



Fruit quality of bilberry (*Vaccinium myrtillus* L.) in boreal forests: Effects of forest stand, understorey, and soil characteristics

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ABSTRACT

The bilberry (*Vaccinium myrtillus* L.) is an essential wild berry species in Northern Europe, valued for its sweet taste and chemical compounds. The growing environment, particularly the light and temperature conditions, affects the quality of bilberry fruits. However, studies of their quality in boreal forests are scarce. We analyzed the total phenolics, anthocyanins (ACN), flavonols, iridoids and sugars of bilberry fruits collected from 28 forests in central Finland, to identify the characteristics of forest structure, understorey, and soil that best indicate fruit quality. Forest structure was characterized by canopy cover (leaf area index, LAI), mean age and dominant tree species. The mean (\pm SD) values of the total phenolics, ACNs, iridoids and sugars in bilberry fruits were 88.7 ± 14.2 , 78.9 ± 13.4 , 0.52 ± 0.11 and 339.1 ± 44.6 mg g⁻¹ d.w., respectively. Based on linear mixed models, forest structure was the strongest predictor of high phenolics and ACNs, while soil organic layer best explained sugar concentrations. Moreover, daily minimum temperatures correlated with higher sugar levels. A significant interaction between the dominant tree species and LAI indicated that light availability increased phenolic content in bilberry fruits in spruce dominated forests. When comparing different forest stand types, bilberry fruits from drained peatland pine forests exhibited the highest levels of ACNs. High ACNs were associated with high graminoid abundance in the understorey. These findings could direct the harvesting of high-quality bilberry fruits and reveal the intricate relationship between bilberry fruit quality, forest stands and site characteristics in natural ecosystems.

1. Introduction

Bilberry (*Vaccinium myrtillus* L., Ericaceae) is a widespread deciduous dwarf shrub understorey species in Europe and Eurasia, well known for its fruits (Ritchie, 1956). Phenolic compounds in bilberry, such as anthocyanins (ACNs) and proanthocyanidins (PA), play a central role in the interaction between the plant and its environment. Phenolics act as defense agents against UV-B, microbes, and herbivores, and their biosynthesis and degradation are part of the plant's defense responses that support long-term performance (Haukioja, 2005; Koskimäki et al., 2009). Phenolic compounds also influence soil processes through litter that affects microbial activity and nutrient cycling (Kaskoniene et al., 2020). Bilberry fruits have traditionally been a part of people's daily diet due to their balanced taste, high nutritional value and health effects (Pires et al., 2020). They are also a potential raw material for the extraction of bioactive compounds, such as anthocyanins and waxes

(Trivedi et al., 2021), also processed into novel products (Pires et al., 2020). Bilberry fruits are rich in flavonoids, especially anthocyanins (ACNs) (Lätti et al., 2008; Mikulic-Petkovsek et al., 2015), which are powerful antioxidants with activity against serious health disorders (Zafra-Stone et al., 2007). The fruits of bilberry contain five different ACNs, with a total of 15 different glycosides identified (Tian et al., 2017). Flavonols, PAs and epicatechin are other less abundant flavonoids present in fruits. In addition, the fruits of bilberry contain phenolic acids (chlorogenic acids, CGA), iridoids and a moderate level of micro-nutrients such as vitamins (Mikulic-Petkovsek et al., 2015; Moyer et al., 2002). Iridoids are heterocyclic monoterpenes found in considerable amounts in many plant species, including members of the Ericaceae family. Iridoids are not frequently reported in the fruits of bilberry in the literature (Heffels et al., 2017; Liu et al., 2020) but have been suggested to have important health benefits for humans (Przybylska et al., 2022). The quality of bilberry fruits can be assessed based on the quantity and

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quality of health-promoting compounds, as well as on the levels of various organic acids and sugars that contribute to the taste of the fruits.

Boreal forests are multilayered systems where canopy structure reduces light intensity and modifies light quality, significantly altering the light environment in the understorey (Pecot et al., 2005; Tonteri et al., 2016). Both light intensity and quality are regulators of the biosynthesis of phenolic compounds, such as ACNs and flavonols (Zoratti et al., 2014). Together with the canopy, the understorey itself can shade bilberry fruit and thus contribute to the regulation of the phenolic concentration in plant tissues (Jaakola et al., 2004; Filippi et al., 2021). In addition to light, temperature is the key factor influencing bilberry phenolic content: bilberries grown at lower temperatures produce fruit with higher phenolic concentrations (Uleberg et al., 2012). The relationship between light and temperature is well documented in studies examining the altitudinal and latitudinal effects on the phenolics of bilberry fruits (Mujanović et al., 2024; Uleberg et al., 2012; Zoratti et al., 2015; Åkerström et al., 2010). Considering soil properties, the presence of a thick soil organic layer is associated with high phenolic content in bilberry fruits (Rohloff et al., 2015; Vaneková et al., 2020), whereas soil fertility, including nitrogen (N) and carbon (C) levels, have a mixed and relatively small effect on bilberry fruit quality (Rohloff et al., 2015; Åkerström et al., 2009).

The sweetness brought by of the soluble sugars and, on one hand, the bitterness resulting from the iridoids, CGAs, epicatechin and proanthocyanins (PAs), determine the taste of bilberry fruits, and effectively influence their quality. Similar to phenolic compounds, soluble sugars, PAs and CGA in bilberry fruits are more abundant at lower temperatures (Uleberg et al., 2012). Little information is available about iridoid concentration in bilberry fruits, except for a few studies (Heffels et al., 2017; Jensen et al., 2002; Mikulic-Petkovsek et al., 2015). The control of their synthesis in plants by environmental factors is poorly known (Martz et al., 2009; Przybylska et al., 2022). Like phenolic compounds, the synthesis of iridoids is induced by biotic stress (Marak et al., 2002). Iridoids are the major chemicals found in the Gentianaceae family where they are responsible for their bitter taste (Rodriguez et al., 1998) but as far as known, no data are available on their impact on the taste of bilberry fruits.

Bilberry is particularly common in pine- and spruce-dominated [*Pinus sylvestris* L. and *Picea abies* (L.) Karsten, respectively] northern boreal forests, where it contributes significantly to boreal biodiversity. Bilberry is associated with relatively shady environments and acidic, nutrient-poor soils characterized by high C:N ratios (Coudun and Gégout, 2007; Pohjanmies et al., 2021). Bilberry yield varies according to the site productivity and the characteristics of the tree stand. Specifically, bilberry yield is higher in mesic heath forests on mineral soil than in peatland forests, and in stands dominated by pine rather than spruce (Miina et al., 2009; Turtiainen et al., 2016). Site-specific variation in bilberry yields (Miina et al., 2009; Turtiainen et al., 2016) and fruit chemical composition (Lätti et al., 2008) have been reported, but information about the effects of natural growing conditions on fruit quality remains scarce. The harvesting and use of wild berries is an essential part of the ecosystem services that provide increasingly valuable non-timber forest products. Therefore, it is important to know if, and how, it is possible to optimize the fruit quality of the naturally growing bilberry in the boreal forest. We analyzed the quality of bilberry fruits collected from four different forest stand types in the middle-boreal forest zone in Finland and using linear mixed model analyses, we determined which of the stand characteristics could be the best predictors of high-quality berries. The four stand types were: pine-dominated peatlands, pine-dominated sub-xeric and mesic forests, and spruce-dominated mesic forests. The stand characteristics included in the study were light (expressed as leaf area index (LAI) under the forest canopy), air temperature up to 4 weeks before berry sampling, tree density, dominant tree species and age, understorey abundance and composition, and soil mineral layer properties (pH, C:N ratio, soil organic matter, SOM). The bilberry fruit parameters studied were

concentrations in total phenolics, ACN, flavonols, iridoids, and soluble sugars.

Due to the reported effect of light on flavonoids (Zoratti et al., 2014, Vaneková et al. 2020), our primary hypothesis is that forest stand and understorey characteristics, such as (LAI), tree density, and high understorey abundance, all of which reduce light availability, will reduce the phenolic compounds in bilberry fruits. Based on previous literature (Uleberg et al., 2012), our second hypothesis is that low temperatures are promoting higher sugar content in bilberry fruits. Consequently, our third hypothesis is that the highest quality bilberry fruits are found in cool and open forests with sparse shrub vegetation. Finally, due to the multilayered structure of boreal forest (Tonteri et al., 2016) and the dependence of phenolics to light, our fourth and last hypothesis is that the forest stand characteristics affecting light availability are the strongest, and soil parameters the weakest predictor of bilberry fruit quality.

2. Material and methods

2.1. Study sites and collection of plant material

The study sites (36 in total) were randomly pre-selected by using the Finnish national geo-portal service (<https://kartta.paikkatietoikkuna.fi/>). In particular, the database including forest site type and stand age in 2017 was used for selection. The age of the pre-selected forest stands varied from 11 to 130 years. Sites were pre-selected to represent the site type of mesic or sub-xeric forest, due to their natural high abundance of bilberry.

The pre-selected sites were visited in early June 2020 and the final selection was made based on the abundance of bilberry ramets and flowers. Finally, 28 of the 36 pre-selected sites were included in the study (Fig. 1, Table S1). While most of the sites were on mineral soil, four of those were in drained peatland forest. Two temperature dataloggers were placed in each site in June, with one positioned about 20 cm above the ground at the height of the bilberry ramets, and the other at a height of 2 m. Temperature was recorded hourly until sampling. Precipitation data for the same period was loaded from Finnish Meteorological Institute (), from the closest meteorological station (Kajaani Petäisenniska). The average monthly temperatures (1961–2020) at the same weather station over June–July–August 2020 were 13.4, 16.3 and 14.0 °C, respectively. Corresponding values for monthly precipitation were 73.2, 176.0 and 53.4 mm, respectively.

Stand characteristics were measured at each study site (Table 1). The basal area of the trees was recorded using a relascope, and the number of trees, mean age, height and volume were measured separately for each tree species, including pine, spruce and deciduous trees. The deciduous trees were mainly silver birch (*Betula pendula* Roth), downy birch (*B. pubescens* Ehrh.) and aspen (*Populus tremula* L.). Canopy measurements were conducted at each study site using a portable photosynthetically active radiation meter AccuPAR Ceptometer LP-80 (Decagon devices, Inc., Pullman, WA USA). AccuPAR LP-80 facilitates non-destructive, indirect measurements of the amount of light transmitted by a tree canopy and calculates the leaf area index (LAI). Four reference measurements were collected in a nearby, unshaded open field, followed by twelve measurements below the tree canopy at height of bilberry ramets to obtain the statistical mean for each study site.

Three circular sampling plots with a radius of 2.82 m (total area 25 m²) were randomly placed within each site (Fig. 1.), at least five meters apart. The abundance of the most common vascular plant species in the field layer, i.e., bilberry, lingonberry (*V. vitis-idaea* L.), crowberry (*Empetrum nigrum* ssp. *nigrum* L.), and heather (*Calluna vulgaris* (L.) Hull), or species groups (graminoids, herbs), was estimated visually using a scale of 1–100 %. Due to the multilayer structure of the vegetation, the total amount of vascular species and species groups may exceed 100 %.

A composite sample of nine soil cores, including the entire organic

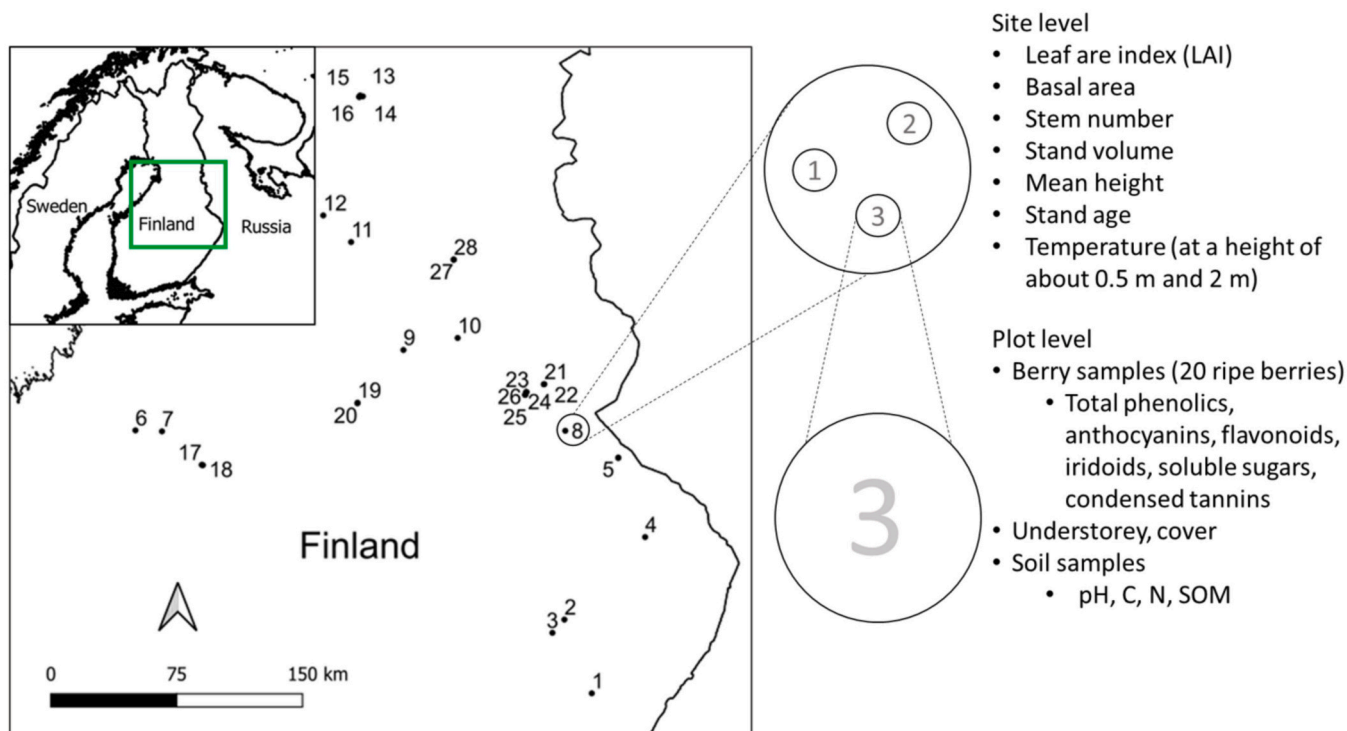


Fig. 1. Locations of the 28 boreal forest sites in central Finland, each containing three study plots. Forest stand characteristics were measured at the forest stand level, and bilberry fruit properties, abundances of dominant understorey species and species groups, and soil organic layer properties were assessed within three plots in each forest site. (C: Carbon, N: nitrogen, SOM: Soil organic matter).

layer, was collected from two lines intersecting in the center of each study plot. Soil samples were kept in cold, homogenized by sieving (mesh 2 mm), and stored at -20°C until analysis.

Twenty fruits were collected at the upper part of the bilberry stems within each plot. The fieldwork period lasted from August 11 to August 26, 2020, starting from the southern sites and gradually moving northwards as the fruit ripened.

2.2. Soil sample analysis

Moisture (105°C , 12 h) was determined gravimetrically from soil samples by TGA-analyzer (LECO TGA-701; Leco Corporation, USA). Soil pH was determined using a combination electrode in a 1:5 (v/v) soil/water suspension. Samples for the total nutrients were digested by the closed wet HNO_3 -HCl digestion method in a microwave (CEM MARS 6; CEM Corporation, USA) and the extract was analyzed by an iCAP 6500 Duo ICP-emission spectrometer (ICP-AES; Thermo Scientific, UK). Total carbon (C) and nitrogen (N) were measured from milled samples on a CHN analyzer (Leco TRUMAC; Leco Corp., St. Joseph, MI). All soil analysis were conducted in accredited laboratory (Natural Research Institute Finland, T04) according to the standard method SFS-EN ISO/IEC 17025:2017.

2.3. Chemical analysis of fruits

About 20 bilberry fruits were collected in sealed plastic bags in each sampling plot and frozen on site to -18°C using a compressor-equipped cooler box. Fruits were kept frozen at -20°C until processing. For extraction, whole bilberry fruits (skin, pulp and seeds) were freeze dried (Labconco, FreeZone plus 4,5 l Cascade), ground into a fine powder using a bead homogenizer (Precellys 24 dual, Bertin) and analyzed as described (Nguyen et al., 2021). Shortly, soluble phenolics were extracted three times in [methanol: H_2O (1:1), 0.1 % HCl] by sonication, followed by shaking for 10 min in the dark. Samples were analyzed

immediately after extraction by UPLC-DAD-ESI-MS/MS (Nexera2, LCMS-8040, Shimadzu, Kyoto, Japan) using a Luna $5\ \mu\text{m}$ C18(2) 100 Å, $250 \times 3\ \text{mm}$ column (Phenomenex, Torrance, USA) and a C18 guard column with solvent A (10 % methanol and 0.1 % formic acid) and solvent B (98 % methanol, and 0.1 % formic acid) and the following gradient: 0–2 min of 5 % B, 15 min of 13 % B, 30 min of 40 % B, 40–50 min of 100 % B (flow $0.3\ \text{mL min}^{-1}$, column oven 40°C). The MS conditions were as follows: nebulizing gas (N_2) $3\ \text{L min}^{-1}$, drying gas (N_2) $15\ \text{L min}^{-1}$, desolvation line 250°C , heat block temperature 400°C , interface voltage 4.5 kV. Quantification was done using MS detection with single ion monitoring and multiple reaction monitoring (MRM) (phenolic acids, flavonols, PAs and ACNs in negative or positive modes (Table S2). Standards for quantification were purchased from Extrasynthese (cyanidin 3-O- glucoside, procyanidins B2, hyperoside) and Merck (catechin, 3-O-chlorogenic acid (CGA)). Calibration curves for MS quantification were done with spiked samples for catechin, CGA, cyanidin 3-O- glucoside, procyanidins B2, hyperoside. UV quantification was used for trans-cinnamic acid (internal standard, 280 nm) and iridoids. However, the quantification of iridoids remains difficult due to the absence of commercial standard. Iridoids have been previously quantified using p-coumaric or monotropein as standard. However, as the UV spectra of the acylated iridoids is related to that of p-coumaric acid ($\lambda_{\text{max}} = 320\ \text{nm}$) we used p-coumaric acid for quantification at 320 nm as previously reported (Mikulic-Petkovsek et al., 2015). “Total phenolics” represents the sum of most abundant soluble compounds: ACNs, flavonols, PAs, CGA and epicatechin. Due to their chemical structure, iridoids were not included in the calculation of total phenolic compound concentrations. Soluble sugars were extracted from 10 to 12 mg of berry freeze-dried powder as described previously (Domisch et al., 2019). Briefly, soluble sugars were extracted three times in water at 80°C and further analysed by HPLC (NexeraX2, Shimadzu Co, Japan) using a ligand-exchange column (Hi-Plex Ca, $300 \times 7.7\ \text{mm}$, Agilent, Santa Clara, CA, USA). Detection was done with an evaporative light scattering detector (Sedex 90LT, Sedere, France). Authentic glucose and

Table 1
Characteristics on the forest stand types in the study (mean \pm SE).

	Mesic spruce	Mesic pine	Peatland pine	Sub-xeric pine
Number of sites	9	10	4	5
Spruce basal area m ²	18.52 (3.08)	1.98 (0.84)	0.99 (0.99)	3.57 (1.46)
Spruce height m	18.14 (1.92)	7.23 (2.51)	3.13 (3.13)	11.14 (4.72)
Pine basal area m ²	2.87 (0.94)	15.47 (2.75)	17.36 (6.65)	16.66 (4.37)
Pine height m	11.31 (3.59)	16.69 (1.56)	12.75 (2.39)	14.94 (4.17)
Deciduous basal area m ²	1.54 (0.72)	2.18 (0.86)	0.50 (0.50)	0.79 (0.79)
Deciduous height m	7.88 (3.17)	7.82 (2.73)	3.25 (3.25)	4.04 (4.04)
Leaf area index (LAI)	2.04 (0.37)	1.46 (0.27)	1.58 (0.32)	1.00 (0.19)
Weighed mean stand age	89.44 (11.08)	53.78 (10.07)	53.40 (11.65)	50.42 (14.54)
Soil N content (mg/g)	1.20 (0.12)	1.17 (0.07)	1.40 (0.27)	1.04 (0.11)
Soil C:N ratio	38.26 (3.81)	39.53 (2.22)	36.81 (4.25)	41.29 (2.20)
Soil organic content %	78.49 (5.06)	79.21 (2.68)	83.33 (7.69)	73.13 (5.50)
Soil pH	3.93 (0.06)	4.01 (0.06)	3.98 (0.11)	3.85 (0.04)
Vaccinium myrtillus %	53.33 (4.74)	45.67 (4.28)	34.17 (13.50)	43.00 (12.25)
Vaccinium vitis-idaea %	12.50 (3.59)	14.15 (3.30)	9.33 (3.23)	22.50 (3.86)
Graminoids %	9.42 (3.23)	10.78 (5.57)	3.21 (2.93)	1.22 (0.95)
Total vegetation %	77.42 (3.05)	75.48 (4.13)	93.46 (5.87)	76.28 (7.78)

fructose were used for quantification. "Sugars" represents the sum of glucose and fructose, the only two soluble sugars detected.

2.4. Statistical analyses

Forest stand types were classified using information on main tree species, site productivity (mesic vs. sub-xeric) based on indicator species abundances and soil type (mineral vs. peatland). The sites represented four stand types, namely spruce dominated mesic sites (Mesic spruce, $n = 9$), pine dominated mesic sites (Mesic pine, $n = 10$), pine dominated peatland sites (Peatland pine, $n = 4$) and pine dominated sub-xeric sites (Sub-xeric pine, $n = 5$). Pictures of forest stand types are shown in [Figure S1](#). The differences in bilberry fruit chemistry between forest stands were analyzed using nonparametric Kruskal-Wallis, performed with PROC NPAR1WAY. The Kruskal-Wallis test was used due to the small sample size and the different sample sizes across forest stand types, and as these tests compare ranks rather than means, the medians of the compounds in the forest stand types are shown.

The temperature effect on bilberry fruit properties was investigated across forest sites ($n = 23$) by analyzing the Pearson correlations (PROC CORR) between the fruit parameters and the average daily minimum, mean, maximum temperature and the daily temperature amplitude over 1, 2, 3, and 4 weeks before the date of sampling. The Pearson' correlations were used as it is the most appropriate analysis for continuous variables that follow a normal distribution and are measured on an interval scale, such as temperature ($^{\circ}$ C). Unfortunately, the loss of five loggers prevented testing the statistical differences in temperatures between the stand types.

Linear mixed models (PROC MIXED) were applied to model the relationships of the concentrations of five chemical groups: total phenolics, ACNs, flavonols, iridoids and sugars, (expressed as mg g^{-1} d.w.) with independent, explanatory environmental variables. Environmental variables were pooled into three groups: variables describing stand characteristics (dominant tree species, LAI, weighed mean age of trees), understorey vegetation (abundances of bilberry and lingonberry, graminoids, and total vegetation), and variables of soil properties (C:N ratio, pH, soil organic matter content SOM).

The separate models for the stand characteristics, understorey vegetation and soil properties were computed in two stages. In the first stage, single-predictor models were computed by the single variables to see their contribution to the responses. In the second stage, the main effects models were made. In the stand characteristic main models, however, average spruce stands were older than pine stands (89 and 52 years, respectively). Hence, we used dominant tree species (spruce, pine) as a categorical factor and analyzed the effects of canopy closure (LAI) and weighed mean stand age in separate interaction models to test the effects of LAI and mean age on the bilberry fruit properties. The results of the interaction models are shown only when the significance level was below 0.1, otherwise the results of the main effect models are reported. Moreover, due to correlation between bilberry and lingonberry in the understorey, and C:N ratio and pH in soil mineral layer (r stronger than ± 0.300) ([Table S3](#)), we created Principal components for the main effects models ([Table S4](#)). Principal component analysis (PCA, PROC PRINCOMP) for bilberry and lingonberry resulted in one significant component where PC1 is positively correlated with bilberry and negatively with lingonberry (here forth referred as 'Vaccinium PC'). The PCA for soil variables C:N ratio and pH resulted in one significant principal component axis where PC1 is positively correlated with C:N ratio and negatively with pH (here forth referred as 'C:N-pH PC'). Main effects models are presented in the Supplementary document. Akaike's Information Criterion (AIC values) for main effects models was used for model comparisons. Prior to the implementation of linear models, the homogeneity and normality of the variances were examined to ensure the suitability of the data. All statistical tests were carried out using SAS 9.4 statistical software (SAS Institute Inc.).

3. Results

3.1. Fruit properties

Evaluation of bilberry fruit quality was based on their soluble phenolic composition, iridoids, and soluble sugar concentrations. The mean (\pm SD) values of total phenolics and ACNs in this study were 88.7 ± 14.2 and 78.93 ± 13.4 mg g^{-1} d.w., respectively ([Table S5](#)). A total of 15 different ACNs were detected, accounting for more than 80 % of the total phenolics. The two most abundant ACNs were cyanidin and delphinidin glycosides (34.3 and 26.2 % of the total ACNs, respectively), followed by malvidin, petunidin and peonidin glycosides (15.7, 13.8 and 10.1 %, respectively). The non-anthocyanin phenolic fraction was composed of flavonols, CGAs, epicatechin and PAs. Quercetin derivatives were the most abundant flavonols, followed by myricetin and kaempferol derivatives (72.5, 24.6 and 2.9 % of the total flavonols, respectively).

Two acylated monotropein derivatives (p-coumaroyl monotropein) were detected in our Finnish bilberry fruits. Reported concentrations of p-coumaroyl-monotropeins in bilberry varied depending on the method used. As its UV spectra is related to its p-coumaroyl group, UV detection has been used in this study and p-coumaroyl-monotropeins were expressed as p-coumaric equivalent, as previously reported ([Mikulic-Petkovsek et al., 2015; Nguyen et al., 2021](#)). Concentrations were in the range from 0.20 to 0.98 mg g^{-1} d.w.

Soluble sugars detected in bilberry fruits were glucose and fructose (42.8 % and 57.2 %, respectively). The average sugar concentration over all samples was 339.1 ± 44.6 mg g^{-1} d.w.

3.2. Correlation between fruit properties and temperature

In 2020, the precipitation in June, July and August were 109, 202 and 53 % of the long-term (1991–2020) monthly averages, respectively. June 2020 was warmer than the average, but temperatures in July and August were considered as normal summer months. Temperature records at the sampling sites showed the seasonal variation (Fig. S2), with a cooler period observed during the sampling period (no frost recorded).

Temperature regimes, mean, minimum and maximum daily temperatures calculated over the 4 weeks before sampling varied among stand types (Table S6). However, because of gaps in the temperature data, stand types could not be used as an explanatory variable in statistical analyses, so temperature data over all stand types was considered.

PAs and flavonols positively correlated with the daily amplitude and maximum temperature (Fig. 2). Significant correlation of both flavonols and PAs with the daily temperature amplitude mirrored their marginal negative correlation with minimum temperature. CGAs concentrations followed similar trends although values were not statistically significant. Total phenolics, ACNs, and epicatechin showed no significant correlations (r weaker than ± 0.300 and $p > 0.05$) with all daily temperature variables (Fig. 2).

Iridoids showed significant a negative correlation with the daily maximum temperature and daily amplitude, and a marginally significant positive correlation with the daily minimum temperatures (Fig. 2), altogether suggesting higher iridoids concentrations when daily temperatures remained stable.

Sugar content was strongly negatively correlated with the daily minimum temperatures but correlated positively with the daily amplitude. A significant negative correlation was also observed with the mean temperatures only one week before sampling. A significant positive correlation was also found with the date of sampling. Indeed, lower temperatures were recorded at the time of sampling (Fig. S2). No other berry parameter correlated significantly with the date of sampling (Fig. 2).

3.3. Fruit quality in relation to forest stand types

Peatland pine stands differed from the other stand types by their higher median concentrations of total phenolics, ACNs, and flavonols (Fig. 3, Table S5), although the difference was significant only for ACNs ($p = 0.045$, Fig. 3). In addition, peatland stands had the lowest median

concentration of sugars, although this was not statistically significant. These peatland pine stands consisted of drained sites, with the lowest abundance of bilberry and lingonberry but the highest total understorey abundance. Compared to the other stand types, their soil organic layer had the highest SOM and soil nitrogen (low C:N ratio) content (Table 1). Moreover, although not statistically tested, peatland pine stands had the lowest average minimum temperature (8.5 °C) and larger temperature amplitude than the other stands (13.1 °C) (Table S6).

From all stand types, sub-xeric pine stands were characterized by the lowest median concentrations of total phenolics and ACNs. (Fig. 3, Table S5). Furthermore, sub-xeric pine stands also had the lowest LAI under the canopy, and the highest abundance of lingonberry than the other stands. (Table 1). In addition, their soil organic layer was poor, as indicated by low pH and nitrogen content and high C:N ratio. Sub-xeric forests were warmer than other forests, as indicated by higher mean (15.9 °C) and maximum temperatures (22.8 °C) compared to the other forest types (Table S6).

Mesic stands did not show any clear correlation between the analyzed compounds, except the iridoids, which were slightly but not significantly higher in mesic pine stands compared to the situation in the other stands (Fig. 3, Table S5). Mesic spruce stands had the highest LAI under the canopy, and they also reached the highest stand age of all stand types (Table 1). In addition, graminoids were most abundant in the mesic forest stand types, regardless of the dominant tree species.

3.4. Stand characteristic models

Tree species or canopy cover measured as LAI alone did not clearly affect the biochemical properties of bilberry fruits. However, their combined effect revealed that total phenolics was dependent on the dominant tree species: in spruce dominated stands, increasing canopy cover, i.e. decreasing light, led to lower concentration of total phenolics, whereas on pine stands, the opposite trend was observed. ACNs followed a similar pattern, showing a decrease with higher LAI in spruce stands and an increase in pine stands, although this trend was less pronounced (Table 2, Fig. 4A and B). The concentration of iridoids was the highest in spruce dominated stands, and their levels also increased with stand age (Table 2, Fig. 4C).

Flavonol and sugar concentrations were not strongly influenced by any of the measured environmental variables, and no clear interactive effects emerged. However, there was a weak tendency for flavonol levels to decline in older stands, but only when tree species was taken into

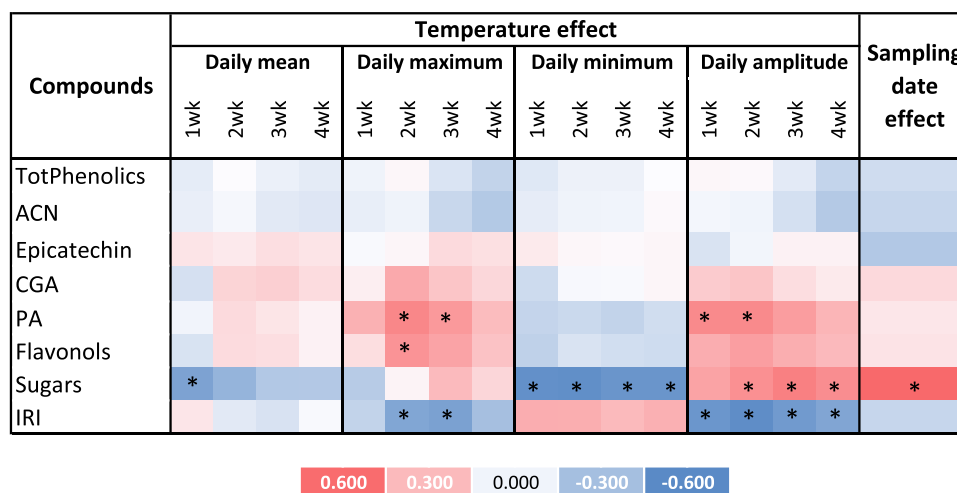


Fig. 2. Heatmap of Pearson's correlation coefficients (r) between concentrations of bilberry fruits' chemical compounds and daily mean, maximum, minimum, and amplitude of temperature over 1–4 weeks before sampling at the study sites ($n = 23$), and the sampling date. Significant correlation coefficients (r stronger than ± 0.300) are indicated by colors of different intensities and significant p values ($p < 0.05$) by a star. (TotPhenolics: Total phenolics, ACNs: anthocyanins, CGA: chlorogenic acids, PA: proanthocyanidins, IRI: iridoids).

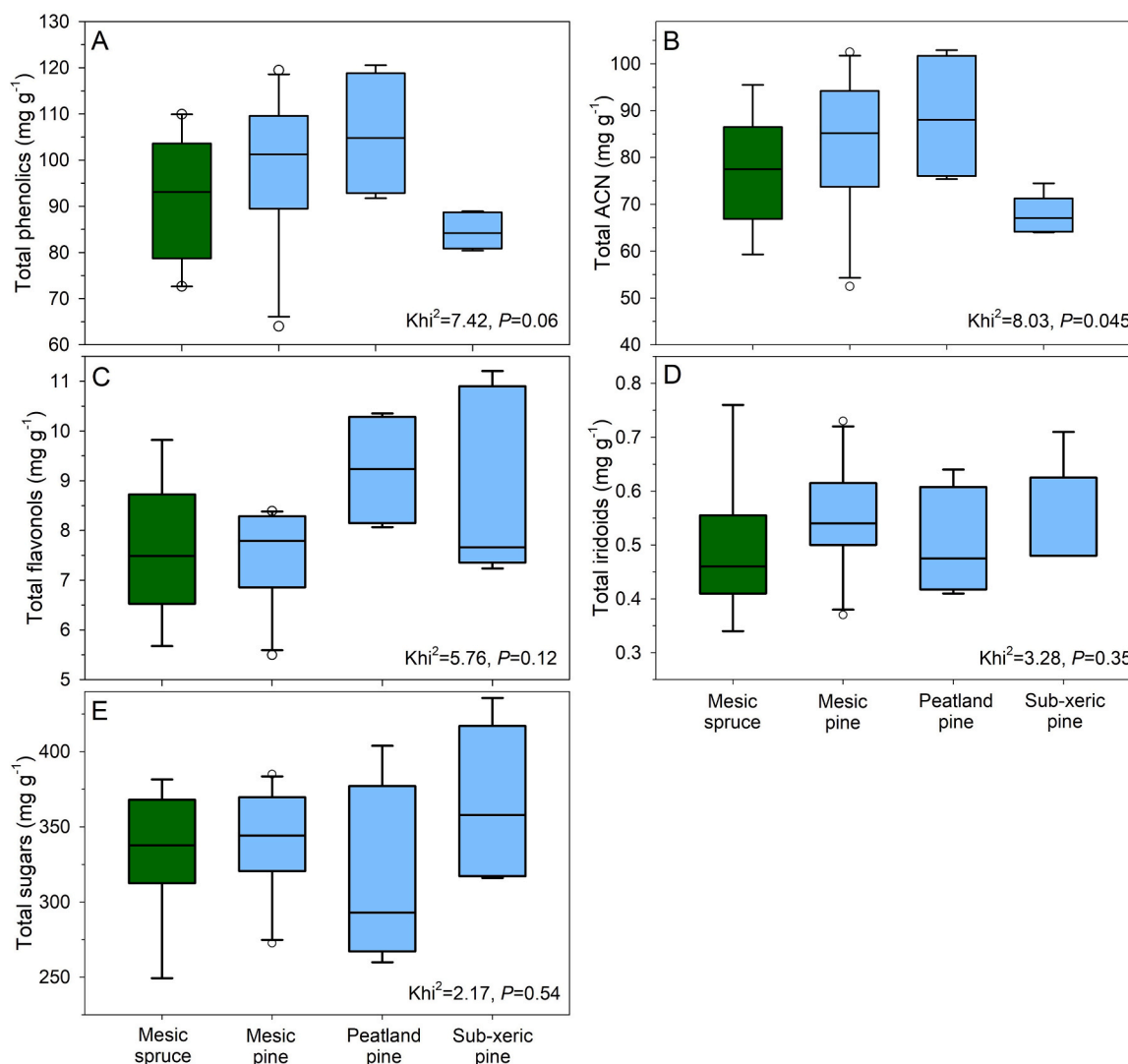


Fig. 3. Box-plot of the concentrations (mg g⁻¹ d.w.) of A) total phenolics, B) anthocyanins (ACNs), C) flavonols, D) iridoids, and E) sugars, and Kruskal-Wallis test statistics in Mesic spruce (n = 9), Mesic pine (n = 10), Peatland pine (n = 4) and Sub-xeric pine (n = 5) stands.

Table 2

Statistical results (p value) of forest stand characteristics models for dominant Tree species x Leaf Area Index (LAI) interaction models, and dominant tree species x weighed mean stand age interaction models. Only p values < 0.1 of interaction terms are shown (detailed statistics of these models are presented in [supplementary Table S7](#)). Interaction terms that were non-significant at the level $p < 0.1$ (marked as n.s.) were removed, and the model was run again with fixed effects only.

	Tree species and LAI			Tree species and mean stand age		
	Tree sp.	LAI	Tree sp. x LAI	Tree sp.	Age	Tree sp. x Age
Total Phenolics	0.163	0.781	0.027	0.266	0.613	n.s.
ACN	0.221	0.678	0.090	0.883	0.236	n.s.
Iridoids	0.528	0.319	n.s.	0.025	0.049	0.019
Flavonols	0.614	0.110	n.s.	0.967	0.062	n.s.
Sugars	0.769	0.958	n.s.	0.707	0.190	n.s.

account (Table 2, Fig. 4D). This suggests that the age structure of the forest may play a minor role in shaping flavonol content, particularly in relation to the dominant tree species. Full statistics for stand models are shown in Table S7.

3.5. Vegetation effects on fruit properties

Vegetation composition appeared to correlate with bilberry fruit chemistry in contrasting ways. Specifically, a dense bilberry layer was associated with lower concentrations of total phenolics and flavonol,

while a dense lingonberry layer correlated with lower concentrations of ACN. In contrast, graminoid-rich vegetation was associated with elevated concentrations of total phenolics and ACNs (Table S8). When broader vegetation structure was taken into account, the influence of individual shrub species diminished. Only the positive association between graminoid abundance and ACNs concentration remained evident, while the single effects of bilberry and lingonberry abundance were no longer apparent (Table 3). Full statistics for vegetation models are shown in Table S8.

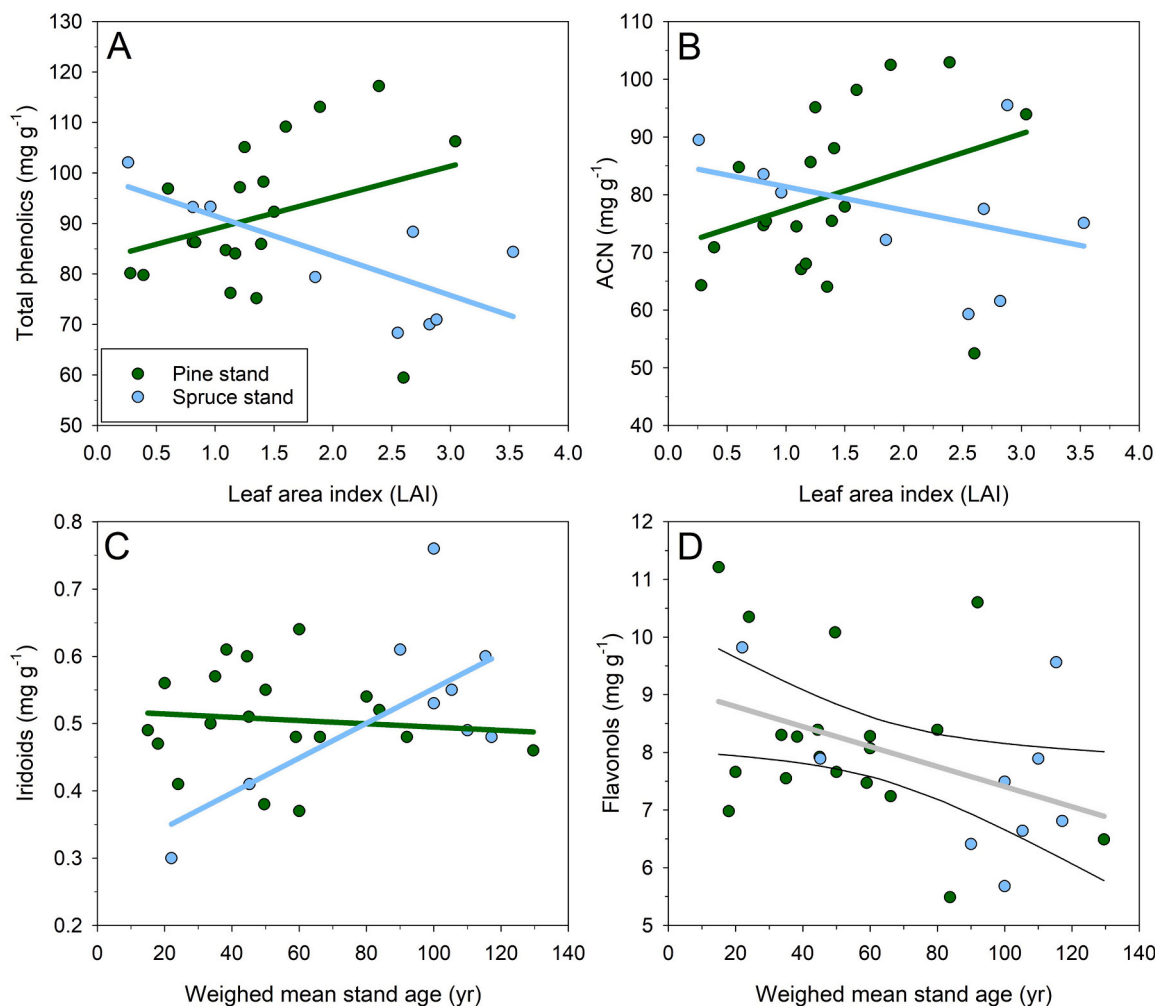


Fig. 4. Predicted concentrations (mg g⁻¹ d.w) of A) total phenolics and B) anthocyanins (ACNs) as a function of Leaf Area Index (LAI), and predicted concentrations of C) iridoids and D) flavonols as a function of stand ages (weighed mean age of trees) in spruce and pine -dominated forest stands.

Table 3

Results of linear mixed models (main effects models) for understory vegetation effects on bilberry (*V. myrtillus*) fruit properties. P-values and direction of effect (+/-) for models with $p < 0.1$. Statistically significant values ($p < 0.05$) are bolded and underlined, and marginally non-significant values ($p = 0.5 - 0.1$) are bolded only. Detailed statistics are presented in [supplementary Table S8](#).

	Main effects models		
	<i>Vaccinium</i> (PC1)	Graminoids	Total vegetation
Total phenolics	0.683	0.126	0.468
ACN	0.591	<u>0.019</u>	0.574
Iridoids	0.196	0.987	0.215
Flavonols	0.200	0.879	0.912
Sugars	0.138	0.114	0.717

3.6. Soil organic layer effects on fruit properties

Soil organic layer properties also played a role in shaping bilberry fruit chemistry. A high soil C:N ratio was linked to lower concentrations of total phenolics and ACNs, but to higher sugar levels. Soil pH, in turn, showed a positive association with several bioactive compounds, including total phenolics, ACNs, and flavonols. In contrast, higher soil organic matter content (SOM) was related to lower concentrations of flavonols and sugars ([Table S9](#)).

When soil variables were combined into broader models, these patterns remained partly visible ([Table 4](#)). A combined increase in C:N ratio

Table 4

Results of linear mixed models (main effects models) for soil organic layer effects on bilberry (*V. myrtillus*) fruit properties. P-values and direction of effect (+/-) for models with $p < 0.1$. Statistically significant values ($p < 0.05$) are bolded and underlined, while marginally significant values ($p = 0.5 - 0.1$) are bolded only. Detailed statistics are presented in [supplementary Table S9](#).

	Main effects models	
	C:N-pH-PC1	SOM
Total phenolics	<u>0.007</u>	0.180
ACN	<u>< 0.001</u>	0.070
Iridoids	0.426	0.542
Flavonols	0.313	<u>0.022</u>
Sugars	<u>< 0.001</u>	<u>< 0.001</u>

and decrease in pH (as reflected by the PC1 component) was still associated with reduced levels of total phenolics and ACNs, but with elevated sugar concentrations. Additionally, higher SOM continued to show a positive link with ACNs, while its negative associations with flavonols and sugars also persisted. Full statistics for vegetation models are shown in [Table S9](#).

3.7. Best-fit models

Based on the AIC comparisons ([Table 5](#)), the stand models showed the best fit for total phenolics, ACNs, and flavonols in bilberry fruits, in

Table 5

Akaike's Information Criterion (AIC) of the main effects models. The AIC values of best fit models are bolded.

	AIC		
	Stand	Vegetation	Soil
Total phenolics	203.1	221.3	215.5
ACN	203.9	215.4	205.0
Iridoids	-24.9	-20.5	-30.3
Flavonols	97.2	112.2	99.8
Sugars	272.7	274.6	261.0

comparison with the understorey vegetation and soil models. However, the stand and soil models were similarly robust predictors of ACNs (difference less than 2 AIC units). The soil models were the strongest predictors for iridoids and sugars.

4. Discussion

In this study, we investigated the composition of bilberry fruits to determine which characteristics of the boreal forest are indicative of good berry quality, based on high phenolics and sugar contents. As previously reported, ACN represented about 80 % of the total soluble phenolics (Lätti et al., 2008), which brings bilberry fruits at the top of the list of foods rich in ACNs (Koponen et al., 2007; Mujanović et al., 2024). The concentrations measured in this study were slightly higher than those reported in earlier studies at similar latitudes (Helström et al., 2024; Kähkönen et al., 2003; Lätti et al., 2008). Iridoids are not always reported in bilberry fruit analyses, although they represent abundant non-anthocyanin compounds (Heffels et al., 2017; Liu et al., 2020). In the absence of authentic standard, the concentrations reported in this study (0.20–0.98 mg g⁻¹ d.w.), or in other studies (0.03–0.15 mg g⁻¹ f.w.) (Mikulic-Petkovsek et al., 2015; Przybylska et al., 2022) remain indicative.

Contrary to our hypotheses, our results suggest that changes in light and temperature have only a subtle effect on the phenolic and ACN concentrations in the boreal forest. However, the responsiveness of bilberry fruit phenolics to light in spruce dominated forest aligns with Vaneková et al. (2020) and may be attributed to canopy structure of the forest. Unlike pine, which has a canopy concentrated at the top of the stem, allowing more light to reach the understorey, spruce has shading foliage and branches distributed along the entire stem. This creates a naturally darker forest floor and greater possibility for light limitation in spruce than pine-dominated forests. Indeed, it has been noted that bilberry fruits in shaded conditions of closed forest have lower contents of total phenolics, ACNs, flavonols, sugars and hydroxycinnamic acids than fruits in sun-exposed sites (Dincheva and Badjakov, 2016; Lätti et al., 2008; Mikulic-Petkovsek et al., 2015; Åkerström et al., 2010). In addition to the canopy, the understorey itself can cause changes in the phenolic content of bilberry fruits through shading (Filippi et al., 2021; Jaakola et al., 2004). However, we did not find any shading effect of understorey on bilberry phenolics. In agreement with our prediction, we found that forest stand characteristics (i.e. forest stand models) best predicted high levels of total phenolics, ACNs and flavonols. Therefore, our findings support the idea that the tree layer regulates bilberry fruit quality by modulating the light environment in the understorey.

Contrary to the general view (Lätti et al., 2008; Rieger et al., 2008; Uleberg et al., 2012; Zoratti et al., 2015; Åkerström et al., 2010) and our expectations, we found no significant correlation between mean temperature and total phenolics or ACNs in bilberry fruits. However, changing daily temperature and warm events during ripening promoted higher concentrations of flavonols and PAs, suggesting that temperature fluctuations, rather than the daily mean, are important regulators of bilberry quality. Earlier studies reported increasing flavonols in bilberry's fruits in cold environments (Uleberg et al., 2012). The low variation in temperature across the forest sites in this study may account

for the weak correlation observed. Our results showed that low daily mean and daily minimum temperature correlated well with high concentrations of soluble sugars. Such plant response to chilling is well described in the literature and allows for preserving cell integrity and functioning (Afzal et al., 2021). In addition to their role as osmoprotectants, soluble sugars have been proposed to be an integrated part of the redox system, detoxifying reactive oxygen species produced in high amount during stress conditions and contributing to stress tolerance especially in tissues with high soluble sugar concentrations (Bolouri-Moghaddam et al., 2010). The strong correlation observed between sugar concentrations and sampling time can partly be explained by the cold spell observed over the period of sampling (see above) but soluble sugars have also been previously shown to continuously increase during the ripening process in bilberry or blueberry fruits (Dare et al., 2022; Uleberg et al., 2012; Zorenc et al., 2016). Finally, this study presents new findings on changes in iridoids under field conditions, showing that their level increases in bilberry fruits with stand age but decrease with fluctuating temperatures. This contrasts with earlier studies on bogbean (*Menyanthes trifoliata* L.), a swamp plant rich in iridoids, where temperature fluctuations appeared to have no effect on their absolute concentrations (Martz et al., 2009).

We found a negative association between soil organic layer characteristics, indicative of low soil fertility, and phenolics in bilberry fruits. This result contrasts with fertilization experiments, suggesting that the phenolic compounds in bilberry fruits are either unresponsive (Vaneková et al., 2020; Åkerström et al., 2009) or exhibit a decreasing trend (Rohloff et al., 2015) as a response to increasing nutrients such as N and P. Notably, the negative correlation observed between soil organic layer C content (as described by high C:N ratios) and both total phenolics and ACNs aligns with the previous findings (Vaneková et al., 2020). In contrast to ACN, soluble sugars tended to be higher at sites with higher C:N ratios. The characteristics of the soil organic layer were only weak predictors of other compounds than sugars and iridoids in bilberry fruits. Still, the role of C and N in the soil organic layer on plant metabolites is complex and may depend on additional factors and local ecological dynamics.

Pine-dominated peatlands showed significantly higher ACN concentrations than the other forest stand types studied. Besides that, forest types showed no differences in the fruit quality variables. Conversely, the models of this study only weakly supported the high ACN concentration of the peatland pine stands. Comparison of the models indicated that forest stand is the strongest predictor of phenolics and ACNs in bilberry fruit. However, lower LAI index, and thus higher light availability, should have resulted in higher phenolic concentrations rather in sub-xeric forests than in the peatland pine forests. Therefore, it seems more likely that the high ACN content observed in peatland stands may be related to the high SOM in the soil organic layer (Rohloff et al., 2015; Vaneková et al., 2020), as suggested by statistical models showing a positive relationship between SOM and ACN concentration in bilberry fruits. Moreover, there were some discrepancies between the results of the understorey vegetation model and the forest stand type characteristics. The abundance of graminoids in the understorey vegetation was associated with higher ACN concentrations in bilberry fruit, but as graminoids were scarce in peatland pine forests, this result was difficult to relate to forest stand type. Typically, graminoids are found in the forest floor of mesic boreal forests, where their occurrence depends both on soil organic layer properties, especially N, and on light availability (Manninen et al., 2009; Strengbom et al., 2004). This inconsistency in our result on the relationship between the bilberry fruit quality, forest stand and site characteristics reflect well the combined influence of environmental factors on bilberry compounds in natural ecosystems.

5. Conclusions

Our study provides valuable information on the effect of environmental factors on the quality of bilberry fruit in their natural habitat in

the boreal forest. The fruit quality was determined here by sugar and phenolic compounds, of which anthocyanins are the most abundant. We validated the effects of light conditions, temperature fluctuations, and soil organic layer characteristics on bilberry fruit quality. Pine-dominated peatland forests had the bilberry fruits with the highest ACN concentrations. Further, in spruce-dominated forests, a higher light availability increased ACN levels, suggesting that the harvesting of high-quality bilberry fruits should be directed to open spruce forests. This information could also be applied in forest management guidelines. Overall, our results reflect the functioning of the boreal forest as a multilayered ecosystem and highlight the complexity of concurrent factors that shape the boreal forest floor environment.

Boreal forests provide a wide range of ecosystem services, of which berry yield and quality can be influenced by forest management. However, further research on the multiple concurrent environmental factors influencing bilberry fruit quality is warranted to fully exploit the potential of the compounds and ensure their adaptation to different forest management activities in a changing environment. This information will support the development of strategies to reconcile multiple uses of forests and ecosystem services in boreal regions.

Abbreviations Used

CAN, anthocyanins; CGA, chlorogenic acids; LAI, leaf area index; PA, proanthocyanidins; SOM, soil organic matter

CRedit authorship contribution statement

Päivi Merilä: Writing – review & editing, Project administration, Funding acquisition. **Outi H Manninen:** Writing – original draft. **Françoise Martz:** Writing – review & editing, Investigation. **Jouni Sorvari:** Writing – review & editing, Visualization, Formal analysis.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2025.123077](https://doi.org/10.1016/j.foreco.2025.123077).

Data availability

Data will be made available on request.

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