diverse subarctic climate. Owing to its distinctive volcanic landscape, the Changbai Mountain area features rich soil types, including alpine frozen soil, mountainous grass forest soil, mountainous brown coniferous forest soil, and mountainous dark brown forest soil from top to bottom. This study primarily focuses on the distribution area of VU at altitudes ranging from 600 m to 2100 m in the Changbai Mountain region. Five concentrated distribution areas of VU at different altitudes were selected as survey areas;

the climatic conditions of each survey area are presented in Table 1, and the climatic indicators are values for multi-year averages. Precipitation and snow cover days increase with altitude, while the temperature index and frost-free periods decrease with altitude. Overall, higher altitudes are associated with greater precipitation, lower temperatures, longer snow cover, and shorter frost-free periods. The study area ranges from 600 m to 2100 m in elevation, with soil types including mountainous dark brown forest soil, mountainous brown coniferous forest soil, mountainous grass forest soil, and alpine frozen soil. The vegetation exhibits a clear belt-like distribution, with the following vegetation types from bottom to top: red pine broad-leaved forest belt (at elevations of 685 m and 900 m), dark coniferous forest belt, birch forest belt, and alpine frozen soil belt. There are no significant differences in crown density (around 0.3) across these vegetation types. The representative broad-leaved tree species in the red pine broad-leaved forest include *Tilia anurensis*, *Fraxinus mandshurica*, and *Betula costata*. Additionally, there are mixed species such as *Acer mono*, *Quercus mongolica*, and *Ulmus japonica*. The shrubs mainly consist of *Corylus mandshurica*, *Deutzia amurensis*, *Eleutherococcus senticosus*, *Vaccinium uliginosum*, and species of Acer. The herbaceous plants primarily include *Brachybotrys paridformis*, *Lilium disticum*, *Aegopodium alpestre*, *Moehringia lateriflora*, *Carex remotiuscula*, and *Carex campylorhina*. The dominant tree species in the dark coniferous forest canopy include *Picea jezoensis*, *Abies nephrolepis*, *Picea koraiensis*, *Larix gmelini*, and *Pinus densiflora*. The shrub layer is mainly composed of *Acer ukurunduense*, *Lonicera edulis*, *Euonymus paueiflorus*, *Vaccinium uliginosum*, and other species. In the herbaceous layer, predominant species include *Maianthemum bifolium*, *Linnaea borealis*, *Carex callitrichos*, and *Actaea acumenata*, among others. The subalpine Betula ermanii forest is a vegetation zone dominated by the single tree species *Betula ermanii*, with only a small number of mixed species such as *Sorbus pohuashanensis* and cold-resistant *Larix gmelini*. Shrubs are sparse in the understory, mainly consisting of *Vaccinium uliginosum*, *Rhododendron chrysanthum*, and *Juniperus sibirica*. The herbaceous layer includes *Synurus deltoides*, *Solidago virgaaurea*, *Aconitum kusnezoffii*, *Sanguisorba officinalis*, and others. The plant species in the alpine tundra zone mainly include *Papaver nudicaule*, *Oxytropis anertii*, *Pedicularis verticillata*, *Aquilegia flabellata*, and others. The main shrub species consist of *Rhododendron chrysanthum*, *Rhododendron confertissimum*, *Phyllodoce caerulea*, *Vaccinium vitis-idaea*, and *Vaccinium uliginosum* L. var. *Alpinum*.

Table 1. Climatic and geographic conditions at the locations of the natural VU populations.

Sample Plot \ Support	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5
Altitude (m)	685	900	1100	1230	2100
Annual precipitation (mm)	679.18	728.95	782.37	810.53	1114.24
Precipitation from June to September (mm)	483.02	518.41	556.4	576.43	792.42
Moisture index	1.91	2.52	3.12	3.43	6.17
Average temperature (°C)	2.79	1.81	0.78	0.27	−4.33
≥5 °C accumulated temperature	2459.77	2123.12	1832.55	1702.53	877.93
Average temperature in January (°C)	−17.33	−17.95	−18.58	−18.89	−21.71
Average temperature in July (°C)	19.63	18.51	17.4	16.84	11.83
Frost-free days	121	112.25	104.14	100.31	71.58
Snow cover days	130.79	144.37	157.94	164.73	225.82
Longitude	128°22′6″	128°31′46″	128°32′30″	128°27′39″	128°9′6″
Latitude	42°32′38″	42°21′26″	42°21′6″	42°19′53″	42°1′46″

2.2. Standard Plot Setting

Based on the distribution characteristics and population traits of VU in the Changbai Mountain region, investigation plots for morphological traits were set up in five concentrated distribution areas of VU at different altitude gradients in 2007. The sampling locations and altitude-related climatic factors are detailed in Table 1, with elevations ranging from 685 m to 2100 m from top to bottom. The sampling method employed a transect approach, with the transect lines and sampling plots set up as shown in Figure 1. Within each population, representative sections were selected, and 15 small plots measuring 1 m × 1 m were set up along a straight line, with a distance of 10 m between adjacent plots. Within each plot, 5 to 10 healthy plants were randomly selected and brought back to the laboratory for measurement of morphological traits.

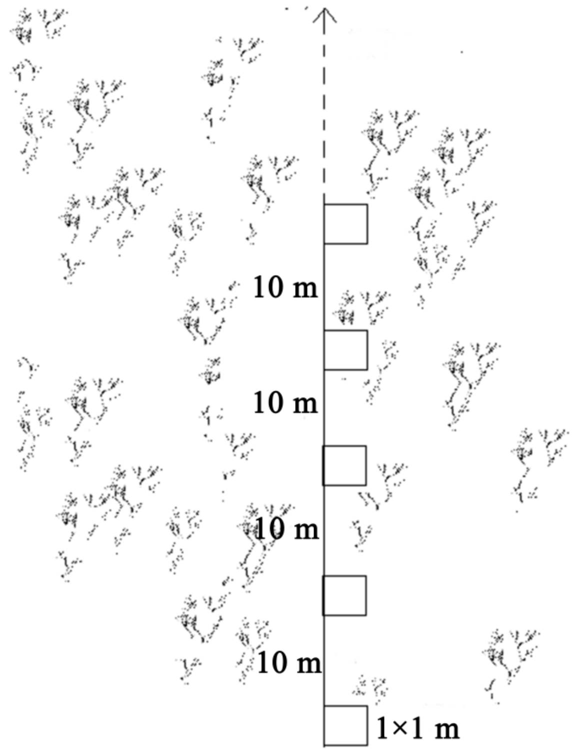

Figure 1. The transect line and sampling plot setup.

The following eight basic traits were measured: leaf length (LL), leaf width (LW), twig length (TL), basal diameter (BD), plant height (PH), clear bole height (CBH), leaf length–width ratio (LL/LW), and plant height-to-basal-diameter ratio (PH/BD). The specific measurement methods were as follows: a vernier caliper was used to measure the longest and widest parts of the leaves, as well as the basal diameter; a ruler was used to measure plant height, canopy base height, and twig length. Within each small plot, 30 measurements were randomly taken for leaf length, leaf width, and twig length, while 5 measurements were randomly taken for basal diameter, plant height, and clear bole height.

2.3. Statistical Analysis

Using nested design analysis of variance (ANOVA), the variation and significance of various fundamental traits in VU were analyzed using the SPSS version 21 software. The linear model is as follows:

$$Y_{ijk} = \mu + S_i + T_{(i)j} + \varepsilon_{(ij)k} \quad (1)$$

where Y_{ijk} is the *k*-th observation value in the *j*-th sample in the *i*-th population; μ is the overall mean; *S* is the population effect (fixed); $T_{(i)j}$ is the effect between samples within the population (random); $\varepsilon_{(ij)k}$ is the experimental error.

To further study the morphological trait variation in natural populations of VU, the coefficient of variation (CV) is used to represent the degree of dispersion for each morphological trait, and the relative range (R′) is used to indicate the extent of extreme differences. The formula for calculating the relative range is as follows:

$$R'_i = R_i / R_0 \quad (2)$$

where R_i is the range within the population; R_0 is the total range of the trait.

By using the components of variance ratio in nested design ANOVA, we can further analyze the proportion of each component of variance in the total variation. The percentage of variance between populations to the total variance is expressed as the average phenotypic differentiation coefficient (Vst) [23]. To analyze the population distribution characteristics of morphological traits in VU, a clustering analysis using the UPGMA method and Euclidean average distance was conducted on 5 VU populations, considering traits such as leaf length, leaf width, twig length, basal diameter, plant height, and clear bole height.

3. Results

3.1. Basic Characteristics of VU Morphological Traits

Given the large differences in altitude and the combined effects of site conditions, regional climate, and genetic types, there are significant differences in traits among populations and within populations of VU (Figure 2).

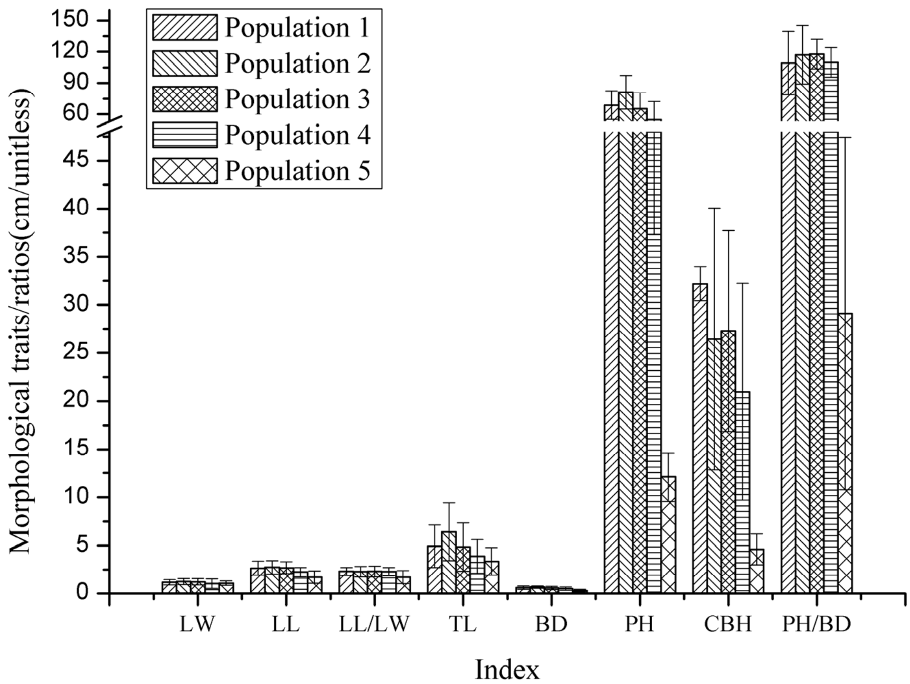

Figure 2. Basic characteristics of VU morphological traits. Note: LW is leaf width; LL is leaf length; LL/LW is the ratio of leaf length to leaf width; TL is twig length; BD is basal diameter; PH is plant height; CBH is clear bole height; PH/BD is the ratio of plant height to basal diameter.

The field survey results indicate that the VU population in Plot 5 consists of the varietal *Vaccinium uliginosum* L. var. *Alpinum*. Among the four VU populations, the maximum leaf length-to-width ratio is 2.31, while the minimum ratio is 2.28, indicating an overall elongated oval shape. Population 2 has the largest leaf size, with a length of 2.73 cm and a width of 1.24 cm, which are the maximum values among the four populations. Conversely, Population 4 has the smallest leaf size, with a length of 2.23 cm and a width of 1.02 cm, which are the minimum values among the four populations (Populations 1–4). The variety of VU found in Population 5 exhibits significant differences in leaf length-to-width ratio compared with VU, with a ratio of 1.72 and nearly circular leaves. The leaf size is smaller, with a length of 1.71cm and a width of 1.07 cm, distinguishing it from VU. The twig length varies between 3.88 and 6.44 cm, with Population 2 having the longest twig length, followed by Population 1 and Population 3, while Population 4 has the shortest twig length, measuring 3.88 cm. The twig length in Population 5 is closer to that of Population 4, measuring 3.34 cm.

Multiple comparison analyses of phenotypic traits were conducted using the LSD method, and the results showed that there are significant differences in basal diameter and plant height among the different populations, similar to the variations observed in leaf size and twig length. The maximum basal diameter and plant height are found in Population 2, measuring 0.66 and 81.14 cm, respectively. Population 1, Population 3, and Population 4 follow with basal diameters of 0.60, 0.56, and 0.50 cm and plant heights of 68.68, 65.37, and 54.79 cm, respectively. The ratio of plant height to basal diameter (PH/BD) reaches its highest value in Population 3, at 117.78. The PH/BD ratios in Populations 1–4 exhibit minor fluctuations with increasing elevation. However, the variety of VU found in Population 5 displays a much shorter plant height, approximately one-third to one-fourth of the height of VU, while the basal diameter is about half of VU's diameter. The plants exhibit a low, stout appearance. The clear bole height decreases with increasing elevation. In Population 1, it measures a maximum of 32.19 cm, accounting for nearly 50% of the total plant height. Population 3 follows with a measurement of 27.29 cm, accounting for 41.74% of the plant height. Population 2 measures 26.45 cm, representing 32.35% of the plant height. Population 5 has the smallest value, with a clear bole height of only 4.61cm, accounting for 38.07% of the plant height.

3.2. Analysis of Variability in VU Populations

Utilizing nested design analysis of variance (ANOVA) to analyze the variability and significance of basic traits in VU, the results indicate that the F-values for both inter-population and intra-population morphological traits reach a highly significant level (Table 2).

Table 2. Statistical analysis results of morphological traits in VU natural populations.

Population	LL	LW	LL/LW	TL	PH	BD	PH/BD	CBH
	F-Value							
Inter-population	44.75 **	5.29 **	49.74 **	82.79 **	63.82 **	21.32 **	37.94 **	14.41 **
Intra-population	16.85 **	8.01 **	16.47 **	29.16 **	56.54 **	39.51 **	53.62 **	46.77 **
	Coefficients of Variation (*CVs*, %)							
1	27.55	25.58	18.32	44.89	27.57	30.90	33.29	44.40
2	25.96	26.59	23.41	46.71	27.74	19.13	29.32	65.47
3	23.49	28.14	24.40	52.00	21.40	27.28	21.77	43.26
4	21.59	50.60	19.18	45.28	30.49	33.51	30.00	49.11
5	22.79	20.46	15.32	36.67	62.46	39.69	65.60	44.69
Total	35.22	31.89	30.47	53.86	53.86	37.32	48.32	66.19
	Relative extreme value (R_i', %)							
1	90.68	19.43	82.36	71.11	71.71	79.81	76.22	71.27
2	41.13	21.42	72.68	71.56	89.12	50.96	61.73	95.36
3	37.08	20.85	76.13	97.33	67.74	79.81	46.11	58.78
4	29.08	96.13	81.82	52.44	69.86	70.19	77.98	54.19
5	14.89	11.98	18.02	22.84	11.99	69.23	29.50	14.51
Total	42.57	33.96	66.20	63.06	62.08	70.00	58.31	58.82

Note: "**" means the difference is significant at the 0.01 level.

The coefficients of variation (CVs) among VU populations are all above 30% (Table 2), indicating a significant level of variability among the populations. Among them, clear bole height exhibits the highest CV at 66.19%, followed by the traits of small branch length and plant height, both at 53.86%, and then by ground diameter, with a variation coefficient of 37.32%. while leaf traits show relatively small CVs, with leaf length slightly larger than leaf width at CV values of 35.22% and 31.89%, respectively. The CV of the ratio between two traits is the smallest among all traits, at 30.47%. Within populations, clear bole height and twig length still demonstrate relatively large CVs. Clear bole height has the largest range of variation in Population 2 at 65.47%, followed by Population 4, Population 5, and Population 1, with the smallest value in Population 3 at 43.26%. Twig length shows a pattern of variation as Population 3 > Population 2 > Population 4 > Population 1 > Population 5, with CVs ranging from 36.67% to 52.00%. Except for the highest value in Population 3 and the lowest value in Population 5, the CV values in the other three populations are relatively close. Plant height and basal diameter have their highest CVs in Population 5, at 62.46% and 39.69%, respectively. Population 4 follows with CVs of 30.49% and 33.51% for plant height and basal diameter, respectively. The smallest CV for plant height is in Population 3 at 21.40%, while the smallest CV for basal diameter is in Population 2 at 19.13%. Leaf traits, except for leaf length with the highest CV of 50.60% in Population 4, show minor variations among different populations, with leaf length ranging from 21.59% to 27.55% and leaf width ranging from 20.46% to 28.14%.

Clear differences were observed among different populations in terms of relative range for each trait (Table 2). Leaf length showed the greatest variation in Population 1, with a range of 90.68%, while the ranges for other sites ranged from 14.89% to 41.13%, decreasing with increasing altitude. The maximum value for leaf width was found in Population 4, at 96.13%, while the range for other sites was relatively small, between 11.98% and 21.42%, with the minimum value found in Population 5. Overall, there was a trend toward decreasing leaf width with increasing altitude. The relative ranges for twig length and basal diameter were highest in Population 3, at 97.33% and 79.81%, respectively, and the overall ranges were large. Except for Population 5, the relative range of twig length was above 50% in all other populations, whereas the same was true for basal diameter. The maximum relative ranges for plant height and clear bole height were both observed in Population 2, at 89.12% and 95.36%, respectively, and the ranges were large for all other populations except for Population 5, where they were less than 50%.

3.3. Differentiation of Morphological Traits in VU Populations

In the current study, the coefficient of differentiation for eight morphological traits in VU populations ranged from 24.64 to 84.95% (Table 3). The trait with the highest phenotypic differentiation coefficient was twig length, followed by plant height, with a Vst of 81.00%, while leaf width had the lowest coefficient. Among the eight traits, twig length, plant height, and leaf length had differentiation coefficients above 75%, indicating that variation among populations was greater than within populations and that they were the main sources of variation. Basal diameter had a differentiation coefficient of 58.15%, slightly greater among populations than within populations, while leaf width and clear bole height had differentiation coefficients below 50%, indicating that within-population variation dominated. The differentiation coefficients for the two proportion values representing leaf type and plant type were also relatively high, at 77.58 and 71.50%, respectively, with large morphological differences among populations and relatively small differences within populations.

Table 3. Components of variance and inter/intra-population phenotypic differentiation coefficients for morphological traits in VU populations.

Traits	Variance Component			Percentage of Variance Portion (%)			Vst (%)
	Among Populations	Within Populations	Random Errors	Among Populations	Within Population	Random Errors	
LL	0.38	0.12	0.23	51.74	16.68	31.58	75.61
LW	0.01	0.02	0.10	5.83	17.84	76.32	24.64
LL/LW	0.24	0.07	0.13	54.07	15.63	30.30	77.58
TL	7.68	1.36	1.45	73.22	12.97	13.81	84.95
PH	729.83	171.18	15.41	79.64	18.68	1.68	81.00
BD	0.02	0.01	0.00	55.16	39.69	5.15	58.15
PH/BD	1657.39	660.54	62.76	69.62	27.75	2.64	71.50
BIH	102.47	112.16	12.25	45.16	49.44	5.40	47.74

3.4. Cluster Analysis of VU Populations According to Morphological Traits

The cluster analysis results revealed that the five VU populations at different altitudinal gradients were divided into four major clusters (Figure 3). The first cluster consisted of Population 5, which showed relatively close similarity to Population 4 in terms of Euclidean distance but differed significantly from Population 2. The second cluster included Population 2, located at an altitude of 900 m, which showed proximity to Populations 1 and 3 based on Euclidean distance while exhibiting some differences from Population 4. The third cluster consisted of Population 4, situated at an altitude of 1230 m, which exhibited relatively close similarity to Population 3 according to Euclidean distance. The fourth cluster comprised Populations 1 and 3, with altitudes of 685 m and 1100 m, respectively. These two sites exhibited the closest relationship in terms of Euclidean distance.

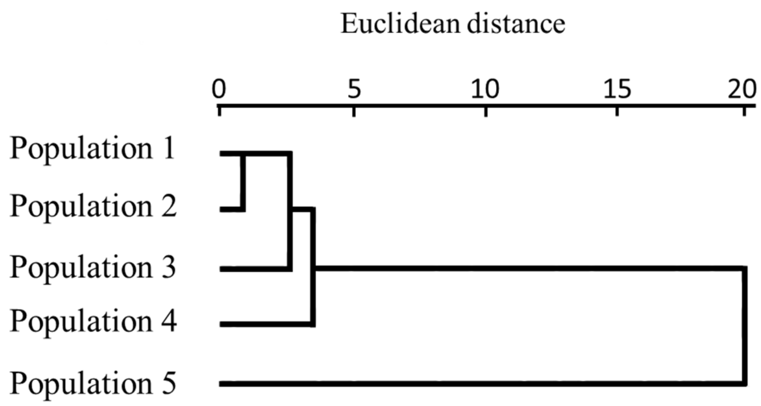

Figure 3. Hierarchical clustering of 5 VU populations based on 8 morphological traits.

3.5. Correlation Analysis between Morphological Traits and Environmental Factors

To explore the relationship between the variability of phenotypic diversity in VU and the environment, this study conducted correlation analysis and significance tests between the morphological traits and ten environmental factors (Table 4). The results showed significant and highly significant correlations between the morphological traits and environmental factors, except for a low correlation between leaf width and twig length with the environmental factors. Among them, clear bole height exhibited extremely significant correlations with basal diameter and various environmental factors. As the altitude, precipitation, and snowfall days increased, clear bole height and basal diameter decreased gradually, with correlation coefficients exceeding 0.98, indicating a highly significant negative correlation. The relationship with temperature factors showed a decrease with decreasing temperature, demonstrating a highly significant positive correlation, with correlation coefficients above 0.98 and R^2 values exceeding 0.92.

The correlation between leaf width and various environmental factors is generally weak, with correlation coefficients below 0.6. However, leaf length shows a close relationship with altitude ($r = -0.954$), annual precipitation ($r = -0.965$), and precipitation from June to September ($r = -0.965$), exhibiting highly significant negative correlations. It also shows significant negative correlations with the moisture index ($r = -0.956$) and snowfall days ($r = 0.956$), as well as significant positive correlations with frost-free periods ($r = 0.939$) and four temperature factors ($0.955 < r < 0.957$). The average value of leaf width has relatively small variations among different sites, ranging from 1.02 to 1.24 (Figure 2). Therefore, the variation in leaf shape is mainly influenced by leaf length, showing the same pattern as observed in the correlation analysis with environmental factors. Twig length varies significantly among different sites, but its correlation with environmental factors is not high, with correlation coefficients below 0.8, and no significant relationships can be observed. The PH and PH/BD show a consistent correlation with environmental factors.

Table 4. Correlation analysis between morphological traits of VU and environmental factors.

Environmental Factors \ Morphological Traits	LL	LW	LL/LW	TL	BIH	PH	BD	PH/BD
Altitude	−0.954 **	−0.586	−0.942 *	−0.78	−0.990 **	−0.947 *	−0.964 **	−0.932 *
Annual precipitation	−0.965 **	0.555	−0.968 **	−0.772	−0.986 **	−0.958 *	−0.971 **	−0.956 *
Precipitation from June to September	−0.965 **	−0.555	−0.968 **	−0.772	−0.986 **	−0.958 *	−0.971 **	−0.956 *
Moisture index	−0.956 *	−0.57	−0.950 *	−0.775	−0.989 **	−0.950 *	−0.966 **	−0.939 *
Average temperature	0.957 *	0.571	0.951 *	0.778	0.988 **	0.951 *	0.967 **	0.940 *
Accumulated temperature (≥5 °C)	0.957 *	0.589	0.893 *	0.766	0.980 **	0.914 *	0.936 *	0.880 *
Average temperature in January	0.956 *	0.57	0.950 *	0.776	0.989 **	0.950 *	0.966 **	0.939 *
Average temperature in July	0.955 *	0.57	0.950 *	0.775	0.989 **	0.950 *	0.966 **	0.938 *
Frost-free days	0.939 *	0.582	0.924 *	0.774	0.987 **	0.935 *	0.954 *	0.912 *
Snow cover days	−0.956 *	−0.57	−0.950 *	−0.775	−0.989 **	−0.950 *	−0.966 **	−0.938 *

Note: "**" means the correlation is significant at the 0.01 level (2-tailed); "*" means the correlation is significant at the 0.05 level (2-tailed). N = 5.

4. Discussion

4.1. Variation Characteristics of VU Populations in Different Altitude Gradients in Changbai Mountain

Changes in altitude are closely related to environmental factors, such as temperature, precipitation, air pressure, and solar radiation, which, in turn, lead to morphological differences in the same plant species at different elevations [9]. In this study, significant variations in morphological traits were found among and within natural populations of VU at different elevations in the Changbai Mountain region. Nesting analysis of variance revealed that the differences in various traits among and within populations were highly significant at a significance level of $\alpha = 0.01$. This finding is similar to the results of studies on phenotypic variations in *Caragana korshinskii* [24], *Syringa oblata* [25], *Alnus cremastogyne* [26], and other species. Based on the coefficient of variation, it can be observed that there is a large degree of variation in morphological traits among VU populations in this study. Except for the insignificant differences between Population 1 and Population 3; Population 2 and Population 3; and Population 4 and Population 5, significant differences were found among the other populations. With increasing elevation, plant height, basal diameter, leaf size, twig length, and clear bole height showed a decreasing trend in each population's habitat. Furthermore, the overall variation range of the VU populations tended to increase with elevation. However, because of the obvious decrease in individual phenotypic variations with increasing elevation, the range of variation within populations showed a decreasing trend with elevation. This means that the traits show larger variation in low-altitude regions compared with high-altitude regions. The observed phenomenon can be attributed to genetic factors and the influence of ecological environmental pressure on the VU population [25,27–30]. In this study, VU plants exhibited maximum values in plant height, basal diameter, leaf size, and twig length in low-altitude regions, particularly in Population 2 at an altitude of 900 m, except for clear bole height. Therefore, the area around 900 m in altitude is considered to be more suitable for the growth of VU.

Overall, the differentiation coefficients of leaf length, leaf width, twig length, plant height, clear bole height, and basal diameter had a mean value of 62.02%. Twig length and plant height exhibited the most distinct differentiation, which is similar to a phenotype differentiation coefficient study on Quercus mongolica (Vst = 53.97) [31]. The variation among populations was greater than within populations, which differed from most related studies, such as those on *Pseudotsuga menziesii* (Vst = 11.1%) [32], *Pinus massoniana* (Vst = 6.44%) [23], *Quercus liaotungensis* (Vst = 35.44%) [33], *Castanea mollissima* (Vst = 13.07%) [30], *Syringa oblata* (Vst = 43.93%) [25], and *Lophura nycthemera* (Vst = 19.5%) [24]. This reflects the complexity of population G×E and the extent of adaptation to environmental stress, which is the result of different environmental selection and the source of population differentiation [24]. The variation between populations also directly reflects geographical and reproductive isolation, and the diversity variation between populations is an important component of intraspecific diversity [34,35]. Through cluster analysis, the five VU populations in this study can be divided into four categories. VU plants in low elevations mainly increase their plant height and leaf size, as well as twig length, to rapidly obtain the required growth resources. However, at high elevations, they produce a series of adaptive measures related to defense, such as reducing leaf size, slow growth (smaller plant height and basal diameter), and reducing twig length, to adapt to the high-altitude environment. Therefore, the adaptation strategies of VU differ at different elevation gradients [7,36]. Research has shown that there is variability in the morphological, endogenous, individual, geographical, and ecological characteristics of generative and vegetative organs, as well as phenological development in the Vaccinium species [5,22,37]. The Vaccinium species can grow across a wide range of altitudes, and their morphological and physiological traits show significant variability with changes in environmental conditions [38].

4.2. The Relationship between Morphological Traits and Environmental Factors for VU in Changbai Mountain

To further reveal the close relationship between the morphological traits of VU and altitude, this study conducted a correlation analysis between VU traits and 10 environmental factors. The results showed a significant correlation between VU morphological traits and environmental factors, characterized by a decrease in leaf length, plant height, clear bole height, and basal diameter with increasing altitude. The negative correlation was statistically significant [7,36]. Along with changes in altitude, precipitation and temperature fluctuations were also important factors affecting vegetation distribution and trait variation [39,40]. The results of this study showed that a decrease in precipitation led to a reduction in leaf size, basal diameter, and plant height in VU traits [41], indicating a significant negative correlation with various morphological traits. Multiple studies have shown that leaf size reduction is a common response to soil water shortage [42,43], thereby reducing the transpiring surface area and avoiding severe decreases in cell water potential and turgor [44]. As temperature decreases with increasing altitude, the morphological changes in VU include reduced leaf size, smaller plant height, basal diameter, and twig length. Therefore, there is a significant positive correlation between VU morphological traits and temperature factors [7]. Among them, the most significant correlation with environmental factors is between VU clear bole height and basal diameter, showing a highly significant negative relationship (R^2 values above 0.90), indicating that VU clear bole height and basal diameter are the most sensitive to variations in environmental factors. The distributions of mountain plants are influenced by their functional traits, which are shaped by climate, soil resources, and microbial activity [45]. The morphological variation of VU may be a result of ecological niche differentiation to avoid competition with coexisting plants, which may mitigate the negative effects of competition caused by high ecological niche overlap [46].

5. Conclusions

The overall population variation in VU showed an increasing trend in magnitude with rising altitude. However, the range of variation within populations decreased with increasing altitude, and the diversity among populations was higher than within populations. Except for leaf width and twig length, which showed a relatively low correlation with environmental factors, the other morphological traits of VU exhibited significant or highly significant correlations with environmental factors. Generally, as altitude increased, leaf length became shorter, and plant height, clear bole height, and basal diameter decreased significantly. These traits showed a negative correlation with altitude. Similar trends were observed with water-related factors, showing a significant negative correlation, while temperature-related factors showed a significant positive correlation. Among them, the clear bole height and basal diameter of VU were the most sensitive to environmental changes. Overall, the optimal growth area for VU appeared to be around an altitude of 900 m. The findings of this study not only contribute to a better understanding of the ecological adaptation mechanisms of plants but also provide a scientific basis for the conservation and restoration of this species. Clarifying the trait variations in VU at different altitudes will help us understand the response mechanisms of this plant to climate change and predict its future adaptability and survival status. Moreover, against the backdrop of global climate change, it is essential to further explore the impacts of climate change, including temperature increases and changes in precipitation patterns, on the distribution, growth, and reproduction of VU. Subsequently, modeling simulations should be considered to predict its potential distribution changes under future climate scenarios, evaluating the effects of global changes on the suitability of its natural reserves and habitats.

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