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Loss in macronutrient pools in bilberry and lingonberry in mesic Scots pine forests after Northern red oak introduction

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Abstract

Forest transformation from coniferous monocultures to mixed stands is being promoted worldwide, including the introduction of fast-growing broadleaved tree species within native stands. Here, we studied how enrichment of temperate European Scots pine (*Pinus sylvestris*) forest by North-American northern red oak *Quercus rubra* impacted macronutrient concentrations in two long-lived and dominant components of the forest understory: bilberry *Vaccinium myrtillus* and lingonberry *V. vitis-idaea*. Study sites were located in forest complexes (central Poland) which occupy continuously reforested lands (hereafter ancient forests) as well as post-agricultural lands (recent forests), all suitable for mesic pine forests. Samples of bilberry and lingonberry leaves, stems, and fruits were collected in pine stands and in adjacent Scots pine-red oak stands, in both ancient and recent forests. Concentrations of macronutrients (C, N, P, K, Ca, S, and Mg) in aboveground biomass components were analysed using standardized chemical procedures. The study revealed intra- and interspecific (bilberry vs. lingonberry) differences in concentrations of all nutrients in leaves, stems, and fruits, except for invariable C concentrations. Macronutrient accumulations in plants were decreased by land-use discontinuity and favoured by enrichment of tree stands by *Q. rubra*. The estimated macronutrient pools were much higher for *V. myrtillus* than *V. vitis-idaea* in all forest types studied. They were lower in forests enriched with *Q. rubra,* both ancient (up to 25.5% for bilberry and 99.9% for lingonberry) and recent (46.9% and 99.9%, respectively), as well as in recent pine forest (46.6% and 81.1%, respectively) than in ancient pine forest. Higher K and S pools (39.3% and 6.5%, respectively) noted for bilberry in an ancient forest with *Q. rubra* were exceptions.

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Despite more effective accumulations of elements at the species level, macronutrient pools of *Vaccinium myrtillus* and *V. vitis-idaea* decreased significantly in the presence of introduced *Q. rubra* due to negative impacts of this broadleaved tree on bilberry and lingonberry cover and biomass. Therefore, the limitation of alien *Q. rubra* planting in sites of mesic pine forest with the abundant occurrence of *V. myrtillus* and/or *V. vitis-idaea* is recommended.

Graphic abstract
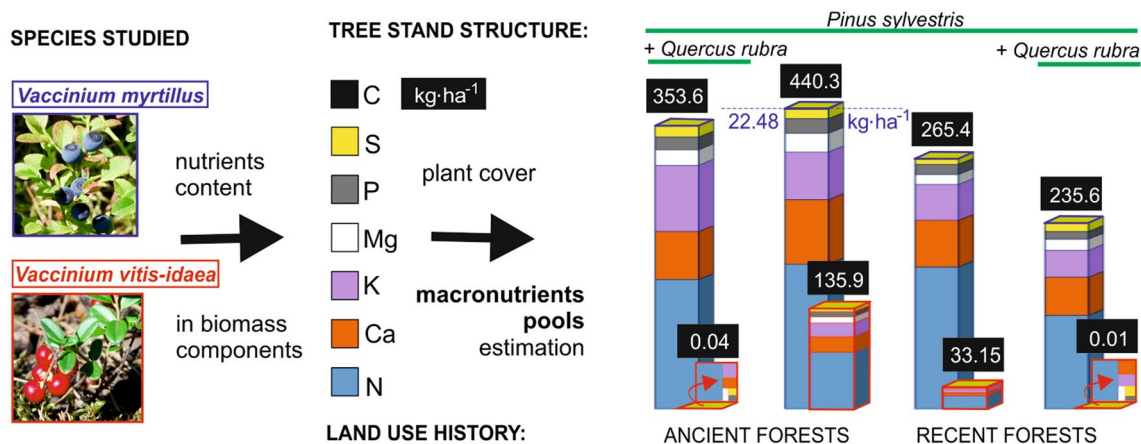
Keyword Coniferous forest transformation · *Quercus rubra* introduction · Carbon sequestration · Nutrient pools · *Vaccinium myrtillus* · *Vaccinium vitis-idaea*

Background

Vaccinium myrtillus L., known as bilberry (Nestby et al. 2011), and *V. vitis-idaea* L., known as lingonberry or cowberry (Luby et al. 1991), are common and dominant components of understory layers in temperate and boreal forests (Timoshok 2000; Turtiainen et al. 2013; Leuschner and Ellenberg 2017a). These long-lived ericaceous dwarf-shrubs play an important role in forest ecosystem functioning and yield valuable non-wood forest products (Woziwoda et al. 2019a, 2021, and references therein). By affecting the restoration of tree seedlings (Maubon et al. 1995; Jäderlund et al. 1996), they constitute one of the major drivers of vegetation dynamics (Nilsson and Wardle 2005; Kolari et al. 2006). *Vaccinium myrtillus* and *V. vitis-idaea* successfully colonize coniferous monocultures, including Scots pine (*Pinus sylvestris* L.) stands commonly planted on post-agricultural soils in Europe (Matuszkiewicz et al. 2013; Woziwoda et al. 2014b). Both species can co-occur at the same sites; however, they differ in adaptation to the environment which is reflected mainly in their leaf longevity: *V. myrtillus* is deciduous, and it sheds leaves every autumn, while evergreen *V. vitis-idaea* sheds 2–4-year-old leaves irregularly (Ritchie 1955, 1956). As *V. myrtillus* and *V. vitis-idaea* achieve high cover and biomass, they play an important role in ecosystem productivity and a regulating role in nutrient fluxes (Eeva

et al. 2018; Grelet et al. 2001). The concentrations of elements in bilberry and lingonberry leaves, stems, fruits, and rhizomes, however, are modified by site conditions (e.g. Fernández-Calvo and Obeso 2004; Zvereva and Kozlov 2005; Jens et al. 2015; Mikulic-Petkovsek et al. 2015; Parzych 2016). Uptake of specific nutrients and accumulation in plants depends on their availability in soils and is modified by the co-occurrence of other nutrients (Barker and Pilbeam 2007; Marschner 2012). Concentrations of elements in plant leaves, stems, and fruits are naturally different, as specific biomass components are composed of different tissues and different biochemical processes occur within them. Furthermore, nutrient concentrations in specific organs change seasonally (Havas and Kubin 1983; Bujor et al. 2018). To avoid nutrient loss with litter, bilberry and lingonberry translocate elements from leaves to stems and rhizomes, and then, while conditions are favourable for growth—re-translocate them to developing tissues (Grelet et al. 2001). The most intensive bioaccumulation of nutrients in aboveground shoots occurs in the full vegetative season, during fruit ripening (Lahdesmaki et al. 1990). This is also a time for collection of bilberry and lingonberry fruits and leaves (a non-wood forest products, NWFP), both for domestic as well as industrial use (e.g. Turtiainen and Nuutinen 2012; Kilpeläinen et al. 2018).

Current studies on the effects of the North-American northern red oak *Quercus rubra* L. introduction to native

European forests revealed strong negative impacts on both *V. myrtillus* (Woziwoda et al. 2019a) and *V. vitis-idaea* (Woziwoda et al. 2021). We found that the cover and aboveground biomass of bilberry and lingonberry were significantly lower in mixed Scots pine-northern red oak forests than in Scots pine monocultures. *Quercus rubra* suppressed the abundance of understory plants (Woziwoda et al. 2014a; Dyderski and Jagodziński 2021), mainly due to its significant effects on-site conditions, i.e. on light transmittance (Dyderski and Jagodziński 2019) and soil physicochemical parameters (Reich et al. 2005; Nicolini and Topp 2005; Bonifacio et al. 2015; Stanek et al. 2020). The continuity of forest land use also impacted bilberry and lingonberry cover and biomass, and differences in their abundances were noted in reforested lands (classified as ancient forests sensu Peterken 1974) *versus* afforested post-agricultural lands (recent forest). However, it is still unknown how these changes affected the chemical composition of plants. The recognition of nutrient concentrations in floral components of the forest understory is of crucial importance for the assessment of the effects of man-made changes in tree stand composition and land-use form, and consequently, for proper forest management. This issue requires urgent clarification also because commercially important *Q. rubra* has been commonly underplanted in European coniferous forests (Woziwoda et al. 2014c; Nicolescu et al. 2020), and at present it spreads spontaneously in an uncontrolled way (e.g. Woziwoda et al. 2018, 2019b; Chmura 2020; Dyderski and Jagodziński 2020a; Dyderski et al. 2020). The recognition of macronutrient concentrations in *V. myrtillus* and *V. vitis-idaea* at the peak of the plant's growing season can be also useful for bilberry and lingonberry pickers, dwellers, and consumers.

In this study, we examined concentrations of macronutrients (C, N, P, K, Ca, S, and Mg) in aboveground shoots of *V. myrtillus* and *V. vitis-idaea* in mesic Scots pine forests and Scots pine-northern red oak forests with different land-use histories. The question was, are there any general patterns in the impacts of former land-use changes and alien tree occurrence on bilberry and lingonberry chemical composition, and especially, does *Q. rubra* impact species-specific bioaccumulation of macronutrients in these long-lived dwarf shrubs? If yes, how are they related to environmental factors, e.g. to light conditions? And finally, how have the bilberry and lingonberry nutrient pools changed in the forest understories of different forest types studied?

Material and methods

The plant material—lingonberry and bilberry shoots, was collected in four forest types: ancient pine forest (AFP, treated as reference), recent pine forest (RFP), ancient pine

forest with introduced *Quercus rubra* (AFQ), and recent pine forest with introduced *Quercus rubra* (RFQ).

Study area

The study site was located in central Poland, in two forest complexes: Aleksandrówek (ancient forest; 51.8599° N, 18.9912° E) and Małyń–Jerwonice (recent forest planted about one hundred years ago on former agricultural lands excluded from cultivation due to low fertility of soils; 51.7803° N, 19.0455° E, ca 10 km from the ancient forest). The mean annual temperature of this area is 8.4 °C, and the mean annual precipitation is 605 mm (Kożuchowski 2011). Soils of the study sites represent Haplic Podzols in the ancient forest, and Albic Brunic Arenosols in the recent forest, according to the World Reference Base for Soil Resources classification system (WRB 2015). The soils developed from Quaternary fluvioglacial sands. They are characterized by medium moisture content (despite coarse granulation), strongly acidic pH (4–5), and a low abundance of nutrients (SHS 2003). Both forest complexes are commercial (timber wood production is the main management goal), but also public, with open access for recreational activity including free berry picking. The ancient pine forest (AFP) is an 86-year-old *P. sylvestris* monoculture, and it is adjacent to a pine forest with *Q. rubra* (AFQ) intentionally planted under a pine canopy a half-century ago. Both ancient forest types studied occupy one forest division with a total area of 12.8 ha, one-third of which has *Q. rubra*. The recent pine forest (RFP) is a 69-year-old monoculture of *P. sylvestris* (2.9 ha), adjacent to a 100-year-old stand of *P. sylvestris* with 35-year-old *Q. rubra* (RFQ), also intentionally planted on the area of 10.95 ha. At present, numerous *Q. rubra* trees form a dense and continuous canopy below crowns of the Scots pine trees, both in ancient and recent forest (Table 1, Fig. 1).

Juveniles of *Q. rubra* and other deciduous tree species (rowan *Sorbus aucuparia*, alder buckthorn *Frangula alnus*, silver birch *Betula pendula*, pedunculate oak *Q. robur*) occur in the shrub layer (b) of the studied forests. The understory vascular plant layer (c) is dominated by bilberry and/or lingonberry dwarf shrubs, and in some places—by grasses: *Deschampsia flexuosa* and *Festuca ovina*. The moss layer (d) covers almost all the ground in both pine forests (AFP and RFP), while it is sparse in forests with *Q. rubra* (AFQ and RFQ) (Fig. 1).

Light environment estimation

To characterize light conditions in the understory layer, we conducted a vegetation survey of 15 randomly sampled plots (100 m^2) per forest type, recording all vascular plant and bryophyte species (see details in Woziwoda

Table 1 Tree stand density, mean trunk circumference at 1.3 m height (± standard deviation) and growing stock of the forests studied: ancient pine forest (AFP, treated as reference), ancient pine forest with introduced *Quercus rubra* (AFQ), recent pine forest (RFP) and recent pine forest with introduced *Q. rubra* (RFQ)

	AFP	AFQ	RFP	RFQ
Tree stand density				
Pinus sylvestris (a1)				
Ind. ha^{-1}	693 ± 118	480 ± 168	847 ± 222	613 ± 141
Trunk circum. (cm)	72.8 ± 13.6	96.5 ± 17.5	78.7 ± 18.0	83.4 ± 15.2
Quercus rubra (a2)				
Ind. ha^{-1}	–	940 ± 555	–	640 ± 558
Trunk circum. (cm)	–	24.5 ± 15.2	–	29.8 ± 8.3
Quercus rubra (b)				
Ind. ha^{-1}	+	500 ± 440	+	250 ± 92
Trunk circum. (cm)	–	10.9 ± 3.9	–	12.7 ± 5.1
*Growing stock (m^3 ha^{-1})	263	263	366	336

Data estimates are from field inventories of this study except for growing stock (asterisk), which is from the Forest Data Bank (FDB 2018) (data published in Woziwoda et al. 2019a). Tree stand labelling: a1—upper tree canopy layer, a2—lower tree canopy layer, b—shrub layer, following Braun-Blanquet (1964)
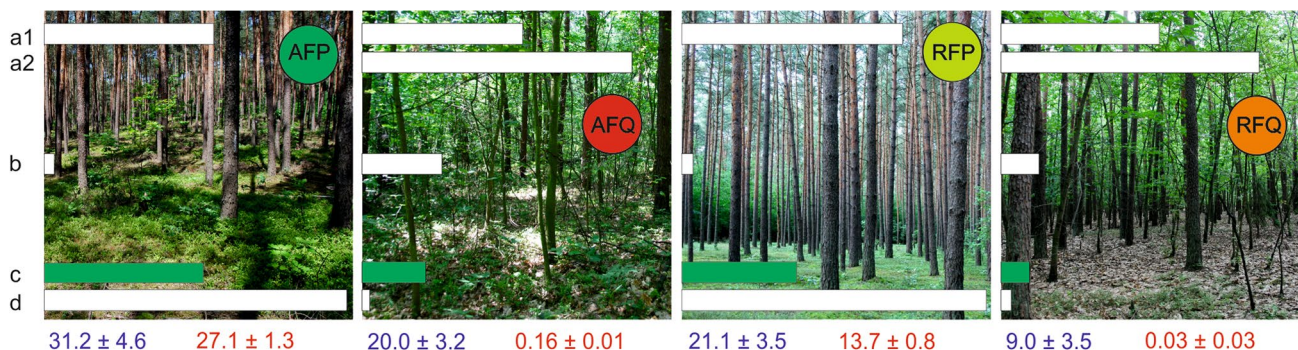
Fig. 1 Forest types studied: ancient pine forest (AFP), ancient pine forest with introduced *Quercus rubra* (AFQ), recent pine forest (RFP), recent pine forest with introduced *Q. rubra* (RFQ), and their structure described by mean cover of forest layers (the picture width = 100% cover of the layer): a1—upper tree canopy layer, a2—lower tree canopy layer, b—shrub layer, c—herb layer (with ericaceous dwarf shrubs), and d—moss layer; and the cover (mean ± standard error) of bilberry *Vaccinium myrtillus* (in blue) and lingonberry *V. vitis-idaea* (in red) noted for each forest type. Data were estimated from our field phytosociological studies made following Braun-Blanquet (1964)

et al. 2021). We recorded the cover of each species using the Braun-Blanquet (1964) scale. To describe the light conditions, we used two indicators widely used in plant community ecology: Ellenberg's light ecological indicator value (EIV.L) from Ellenberg and Leuschner (2010) and specific leaf area (SLA, expressed in cm^2 g^{-1}) obtained from the LEDA database (Kleyer et al. 2008) and Paź-Dyderska et al. (2020). For each plot, we calculated community-weighted mean values of EIV.L and SLA, i.e. mean weighted by species cover. For EIV.L, we used data for vascular plants and bryophytes and vascular plants only, while SLA reflected only the vascular plant community. We decided to analyse EIV.L for both vascular plants and bryophytes, as the latter dominate the understory in AFP and RFP and are also responsive to light availability (Dyderski and Jagodziński 2020b). We used one-way ANOVA followed by Tukey's *posteriori* test to assess the

differences in EIV.L and SLA community-weighted mean values among forest types studied.

Samples collection

Vaccinium myrtillus and *V. vitis-idaea* aboveground shoots (ramets) were collected in June–July (for bilberry) and August–September (for lingonberry) 2017, in 400 research plots in total (50 research plots, each 50 × 50 cm in area, set up in the Scots pine forests with and without *Q. rubra*, in each of the two localities, and located randomly in clumps of *V. myrtillus* and *V. vitis-idaea*; for more information see Woziwoda et al. 2019a, 2021). Bilberry and lingonberry sampling in different months was necessary due to phenological differences in the development of their shoots and berries—in the study area, bilberry fruits one month earlier than lingonberry,

and shoots were collected at the peak of the species-specific fruiting season. Sampling time variation allowed us to avoid mistakes connected with seasonal changes in nutrient accumulation in specific components (i.e. leaves, stems, and fruits) caused by translocation of elements within the plant.

Ramets (ten in each plot, randomly chosen) of both species studied, separated into stem, leaves, and fruits, dried and packed in marked closed polyethylene bags (Woziwoda et al. 2019a, 2021), were used for studies. For chemical analysis, ten samples of lingonberry and bilberry leaves and stems, each at around 10 g of mass, were separated from dried material gathered for each of the four variants studied (160 samples in total). Ten-gram-samples contained dried plant material composed from samples deposited in subsequently numbered bags. In the same way, 40 ten-gram-samples of bilberries (ten samples for each of four variants) and 20 ten-gram-samples of lingonberries (ten samples for each of two pine forest variants; in forests with *Q. rubra* lingonberry did not produce fruits, Woziwoda et al. 2021) were composited from samples of dried berries. Samples of leaves, stems, and fruits (biomass components)—220 in total, were sent to the laboratory for chemical analysis.

Laboratory analyses

The plant material was homogenized in a laboratory grinder (IKA A11, Germany). Until the time of analyses, the samples had been kept in leak-proof, closed polyethylene bags. To determine the total phosphorus and metallic elements, the plant samples (0.5 g) were digested in a solution of 65% HNO_3 acid and 30% H_2O_2 (1:1 v/v) in a closed system. Then, the samples were supplemented with deionized water (Hydrolab, HLP 10, Poland) to a volume of 50 ml. The concentration of P was determined by spectrophotometry with a molybdenum-blue method (5001 Hitachi, Japan). The concentrations of Mg and Ca were determined by atomic absorption spectrometry, and K was determined by atomic emission spectrometry (AAS 2100, PerkinElmer, USA). Element concentrations were expressed on a dry weight basis. The wavelengths at which the various metals were detected were as follows: K 766.5 nm, Mg 285.2 nm, and Ca 422.7 nm. The tests were carried out following the original standards (Merck KGaA, 1 g/1000 mL). All analyses were carried out in three replicates, and the samples were represented by average values (the variance of the replicates was checked, and outliers were skipped). Total concentrations of organic C, N, and S were determined by dry combustion using the MacroCube CHNS analyser (Elementar, Germany).

Quality assurance/quality control (QA/QC)

The QA/QC of the analytical procedures was carried out by analysing the standard certified reference material of plants (CRM 060), adopting the same procedures as for the analysed samples. The results of the experimental measurements agreed with the recommended reference value material. Analysis of most of the elements is accurate within a 3% analytical error. Recoveries were calculated as a ratio of the determined value to the certified one and were within the confidence intervals of the certified values. Recoveries were as follows: $99 \pm 2\%$ (P), $98 \pm 3\%$ (K), $98 \pm 2\%$ (Mg), $97 \pm 3\%$ (Ca). Birch leaf certified reference material (B2166, Elemental Microanalysis) was used to ensure the quality of C, N, and S analyses.

Data analyses

All analyses were conducted using R software (R Core Team 2019). We compared the chemical composition of studied plants using redundancy analysis (RDA)—a constrained version of principal components analysis. In RDA, we used scaled (i.e. subtracting the mean and dividing by SD) macronutrient concentration and C:N ratio. As constraints, we assumed species, forest variant, and biomass component. We conducted RDA using the *vegan* package (Oksanen et al. 2018). Before analyses, we ensured that variables are not intercorrelated using variance inflation factors. Then, we compared the full model with the null model using Akaike's Information Criterion (AIC) and we tried to reduce model AIC by reducing the number of variables. We also used variance partitioning to show how much variability is explained by a particular variable.

We calculated the mean concentrations of studied macronutrients and mean nutrient masses in plant tissues for each treatment. To calculate nutrient pools, we used data from previous studies on biomass allocation (Woziwoda et al. 2019a, 2021). We used mean biomass allocation into stems, leaves, and fruits in each forest variant, mean ecosystem-level dry biomass, and mean nutrient concentrations to obtain a pool of each nutrient for bilberry. For lingonberry, we used mean biomasses of components, mean lingonberry cover, and mean nutrient concentrations to obtain nutrient pools. We referred to AFP as a reference, calculating differences connected with land-use change (ancient *versus* recent forest) and with *Q. rubra* (pine *versus* red oak). We calculated how SE of estimation is propagated following: $\frac{SE_{pool}}{pool} = \sqrt{\frac{SE_{x1}^2}{x1} + \frac{SE_{x2}^2}{x2} + \frac{SE_{x3}^2}{x3}}$, where pool—total nutrient pool in the ecosystem (mass of a particular element in organs of the species studied), $\times 1 - \times 3$—variables used in

Table 2 Ranges, mean, and SE values of community-weighted mean Ellenberg's ecological indicator values of light requirements for both bryophytes and vascular plants (EIV.L) and vascular plants only (EIV.L vascular), and specific leaf area (SLA) of understory vegetation ($n = 15$ per variant) in ancient pine forest (AFP), ancient pine forest with introduced *Quercus rubra* (AFQ), recent pine forest (RFP), recent pine forest with introduced *Q. rubra* (RFQ), assessed using one-way ANOVA

| Variable	Variant	min	mean	SE	max	Tukey test
SLA	AFP	119.62	168.96	8.00	221.42	C
	AFQ	156.29	239.22	6.28	260.05	A
	RFP	129.48	199.01	8.72	240.64	Bc
	RFQ	145.88	206.11	11.66	257.34	Ab
EIV.L	AFP	5.51	5.76	0.05	6.15	A
	AFQ	4.89	5.08	0.04	5.50	C
	RFP	5.63	5.78	0.03	6.00	A
	RFQ	4.80	5.37	0.10	5.92	B
EIV.L vascular	AFP	5.07	5.52	0.10	6.45	A
	AFQ	4.76	5.16	0.08	6.25	A
	RFP	5.07	5.29	0.07	6.02	A
	RFQ	5.00	5.37	0.17	7.00	A

Variants marked with the same letter did not differ statistically significantly ($p > 0.05$), according to Tukey's *posteriori* test

calculations, SE—standard error. We used SE instead of SD or variance due to uneven sample size, which affects error calculations. Then, to show nutrient pools in each treatment we summed nutrient pools in each biomass component, assuming additive error propagation. We assessed the impacts of land-use history and *Q. rubra* invasion using ANOVA. We quantified the influences of both factors and their interaction using the *modEva::varPart()* function (Barbosa et al. 2013). After ANOVA, we compared the significance of mean values by Tukey *posteriori* tests and we calculated marginal mean values of each treatment using the emmeans package (Lenth 2019). The same procedure was applied at the concentration and ecosystem level.

Results

Difference in light conditions among forest types

Regardless of the indirect light availability indicator used, ANOVA revealed significant differences among forest types analysed ($F_{3,56} = 33.72$, $p < 0.0001$ and $F_{3,56} = 10.05$, $p < 0.0001$ for EIV.L and SLA, respectively). Considering only vascular plant species, the community-weighted mean of EIV.L did not differ statistically significantly ($F_{3,56} = 1.84$, $p = 0.151$). AFP had the lowest SLA, indicating the highest light availability, as well as the highest value of EIV-L. RFP did not differ statistically significantly from AFP both in terms of EIV-L and SLA community-weighted means. Results indicate lower light availability in forests with *Q. rubra* (Table 2).
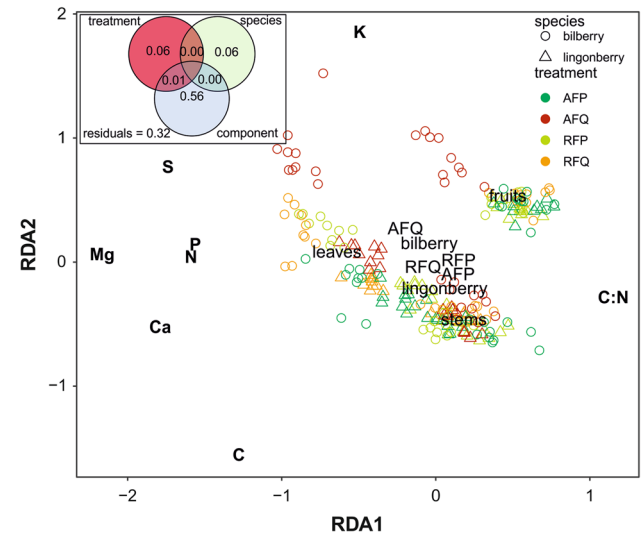
Fig. 2 Redundancy analysis (RDA) showing patterns of macronutrient composition within the studied samples. Points represent samples, bold labels—numeric variables, regular font labels—constraining factors. Upper-left subplot: Venn diagram representing variance partitioning among RDA constraints. RDA AIC = 214.44, AIC of null model (without constraints) = 458.47. Significance of constraints fitness: Table 3

Table 3 The fit of environmental traits to redundancy analysis (RDA) results evaluated using a PERMANOVA test (999 iterations)

Constraining variable	df	variance	F	Pr (>F)
Forest type	3	0.650	18.560	0.001
Species	1	0.467	39.992	0.001
Biomass component	2	4.396	188.231	0.001
Residuals	213	2.487	–	–

Variability of macronutrient concentrations

Analysis of macronutrient concentration patterns showed that the main driver of variability was the biomass component (leaves, stems, fruits), responsible for 56% of variability explained by the model (Fig. 2, Table 3). Species (lingonberry or bilberry) and forest type (AFP, AFQ, RFP, RFQ) each explained 6% of the variability. The ordination diagram revealed a clear distinction between fruits (upper right part of the plot) and other components, as well as between leaves and stems (between the labels of 'lingonberry' and 'stems'). All these factors significantly drove the chemical composition of berries. We found more samples from pine forests with *Q. rubra* at the left side of the ordination diagram, but no differences between ancient and recent forests.

Macronutrient concentrations in biomass components: differentiation between species and among forest types

For bilberry, we found higher concentrations of macronutrients in leaves than in stems and fruits (Fig. 3). Differences in C concentration among forest types were negligible. Higher leaf N and K concentrations, as well as lower C:N ratios, were noted in *V. myrtillus* from the recent pine forest and both pine forests with *Q. rubra* than from ancient pine forest. The concentration of P was the highest in leaves of bilberry from the recent pine forest and ancient pine forest with *Q. rubra*. In stems, we found the highest N and Ca concentrations in RFP, while stem K concentration was higher in AFQ than in the other three forest types. Concentrations of N, S, K, and Mg in fruits were also higher in AFQ than in other forest types.

The presence of *Q. rubra* was the most important factor for most leaf nutrients studied, while stem nutrients were more affected by land-use history (Fig. 4). *Q. rubra* mostly affected S and Mg concentrations all biomass components of bilberry, as well as leaf N, K, and Ca concentrations, while land-use change mostly affected stem N, K, and Ca concentrations, as well as stem C:N ratio.

For lingonberry, we found higher concentrations of macronutrients in leaves than stems, except C, for which concentrations were aligned (Fig. 5). In pine forests with *Q. rubra* (AFQ and RFQ), we found higher N and S leaf concentrations, and lower C:N ratio and P concentration (in AFQ only) than in pine forests. Leaf K concentration was higher in AFQ than in other forest types. We also found lower stem N concentrations in RFQ than in the other three forest types, as well as lower stem K concentration in recent than in ancient forests.

Leaf macronutrient concentrations were more affected by *Q. rubra* than by land-use change (Fig. 4), especially for N, S, and P concentrations, and C:N ratio. To a lesser degree,

this factor also affected stem macronutrient concentrations (Mg, Ca, S, P, and N), as well as C:N ratio. Stem K concentration, however, was mostly affected by land-use change. *Vaccinium vitis-idaea* did not produce berries in pine forests with *Q. rubra,* both ancient and recent (Woziwoda et al. 2021), so macronutrient concentrations in lingonberries were the most affected by this species (*Q. rubra* limited allocation of elements in fruits to zero). Fruit macronutrient concentrations in both pine forests were more affected by land-use change than leaf and stem concentrations (Fig. 4).

Nutrient pools in forest understory

The estimated macronutrient pools were much higher for *V. myrtillus* than *V. vitis-idaea* in all forest types studied (Table 4). Land-use change and *Q. rubra* affected nutrient pools of lingonberry more (up to 99.9%) than bilberry (up to 46.9%; Table 4). Land-use change decreased (in comparison with AFP) the P pool in bilberry more than *Q. rubra*, but increased K and S pools, in comparison with ancient pine forest (39.3% and 6.5%, respectively). However, for bilberry, the highest nutrient pool decreases were found in the recent pine forest with *Q. rubra*, with the C and P pools most affected (46.5% and 46.9% lower, respectively). For lingonberry, the extremely high decreases in nutrient pools (for all elements studied) were found in both forests with *Q. rubra* (Table 4). The lowest decreases (but still exceeding 70%) were found in the recent pine forest, with the S and C pools least affected (73.2% and 75.6% lower, respectively) and Ca and Mg pools most affected (81.1% and 80.6% lower, respectively).

Discussion

In line with our expectations, the biomass components were the main drivers of the variability of nutrient concentrations. The low species-specific differences in macronutrient concentrations were also expected as both species studied are congeneric. However, species-specific differences occurred, as the species studied differ in life strategy (deciduous vs. evergreen), which is reflected in their chemical composition (Grelet et al. 2001; Barker and Bryson 2007). The most important differences in species-specific macronutrient concentrations revealed here were those indicating the different reactions of *V. myrtillus* and *V. vitis-idaea* to changes in light condition after deciduous tree introduction and past changes in land use (ancient *vs.* recent forests). Differences in macronutrient concentrations in plant species studied could also result from nutrient availability in soils or modifications of nutrient uptake due to the occurrence of other elements (Barker and Pilbeam 2007; Marschner 2012); further studies are needed.

Fig. 3 Mean (+ SE) concentrations of macronutrients and C:N ratios in *Vaccinium myrtillus* growing in four forest types: AFP—ancient pine forest, AFQ—ancient pine forest with introduced *Q. rubra*, RFP—recent pine forest, RFQ—recent pine forest with introduced *Q. rubra*. Groups denoted by the same letters did not differ statistically significantly ($p < 0.05$) according to the Tukey *posteriori* tests. For models—see Appendix A
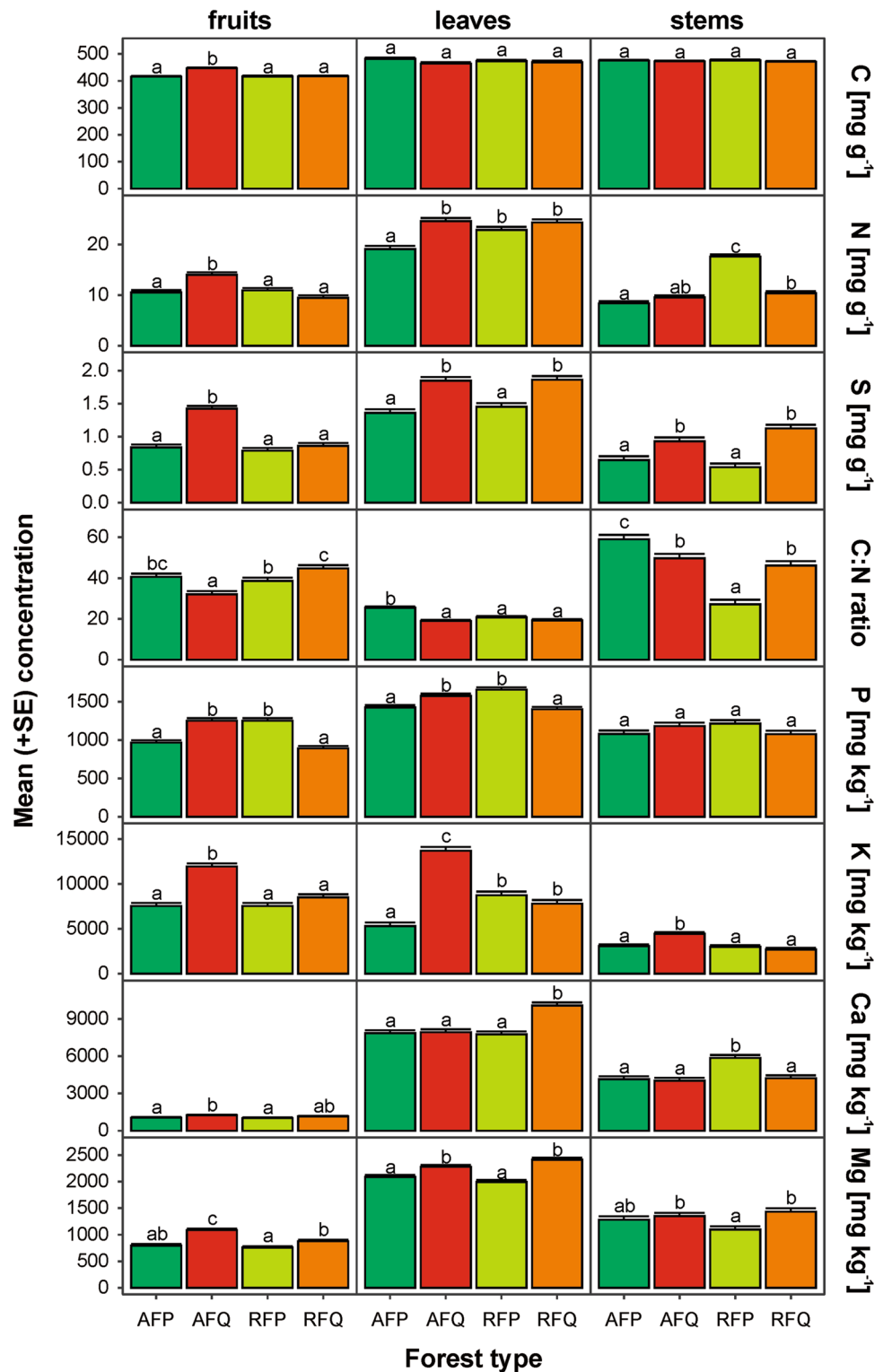

Vaccinium myrtillus and *V. vitis-idaea* shoots were mainly composed of carbon, and so its high concentration (nearly 50% of dry mass) was expected. No intra- and interspecific differences in C concentration were found in bilberry and lingonberry leaves, stems, or fruits, both within and between mesic pine forest types studied. However, results of this study combined with our earlier data (Woziwoda et al. 2019a, 2021) revealed the important roles of *V. myrtillus* and *V. vitis-idaea* in C sequestration and storage in the Scots pine forest ecosystems, consistent with data from other European

Fig. 4 The proportion of variance explained by *Q. rubra*, land-use change (ancient-recent forest), and their interactions in models of macronutrient concentrations and C:N ratios in bilberry *Vaccinium myrtillus* and lingonberry *V. vitis-idaea*. For models—see Appendix A
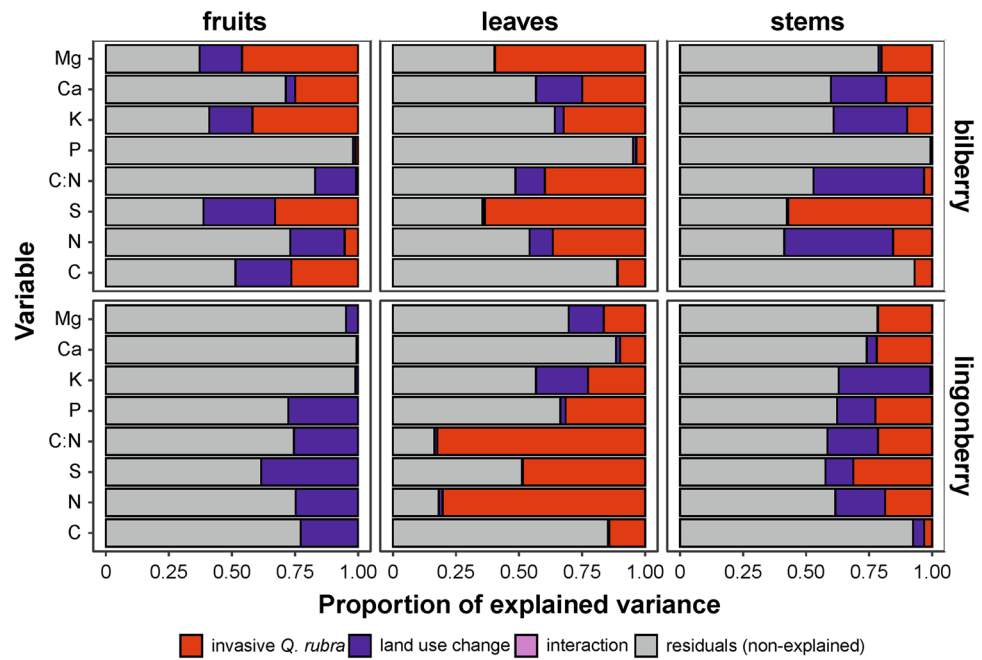

coniferous forests (Nilsson and Wardle 2005; Kolari et al. 2006; Rodriguez and Kouki 2015). As bilberry colonizes recent forests faster than lingonberry (Matuszkiewicz et al. 2013) and is more resistant to negative impacts of introduced alien oak (Woziwoda et al. 2014a, 2019a), it seemed to be more important for C storage. Indeed, the estimated C pool of aboveground shoots of *V. myrtillus* was eight times higher in pine monoculture planted on post-agricultural soil, and multiple times higher in both recent and ancient forests with *Q. rubra,* than *V. vitis-idaea* C pools (Table 4). Moreover, in reference plots (ancient pine forest) the estimated C pool of *V. myrtillus* was also more than three times higher than the *V. vitis-idaea* C pool.

The different concentrations of the next major element—nitrogen, noted in leaves, stems, and fruits were also expected (Barker and Bryson 2007; Marschner 2012). However, we found that whole aboveground shoots of *V. myrtillus* in recent forest and *V. vitis-idaea* in the ancient and recent forests contained less N in stands with *Q. rubra* than in pure Scots pine stands. The highest N concentration in leaves in mixed stands was linked with lower exposure of plants to sunlight (see Table 2), and light conditions strongly affect the growth, performance, and chemical composition of bilberry and lingonberry plants (Sjönberg et al. after Atlegrim 1989; Messier et al. 1998; Frelich et al. 2003; Uleberg et al. 2012; Nestby et al. 2011, 2014b). Both species studied react to decreases in light availability by specific leaf area (SLA) increases (Paź-Dyderska et al. 2020), and SLA is positively correlated with N concentration (Wright et al. 2004; Díaz et al. 2016). Higher N concentration noted in bilberry than lingonberry leaves can also result from the

tendency of N to concentrate in the most intensively growing points of the plant (Tegeder and Masclaux-Daubresse 2018), i.e. in deciduous bilberry leaves. N accumulated in plants is naturally re-used by them in growing tissues. However, within-plant N management varies depending on whether the plant is evergreen (lingonberry) or deciduous (bilberry) (Barker and Bryson 2007). *Vaccinium myrtillus* remobilizes N to intensively growing deciduous leaves and new shoots from previous year stems and roots, while *V. vitis-idaea* retranslocates N predominantly from previous year evergreen leaves (Grelet et al. 2001). Moreover, N remobilization from older lingonberry leaves to new ones occurs slowly during the vegetative season, while remobilization of N from long-lived bilberry stems and roots to seasonal leaves occurs faster. All these facts resulted in higher N concentrations noted in lingonberry stems than leaves in both pine forests, while in mixed forests more N was noted in leaves, as leaves are bigger there (Paź-Dyderska et al. 2020) and grow more intensively. However, intraspecific SLA plasticity in *V. vitis-idaea* is low (Paź-Dyderska et al. 2020), and this evolutionary incapacity can be responsible for lingonberry decline after broadleaved tree planting (or their spontaneous encroachment) (Woziwoda et al. 2018) in the Scots pine stands. Admittedly, slow biomass turnover supports efficient internal N-cycling and favours N accumulation (Grelet et al. 2001); however, lingonberry shoots contained less N than bilberry shoots. Results of this study confirmed that *V. myrtillus* more effectively uptakes nutrients from the soil than *V. vitis-idaea* (Sjönberg et al. after Atlegrim 1989; Parzych 2016). The lower N concentrations in whole (aboveground) shoots found in mixed forests than in pine forests could also

Fig. 5 Mean (+SE) concentrations of macronutrients and C:N ratios in lingonberry *Vaccinium vitis-idaea* growing in four forest types: AFP—ancient pine forest, AFQ—ancient pine forest with introduced *Q. rubra*, RFP—recent pine forest, RFQ—recent pine forest with introduced *Q. rubra*. Groups denoted by the same letters did not differ statistically significantly ($p < 0.05$) according to the Tukey *posteriori* tests. For models—see Appendix A
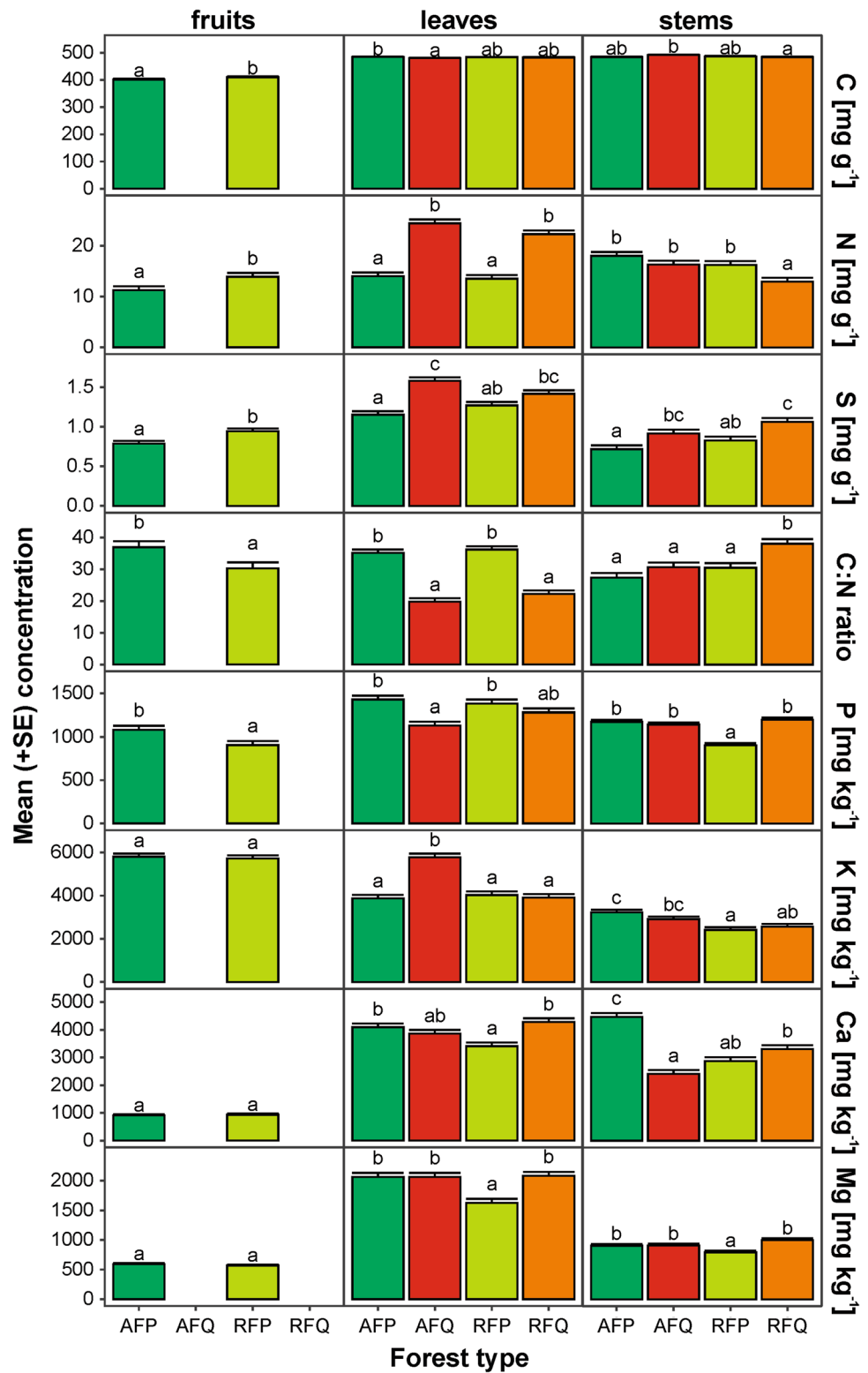
result from lower N availability, as even fertile forest soils are impoverished in N in the presence of *Q. rubra* (Nicolini and Topp 2005; Stanek et al. 2020).

Nitrogen, along with phosphorus and sulphur, is present mainly as a constituent of nucleic acids and fatty phospholipids, and all of these elements are accumulated mainly at intensively growing green parts of plants (Haneklaus et al. 2007). The uptake and assimilation of N, S, and P by plants are strongly interrelated and dependent upon each other (Haneklaus et al. 2007; Sanchez 2007). Sulphur is

Table 4 Estimated macronutrient pools (kg ha^{-1}) of bilberry *Vaccinium myrtillus* and lingonberry *V. vitis-idaea* in ancient pine forest (AFP; reference), ancient pine forest with introduced *Q. rubra* (AFQ), recent pine forest (RFP), and recent pine forest with introduced *Q. rubra* (RFQ), and difference (%) in AFQ, RFP, and RFQ macronutrient pools in comparison with AFQ. Data on biomass allocation of both species per each forest stand are available in Woziwoda et al. (2019a) for bilberry and Woziwoda et al. (2021) for lingonberry

Element	AFP	Propagated error	AFQ	Propagated error	Difference (%)	RFP	Propagated error	Difference (%)	RFQ	Propagated error	Difference (%)
Vaccinium myrtillus											
C	440.31331	57.24534	353.57220	25.05422	− 19.70	265.40714	17.53191	− 39.72	235.60600	11.84699	− 46.49
N	10.81007	1.49335	9.65832	0.80918	− 10.65	10.59134	0.73720	− 2.02	6.97572	0.43863	− 35.47
Ca	4.82596	0.66487	3.59460	0.31193	− 25.52	3.49662	0.25417	− 27.55	2.85726	0.19283	− 40.79
K	3.55059	0.52300	4.94732	0.41833	39.34	2.67385	0.23500	− 24.69	2.00172	0.15836	− 43.62
Mg	1.40518	0.19081	1.15710	0.09494	− 17.65	0.75084	0.05924	− 46.57	0.84248	0.05261	− 40.04
P	1.09236	0.14742	0.95144	0.07574	− 12.90	0.75124	0.05541	− 31.23	0.57971	0.03631	− 46.93
S	0.80257	0.11899	0.85456	0.07770	6.48	0.45051	0.04571	− 43.87	0.65629	0.04449	− 18.23
Vaccinium vitis-idaea											
C	135.90160	6.73098	0.04020	0.00366	− 99.97	33.14511	1.92670	− 75.61	0.00572	0.00056	− 99.995
N	4.27941	0.29915	0.00175	0.00017	− 99.96	0.98934	0.07700	− 76.88	0.00022	0.00002	− 99.994
Ca	1.16557	0.06855	0.00027	0.00003	− 99.98	0.21997	0.01575	− 81.13	0.00005	0.00000	− 99.996
K	1.04301	0.06689	0.00038	0.00004	− 99.96	0.23682	0.01714	− 77.29	0.00004	0.00000	− 99.996
Mg	0.46956	0.02786	0.00013	0.00001	− 99.97	0.09094	0.00646	− 80.63	0.00002	0.00000	− 99.996
P	0.37765	0.02172	0.00009	0.00001	− 99.98	0.08300	0.00548	− 78.02	0.00001	0.00000	− 99.996
S	0.28364	0.01902	0.00011	0.00001	− 99.96	0.07613	0.00543	− 73.16	0.00002	0.00000	− 99.995

essential for chloroplast growth and function; it is a component of the iron–sulphur complexes of the electron transport chains in photosynthesis (Haneklaus et al. 2007). We found that *Q. rubra* occurrence favoured S accumulation both in *V. myrtillus* and *V. vitis-idaea* leaves, irrespective of the forest land-use history. The noted high S concentrations in bilberry and lingonberry fruits were expected as the sulphur-containing amino acids (cysteine and methionine) are present at high levels in seed storage proteins (Tabatabai 1986).

Uptake of the next element—phosphorus—from the soil is positively correlated with N uptake (Marschner 2012), and high N and P availability in soils increases bilberry fruit yield and shoot growth (Nestby et al. 2014a). However, intensive plant growth and fruiting occur only if both elements are available in high amounts or eventually high N concentration is noted, while even high P with low N availability is insufficient for proper plant development (Nestby et al. 2014a). Our study showed that in the presence of *Q. rubra*, *V. myrtillus* increased P accumulation in the ancient forest, but decreased it in the recent forest, while *V. vitis-idaea* had decreased P accumulations in the presence of oak in both recent and ancient forests. The higher P concentration in bilberry plants growing under the closed pine-red oak canopy can be related to more intensive photosynthesis in sites with denser shade, and P is involved in this process (Van Heerwaarden et al. 2003). A large amount of P is naturally stored within seeds in anticipation of their germination, so more P noted in bilberries in recent pine forest without than with *Q. rubra* can be explained by limited seed set production in dense shade conditions (Eckerter et al. 2019). However, higher P concentration in fruits collected in an ancient forest with *Q. rubra* than in an ancient pine forest contradicts this theory (unless bilberries from ancient forest contained more seeds; further studies are necessary).

Potassium, unlike other major elements, does not enter into the composition of any of the important plant constituents, but it is involved in numerous metabolic processes, and it usually occurs in all biomass components in substantial amounts (Marschner 2012). Regulating internal plant moisture and being involved in maintaining the water status of the plant by control of the turgor pressure of plant cells and the opening and closing of its stomata, K is an essential contributor to photosynthesis and respiration (White and Karley 2010). The aforementioned functions explain much higher K concentration in *V. myrtillus* and *V. vitis-idaea* leaves than stems, as well as its higher concentration in bilberry shoots collected in forests with than without *Q. rubra* (Figs. 3, 5). The latter is interesting, as forest soils occupied by *Q. rubra* are strongly impoverished in K (Nicolini and Topp 2005; Stanek et al. 2020). We hypothesise that the noted soil impoverishment can result not only from more intensive nutrient uptake by *Q. rubra*—as was stated in previous studies—but also due to increased absorption of elements by native understory "survivors" (further study is needed). Thin bilberry leaves contained more than twice as much K than lingonberry leaves, and much higher K bioaccumulation in thin than leathery leaves was expected, although both species responded to increased loss of moisture in low light habitats (Leuschner and Ellenberg 2017b) by SLA increase (Paź-Dyderska et al. 2020). The high K concentrations in bilberry and lingonberry berries (Figs. 3, 5) resulted in turn from substantial participation of this element in natural processes of fruit ripening and coloration (Upton 2001; Chu et al. 2011).

The high magnesium concentrations in leaves of both species, slightly higher for deciduous bilberry, are explained by the role of Mg in plants (an important constituent of the chlorophyll molecule and effective activator in numerous enzyme reactions closely related to energy-supplying P-compounds; Marschner 2012). Higher Mg concentration in shoots collected in mixed than pine forests (except lingonberry in the ancient pine forest) can also be explained by more intensive photosynthesis ongoing in plants in light deficiency under a closed canopy. The lower Mg concentration in the whole lingonberry shoots from mixed pine-oak stands than those from pine monocultures can result from the lack of fruits in the former (Woziwoda et al. 2021), as during fruit ripening magnesium is remobilized from vegetative to reproductive tissues (Merhaut 2007). Fruiting limitation in the ancient forest, however, did not change Mg bioaccumulation in lingonberry vegetative organs, while in recent forests Mg concentrations in leaves and stems were slightly higher in forests with than without *Q. rubra*.

Both N absorption from the soil to the plant as well as K transport within are regulated by calcium availability, and the more N and K, the more Ca in plant tissues (Marschner 2012). This element is a constituent of cell walls, especially in leaves (Vergutz et al. 2012) and, like Mg, it is involved (among others) in the activation of enzymes necessary for photosynthesis, hence, the naturally high amounts of Ca found in green biomass components of both species. High amounts of Ca in long-living plant parts like stems or evergreen (lingonberry) leaves are explained by its tendency to accumulate in plants with plant age (Marschner 2012). However, more than twice as much Ca was found in bilberry than in lingonberry leaves, and the highest Ca concentration was noted in *V. myrtillus* growing in the recent pine forest with *Q. rubra*. It can be connected to species-specific leaf structure (thinner in bilberry while thicker and leathery in lingonberry) and site-specific rate of water circulation. Calcium ions (immobile in a plant) are transported from the soil to the plant tissues with water by the xylem system. Thinner leaves transpire faster, and in sites with dense shade plant transpiration accelerates (Sjönberg et al., after Atlegrim 1989; Leuschner and Ellenberg 2017b). Faster transpiration means faster water movement within a plant,

and consequently more intensive Ca uptake (but see: Pilbeam and Morlay 2007). For lingonberry, rapid Ca uptake in high amounts is a very marked characteristic of nutrient absorption (Ingestad 2006). Higher Ca concentration noted in *V. vitis-idaea* stems in ancient pine forests may be in turn linked with the lingonberry strategy for specific biomass accumulation during generative reproduction. In the previous study (Woziwoda et al. 2021), we found that some fruiting shoots (noted exclusively in pine stands without *Q. rubra*) almost completely reduced their leaf biomass. Consequently, the plant transpiration and photosynthesis had to be "taken over" by green stems which resulted in higher Ca accumulation within.

We are aware that conclusions drawn from our study might be biased by the low replicability (connected with very high labour demand)—each forest type is represented by only one study site, and research plots are probably not independent. This may limit the transferability of the results, and one should be cautious when inferring results and conclusions for other forests. However, despite the lack of replications, assessments of the effects of introduced (invasive) woody species on the biomass of native plants in forests with different histories of land use are scarce, and our study provides novel data that could be used in designing further researches. Lingonberry and bilberry plant biomass components were not separated into the current growing season and older parts of stems and leaves, so results show both long-term and one-season accumulations of nutrients in long-lived stems and evergreen lingonberry leaves, as well as one-season accumulations of nutrients in deciduous bilberry leaves, and fruits of both species.

The second disadvantage of the study is a lack of direct light availability measurements, as light availability is a crucial factor determining plant biomass and nutrient allocation (Karolewski et al. 2013; Czapiewska et al. 2019). However, we used indirect methods, based on functional traits and indicator values of plants (Ellenberg and Leuschner 2010), that are related to light availability (Dzwonko 2001; Jagodziński et al. 2016). As we used vegetation surveys, we assessed community-based responses that neglected intraspecific variability of particular species (Paź-Dyderska et al. 2020), but provided an average response of all species, weighted by their abundance. Moreover, SLA has higher inter- than intraspecific variability (Paź-Dyderska et al. 2020) that allows for conclusions on plant community characteristics. We found a lack of differences among forest types in EIV.L for vascular plants only, but including bryophytes in the analysis revealed higher EIV.L in forest types without *Q. rubra*. Lack of differences accounting for vascular plants results from the low cover of the herbaceous layer, and therefore lower species richness. Bryophytes seem to be more sensitive to the limitation of light availability than vascular plants, similarly as in a multi-comparison study on

invasive tree species effects on bryophytes (Dyderski and Jagodziński 2020b). Our results confirmed previous findings of shading by red oak (Niinemets 2010; Jagodziński et al. 2018; Dyderski et al. 2020). However, the ability of *Q. rubra* to shade the understory is not connected with its functional advantage, but rather with its ability to grow beneath a *P. sylvestris* canopy (Dyderski and Jagodziński 2019). Therefore, the effect of *Q. rubra* can be similar to native oak species. For example, in Western Poland stands with *Q. rubra* transmitted $3.9 \pm 0.5\%$ of open-sky light, stands with *Q. petraea* transmitted $5.7 \pm 0.6\%$, while non-invaded *P. sylvestris* stands transmitted $10.2 \pm 1.8\%$ of full light (Dyderski and Jagodziński 2020a).

However, as *Q. rubra* is classified in Poland and other European countries as an invasive alien species (Dyderski et al. 2020, and references therein), the effects of its introduction require more attention than of other broadleaved (native) species occurrence. Admittedly *Q. rubra* planting in Polish forests is currently limited, but it still can be used in the transformation of recent Scots pine forests occupying post-agricultural soils to mixed forests. Moreover, mature red oak trees already occur in high numbers in numerous localities in forests (Woziwoda et al. 2014a, b, c), and *Q. rubra* spreads effectively in an uncontrolled way (Woziwoda et al. 2018, 2019b; Chmura 2020; Dyderski and Jagodziński 2020a). Our earlier studies indicated that *V. myrtillus* and *V. vitis-idaea* declined in *Q. rubra* presence (Woziwoda et al. 2019a, 2021). Decreases in macronutrient pools revealed here for bilberry and lingonberry confirm earlier observations on strong negative effects of this alien tree introduction both on native flora and (consequently) NWFP availability (Woziwoda et al. 2019a, 2021). Differences in nutrient concentrations found for *V. myrtillus* and *V. vitis-idaea* in the Scots pine and Scots pine-red oak forests result from changes in abiotic conditions caused by underplanting broadleaved tree species. Decreases in macronutrient pools indicate changes in nutrient accumulations in forest understories which can have far-reaching consequences for nutrient cycling within forest ecosystems. Therefore, we suggest controlling the occurrence of alien *Q. rubra* (as well as other broadleaved species) in pine monocultures and limiting its underplanting in Scots pine monocultures, especially in areas with abundant *V. myrtillus* and *V. vitis-idaea*.

Conclusions

Forest land-use discontinuity and enrichment of the Scots pine monocultures with *Q. rubra* significantly affected macronutrient bioaccumulation in aboveground shoots of *V. myrtillus* and *V. vitis-idaea*. We found intra- and interspecific (bilberry *vs.* lingonberry) differences in N, S, P, K, Ca, and Mg concentrations and no differences in C concentrations in bilberry and

lingonberry leaves, stems, and fruits. Forest land-use continuity favoured the accumulation of nutrients in *Vaccinium myrtillus* and *V. vitis-idaea* aboveground biomass components, except P in bilberry. Macronutrient concentrations were also higher in both species in pine forests "enriched" with *Q. rubra*, both recent and ancient. However, despite the more effective accumulation of elements in *Q. rubra* presence at the species level, at the ecosystem level macronutrient pools of *V. myrtillus* and *V. vitis-idaea* were significantly lower, and the decreases noted resulted from significant changes in bilberry and lingonberry cover and biomass, as a response of both species on forest stand transformation. Therefore, the limitation of *Q. rubra* occurrence in mesic Scots pine forests in areas with abundant bilberry and lingonberry cover is recommended.

Declarations

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