https://doi.org/10.17221/147/2023-HORTSCI

Variations in bog bilberry fruit characteristics along an altitudinal gradient on Changbai Mountain, China

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Citation: Li J., Qi Q., Zhang Q., Wang M., Liu Y., Sun X., Mu Y., Yang C. (2025): Variations in bog bilberry fruit characteristics along an altitudinal gradient on Changbai Mountain, China. Hort. Sci. (Prague), 52: 111–119.

Abstract: To better understand the influence of altitude on fruit characteristics of bog bilberry (*Vaccinium uliginosum* L.), here we investigated the adaptation of its fruit morphological and chemical traits to the environment at six growing positions along an altitudinal gradient (706, 957, 1 226, 1 315, 2 000 and 2 190 m) on the northern slope of Changbai Mountain, China. Fruit longitudinal diameter, fruit transverse diameter and fruit weight decreased significantly with increasing altitude. Vitamin B_1 content reached its highest at 2 190 m, while both vitamin B_2 and vitamin C contents reached their highest and lowest at 1 226 and 706 m, respectively. Anthocyanin content and DPPH (1,1-diphenyl-2-picrylhydrazyl) free radical scavenging ability initially decreased and then improved with increasing altitude. We observed a highly significant ($P < 0.001$) negative correlation between external fruit quality traits (fruit length, diameter and weight) and internal fruit quality traits (vitamins B_1, B_2, C and anthocyanin), and found that environmental factors significantly influenced fruit characteristics. Taken together, we concluded that on the northern slope of Changbai Mountain, bog bilberry fruits were larger at low altitudes, fruits at mid altitudes contained higher vitamins B_2 and C, while high altitude (especially at 2 190 m) was beneficial for vitamin B_1, anthocyanin, and DPPH free radical scavenging ability.

Keywords: altitude; fruit antioxidant capacity; fruit appearance characteristics; fruit vitamin content; Changbai Mountain *Vaccinium uliginosum* L.

The bog bilberry (*Vaccinium uliginosum* L.) is a perennial deciduous shrub in the family of *Ericaceae*, and is widely distributed in China, Mongolia, Japan, South Korea, North Korea, Europe, North America and elsewhere. It is an important economic forest understory plant in high-latitude areas of the northern hemisphere. In China, wild bog bilberries are mainly found in the Daxing'anling, Xiaoxing'anling and Changbai Mountain areas, making them the most widely distributed and abundant wild blueberries (Su et al. 2016; Wang et al. 2022b; Zhang et al. 2023). The ripe fruit is blue-purple, covered with white frost, and the flesh is white and juicy. It tastes sour, sweet, and slightly astringent, is rich in functional active components (24 anthocyanins, 32 flavones, 24 organic acids, 28 aromatic components) and a variety of nutrients (e.g. mineral elements, vitamins and amino acids) (Su et al. 2016). Therefore, bog bilberry fruits have powerful antioxidant, anti-ageing, anti-inflammatory, anticancer, vision health properties and cardiovascular disease and cerebral nerve ageing prevention quali-

Supported by the National Natural Science Foundation of China (Project No. 32171770) and Central Finance Forestry Science and Technology Extension Demonstration Project (Project No. JLT2019-04).

https://doi.org/10.17221/147/2023-HORTSCI

ties, which have attracted much attention in food science and medicine (Kopystecka et al. 2023). They are one of the most promising small berries for development and utilisation in Northeast China, and artificial management of their resources has also become an important industry for the development of the Changbai Mountain area forest economy. However, due to irregular harvesting and environmental variability for many years, wild bog bilberry resources have decreased in area, their yield has declined, and quality fluctuated, which has affected their long-term production and management (Wei et al. 2023). Habitat conditions are the basis for fruit quality development. Therefore, an in-depth understanding of habitat effects on bog bilberry fruit quality and fruit yield is imperative for the development of the industry and is important for future utilisation and promotion of the fruit.

Altitude directly determines tree growth environment and is one of the important ecological factors affecting fruit quality and yield. Different altitudes have large differences in light, temperature, moisture and soil, which in turn have significant effects on plant growth and fruit development (Kergunteuil et al. 2018; Naryal et al. 2020; Fischer et al. 2022). Many studies have shown that fruit quality and yield vary with altitude; for example, Karagiannis et al. (2020) found that the high-altitude environment suppresses apple redness and colour index. Wen et al. (2023) revealed that the total anthocyanin content of fruits of six highbush blueberry varieties improved with an increasing altitude, as did the amino acid content of fruits of four highbush blueberry varieties. Fischer et al. (2007) discovered that cape gooseberry fruit number, dry matter content, and sucrose content decreased significantly at high altitudes, and Naryal et al. (2020) found that for every 100 m increase in altitude, apricot fruits show a 0.5 g decrease in fruit weight, a 1.9% decrease in water content, and a 1.2° Brix increase in soluble solids. Vegetation distribution in the Changbai Mountain area varies significantly with changes in slope, with the northern slope having a complete vertical spectrum (Wang et al. 2022a). Therefore, environmental heterogeneity at different altitudes will likely lead to differences in fruit development and quality formation.

Anthocyanins are the main antioxidant components in bog bilberry fruits (Zeng et al. 2020). Aging and many chronic diseases (including cancer) are related to the excessive production of free radicals, and antioxidants can effectively overcome the harm caused by both. Therefore, antioxidants are one of the most important functional demands in the current market and one of the main healthcare research and development directions. Finding antioxidant-active substances from plant sources has become a hot research topic today (Taruscio et al. 2004; de Oliveira et al. 2007; Rangkadilok et al. 2007; Wang et al. 2023). Vitamins B_1, B_2, and C are water-soluble, and although human demand for them is not high, they play an important role in maintaining normal human metabolism and physiological functions. These vitamins cannot be synthesised in the human body due to their physical and chemical properties, so must be supplied from food. However, they are easily affected by external conditions, making them nutrients that humans often lack (Said 2011; Song et al. 2012; Paunović et al. 2020). In this study, we focused on wild bog bilberry fruits continuously distributed on the northern slope of Changbai Mountain and compared their appearance quality (fruit longitudinal diameter, fruit transverse diameter and fruit weight), vitamin (vitamin B_1, vitamin B_2 and vitamin C) contents, as well as antioxidant capacity [anthocyanin content and DPPH (1,1-diphenyl-2-picrylhydrazyl) free radical scavenging ability]. Furthermore, we explored the following three patterns: (*i*) changing patterns of external and internal fruit quality with altitude, (*ii*) intrinsic correlation between fruit quality indicators and their relationship with altitude, and (*iii*) dominant habitat factors affecting fruit quality.

MATERIAL AND METHODS

Study area overview. Changbai Mountain (41°23'–42°36' North longitude, 126°55'–129°08' East latitude), located in the southeastern Jilin Province, on the boundary mountain between China and North Korea, is the highest mountain on the east coast of the Eurasian continent. Its north, west, and south slopes are located in China, and its highest peak is the Baiyun Peak, which reaches 2 691 m. The Changbai Mountain National Nature Reserve (1 964.65 km^2) is one of China's key protected forest areas and is listed on the IUCN Nature Reserves "Green List" (2022). The Changbai Mountain area has a north-temperate continental monsoon alpine climate. Annual precipitation reaches a maximum of 1 400 mm and a minimum of 700 mm, while summer precipitation accounts for > 70% of annual

https://doi.org/10.17221/147/2023-HORTSCI

precipitation. It is relatively humid throughout the year, with an average relative humidity of 70%. The annual average temperature can reach as low as 2 °C, and the annual average temperature difference between the top and the foot of the mountain can reach more than 10 °C. Annual sunshine time is not more than 2 300 h; the frost-free period is 3 to 4 months and only about 2 months at the top of the mountain. The vegetation in the Changbai Mountain area, from the temperate zone at low altitude to the frigid zone at high altitude, can be divided vertically into coniferous and broad-leaved mixed forest, mountain coniferous forest, subalpine *Betula ermanii* forest, and the alpine tundra zone. Soils are also vertically differentiated into dark brown forest soil, brown coniferous soil, mountainous herbaceous forest soil, and mountain tundra soil (Qi et al. 2022; Wang et al. 2022a).

We conducted a comprehensive survey of the wild bog bilberry resources in Changbai Mountain Nature Reserve and found that the northern slope of Changbai Mountain at altitudes 700–2 200 m has a continuous and concentrated distribution of wild bog bilberries. Therefore, we established an altitudinal transect for bilberry sampling. Typical sample plots were located at 706, 957, 1 226, 1 315, 2 000, and 2 190 m and environmental conditions at each altitude were determined (Table 1; Hao et al. 2003).

Sampling methods and trait determination. Three typical sample plots were established at each altitude, and in each plot (30 × 30 m), 20 plants (replicates) of healthy and close to 10-year-old bog bilberries were randomly selected, approximately 20 g mature fruit samples were manually collected in the middle and upper periphery of the canopy of each sample plant, and fruit traits measured in the laboratory. Fruit longitudinal diameter (FLD, mm) and fruit transverse diameter (FTD, mm) were measured by vernier callipers (accuracy – 0.01 mm), and fruit weight (FW, g) was measured with an electronic balance (accuracy – 0.001 g). Vitamin B_1 (VB_1, mg/100 g) and B_2 (VB_2, mg/100 g) contents were determined according to GB 5009.84-2016 National Food Safety Standard for Determination of Vitamin B_1 in Foods and National Food Safety Standard for Determination of Vitamin B_2 in Foods, respectively. Vitamin C (VC, mg/100 g) content was determined according to GB 6195-86 Determination of vitamin C in vegetables and fruits (2,6-dichloroindophenol titration method). Anthocyanin (ACN, mg/g) content was determined using the pH differential method (Song et al. 2013), and DPPH free radical scavenging abil-

Table 1. Wild bog bilberry habitat conditions at different altitudes

Type	Environmental factors	Altitude (m)					
		706	957	1 226	1 315	2 000	2 190
Meteorological condition	AAT	2.83	1.29	0.27	–0.75	–3.82	–4.84
	> 5 °C CT	2 459.77	1 972.49	1 702.53	1 469.52	944.97	815.97
	Jan. AT	–17.33	–18.27	–18.89	–19.52	–21.40	–22.03
	Jul. AT	19.63	17.95	16.84	15.73	12.39	11.27
	AAP	679.18	755.19	810.53	869.92	1 075.53	1 154.34
	Jun. ~ Sep. P	483.02	537.07	576.43	618.67	764.89	820.94
	FFS	121.00	108.12	100.31	93.06	74.31	68.94
	SCD	130.79	151.16	164.73	178.31	219.04	232.61
	DI	0.67	0.56	0.50	0.44	0.31	0.28
Soil condition	OM	4.93	4.96	2.49	2.92	1.21	0.68
	SAN	663.02	819.94	451.68	532.24	273.31	244.54
	SAP	35.68	27.26	41.55	18.86	2.61	5.79
	SAK	1 225.77	1 228.48	731.45	542.67	296.02	335.76

AAT – annual average temperature (°C); > 5 °C CT – > 5 °C cumulative temperature (°C); Jan. AT – average January temperature (°C); Jul. AT – average July temperature (°C); AAP – average annual precipitation (mm); Jun. ~ Sep. P – precipitation from June to September (mm); FFS – frost-free period (days); SCD – days of snow accumulation (days); DI – drying index; OM – organic matter (g/kg); SAN – soil available nitrogen (mg/kg); SAP – soil available phosphorus (mg/kg); SAK – soil available potassium (mg/kg)

https://doi.org/10.17221/147/2023-HORTSCI

ity (DPPH, %) measurement followed the method of Zhu et al. (2019).

Data processing. Significant differences in fruit traits across altitudinal gradients were analysed using one-way ANOVA, multiple comparisons were performed by Fisher's LSD (least significant difference) method (α = 0.05), and data were expressed as mean ± standard error (SE). Pearson correlation analysis was performed using two-tailed significance tests. The relationship between fruit traits and environmental factors was studied using stepwise regression and principal component analysis (PCA). Analysis of variance, multiple comparisons, correlation analysis, path analysis and stepwise regression analysis were performed using R studio version 4.1.1, while PCA was implemented using Canoco version 5.0.

RESULTS AND DISCUSSION

Fruit appearance characteristics. Environmental factors vary along altitudinal gradients, and therefore, plant growth, development and physiological characteristics will also vary regularly (Kergunteuil et al. 2018; Abbas et al. 2022). Plants growing at high altitudes experience different combinations of light, temperature, and moisture compared to those at low altitudes because the growing season is shorter, plants have less access to resources, carbohydrate accumulation is significantly reduced, and plants tend to be smaller, with a consequent reduction in fruit size (Körner et al. 1989; Soethe et al. 2008; Li et al. 2017; Wen et al. 2023). On Changbai Mountain, bog bilberry FLD, FTD and FW decreased with increasing altitude. FLD at altitudes 957 m ($P = 0.003$), 1 226 m ($P < 0.001$), 1 315 m ($P < 0.001$), 2 000 m ($P < 0.001$) and 2 190 m ($P < 0.001$) were significantly lower than at 706 m. FLD at 2 190 m was 17.01% lower than at 706 m (Figure 1A). Significant differences were found between the FTD of bog bilberries at 706 m and at altitudes 1 315–2 190 m ($P = 0.014$, $P < 0.001$, $P < 0.001$), and the FTD of bog bilberries at altitudes 2 000 and 2 190 m were significantly lower than at other altitudes, with the FTD at 2 000 and 2 190 m being lower than at 706 m by 15.82 and 24.93%, respectively (Figure 1B). The FWs of bog bilberries at altitudes 957–2 190 m were significantly ($P < 0.001$) lower than at 706 m, and those at 2 000 and 2 190 m were significantly lower than at other altitudes, with those at 2 000 and 2 190 m being 66.52 and 77.88% lower than at 706 m, respectively (Figure 1C).

Fruit vitamin contents. As the altitude increased, VB_1 and VB_2 contents showed an increasing-decreasing-increasing pattern, and both of them entered the decreasing inflexion point at altitude 1 315 m. VB_1 content at altitude 2 190 m (Figure 1D) and VB_2 content at 1 226 m (Figure 1E) were significantly ($P < 0.001$) higher than at other altitudes, the former of which was 35.49% higher than at 1 315 m, and the latter which was 37.75% higher than at 706 m. At altitudes 706–1 226 m, bog bilberry VC content increased with increasing altitude. VC content (130.13 mg/100 g) at altitude 1 226 m was significantly higher than at other altitudes, and VC content at altitude 2 000 m (121.40 mg/100 g) was second only to altitude 1 226 m. VC contents at 1 226 m and 2 000 m were 7.86 times ($P < 0.001$) and 7.34 times ($P < 0.001$), respectively, greater than that at 706 m. VC contents at altitudes 1 315 and 2 190 m were similar (95.59 mg/100 g and 96.62 mg/100 g; $P = 0.67$) (Figure 1F). VB_2 and VC contents reached the highest and lowest values at altitudes 1 226 m and 706 m, respectively, suggesting that the mid-altitude section with sufficient light and the suitable temperature was more favourable for VB_2 and VC synthesis. Relatively higher temperatures and less precipitation at low altitudes (Table 1) may have restricted the accumulation of the two within the fruits.

Fruit antioxidant capacity. Bog bilberry ACN content initially decreased and then increased with increasing altitude. ACN content at altitudes 2 000 and 2 190 m was significantly higher than at other altitudes (1.89 mg/g and 2.27 mg/g), which was 19.34% ($P = 0.002$) and 33.03% ($P < 0.001$) higher than at 1 226 m (1.52 mg/g) (Figure 1G). Bog bilberry DPPH initially decreased and then increased with increasing altitude. DPPH at 1 315 m was significantly ($P < 0.001$) lower than at other altitudes. DPPH at altitudes 2 190, 2 000, 1 226, 957 and 706 m was 3.51 times ($P < 0.001$), 3.22 times ($P < 0.001$), 2.87 times ($P < 0.001$), 3.26 times ($P < 0.001$), and 3.33 times ($P < 0.001$) higher than at 1 315 m, respectively (Figure 1H). Overall, anthocyanins and DPPH free radical scavenging ability at mid-altitudes (1 226–1 315 m) were relatively low, while bog bilberry antioxidant capacity at high altitudes increased. It reveals that harsh environmental conditions at high altitudes (especially strong light and UV) lead to the production of a large number of free radicals in bog bilberries, inducing the synthesis

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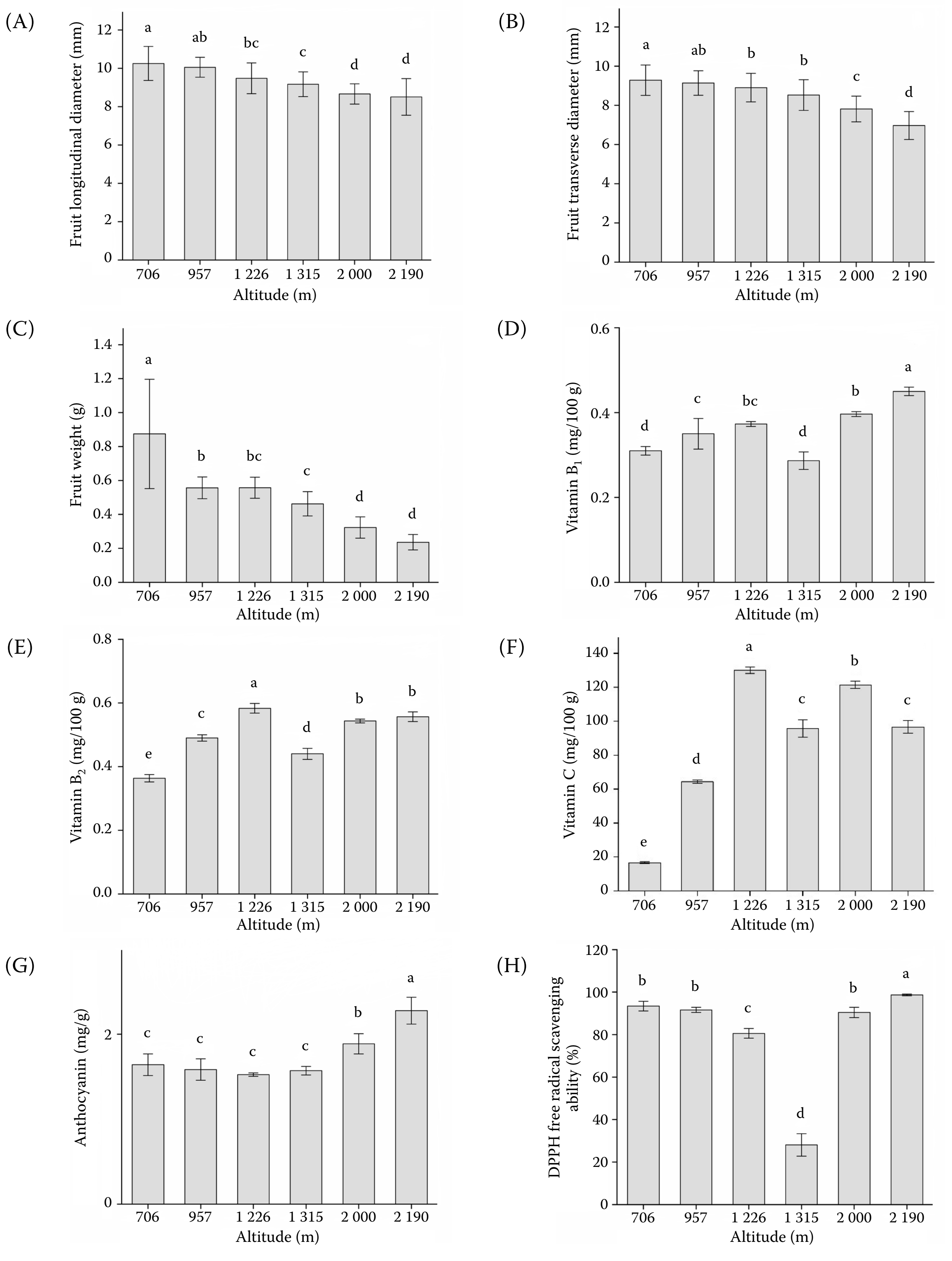

Figure 1. Average values of bog bilberry fruit traits at different altitudes

Error bars represent standard errors (SE); [a–e]different lowercase letters above the bars are significantly different at the level α = 0.05 according to Fisher's LSD (least significant difference) test

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of flavonoids mainly composed of anthocyanins. The bilberry cytoplasmic membrane structure and the antioxidant enzyme system changed to protect various organs and enhance its ability to resist adversity (Zeng et al. 2020; Wang et al. 2022c).

Correlation between fruit traits and between altitudes and fruit traits. There were different degrees of intrinsic correlations between bog bilberry fruit quality characteristics. FLD, FTD, and FW showed a highly significant ($P < 0.001$) positive correlation with each other, and there was a highly significant ($P < 0.001$) negative correlation between the FLD, FTD and FW and VB_1 content, VB_2 content, VC content and ACN content (Figure 2). VB_1, VB_2 and VC contents showed a highly significant ($P < 0.001$) positive correlation with each other, indicating that the three synergistically regulated fruit formation quality. Antioxidation is an important healthcare function of bog bilberries, and anthocyanins are the main functional components of its fruits (Häkkinen, Törrönen 2000; Zoratti et al. 2015). The negative relation between ACN and fruit size (i.e. FLD, FTD and FW), as described above, may be that smaller fruits have a higher concentration of ACN than big ones. However, we found a highly significant positive correlation between ACN and DPPH ($P < 0.001$), indicating that anthocyanins are important contributors to the DPPH free radical scavenging ability of bog bilberries. There was a highly significant ($P < 0.001$) positive correlation between ACN content with VB_1 ($P < 0.001$) and VB_2 content ($P < 0.01$), a highly significant positive correlation between DPPH and VB_1 content ($P < 0.001$), and a significant positive correlation between the DPPH and VB_2 content ($P < 0.05$), indicating that VB elements were able to effectively synergise the scavenging of DPPH free radicals and antioxidant activity, with the synergistic effect of VB_1 being stronger than that of VB_2.

There were highly significant ($P < 0.001$) negative correlations between altitude and FLD, FTD and FW, and highly significant ($P < 0.001$) positive correlations with VB_1, VB_2, VC and ACN contents, suggesting that higher light and UV radiation, cooler temperatures, and greater diurnal temperature differences at increased altitude promotes VB_1 and anthocyanin accumulation in bog bilberry fruits and enhances the DPPH free radicals scavenging efficiency. Additionally, the correlation coefficient between altitude and FW (–0.85) was the highest, followed by ACN content (0.78), and the lowest was with DPPH (0.11) (Figure 2). The absolute value of the path coefficients can be directly used to compare the importance of the role of altitude on fruit characteristics, where the direct and indirect path coefficients reflect the magnitude of direct and indirect effects caused by altitude, respectively. The path analysis results (Table 2) show that the direct effects of altitude on FLD, FW and VB_2 were all negative, while on VC, ACN, and DPPH were positive. The indirect effects of altitude gradient on VB_2, VC and ACN were all negative, while on FLD, FW,

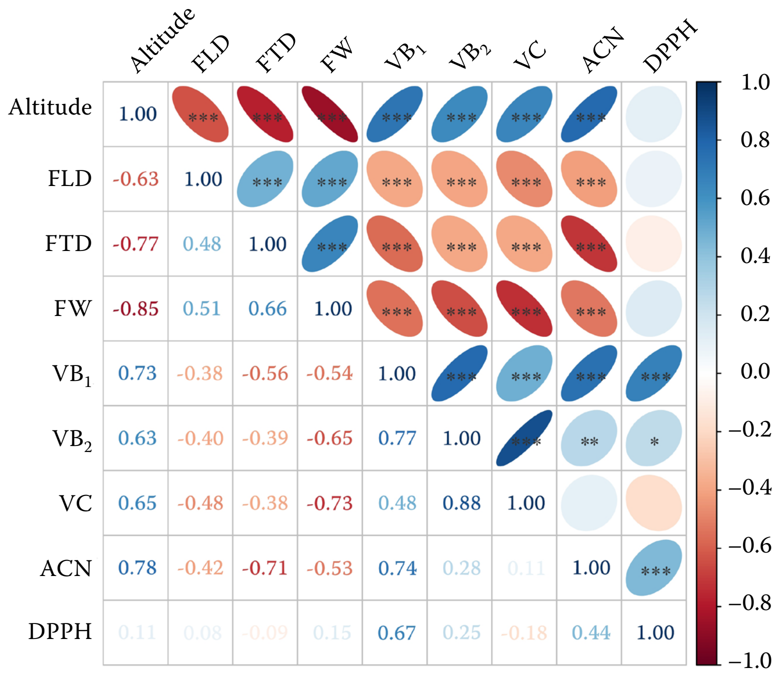

Figure 2. Pearson correlation coefficients (r) between bog bilberry fruit traits and between altitude and fruit traits

Colours and numbers indicate the strength of the correlation (red – negative correlation, blue – positive correlation), the darker the colour, the closer the correlation. Numbers represent the Pearson correlation coefficient (r)

FLD – fruit longitudinal diameter; FTD – fruit transverse diameter; FW – fruit weight; VB_1 – vitamin B1 content; VB_2 – vitamin B2 content; VC – vitamin C content; ACN – anthocyanin content; DPPH – DPPH free radical scavenging ability

*,**,***significant levels at $P < 0.05$, 0.01, 0.001, respectively

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Table 2. Path analysis of bog bilberry fruit traits and altitude

Fruit trait	Correlation coefficient	Direct path coefficient	Indirect path coefficient						
			FLD	FW	VB_2	VC	ACN	DPPH	total
FLD	–0.63	–0.055	–	–0.028	0.022	0.026	0.023	0.004	0.047
FW	–0.85	–0.163	–0.083	–	0.106	0.119	0.086	–0.024	0.204
VB_2	0.63	–0.502	0.201	0.326	–	–0.442	–0.141	–0.126	–0.182
VC	0.65	0.983	–0.472	–0.718	0.865	–	0.108	–0.177	–0.394
ACN	0.78	0.703	–0.295	–0.373	0.197	0.077	–	0.309	–0.085
DPPH	0.11	0.239	0.019	0.036	0.060	–0.043	0.105	–	0.177

FLD – fruit longitudinal diameter; FW – fruit weight; VB_2 – vitamin B_2 content; VC – vitamin C content; ACN – anthocyanin content; DPPH – DPPH free radical scavenging ability

and DPPH were positive. Moreover, altitude had maximum direct and indirect effects on VC while minimum direct and indirect effects on FLD. The direct effects on FLD, VB_2, VC, ACN and DPPH were higher than the indirect effects, while the indirect effect on FW was higher than the direct effect. It can be inferred that a great direct effect did not necessarily lead to a great indirect effect, and altitude had greater effects on VC, VB_2 and ACN.

Effects of environmental factors on bog bilberry fruit traits at different altitudes. Principal components (Figure 3) and stepwise regression (Table 3) analyses jointly showed that climate and soil factors have a significant impact on bog bilberry exter-

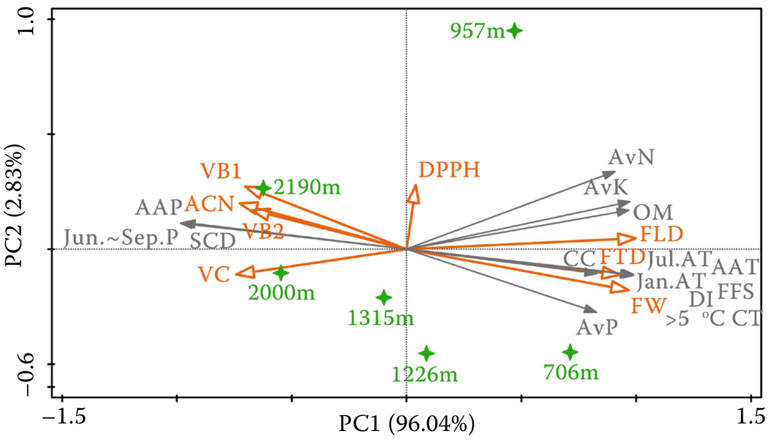

Figure 3. PCA analysis of bog bilberry fruit characteristics and environmental factors

PCA – principal component analysis; PC1,2 – principal components

Table 3. Stepwise regression analysis of bog bilberry fruit traits and environmental factors

Model normalisation factor	R^2	F	P
FLD = 0.536 × DI + 0.476 × SAK + 7.583	0.993	368.185	< 0.001
FTD = –0.981 × Jun. ~ Sep. P + 12.620	0.954	158.574	< 0.01
FW = 6.904 × > 5 °C CT + 5.923 × DI + 0.827	0.988	208.394	< 0.01
VB_1 = –3.475 × SAK + 0.365	0.769	14.775	0.018
VB_2 = –0.876 × SAK + 0.533	0.709	13.182	0.022
VC = –0.883 × SAP + 72.631	0.724	14.100	0.020
ACN = 7.812 × Jun. ~ Sep. P + 6.970 × SCD + 0.120	0.846	17.677	0.014
DPPH = 0.877 × > 5 °C CT + 88.375	0.711	13.307	0.022

FLD – fruit longitudinal diameter; FTD – fruit transverse diameter; FW – fruit weight; VB_1 – vitamin B_1 content; VB_2 – vitamin B_2 content; VC – vitamin C content; ACN – anthocyanin content; DPPH – DPPH free radical scavenging ability; > 5 °C CT – > 5 °C cumulative temperature; Jun. ~ Sep. P – precipitation from June to September; SCD – days of snow accumulation; DI – drying index; SAP – soil available phosphorus; SAK – soil available potassium

https://doi.org/10.17221/147/2023-HORTSCI

nal and internal fruit quality, and different degrees of influence. The cumulative explanation of the first two axes of the PCA plot was 98.87%, and the explanation ratios of the first and second axes were 96.04 and 2.83%, respectively (Figure 3). FLD, FTD and FW showed positive correlations with VB_1, VB_2, VC, and ACN content but not AAP, Jun. ~ Sep. P, and SCD. The drop point distribution of low altitudes was relatively closely related to FLD, FTD and FW, indicating better appearance quality of bog bilberry fruits at low altitudes (especially at 706 m). However, the drop point distribution of high altitudes was closely related to fruit VB_1, VB_2, VC and ACN content. FLD was more likely to be affected by DI and SAK, with a 99.3% explanation value, while Jun. ~ Sep. P affected FTD, with a 95.4% explanation value (Table 2). FW was mainly affected by the > 5 °C CT and DI, with a 98.8% explanation value, while SAK had more obvious effects on both VB_1 and VB_2 contents, with explanation values of 76.9 and 70.9%, respectively. SAP had more obvious effects on VC content, with a 72.4% explanation value, while ACN content was most affected by Jun. ~ Sep. P and SCD, with an 84.6% explanation value, and > 5 °C CT had an explanation value of 71.1% on DPPH (Table 3).

CONCLUSION

We investigated the effects of altitude on bog bilberry fruit appearance, vitamin content and antioxidant capacity. The high nutrient content and antioxidant capacity within bog bilberry fruit indicate that it is a high-quality raw material for functional food processing. Altitude effects on bog bilberry fruit quality reflect the combined effects of various environmental factors. Fruit appearance quality decreased with increasing altitude, meaning that fruits at low altitudes were bigger. Although changing patterns of individual internal fruit quality indicators with increasing altitude were inconsistent, environmental conditions at mid to higher altitudes were more favourable for the formation of bog bilberry fruit internal quality. Specifically, fruit at mid altitudes had higher VB_2 and VC contents, while at high altitudes, the fruit had relatively higher VB_1, ACN, and DPPH radical scavenging ability. Moreover, the highest anthocyanin level was found in bog bilberry fruits at 2 190 m. Additionally, we demonstrated that habitat conditions along an altitudinal gradient are closely related to their fruit development. Except for the meteorological and soil factors as covered in Table 1, vegetation is also an important indirect factor as the canopies of higher trees at the lower altitudes will create a shadow effect and also have an impact on the light quality that will again influence the quality of the berries. The above results can provide a point of reference for the precise cultivation, development and utilisation of wild bog bilberries on the northern slope of Changbai Mountain to obtain high benefits for market needs, as well as the protection of natural habitats.

REFERENCES

Abbas M., Sharma G., Dambire C., Marquez J., Alonso-Blanco C., Proaño K., Holdsworth M.J. (2022): An oxygen-sensing mechanism for angiosperm adaptation to altitude. Nature, 606: 565–569.

de Oliveira A.C.D., Valentim I.B., Silva C.A., Bechara E.J.H., Barros M.P.D., Mano C.M., Goulart M.O.F. (2009): Total phenolic content and free radical scavenging activities of methanolic extract powders of tropical fruit residues. Food Chemistry, 115: 469–475.

Fischer G., Ebert G., Lüdders P. (2007): Production, seeds and carbohydrate contents of cape gooseberry (*Physalis peruviana* L.) fruits grown at two contrasting Colombian altitudes. Journal of Applied Botany and Food Quality, 81: 29–35.

Fischer G., Parra-Coronado A., Balaguera-López H.E. (2022): Altitude as a determinant of fruit quality with emphasis on the Andean tropics of Colombia. A review. Agronomía Colombiana, 40: 212–227.

Hao Z.Q., Guo S.L., Ye J. (2003): Canonical correspondence analysis on relationship of woody plants with their environments on the northern slope of Changbai Mountain. Chinese Journal of Plant Ecology, 27: 733–742. (in Chinese)

Karagiannis E., Michailidis M., Tanou G., Scossa F., Sarrou E., Stamatakis G., Samiotaki M., Martens S., Fernie A.R., Molassiotis A. (2020): Decoding altitude-activated regulatory mechanisms occurring during apple peel ripening. Horticulture Research, 7: 120.

Kergunteuil A., Descombes P., Glauser G., Pellissier L., Rasmann S. (2018): Plant physical and chemical defence variation along elevation gradients: A functional trait-based approach. Oecologia, 187: 561–571.

Kopystecka A., Kozioł I., Radomska D., Bielawski K., Bielawska A., Wujec M. (2023): *Vaccinium uliginosum* and *Vaccinium myrtillus* – Two species – One used as a functional food. Nutrients, 15: 4119.

Körner C., Neumayer M., Menendez-Riedl S.P., Smeets-Scheel A. (1989): Functional morphology of mountain plants. Flora, 182: 353–383.

https://doi.org/10.17221/147/2023-HORTSCI

Häkkinen S.H., Törrönen A.R. (2000): Content of flavonols and selected phenolic acids in strawberries and *Vaccinium* species: Influence of cultivar, cultivation site and technique. Food Research International, 33: 517–524.

Li M.F., Yao Y.Y., Ding Y.L., Ge L., Cao X.L., Li J., Yang D.L. (2017): Effect of altitude on fruit characteristics, bioactive compounds and antioxidant capacity in *Podophyllum hexandrum*. Acta Prataculturae Sinica, 26: 162–168. (in Chinese)

Naryal A., Dolkar D., Bhardwaj A.K., Kant A., Chaurasia O.P., Stobdan T. (2020): Effect of altitude on the phenology and fruit quality attributes of apricot (*Prunus armeniaca* L.) fruits. Defence Life Science Journal, 5: 18–24.

Paunović S.M., Mašković P., Milinković M. (2020): Determination of primary metabolites, vitamins and minerals in black mulberry (*Morus nigra*) berries depending on altitude. Erwerbs-Obstbau, 62: 355–360.

Qi Q.G., Yan J.Y., Zhang Q.C., Jiang W.Q., Zhao J.S., Xu X.Y. (2022): Variation of species diversity in *Lonicera caerulea* communities with altitude gradient in north slope of Changbai Mountain. Journal of Northeast Forestry University, 50: 35–41. (in Chinese)

Rangkadilok N., Sitthimonchai S., Worasuttayangkurn L., Mahidol C., Ruchirawat M., Satayavivad J. (2007): Evaluation of free radical scavenging and antityrosinase activities of standardized longan fruit extract. Food and Chemical Toxicology, 45: 328–336.

Said H.M. (2011): Intestinal absorption of water-soluble vitamins in health and disease. Biochemical Journal, 437: 357–372.

Soethe N., Wilcke W., Homeier J., Lehmann J., Engels C. (2008): Plant growth along the altitudinal gradient – Role of plant nutritional status, fine root activity, and soil properties. In: Beck E., Bendix J., Kottke I., Makeschin F., Mosandl R. (eds): Gradients in a Tropical Mountain Ecosystem of Ecuador. Ecological Studies, vol. 198. Heidelberg, Springer: 259–266.

Song C.M., Ma H.B., Du J., Ge H.J., Zhang X.H. (2012): Nutritional survey of the vitamin B_1, B_2 and C of university students in Jilin. Journal of Jilin Medical College, 33: 69–71. (in Chinese)

Song D.Q., Meng X.J., Wang C.Y., Wang G.Q., Lv C.M. (2013): Determination of blueberry anthocyanins through pH differential method. Journal of Shenyang Agricultural University, 44: 231–233. (in Chinese)

Su S., Wang L.J., Wu J., Li B., Wang W.W., Wang L.S. (2016): Review: Chemical compositions and functions of *Vaccinium uliginosum*. Chinese Bulletin of Botany, 51: 691–704. (in Chinese)

Taruscio T.G., Barney D.L., Exon J. (2004): Content and profile of flavanoid and phenolic acid compounds in conjunction with the antioxidant capacity for a variety of northwest *Vaccinium* berries. Journal of Agricultural and Food Chemistry, 52: 3169–3176.

Wang C.L., Jing J.H., Xu J.W., Jin Y.H., Zhang Y.J., Chen X.Y. (2022a): Analysis of population differences in *Betula ermanii* Cham. between the northern and western slopes of Changbai Mountain. Plant Science Journal, 40: 21–30. (in Chinese)

Wang H., He D.R., Zhou L., Sha G., Zhou L.P. (2022b): Research progress of *Vaccinium uliginosum* L. Territory & Natural Resources Study, 5: 75–78. (in Chinese)

Wang X.P., Li X., Li Z.R., Ling C.T., He Y.M., Li Y. (2022c): Research progress on the characteristics and mechanisms of transgenerational plasticity of plants in response to enhanced UV-B radiation. Plant Physiology Journal, 58: 797–805. (in Chinese)

Wang H., Li M.S., He D.R., Wang C.L., Zhou L.P. (2023): Protective effects of *Vaccinium uliginosum* on hydrogen peroxide-induced cellular oxidative stress injury in cardiomyocytes and UPLC-MS Analysis. Food and Nutrition in China, 29: 45–50. (in Chinese)

Wei D.W., Sun B., Wang F.D. (2023): Effects of mechanical tending on plant morphology, photosynthesis and fruit yield of *Vaccinium uliginosum*. Forestry Science & Technology, 48: 14–17. (in Chinese)

Wen G.Q., Zhao L.Q., Zhou Y., Liao Y.J., Nie F. (2023): The growth status of six varieties of highbush blueberries in different elevation areas in Guizhou province. South China Fruits, 52: 145–150. (in Chinese)

Zhang J.Z., Yuan L., Yu Z.M., Wang L.M., Lv P. (2023): Absorption characteristics and pollution evaluation of Pb and Cd by *Vaccinium uliginosum* L. in the Greater Khingan Mountains. Chinese Journal of Soil Science, 54: 703–712. (in Chinese)

Zeng Q., Dong G., Tian L., Wu H., Ren Y., Tamir G., Huang W., Yu H. (2020): High altitude is beneficial for antioxidant components and sweetness accumulation of rabbiteye blueberry. Frontiers in Plant Science, 11: 573531.

Zhu M.T., Huang Y.S., Wang Y.L., Shi T., Zhang L.L., Chen Y., Xie M.Y. (2019): Comparison of (poly)phenolic compounds and antioxidant properties of pomace extracts from kiwi and grape juice. Food Chemistry, 271: 425–432.

Zoratti L., Jaakola L., Häggman H., Giongo L. (2015): Anthocyanin profile in berries of wild and cultivated *Vaccinium* spp. along altitudinal gradients in the Alps. Journal of Agricultural and Food Chemistry, 63: 8641–8650.

Received: November 23, 2023
Accepted: August 16, 2024
Published online: May 23, 2025