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Review Article

The effect of environmental conditions on the growth and productivity of lingonberry (*Vaccinium vitis-idaea* L.)

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Abstract

The growth and productivity of wild lingonberry (*Vaccinium vitis-idaea* L.) are closely influenced by various environmental factors, including soil composition, climate, light availability, and water levels. This review explores how these conditions and abiotic stress affect lingonberry populations in diverse habitats, from lowland regions to mountainous terrain. Light plays a critical role in flavonoid and anthocyanin synthesis, with solar radiation and photoperiod directly impacting fruit development. Additionally, altitudinal gradients influence the accumulation of polyphenols and vitamin C, while reducing plant height and pollinator activity. Soil types such as cambisols and podzols, often found in subalpine and alpine areas, are favorable for lingonberry growth. Climate factors, particularly winter temperatures and precipitation, significantly affect flowering success, with low temperatures and lack of snow cover negatively impacting fruit production. Forest type and density, including competing vegetation and nutrient availability, further determine the distribution and health of lingonberry populations. This review emphasizes the importance of favorable environmental conditions in promoting the vitality and yield of wild lingonberry, with potential implications for conservation efforts aimed at sustaining its productivity in natural habitats.

Keywords: abiotic stress, altitude, nutrient accumulation, polyphenols, soil, wild lingonberry

Introduction

Biological diversity is essential for maintaining the healthy functioning of ecosystems and for providing critical ecosystem services for people. Ensuring healthy biodiversity not only supports the functioning of ecosystems but also enhances the economic potential of the natural resources they provide. From an economic perspective, *Vaccinium vitis-idaea* L. holds significant value due to its culinary and therapeutic uses. Its berries

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are highly prized for their rich antioxidant and vitamin content, making them widely used in the food industry and in nutritional supplements. Nordic countries, such as Finland and Sweden, economically benefit from the harvesting and export of these berries, which are considered delicacies in many other regions of the world (Kowalska, 2021). Due to the importance of this species, many specimens have been collected and preserved in herbaria since 1800 to be investigated and studied by future generations. *Vaccinium* species from Romania and other countries around the world are present in the "Al. Beldie" Herbarium at the National Institute for Research and Development in Forestry "Marin Drăcea" (INCDS), Bucharest, where they are preserved in very good conditions, allowing all specific details to be observed. Most of the specimens are of *V. vitis-idaea* and have been collected from Romania (Maramureș, Transylvania, Caraș-Severin, Parâng, Ceahlău, Bucegi, Țibleș) and even from Finland. The oldest specimen dates from 1880, while the most recent is from 1974. These specimens were collected and identified by renowned botanists such as S. Pașcovschi, P. Cretzoiu, A. Haralamb, and C. C. Georgescu (Scărlătescu *et al*., 2017).

To fully understand the productive potential and fruit quality of *V. vitis-idaea*, it is essential to consider the influence of the species' genotype and the environmental factors specific to the areas where the species grows. The unique site conditions and historical evolution of this ecosystem result in significant variation in the vegetation and structure of the alpine forests and meadows where the species commonly thrives. Therefore, analyzing this complex interaction can provide a deep insight into the species' adaptations and production potential in a distinct ecological context (Gustavsson, 2001). As is well known, the accumulation of biologically active compounds in plants depends on their geographical origin, climatic and environmental conditions, as well as their genotype (Kaškonienė *et al*., 2016).

Description of the species and ecological requirements

V. vitis-idaea (lingonberry, cowberry or redberry) is an indigenous species with a very wide distribution, similar to the bilberry. It is a very small, erect shrub with round, unbranched stems and shoots. Another common name for this plant in Romanian is "afin roșu" (red bilberry), and it is a bushy shrub that can reach a height of 10-40 cm (Stănescu, 1979).

The stem is cylindrical and branched and the root system is composed of fibrous roots and underground stems (as shown in Figure 1). The rhizomes, which are dichotomously branched, feature numerous fine roots resembling thin hair-like structures. Reported maximum rooting depths range from 5 to 28 cm and are thought to be influenced by the thickness of the organic soil horizons. The variability in rooting depth likely reflects environmental conditions and soil composition, which play a significant role in determining the extent of rhizome growth and anchorage (Smith, 1969).

Vaccinium vitis-idaea commonly sprouts from rhizomes or buds located on the surviving portions of aerial stems after fires damage or consume the aboveground material. Additionally, sprouting from stumps or "rhizocorms" has been reported. Regeneration from seeds is highly uncommon, and although the surviving portions of the aerial stems produce new shoots relatively quickly, sprouting from rhizomes may not occur until the following year (Viereck *et al*., 1980).

(a) (b)

Figure 1. Representation of the root system: (a) Stems growing from a common root; (b) Soil-cross section showing underground interaction of *V. vitis-idaea* and *V. myrthillus* (source: original)

The leaves (Figure 2) are evergreen, measuring 1-3 cm in length, leathery, and obtuse or rounded in shape. They are dark green on the upper surface and have sparse, brown spots on the underside. The leaves can remain green for up to 3 years (Hall and Shay, 1981). The location of the shoots was influenced by shade, with an increase in the number of terminal shoots as shading intensified. This effect reached a maximum of 45% under dense shading conditions, indicating that shading plays a significant role in determining shoot distribution. Such conditions likely promote the growth of shoots in areas with less direct sunlight, allowing the plant to adapt to its environment and maximize its chances of survival in shaded habitats (Smith, 1962.

(a) (b)

Figure 2. Leaf structure: (a) Highlighting the shape, colour and brown spots on the underside of leaf; (b) Leaves positioning on the stem (source: original)

Phenological development can be closely related to the timing of snowmelt, as it marks the onset of seasonal growth. In the interior of Alaska, plants typically reach their peak bloom about six weeks after the snow has melted, with the first visible signs of growth appearing approximately two weeks following the snowmelt. This relationship between snowmelt timing and plant growth highlights the importance of temperature and environmental conditions in the early stages of development. However, unusually cold temperatures can delay phenological processes, affecting the overall growth cycle. Roots and rhizomes, which are vital for the plant's growth, experience two periods of active growth each year: one in early spring and another in the fall. These growth phases are critical for the plant’s survival, as they contribute to root and rhizome development, ensuring the plant can withstand harsh environmental conditions and thrive when favorable conditions return.

The flowers are white, slightly tinged with red (Figure 3), and appear in clusters of 4 to 6 on a slightly drooping raceme. They are 4 to 6 mm in length and possess 4 to 5 petals, with 8 to 10 stamens. The flowers develop from buds initiated in the previous year (Holloway, 1983).


(a)


(b)

Figure 3. Lingonberry flowers: (a) The structure of the flowers; (b) Arrangement of racemes on the plant (source: original)

The fruits (lingonberries) are red berries, mostly globular in shape, but berries of various shapes have been found (Figure 4). Generally, lingonberries contain about 7 seeds. They are edible and have numerous nutritional and nutraceutical properties. Plants typically bear fruit for the first time at 3 to 4 years of age in most locations. However, British studies indicate that lingonberry produces few flowers until the shrub reaches the age of 5 to 10 years (Blomhoff *et al.*, 2023).

Figure 4. Fruit shape variability (source: original)

Originally from the northern temperate regions of Eurasia and North America, lingonberry grows wild in diverse habitats, ranging from lowlands to mountainous areas (Figure 5), and generally prefers acidic soils to pure peat bogs. It is highly resistant to low temperatures, drought, and a wide range of environments, from exposed, dry slopes and peat soils to isolated marshlands (Ștefănescu *et al.*, 2020, Vilkickyte *et al.*, 2022).

Lingonberry (*V. vitis-idaea*) is a species that grows abundantly in Europe, Asia, and North America, similar to the bilberry. It reaches approximately 72° N in Siberia and 76° N in Greenland, in the boreal and subarctic regions of the Northern Hemisphere. It is rarely found in lowland areas in our region, but is often present at high altitudes, particularly from the timberline upwards, continuing into subalpine and alpine zones, among dwarf pine thickets and other plant communities specific to these areas. Ecologically, it closely resembles the bilberry, being even more oligotrophic and acidophilic. However, it is not as detrimental to forest regeneration, as despite contributing to the formation of raw humus, it compacts the soil to a lesser extent (Stănescu, 1979).

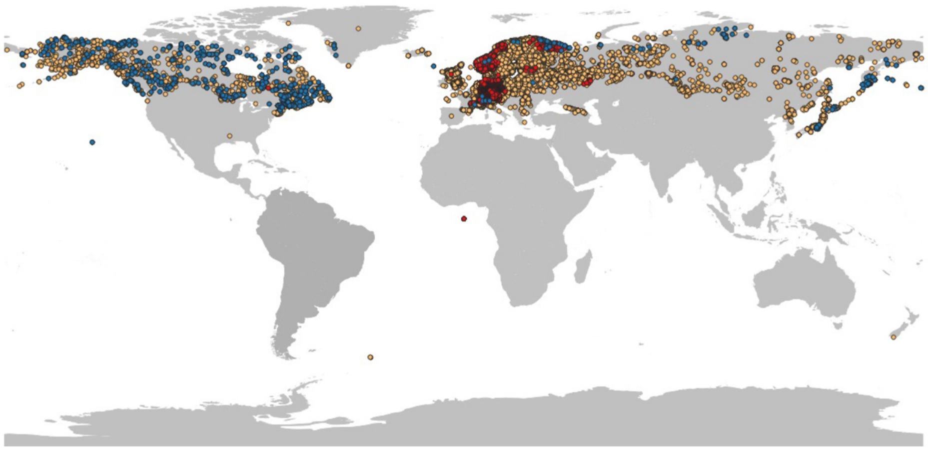

Figure 5. The distribution area of the two subspecies of *V. vitis-idaea* L. *V. vitis-idaea* ssp. *minus* (blue), *V. vitis-idaea* ssp. *vitis-idaea* (red), *V. vitis-idaea* L. ssp. unidentified (yellow) (source: *https://www.gbif.org/occurrence/map?taxon_key=2882835&advanced=1*, 10.10.2024)

Although it has a narrower climatic range than the bilberry and is highly resistant to low temperatures (oligothermic), it sometimes grows in areas with advanced dryness caused by intense sunlight and wind exposure on shallow soils, such as in high-altitude regions. Nevertheless, it demonstrates greater tolerance to soil moisture and can withstand excess soil moisture (a mesoxerophytic-hygrophytic species), similar to the bilberry. This plant thrives in most forests of the Northern Hemisphere. Sites with low pH soils, low base saturation, and low calcium content are the most suitable for lingonberry (Zheng *et al*., 2019). In terms of soil requirements, it is very similar to the bilberry, growing on skeletal soils with low fertility, strongly acidified, and poor in minerals (oligobasic-extremely oligobasic, oligotrophic-extremely oligotrophic, acidophilic-extremely acidophilic). It is drought-resistant (Stănescu, 1979).

Many biotic and abiotic factors, such as temperature, water availability and quality, light, soil properties, plant physiology, and genetics, influence the growth, development and biochemical composition of fruits (Figure 6) of lingonberries, as is the case with any other plant (Karlsons *et al.*, 2021). Plant physiological processes are affected by numerous variables, and the yield of their secondary metabolites occurs under the influence of several conditions. Biotic factors include interactions with neighboring plants and pathogens, vegetation cover, as well as species richness and evenness, while abiotic factors consist of light exposure, temperature, humidity, water availability, macronutrients, soil properties, as well as altitude and growth location (Vilkickyte and Raudone, 2021; Vrancheva *et al.*, 2021). For example, a study that examined phenological and geographical effects in *Vaccinium vitis-idaea* leaves showed that differences in climatic, physiological, and geographical conditions influence the adaptation of lingonberry leaves and their phytochemical properties. The study demonstrated continuous biosynthesis and storage of 30 phenolic compounds and 13 triterpenoids throughout the year, suggesting seasonal availability. Harsh weather conditions and cold acclimation positively impacted the content of these compounds, indicating that lingonberry leaves should be preferably collected in the autumn and early spring. Distinct chemotypes of lingonberry with varying levels of secondary metabolites, related to habitat differences, were found in Lithuania, suggesting that factors such as macronutrient status, soil quality, light, temperature, and humidity regimes can influence the phytochemical content of lingonberry leaves. The observed variability in phytochemical profiles should be understood as the result of a complex interaction of biotic and abiotic factors, rather than a single factor (Vilkickyte and Raudone, 2021).

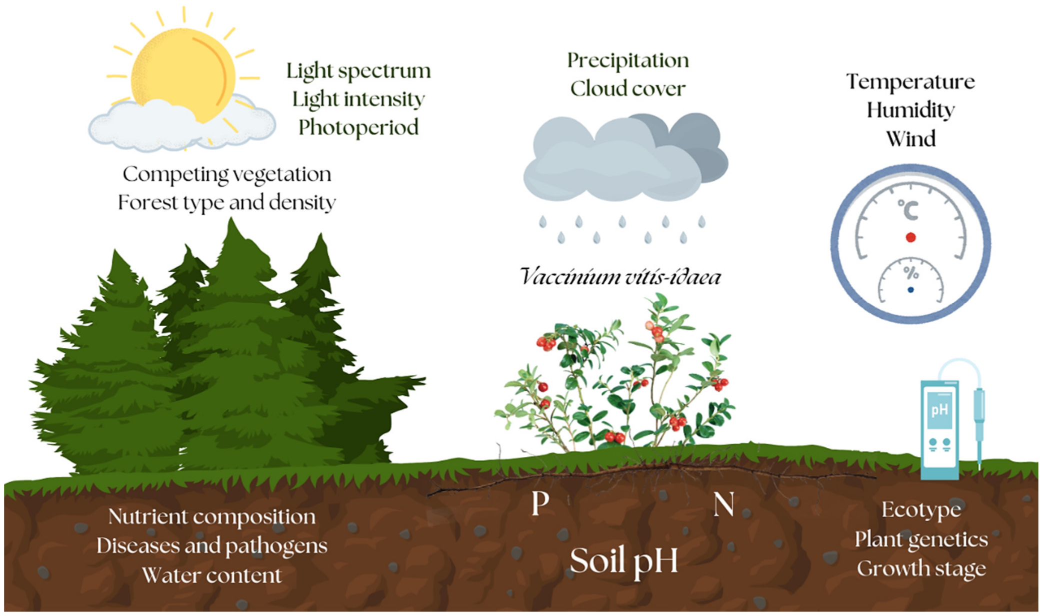

Figure 6. The factors influencing the biochemical composition of lingonberries (source: original)

Light and solar radiation

Considered the most important factor influencing biomass production, plant growth, and biomass yield, light has several qualities or characteristics: photoperiod, spectrum, and intensity. These vary depending on the season and the location on Earth. These differences are caused by the Earth's tilt of approximately 23.45° in relation to the sun. Solar inclination affects the photoperiod because, during the summer months, areas above the Arctic Circle experience 24 hours of daylight. In winter months, direct sunlight is absent. The flowering period of lingonberry occurs from May to June, leading to significant variations in the photoperiod of flowering and fruiting. However, the fruit ripening period (early autumn) is close to the equinox, when days and nights are of equal length, and the ripening of berries in areas of different latitudes is influenced only slightly by the differences in photoperiod. The light scattering properties of the ozone layer are influenced by the angle at which the emitted ray enters, altering the length of the path it travels through the atmosphere. This aspect also impacts the growth and development processes of plants (Mølmann *et al.*, 2021; Zoratti *et al.*, 2015).

The content and composition of flavonoids in many berries are influenced by variations in light spectrum. Additionally, the biosynthesis of anthocyanins is affected by the properties of the light spectrum, which impacts the mechanisms of signal transduction and transport. The energy reaching the Earth's surface is influenced by a series of factors, including variations in the meteorological conditions of that region, as well as the degree of cloud cover that affects light penetration to the ground (Huld and Pinedo-Pascua; Mølmann *et al.*, 2021; Samkumar *et al.*, 2022). Geographical location, time of day, season, site conditions, and weather conditions are the factors that influence the light reaching plants. Previous studies on berries demonstrate that the profile and content of secondary metabolites are related to the amount of solar radiation reaching the plants (Chiang *et al.*, 2019; Karppinen *et al.*, 2016).

Altitude

Altitudinal gradients not only create variations in temperature but also affect snow depth and the timing of snowmelt, both of which significantly impact plant phenology and the duration of the growing season.

Studies have shown that anthocyanin synthesis in berries is increased by ultraviolet radiation at high altitudes. As a result, the antioxidant capacity in photosynthetic organs increases with the level of solar radiation. However, the structure of polyphenols differs depending on genotype and environment. It has been observed that the accumulation of polyphenols, anthocyanins, and vitamin C increases with altitude. An experiment conducted at various altitude levels, ranging from 750 meters to 2000 meters, demonstrated that plants exhibited a decrease in annual growth and height as altitude increased. In addition, the number and activity of pollinators significantly decrease at high altitudes, which affects fruit production. At altitudes above 950 meters, a reduced leaf area and higher stomatal density were observed. This was likely caused by the increased solar radiation. In these studies, it was noted that altitude not only increased the number of seeds per fruit but also the fruit weight. However, the intensity of flowering and fruit production were not significantly affected by altitude (Jovanevi *et al.*, 2011; Rieger *et al.*, 2008).

Type of forest and soil

In terms of phenotype, *V. vitis-idaea* has shown plasticity to environmental changes. However, the importance of genetic factors and environmental influences has not been fully understood and elucidated. Initial experiments, using wild populations, could explain some of the contradictory conclusions. For example, Eriksson *et al.*, (1979) noted that the lingonberry cover in Swedish pine forests was 8-9%, while in denser spruce forests it was 4%. At the same time, in field cultivation experiments conducted by Lehmushovi and Hiirsalmi, (1973), it was found that shading (10-25% of full light) increased the average height of the shoots. On the other hand, Holloway et al., (1982), working with a specific clone, observed greater vegetative growth in full sunlight compared to 44%, 56%, and 73% shade.

In a study conducted in Norway, it was demonstrated that the frequency of *V. vitis-idaea* shrubs does not vary based on forest density, with an average cover of 5-7%, being more abundant in pine forests in Scotland, as opposed to spruce forests in Norway. This finding differs from the results obtained for bilberry, where abundance was shown to be correlated not only with forest age but also with forest composition (Kardell, 1979).

In Romania, the most widespread type of soil in forested areas is represented by districambosol (cambisols) - 22,923.85 km^2, followed by podzol (spodosols). Knowing the distribution range of the *V. vitis-idaea* species and its preference for high altitudes, starting from the timberline upwards through subalpine and alpine zones, we can affirm that the species primarily vegetates in areas with cambisols and spodosols (Dincă *et al.*, 2014; Stănilă and Dumitru, 2016).

Plant metabolism depends on the diversity of nutrients in the soil. Additionally, plant metabolites can be affected by a variety of factors such as harmful insects, fungi, competing vegetation, salinity, drought, pesticides, or heavy metals. Acidity, the content of essential elements such as nitrogen, potassium, phosphorus, and conductivity have been shown to impact the metabolism of *V. vitis-idaea* the most (Sharma *et al.*, 2019; Vilkickyte and Raudone, 2021).

Temperature and precipitation

The habitat and climate significantly influence the properties of the fruits. Polyphenolic compounds are often synthesized to survive external abiotic stress (Urbonaviciene *et al.*, 2023).

Studies conducted on bilberry (*V. myrtillus* - which is often known to grow in association with lingonberry and shares similar ecological requirements) have shown that low winter temperatures are dangerous for bilberry plants and can cause significant or even total damage if they do not have a protective layer of snow. When plants overwinter without a snow cover, their metabolism slows down in the spring, leading to a reduction in the number of flowers and fruit production. Bilberries require approximately 1.600 hours of temperatures below 40 °C to inactivate dormancy mechanisms. During flowering, low temperatures below -3 °C, along with late frosts, destroy the flowers, significantly affecting fruit production, which may be entirely absent. Therefore, abundant flowering in warm weather, along with precipitation after late spring frost, can ensure adequate production. Additionally, a proper supply of nitrogen has a positive effect on cold resistance (Martinussen, 2009; Nestby *et al.*, 2010).

For some small-fruited species, temperatures between ten to fifteen degrees Celsius increase anthocyanin content, while for other species, such as strawberries, temperatures above thirty degrees Celsius are needed. Furthermore, Åkerström *et al.* argue that significant differences between night and day temperatures favor anthocyanin synthesis. Although temperature may indirectly affect pollination and production. Pollination in lingonberry is promoted at temperatures between 15 and 20 °C, whereas fruit set decreases at temperatures exceeding 25 °C (Janick, 2001). Nevertheless, Uleberg and colleagues' studies demonstrated no significant differences in production between bilberry plants grown at different temperatures (Åkerström *et al.*, 2010; Nestby *et al.*, 2010; Uleberg *et al.*, 2012).

Anthropic factor

In areas affected by human activities, such as intensive agriculture and mining, soil salinity levels increase (Fadaei *et al.*, 2020). Wild fruits are not included in Romanian legislation, but for the commercialization and consumption of fresh fruits and vegetables, there are well-established permissible limits. The maximum limits for heavy metals in fresh fruits are: 0.5 mg/kg for As and Pb, 0.05 mg/kg for Cd, and 5 mg/kg for Cu and Zn.

Organ damage (such as to the kidneys, liver, and bones) and a variety of diseases can be caused by heavy metals in the human body. Additionally, an excessive amount of heavy metals in the body can lead to toxicity or a deficiency of trace elements. When the body is exposed to contamination, symptoms become visible and can be quickly observed by doctors, while lower exposure may lead to biochemical effects (Huzum *et al.*, 2017).

Authors' Contributions

Conceptualization: CMA, MB and AFS; Literature and data organization: CMA, AMT and IMM; Formal analysis; Photography: CMA; Interpretation and selection of relevant information: AMT and IMM; Writing - original draft: CMA, AMT and IMM; Writing - review and editing: MB and AFS. All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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