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Ionome of Lithuanian Populations of Purple Loosestrife (*Lythrum salicaria*) and Its Relation to Genetic Diversity and Environmental Variables

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Abstract: Fifteen riparian populations of Lithuanian *Lythrum salicaria* were assessed for leaf macronutrient, micronutrient and non-essential element concentrations and compared to the former obtained molecular data at amplified fragment length polymorphism (PLP.AFLP) loci. Inductively coupled plasma mass spectrometry was used to profile the contents of 12 elements in the leaves. The leaf nutrient concentrations were within normal ranges for growth and development and heavy metal concentrations did not reach toxic levels. The concentrations of macroelements such as nitrogen, potassium, calcium and magnesium were in the range of 23,790–38,183; 7327–11,732; 7018–12,306; and 1377–3183 µg/g dry mass (d. m.), respectively; the concentrations of micronutrients such as sodium, iron, zinc and copper varied in the ranges of 536–6328; 24.7–167.1; 10.88–26.24; and 3.72–5.30 µg/g d. m., respectively, and the concentrations of non-essential elements such as lead, nickel, chromium, and cadmium were in the intervals of 0.136–0.940; 0.353–0.783; 0.207–0.467; and 0.012–0.028 µg/g d. m., respectively. When comparing the maximum and minimum values for site elements of *L. salicaria*, the concentration of N varied by 1.6, K—1.6, Ca—1.8, Mg—2.3, Na—6.1, Fe—6.8, Zn—2.4, Cu—1.5, Pb—6.9, Ni—2.2, Cr—2.2, and Cd—2.3 times. The coefficient of variation (CV) of element concentrations in sites was moderate to large: N—15.4%, K—14.3%, Ca—18.6%, Mg—24.8%, Na—50.7%, Fe—47.0%, Zn—24.9%, Cu—14.5%, Pb—57.1%, Ni—30.11%, Cr—26.0%, and Cd—38.6%. *Lythrum salicaria* populations growing near regulated riverbeds were characterized by significantly ($p < 0.05$) lower concentrations of Ca and Mg, and significantly ($p < 0.05$) higher concentrations of N, K, Fe, Na, Ni, Cr and Cd. The PLP.AFLP was negatively correlated with concentrations of N, Na, Fe, Ni, Cr, and Cd. The *L. salicaria* population with the lowest leaf N and Na concentration showed the highest genetic polymorphism (PLP.AFLP = 65.4%), while the least polymorphic population (PLP.AFLP = 35.0%) did not show extreme concentrations of either element. In conclusion, our elemental analysis of *L. salicaria* populations showed that ionomic parameters are related to genomic parameters, and some habitat differences are reflected in the ionomes of the populations.

Keywords: invasive alien species; riparian vegetation; macrophyte; elements; macronutrients; micronutrients; heavy metals; phytoremediation; molecular markers; AFLP

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1. Introduction

Wetlands are very valuable habitats with the greatest diversity of plant and animal species. These areas are very important because they reduce the impact of extreme climate conditions. Wetlands are permanently disturbed by anthropogenic activities; as a result, these ecosystems are becoming increasingly sensitive [1].

Alterations of physical and chemical nature by humans make wetlands highly susceptible to plant invasions. Because of the growing damage caused by the spread of non-native species, biologists are increasingly focusing on understanding aquatic invasions [2].

Purple loosestrife (*Lythrum salicaria* L.), a member of the order *Myrtales*, family *Lythraceae*, is a tall perennial herb with tristylous reddish-purple flowers. Due to its amphibian lifestyle, it grows either submerged under water or above water. It is found along riverbanks and ditches, on the edges of lakes, in marshes and in wet meadows. *Lythrum salicaria* is naturally growing in Europe and temperate Asia. It belongs to an invasive species with long lag phases from introduction to eventual spread [3]. In the early 1800s, it arrived in North America and, since the 1930s, has become invasive [4]. To date, *L. salicaria* is attributed to the most aggressive species, forming monospecific communities in the wetlands of the United States and southern Canada [5].

Intensive use of fertilizers, urban and industrial activities are causing leakages of an excess of nutrients, which drain into aquatic ecosystems. As a result, lakes and rivers gradually become eutrophic [6–8]. Regarding the condition of rivers, parameters of the abiotic environment are usually recorded [9] together with macrophyte composition and coverage data [10,11]. The requirement of species for soil nutrients is estimated either by examining the concentration of soil elements or by employing Ellenberg indicator values (EIV) [12]. As indirect evidence of the abundance of nutrients in the soil, there are various plant growth data, for example, the mass of the aboveground part of all growing species per unit area or the mass of the aboveground part of a single individual [13]. The most accurate information about the condition of a plant could be obtained by measuring the concentration of nutritional elements in the leaves [13,14]. For a long time, amounts of macro- and microelements have been well examined for important forest tree species and cultivated food plants [15].

In the second half of the last century, many efforts were made to collect knowledge about the morphology, especially the flower structure, of *L. salicaria* [16], pollination, reproduction [17], cytology [18], DNA polymorphism [19–22], secondary metabolites [23] and interaction with other plant species [24–26], and various measures to control and eradicate the species have been examined [27–29]. Finding the best solutions to improve the management of invasive wetland plants requires filling gaps in knowledge about exotic species [30].

For many alien species, the situation is inadequate when comparing data collected within invasive areas and in the area of the natural distribution range. This also applies to *L. salicaria*. The majority of investigations of this species have been carried out only in North America [4,16,20,24,31–34], with a much smaller proportion of data covering both invasive and natural areas [19,21] or only natural areas [22,35]. Ionome investigations are gaining increasing attention [36]. Nutrients are responsible for maintaining the functions of organisms. They affect physiological processes and lead to morphological and quantitative changes in plant growth and development. So far, nutritional topics related to invasive species have not received enough attention [37,38]. Soil nutrient richness was the most important factor, accounting for more than 20% of the variance in coverage of invasive herbaceous plants [37]. Despite more than half a century of extensive research on *L. salicaria* as an invasive species, to our knowledge, more extensive ionomic data on *L. salicaria* populations from invasive or pristine areas are still lacking. As nutrient loads (such as N or P) are reduced in large parts of wetlands, the wise use of these habitats will remain an important strategy for the future [39].

Ionomic data on *L. salicaria* have been obtained from several studies in experimental wetlands with artificially simulated pollution [40–44]; under such circumstances, the knowledge acquired cannot be transferred to naturally growing plants. In the Baltic countries, *L. salicaria* is a common riparian species along the edges of water bodies, growing near lakes, ponds, rivers and ditches. In contrast to the dense coverage of this plant within the invasive areas of North America, the coverage by *L. salicaria* in permanently over-moistened habitats of Poland is not high (5%) [45]; a similar situation in terms of its coverage is also found on the banks of riparian sites of Lithuania [10]. Our recent investigations of the genetic diversity of *L. salicaria* populations in Lithuania revealed significant population differentiation in polymorphism loci of amplified fragments of DNA (AFLP) [22]. There is a growing worldwide interest in linking the molecular properties of organisms to physiology, including the ionome [46–53].

The aim of the study was to evaluate the concentrations of macroelements (N, K, Ca, Mg), microelements (Fe, Na, Zn, Cu) and non-essential elements (Pb, Ni, Cr, Cd) in the leaves of *L. salicaria* populations in 15 sites in Lithuania. Special tasks were to relate elemental data of the species with the extent of polymorphism at AFLP loci; and to evaluate the influence of distinct habitats with respect to (1) river basin (Nemunas, Lielupė and Seaside Rivers basins), (2) land cover and use type (agricultural areas, artificial areas and forest), and (3) riverbed origin (natural and regulated).

2. Materials and Methods

2.1. Study Area

Purple loosestrife (*Lythrum salicaria* L.) was collected from 15 sites in Lithuania. In addition to elemental analysis, molecular diversity at amplified fragment length polymorphism (AFLP) loci was also examined at those sites, as previously described [22]. The selected sites belong to three river basins—Nemunas, Seaside Rivers and Lielupė basin (Figure 1).

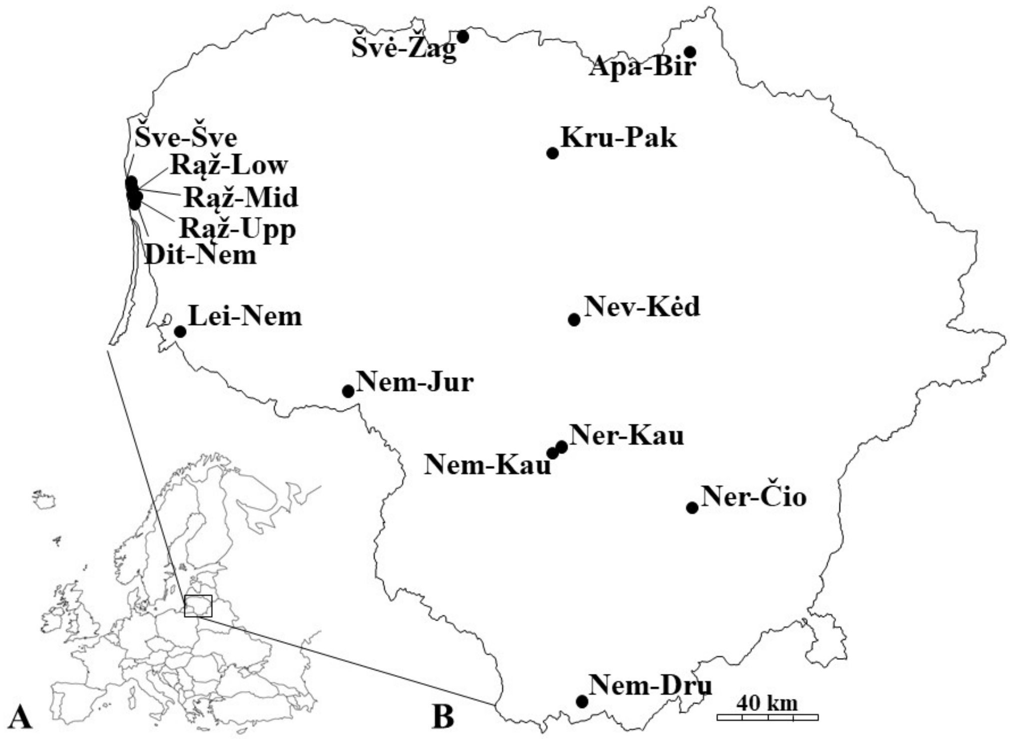

Figure 1. Location of Lithuania (**A**), and 15 sites with purple loosestrife (*Lythrum salicaria*) growing in the country (**B**).

The sampling area extended between 54°01′12.9′′ and 56°21′36.6′′ North and between 21°03′21.8′′ and 24°45′57.8′′ East (Table 1).

Table 1. The names and geographical locations of 15 populations of *Lythrum salicaria* in Lithuania (Figure 1) selected for element (macro-, microelement and non-essential) and AFLP [22] analysis.

Name of Population	River	River Basin	Location	Latitude (°N)	Longitude (°E)
Nem-Dru	Nemunas	Nemunas	Druskininkai	54°01′12.9″	23°58′53.9″
Ner-Čio	Neris	Nemunas	Čiobiškis	54°56′55.9″	24°40′28.0″
Ner-Kau	Neris	Nemunas	Kaunas	54°58′46.2″	24°01′37.7″
Nem-Kau	Nemunas	Nemunas	Kaunas	54°53′35.9″	23°53′21.0″
Nev-Kėd	Nevėžis	Nemunas	Kėdainiai	55°17′58.3″	23°59′45.5″
Nem-Jur	Nemunas	Nemunas	Jurbarkas	55°05′35.1″	22°43′48.9″
Lei-Nem	Leitė	Nemunas	Sausgalviai	55°15′57.6″	21°27′18.4″
Rąž-Upp	Rąžė	Seaside Rivers	Palanga	55°54′39.8″	21°04′28.9″
Raž-Mid	Rąžė	Seaside Rivers	Palanga	55°54′59.3″	21°03′56.4″
Rąž-Low	Rąžė	Seaside Rivers	Palanga	55°55′14.1″	21°03′21.8″
Dit-Nmr	Ditch	Seaside Rivers	Nemirsėta	55°52′50.1″	21°03′50.2″
Šve-Šve	Šventoji	Seaside Rivers	Šventoji	56°02′02.1″	21°05′12.3″
Švė-Žag	Švėtė	Lielupė	Žagarė	56°21′36.6″	23°15′07.5″
Apa-Bir	Apaščia	Lielupė	Biržai	56°11′16.7″	24°45′57.8″
Kru-Pak	Kruoja	Lielupė	Pakruojis	55°58′52.2″	23°51′15.8″

2.2. Sampling and Element Analyses

Samples of *L. salicaria* leaf material were taken during the period of intensive flowering, 1–10 August 2015. In order to examine the concentration of macroelements, microelements and non-essential elements, healthy mature leaves, undamaged by fungi or insects, were collected from the middle part of the main shoot. Three batches of leaves were collected at each site for elemental analysis. The dried plant material was ground with a tungsten carbide grinder Retsch MM400 (Haan, Germany). The Kjeldahl method [54,55] was used to determine nitrogen concentration. For analyses, 0.2 g of *L. salicaria* leaves was digested in a Kjeldahl digestion unit DK-20S and subsequently analyzed with an automatic analyzer UDK 159 (VELP Scientifica, Usmate Velate, Italy). Quality assurance was achieved using standard reference materials SRM1515, SRM1575 and CRM125045.

For metal analyses with ICPS-MS, the mineralization of the ground material was performed in a high performance An Anton Paar Multiwave 3000 microwave digestion system using HNO_3 and H_2O_2 solutions. Eleven essential and non-essential elements were analyzed with ICPS-MS (Thermo Scientific Element 2) according to the ISO 17294-2:2016 standard as it was done before [56–58]. The MERC ICP Multi-element solution IV standard was used for ICP-MS calibration.

2.3. Classification of Environment

Revealing the possible influence of the river and its environment on the nutritional status of the plant (evaluated by the concentration of leaf elements), the populations were grouped in several ways, as was done in the case of molecular analysis [22]: (1) three groups according to the river basin: Nemunas basin (Nem-Dru, Ner-Čio, Ner-Kau, Nem-Kau, Nev-Kėd, Nem-Jur, Lei-Nem; Figure 1, Table 1), Seaside Rivers basin (Rąž-Upp, Rąž-Mid, Rąž-Low, Dit-Nmr, Šve-Šve) and Lielupė basin (Švė-Žag, Apa-Bir, Kru-Pak); (2) three groups according to the land adjacent to the riverbank: artificial surfaces (ART; Nem-Kau, Rąž-Upp, Rąž-Mid, Rąž-Low, Dit-Nmr, Švė-Žag, Apa-Bir, Kru-Pak), agricultural areas (AGR; Nem-Dru, Ner-Čio, Ner-Kau, Nev-Kėd, Nem-Jur, Šve-Šve), forest and semi-natural areas (further in the text, named under forest areas, abbr. FOR; Lei-Nem), employing the CORINE Land Cover database (classification level (1) available for 2000 and 2006 [59]); (3) two groups according to riverbed origin: natural (Nem-Dru, Ner-Čio, Ner-Kau, Nem-Kau, Nev-Kėd, Nem-Jur, Šve-Šve, Švė-Žag, Apa-Bir, Kru-Pak) and regulated (Lei-Nem, Rąž-Upp, Rąž-Mid, Rąž-Low, Dit-Nmr) [60].

2.4. Data Analysis

Descriptive statistics were performed using the R software package (version 4.2.2) and the R package DescTools (version 0.99.42) [61,62]. The Kruskal–Wallis test was used to compare element concentrations between populations and between groups of populations. The R package compareGroups was used for this (version 4.5.1) [63]. The coefficient of variance (CV, in %) was calculated to characterize the heterogeneity of element concentrations at *L. salicaria* sites.

To relate physiological (element concentrations) and genetic data (percentage of polymorphic AFLP loci (PLP.AFLP) of *L. salicaria*, Spearman rank correlations were calculated by plotting a correlogram using the R package corrplot (version 0.90) [64]. Principal component analysis was performed for 12 physiological variables (concentrations of macroelements N, K, Ca, Mg, microelements Na, Fe, Zn and Cu, and non-essential elements Pb, Ni, Cr and Cd) and the molecular variable PLP.AFLP [22], using the statistical software R.

3. Results

3.1. Comparison of Populations Based on Elemental Concentrations

The median concentrations of macroelements in the leaves of Lithuanian populations of *L. salicaria* were within the following ranges (Figure 2): (1) N—23,790–38,183 µg/g d. m. (populations with extreme N concentrations, Kru-Pak and Nem-Kau, differed by a factor of 1.605); (2) K—7327–11,732 µg/g d. m. (populations with extreme K concentrations, Nem-Kau and Nem-Jur, differed by a factor of 1.601; (3) Ca—7018–12,306 µg/g d. m. (populations with extreme Ca concentrations, Kru-Pak and Nem-Jur, differed by a factor of 1.753); (4) Mg—1377–3183 µg/g d. m. (populations with extreme Mg concentrations, Kru-Pak and Nem-Jur, differed by a factor of 2.311). Multiple comparisons using the Kruskal–Wallis test did not reveal significant differences between populations in leaf concentrations of N, K, Ca and Mg.

The median concentrations of Na and microelements in the leaves of Lithuanian populations of *L. salicaria* were within the following ranges: (1) Na—536–6328 µg/g d. m. (populations with extreme Na concentrations, Kru-Pak and Šve-Šve, differed by a factor of 6.115); (2) Fe—24.7–167.1 µg/g d. m. (populations with extreme Fe concentrations, Ner-Čio and Raž-Mid, differed by a factor of 6.763); (3) Zn—10.88–26.24 µg/g d. m. (populations with extreme Zn concentrations, Nem-Jur and Nev-Kėd, differed by a factor of 2.413); (4) Cu—3.72–5.30 µg/g d. m. (populations with extreme Cu concentrations, Nem-Kau and Raž-Mid, differed by a factor of 1.448). Multiple comparisons using the Kruskal–Wallis test did not reveal significant differences between populations in leaf concentrations of Na, Fe, Zn and Cu.

The median concentrations of non-essential elements in the leaves of Lithuanian populations of *L. salicaria* were within the following ranges: (1) Pb—0.136–0.940 µg/g d. m. (populations with extreme Pb concentrations, Ner-Čio and Nem-Kau, differed by a factor of 6.884); (2) Ni—0.353–0.783 µg/g d. m. (populations with extreme Ni concentrations, Apa-Bir and Raž-Low, differed by a factor of 2.218); (3) Cr—0.207–0.467 µg/g d. m. (populations with extreme Cr concentrations, Nem-Jur and Raž-Low, differed by a factor of 2.218); (4) Cd—0.012–0.028 µg/g d. m. (populations with extreme Cd concentrations, Kru-Pak and Nem-Jur, differed by a factor of 2.349). Multiple comparisons using the Kruskal—Wallis test did not reveal significant differences between populations in leaf concentrations of Pb, Ni, Cr and Cd.

When comparing the maximum and minimum site values for elements of *L. salicaria*, the concentration of N varied by 1.6 times ($p < 0.05$), K—1.6 ($p < 0.05$), Ca—1.8 ($p < 0.05$), Mg—2.3 ($p < 0.05$), Na—6.1 ($p < 0.05$), Fe—6.8 ($p < 0.05$), Zn—2.4 ($p < 0.05$), Cu—1.5 ($p > 0.05$), Pb—6.9 ($p < 0.05$), Ni—2.2 ($p < 0.05$), Cr—2.2 ($p < 0.05$), and Cd—2.3 ($p < 0.05$). The coefficient of variation (CV) of element concentrations in sites was moderate to large: N—15.4%, K—14.3%, Ca—18.6%, Mg—24.8%, Na—50.7%, Fe—47.0%, Zn—24.9%, Cu—14.5%, Pb—57.1%, Ni—30.11%, Cr—26.0%, and Cd—38.6%.

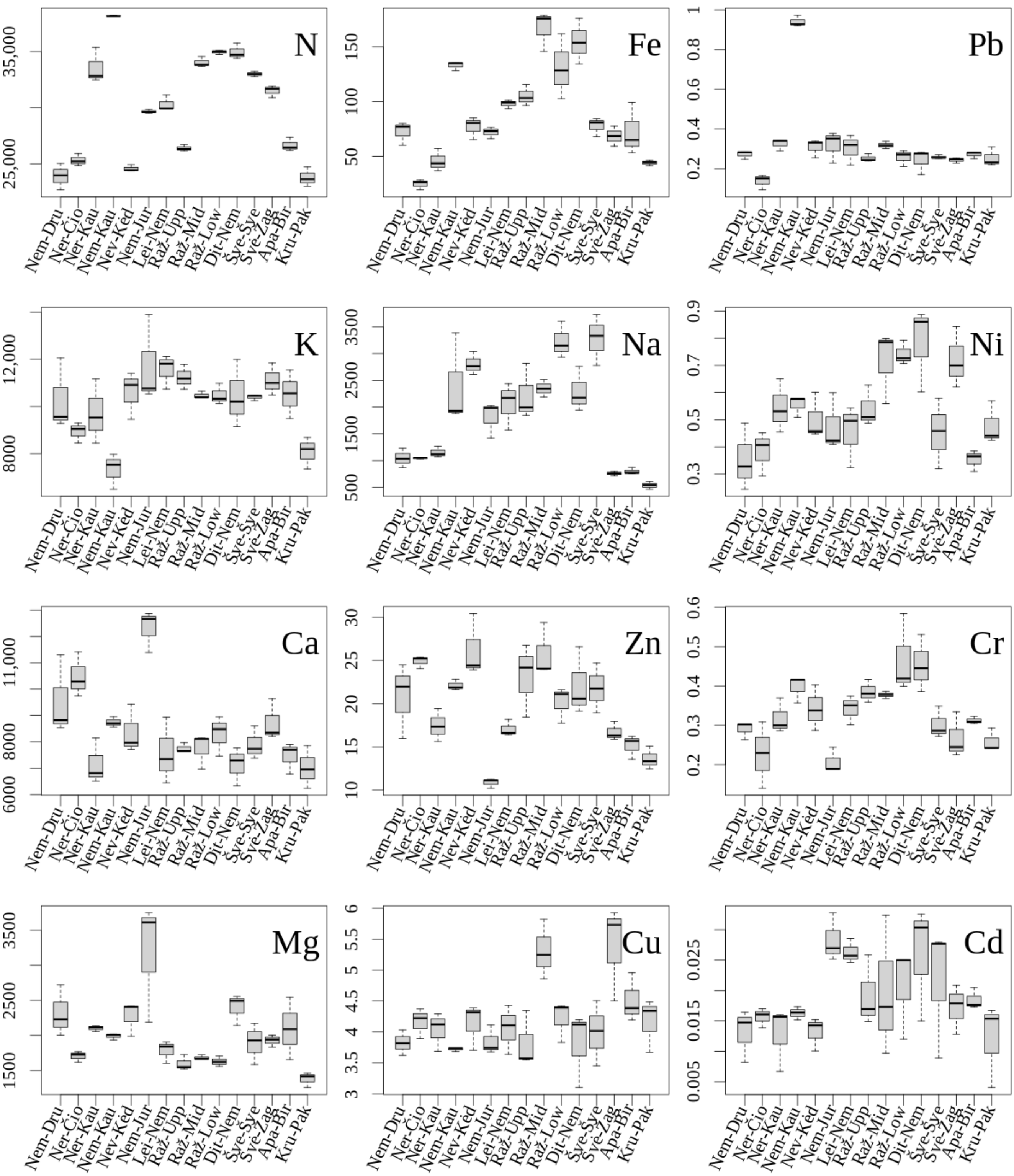

Figure 2. Median values (box–whisker plots) of the leaf element concentrations (µg/g d. m. in y axes) in *L. salicaria* populations in Lithuania. The central line of each box indicates the median value; the boxes, the lower (25%) and upper (75%) quartiles; and the whiskers are from the 10th to 90th percentiles (typical range). The median (central horizontal line) with 25/75 percentiles (boxes), 10/90 percentiles (bars); the number of replicates per population n = 3.

3.2. Comparison of Groups of Populations

Among the investigated populations of *L. salicaria*, 47% of the populations belonged to the Nemunas basin, 33% to the Seaside Rivers basin and 20% to the Lielupė basin. The leaves of the *L. salicaria* populations in the Nemunas basin were characterized by the following element concentrations (median value for the group of populations in μg/g d. m.) (Figure 3): N—29,620, K—9563, Ca—8822, Mg—2018, Na—1573, Fe—76.6, Zn—21.6, Cu—3.89, Pb—0.32, Ni—0.46, Cr—0.30, and Cd—0.02.

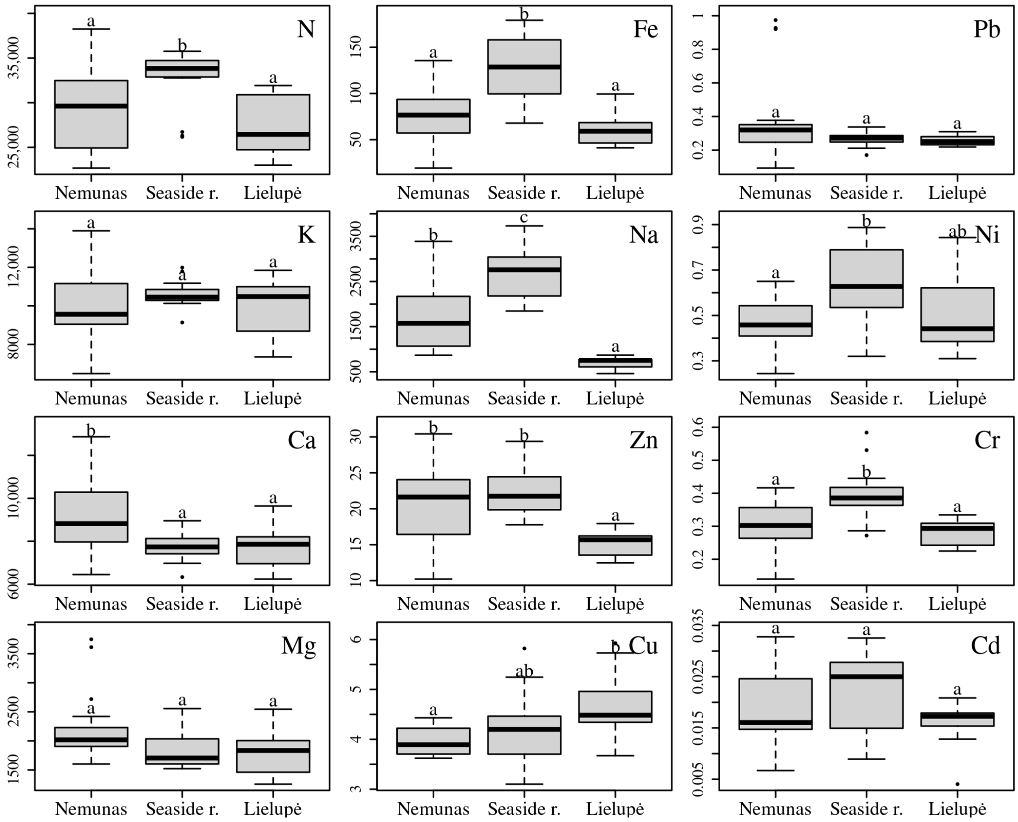

Figure 3. Median values (box–whisker plots) of the leaf element concentrations (μg/g d. m. in y axes) of *L. salicaria* populations, growing in the Nemunas, Seaside Rivers and Lielupė basins. The central line of each box indicates the median value; the boxes, the lower (25%) and upper (75%) quartiles; the whiskers are from the 10th to the 90th percentile (typical range); the points are outliers. Population groups marked with different letters differ significantly ($p < 0.05$).

The leaves of *L. salicaria* populations collected in the Seaside Rivers basin were characterized by the following concentrations of elements (median value for the group of populations in μg/g d. m.) (Figure 3): N—33,830, K—10,452, Ca—7736, Mg—1705, Na—2760, Fe—129, Zn—21.7, Cu—4.20, Pb—0.27, Ni—0.63, Cr—0.39, and Cd—0.02. The leaves of *L. salicaria* populations collected in the Lielupė basin were characterized by the following element concentrations (median value for the group of populations in μg/g d. m.): N—26,450, K—10,482, Ca—7859, Mg—1834, Na—752, Fe—59.1, Zn—15.7, Cu—4.48, Pb—0.25, Ni—0.44, Cr—0.29, and Cd—0.02. Significant ($p < 0.05$) river basin-related differences were documented for the N, Ca, Mg, Fe, Na, Zn, Cu, Ni and Cr elements. The river basin did not have a significant effect on the concentrations of K, Mg, Pb and Cd. The leaves of *L. salicaria* populations collected in the Nemunas basin were characterized by significantly ($p < 0.05$) higher concentrations of Ca (compared to the populations of the Lielupė and Seaside Rivers basins) and Zn (compared to the populations of the Lielupė basin), and significantly lower concentrations of N, Fe, Na, Cu, Ni and Cr, (compared to the populations of the Seaside Rivers basin) (Figure 3). The populations of the Seaside Rivers basin were characterized by significantly ($p < 0.05$) higher concentrations of N, Fe, Na, Ni and Cr (compared to the populations of the Nemunas and Lielupė basins), and significantly ($p < 0.05$) lower concentrations of Ca (compared to the populations of the Nemunas basin) (Figure 3). Populations of the Lielupė basin were characterized by significantly higher concentrations of Cu (compared to the populations of the Nemunas basin), and significantly ($p < 0.05$) lower concentrations of N, Fe and Cr (compared to the populations of the Seaside Rivers basin), Ca (compared to the populations of the Nemunas basin) Na, and Zn (compared to the populations of the Nemunas and Seaside Rivers basins) (Figure 3).

Among the *L. salicaria* populations studied, according to land cover and use, 53% of populations grew adjacent to artificial areas, and 40% of the populations were located adjacent to agricultural areas. Only one population (7%) of *L. salicaria* grew near the forests. The leaves of *L. salicaria* populations growing next to artificial areas were characterized by the following concentrations of leaf elements (median value for the grouped populations (μg/g d. m.)) (Figure 4): N—33,000; K—10,388; Ca—7905; Mg—1894; Na—3281; Fe—77.80; Zn—21.80; Cu—3993; Pb—0.259; Ni—0.453; Cr—0.302; Cd—0.022.

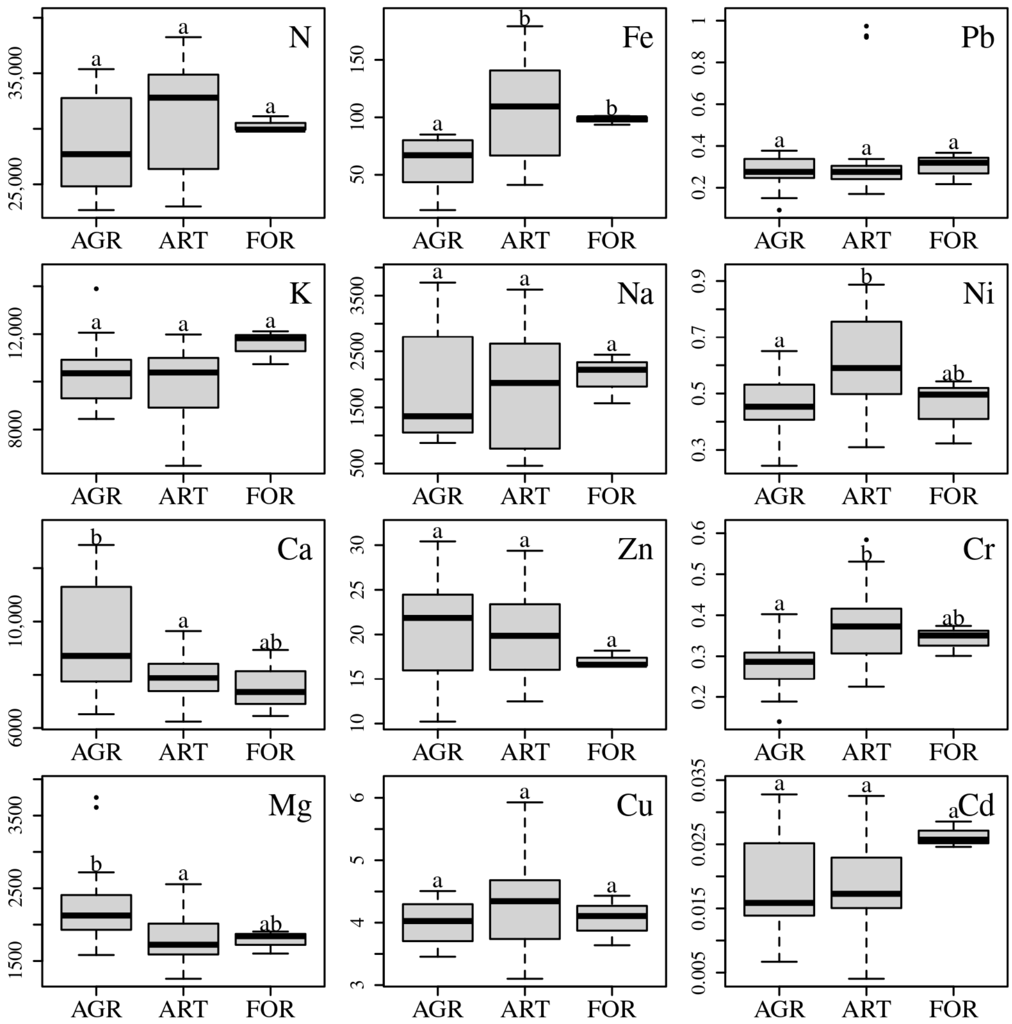

Figure 4. Median values (box–whisker plots) of leaf element concentrations (μg/g d. m. in y axes) of *L. salicaria* populations growing near different type of land (according to cover and use): agricultural areas (AGR), artificial areas (ART) and forest (FOR). The central line of each box indicates the median value; the boxes, the lower (25%) and upper (75%) quartiles; the whiskers are from the 10th to the 90th percentiles (typical range); the points are outliers. Population groups marked with distinct letters differ significantly ($p < 0.05$).

The leaves of populations growing near agricultural areas were characterized by the following concentrations of elements (median values of grouped populations (μg/g d. m.): N—31,308; K—9958; Ca—7860; Mg—1837; Na—1822.5; Fe—110; Zn—19.85; Cu—4.368; Pb—0.348; Ni—0.611; Cr—0.365; Cd—0.019. Populations near agricultural land were characterized by significantly ($p < 0.05$) higher concentrations of such elements as Ca and Mg (compared to artificial areas) and significantly ($p < 0.05$) lower concentrations of Fe (compared to artificial and forest areas) and Ni and Cr (compared to artificial areas), while land cover and use type did not affect the concentrations of N, K, Na, Zn, Cu, Pb and Cd (Figure 4).

According to the nature of riverbeds, 67% of *L. salicaria* populations grew alongside natural riverbeds (N) and 33% alongside regulated riverbeds (R). The leaves of natural riverbed *L. salicaria* populations contained the following concentrations of elements (median values, μg/g d. m.) (Figure 5): N—28,440; K—9904; Ca—8444; Mg—2007; Na—1093; Fe—67.0; Zn—18.4; Cu—4.12; Pb—0.28; Ni—0.46; Cr—0.30; Cd—0.02. The leaves of *L. salicaria* populations of regulated riverbeds contained the following concentrations of elements (median values, (μg/g d. m.): N—33,830; K—10,722; Ca—7653; Mg—1705; Na—2345; Fe—129; Zn—21.1; Cu—4.20; Pb—0.28; Ni—0.63; Cr—0.39; Cd—0.02. *Lythrum salicaria* populations growing near natural riverbeds were characterized by significantly ($p < 0.05$) higher concentrations of Ca and Mg and significantly ($p < 0.05$) lower concentrations of N, K, Fe, Na, Ni, Cr and Cd, and the origin of riverbeds had no significant influence on Zn, Cu and Pb concentrations (Figure 5).

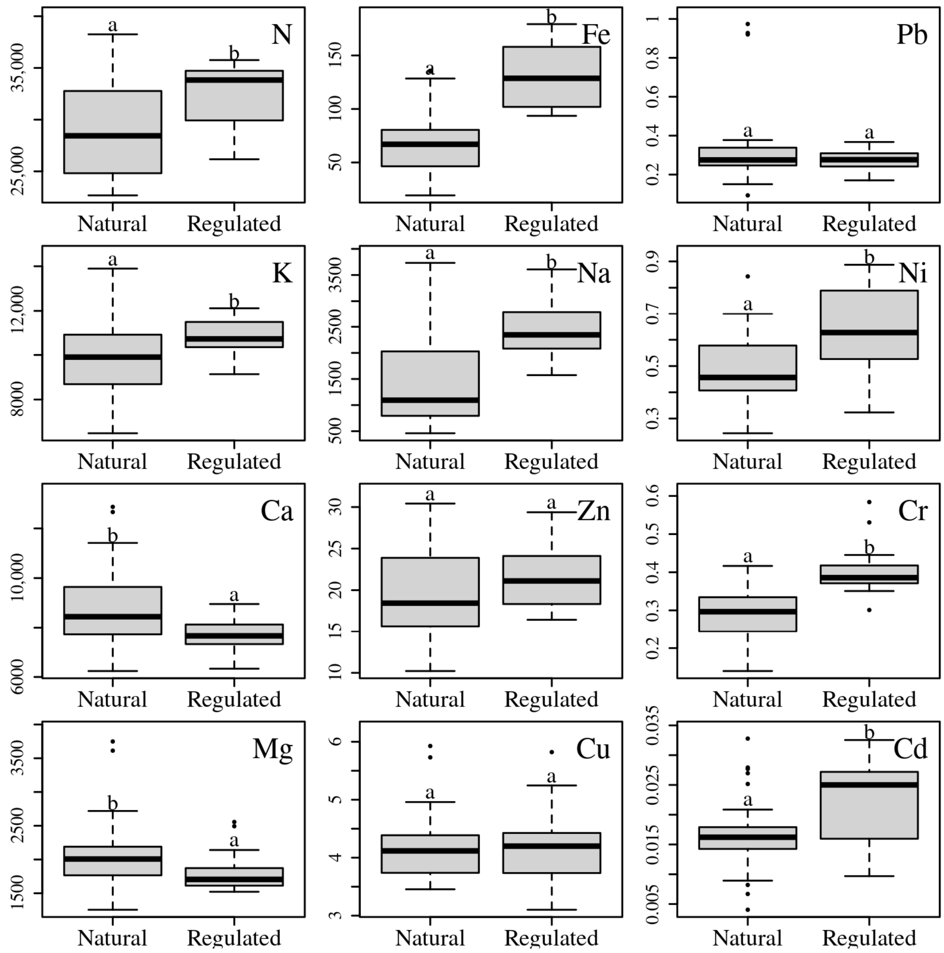

Figure 5. Median values (box–whisker plots) of leaf element concentrations (μg/g d. m. in y axes) of *L. salicaria* populations growing near natural and regulated riverbeds. The central line of each box indicates the median value; the boxes, the lower (25%) and upper (75%) quartiles; the whiskers are from the 10th to 90th percentiles (typical range); the points are outliers. Population groups marked with distinct letters differ significantly ($p < 0.05$).

3.3. Relations between Element and Molecular Data

Looking for relationships between physiological and genetic parameters of *L. salicaria* populations, Spearman rank correlations between element concentrations and PLP.AFLP (percentage of amplified fragment length polymorphic loci) were calculated (Figure 6).

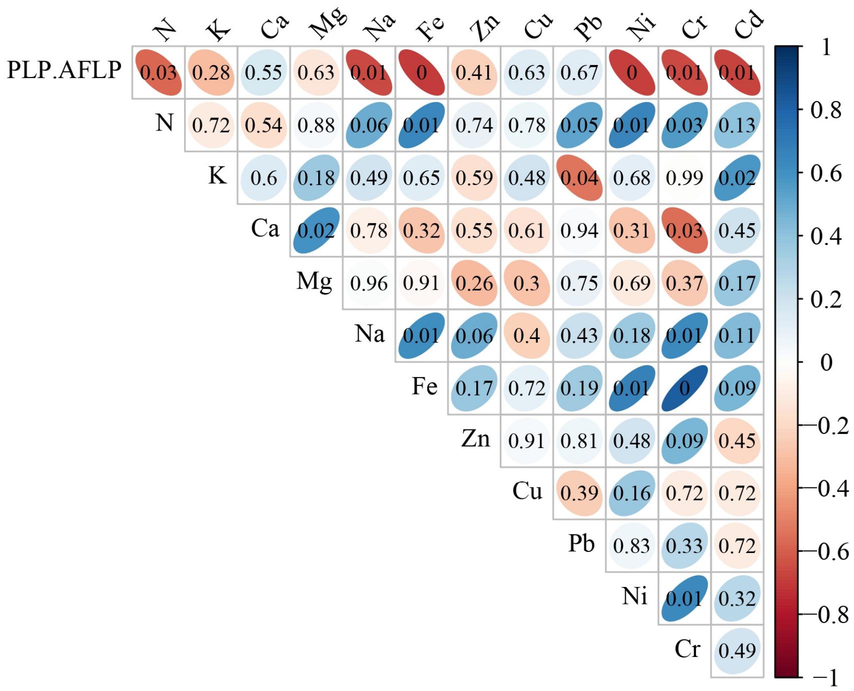

Figure 6. The correlogram of Spearman rank correlation coefficients (Rs) (from −1 to 1) for all pairs of variables of *Lythrum salicaria* populations. Blue color represents positive and red color, negative, correlations. Color intensity indicates the strength of correlation, so the stronger the correlation, the darker the figures. Correlation numbers inside colored figures indicate level of significance; thin ellipsoid figures show significance ($p < 0.05$) while figures towards a spherical shape show insignificant correlations. PLP.AFLP—percentage of amplified fragment length polymorphic loci. N, K, Ca, and Mg—macroelements. Na—beneficial element. Fe, Zn, Cu—micronutrients. Pb, Ni, Cr, and Cd—non-essential elements.

Concentration of N was positively correlated with concentrations of Na (Rs = 0.536, $p < 0.0396$), Fe (Rs = 0.643, $p < 0.0097$), Ni (Rs = 0.679, $p < 0.0054$), and Cr (Rs = 0.631, $p < 0.0117$). The concentration of K was positively correlated with the concentration of Cd (Rs = 0.591, $p < 0.0204$). The concentration of Na was positively correlated with the concentrations of Fe (Rs = 0.732, $p < 0.0019$), Zn (Rs = 0.557, $p < 0.031$), and Cr (Rs = 0.66, $p < 0.0075$). The concentration of Fe was positively correlated with the concentrations of N (Rs = 0.643, $p < 0.0097$), Na (Rs = 0.732, $p < 0.0019$), and Cr (Rs = 0.854, $p < 0.001$). The concentration of Zn was positively correlated with the concentration of Na (Rs = 0.557, $p < 0.031$). The concentration of Ni was positively correlated with the concentration of N (Rs = 0.621, $p < 0.0135$). The concentration of Cr was positively correlated with the concentrations of N (Rs = 0.631, $p < 0.0117$), Na (Rs = 0.66, $p < 0.0075$), and Ni (Rs = 0.621, $p < 0.0135$). The concentration of Cd was positively correlated with the concentration of K (Rs = 0.591, $p < 0.0204$). The concentrations of Ca, Mg, Zn, Cu, and Pb did not correlate with any other element concentration.

The PLP.AFLP was negatively correlated with concentrations of N (Rs = −0.657, $p < 0.0078$), Na (Rs = −0.793, $p < 0.0004$), Fe (Rs = −0.721, $p < 0.0024$), Ni (Rs = −0.538, $p < 0.0386$), Cr (Rs = −0.584, $p < 0.0221$), and Cd (Rs = −0.781, $p < 0.0006$).

In order to clarify which parameters were most important for the variability of *L. salicaria* populations, a principal component (PC) analysis was performed (Figure 7) using concentrations of elements and PLP.AFLP variables.

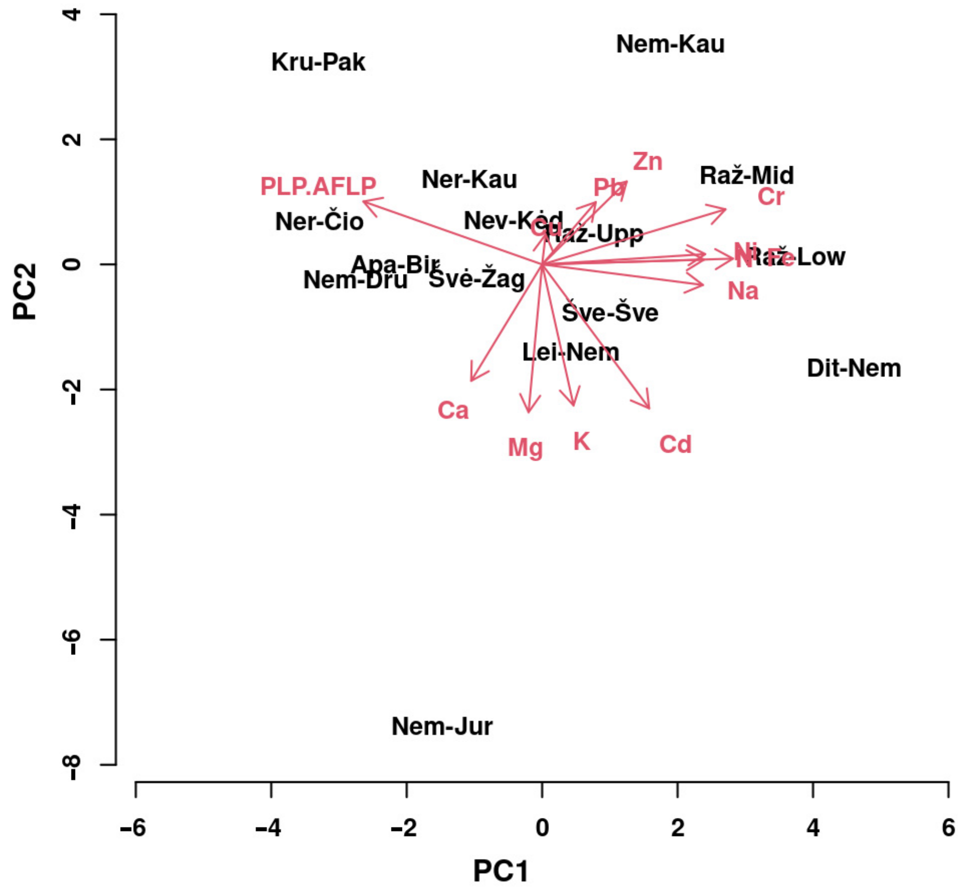

Figure 7. Biplot of the principal component analysis for the first two principal components of a model testing variation of *Lythrum salicaria* populations depending on PLP at AFLP loci and concentrations of macronutrients (N, K, Ca, and Mg), Na, micronutrients (Fe, Zn, and Cu), and non-essential elements (Pb, Ni, Cr, Cd). Titles of populations are in black letters (Figure 1; Table 1), and red arrows with letters denote variables.

Our study showed that the first four PCs were quite informative, accounting for 79.76% of the overall variance for the entire set of variables. For separate principal components PC1, PC2, PC3, and PC4, the variance (with eigenvalues) was as follows: 36.38% (4.730), 19.50% (2.535), 14.11% (1.834), and 9.77% (1.270), respectively. PC1 variability was mainly caused by the concentrations of Fe, Cr, PLP.AFLP, and concentrations of Ni, N, Na, and Cd; the contribution of concentrations of most elements was positive, with the exception of Ca and Mg. For variability of PC2, concentrations of Mg, Cd, K, Ca and Zn, and PLP.AFLP were the most important; contributions of Zn, PLP.AFLP, Pb, Cr, Cu, Na, Ni, Fe and N were positive; and contributions of Mg, Cd, K, Ca and Na were negative. According to the variability of the parameters, displayed in the biplot of two principal components, the importance of the variables (in descending order) in PC1 was as follows: Fe > Cr > PLP.AFLP > Ni > N > Na > Cd > Zn > Ca > Pb > K > Mg > Cu, and the order of importance of the variables in PC2 was different: Mg > Cd > K > Ca > Zn > PLP.AFLP > Pb > Cr > Cu > Na > Ni > Fe > N.

The most extreme locations in the PC biplot were characteristic for populations of the Seaside Rivers basin (Dit-Nem, and Raž-Mid), Nem-Kau, Nem-Jur, and Kru-Pak. Compared to the remaining populations, (1) PLP.AFLP was the highest (65.4%,) and the concentrations of N and Ca, Mg and Na were the lowest, for population Kru-Pak; (2) the least-polymorphic population (PLP.AFLP = 35.0%), Dit-Nem, did not show extreme concentrations of either element; (3) the concentrations of N and Pb were the highest and the concentrations of K and Cu the lowest for population Nem-Kau; (4) the concentrations of K, Ca, Mg and

Cd were the highest, and the concentrations of Zn and Cr were the lowest, for population Nem-Jur; (5) Rąž-Mid had the highest concentrations of Fe and Cu.

4. Discussion

Despite the fact that *L. salicaria* is widely distributed in the world as a naturally growing or invasive species, element data for this species were not found in the most extensive European and Asian studies of ionomics [13,14,65–67]. The concentrations of elements in the leaves, more often in the aboveground or in undetermined parts of *L. salicaria* growing in the natural environment, have been documented only in rare cases [68–73]. Recently, ionome analyses of *L. salicaria* have mostly been performed in hydroponic experiments with nutrient and/or heavy metal additions [74,75], so the comparison of our data with such cases is very relative.

4.1. Macroelements

Nitrogen. Nitrogen concentrations in Lithuanian *L. salicaria* (23,790–38,183 µg/g d. m., leaves, Figure 2) were similar to the nitrogen concentration in this species in the flood model (15,000–21,000 µg/g d. m., aboveground part) [75]. When *L. salicaria* was grown in a medium with nitrogen, phosphorus and potassium for 70 days, the nitrogen concentration was higher (42,000 µg/g d. m.) [76]. Compared to the other riparian species of Lithuania (*Phalaris arundinacea*, *Bidens frondosa*, *Phragmites australis*, *Echinocystis lobata*), *Lythrum salicaria* demonstrated the lowest leaf N concentration [77]. Very often, riparian community data are discussed in relation to the nutritional state of the species [78]. Compared to the abundance of other Lithuanian macrophytes [10], the abundance of *L. salicaria* individuals is not high. In contrast to our sampling sites, within the invasive range (wetlands of North America), *Lythrum salicaria* is forming dense monolithic stands [3–5]. Nitrogen is the most important element for biomass production. *Lythrum salicaria* may have encountered excess nitrogen in the invaded areas. Compared to the other species studied by us, *L. salicaria* showed the largest differences in nitrogen concentration between populations. Such a fact indicates the potential of the species to use higher amounts of nitrogen. Our nitrogen data are supported by the indicator value of soil nutrient richness (nitrophobic–nitrophil interval 1–9) [12], according to which *L. salicaria* was defined as a species growing in various soils. A soil richness study of *L. salicaria* in the Czech Republic showed an average indicatory value (5.6) among other species, with soil richness ranging from 2.4 to 7.1 [79]. The worldwide invasion success of European species is likely to have been promoted by the global increase in nutrient-enriched sites. It is postulated that alien plants are successful invaders because they have a broader capability for nutrient consumption than native plants [80,81]. In addition, it has been shown that species from more productive habitats are more invasive [79]. Greenhouse experiments on water and nitrogen additions to invasive *Bidens frondosa* and native *B. tripartita* revealed higher phenotypic plasticity for the alien species [68]. It has been shown that in eutrophic environments, *Lythrum salicaria* may invest nitrogen in building root biomass; thus, cultivation of the plants in constructed wetlands can successfully reduce the nitrogen concentration from wastewater [82].

The potential of the species to use elevated amounts of nitrogen, revealed in our study, corresponds to numerous phytoremediation studies. Cultivation of *L. salicaria* in a eutrophic environment (constructed wetland) successfully reduced the nitrogen concentration in wastewater [82]. In constructed wetland conditions, *L. salicaria* was a valuable nitrogen absorber which could be used to remove excess nitrogen [44]. This plant effectively removed nitrogen from antibiotic-contaminated wetlands [83]. In artificial wetlands with *L. salicaria* and *Canna indica,* the plants removed more than 90% of nitrate, ammonia or total of nitrogen [42]. In the studies with supplied contaminants, most often, only the nitrogen effect is examined. Wide-scope analyses of experimental data revealed that an excess of N might aggravate the uptake of phosphorus, and the consumption of other elements might be disturbed [84]; thus, a bigger set of elements should be included in phytoremediation assessments of *L. salicaria*.

Potassium. Potassium, along with calcium, is the most abundant element in leaves after nitrogen, highlighting its major contribution to plant functioning [85]. The potassium concentrations (7327–11,732 μg/g d. m., leaves) of Lithuanian *L. salicaria* were similar to the data on *L. salicaria* (5000–18,000 μg/g d. m., aboveground parts) in the flood simulation experiment [75]; a higher potassium concentration (16,500 μg/mg d. m., aboveground parts) was determined in *L. salicaria* growing in the flood plains of the Tisza River [68,69]. *Lythrum salicaria* growing in the flood plains of the Tisza River contained less potassium and much more sodium than meadow-hays [68]. After 70 days of incubation of *L. salicaria* in a medium containing nitrogen, phosphorus and potassium, very high concentrations of potassium (80,000 μg/g d. m., leaves) [76] were documented, in parallel with changes in plant architecture, dry mass of the aboveground part and leaf area.

Calcium. The calcium concentrations in Lithuanian *L. salicaria* (7018–12,306 μg/g d. m., leaves) were very similar to concentrations of calcium of *L. salicaria* from Rhodes Island in Greece (892–1247 μg/g d. m. leaves) [72] and *L. salicaria* in the flood simulation experiment (5000–18,000 μg/g d. m. aboveground parts) [75] and lower than the concentration of calcium of *L. salicaria* in the flood plains of the Tisza River (15,800 μg/mg d. m., aboveground part) [68,69]. After 70 days of incubation of *L. salicaria* in a medium containing nitrogen, phosphorus and potassium, higher concentrations of calcium (80,000 μg/g d. m., leaves) [76] were determined, similar to what was obtained in the case of potassium.

Magnesium. In addition to the well-known role of magnesium in the vitality of plants [86], it was shown that Mg inhibits the absorption of heavy metals and therefore reduces their toxicity in plants [87]. The magnesium concentrations in Lithuanian *L. salicaria* (1377–3183 μg/g d. m., leaves) encompassed the magnesium concentration of *L. salicaria* in the flood plains of the Tisza River (2640 μg/g d. m.) [69] and were lower than magnesium concentrations in *L. salicaria* on Rhodes Island, Greece (3469–4741 μg/g d. m., leaves) [72].

4.2. Microelements

Iron. It was estimated that a concentration of Fe > 500 μg/g d. m. is phytotoxic [87]. The iron concentrations in Lithuanian *L. salicaria* (24.7–167.1 μg/g d. m., leaves, Figure 3) were lower compared to *L. salicaria* in the flood plains of the Tisza River (254 μg/g d. m., aboveground parts) [69] and nearly twice the concentration in *L. salicaria* (328 μg/g d. m., aboveground parts) found in the tidal wetlands of Belgium and The Netherlands [88].

Sodium. Sodium is beneficial to many species at lower levels of supply and essential in some species (e.g., C_4) [89]. According to the salt indicator value of 1 (on a scale of 0–9 for salt), [12] *L. salicaria* is salt tolerant; it usually grows in low-salt to salt-free soils, while most of the riparian species of Lithuania have a salt indicator value of 0 (glycophytes, which do not tolerate salts). Some of our selected populations grew close to the sea, where the atmosphere is enriched by sodium-containing aerosols. The sodium concentrations in *L. salicaria* were lower in the flood plains of the Tisza River (520 μg/g d. m., aboveground parts) [69].

Zinc. Zinc enters the environment through sewage sludge and municipal waste [90]. The concentration of zinc in plants ranges from 15 to 100 μg/g d. m. [54]. At low concentrations, zinc acts as a micronutrient but becomes toxic when its concentration in the plant reaches 100 μg/g d. m. [87], and at a concentration of 300 μg/g d. m., visible symptoms of leaf damage appear. There is evidence that zinc is able to alleviate cadmium-induced toxicity [91]. The zinc concentrations in Lithuanian *L. salicaria* (10.88–26.24 μg/g d. m., leaves) were comparable to the zinc concentrations in *L. salicaria* from Sevan Lake in Armenia (the number was taken from figure, ~20 μg/g d. m., leaves) [71]. Two or more times' higher concentrations of zinc were found in *L. salicaria* from the tidal wetlands of Belgium and The Netherlands (59.6 μg/g d. m., aboveground parts) [88], in *L. salicaria* near Köprüören Pond in Turkey (110 μg/g d. m., aboveground parts) [92], in *L. salicaria* from Rhodes Island in Greece (87.7–178.4 μg/g d. m. leaves) [72], and in *L. salicaria* from the flood plains of the

Tisza River (172.8 µg/g d. m., aboveground parts) [69]. Comparative analyses showed that *L. salicaria* accumulates more Zn than other hydrophytes [69,71]. After seven days of growth of *L. salicaria* seedlings in the solutions of zinc (up to 100 mg/L zinc), the concentration of zinc accumulated in the leaves reached 1084.7 µg/g d. m. Considering the high capacity of *L. salicaria* to accumulate zinc and tolerate high zinc concentrations, this species might be used for phytoremediation [93].

Copper. At low concentrations, Cu, like Zn, normally acts as a micronutrient but becomes toxic when its concentration in the plant increases [87]. Copper concentrations in Lithuanian *L. salicaria* (3.72–5.30 µg/g d. m., leaves) were the same as in *L. salicaria* from Lake Sevan in Armenia (the number was taken from the figure, ~5 µg/g d. m., aboveground parts) [71] or from the tidal wetlands of Belgium and The Netherlands (6.81 µg/g d. m., aboveground parts) [88]. Almost twice the copper concentrations were found in *L. salicaria* from the flood plains of the Tisza River (9.8 µg/g d. m., aboveground parts) [69] and Rhodes Island in Greece (10.0–14.4 µg/g d. m., leaves) [72].

4.3. Heavy Metals

The toxicity of heavy metals is an important factor limiting plant growth and development [94–96]. Metal stress responses have been extensively examined among food species [97], with inconclusive information on naturally growing macrophytes [91] receiving unused fertilizers and pesticides. In the Baltic region, much attention has been paid to the study of heavy metals in conifers and mosses [98–101], while the data on elements of herbaceous angiosperms are still very scarce [102].

Lead. The toxic concentrations of lead for plants are >27 µg/g d. m. [87]. As in aboveground parts of vegetation collected from the buffer zones of wetlands in Lithuania [103], the lead concentrations in Lithuanian *L. salicaria* were within the background values (0.136–0.940 µg/g d. m. leaves, Figure 3) and similar to the lead concentrations in *L. salicaria* in Lake Sevan, Armenia (the number was taken from the figure, ~0.1 µg/g d. m., aboveground parts) [71] or to tidal wetlands of Belgium and The Netherlands (1.02 µg/g d. m., aboveground parts) [92] as well as to Rhode Island, Greece (0.1–1.5 µg/g d. m., leaves) [72]. Growth of *L. salicaria* in lead-containing soil reduced the aboveground mass, but the belowground parts of the plant remained intact due to the ability to replace damaged shoots with new ones developing from healthy roots [40,41]. Evaluating the effects of lead concentrations (up to 2000 mg/L) on the growth of *L. salicaria* revealed tolerance to lead contamination [40].

Nickel. Nickel concentrations in Lithuanian populations of *L. salicaria* were low (0.353–0.783 µg/g d. m., leaves) and were very similar to *L. salicaria* from the tidal wetlands of Belgium and The Netherlands (0.489 µg/g d. m., aboveground parts) [92] or lower than in Rhodes Island in Greece (0.5–1.5 µg/g d. m., leaves) [72] or Lake Sevan in Armenia (number was taken from figure, ~1.2 µg/g d. m., aboveground parts) [71]. After 15 days of hydroponic cultivation of *L. salicaria* seedlings in a medium enriched with nickel up to 100 mg/L, the plants accumulated significantly more nickel (418.4 µg/g d. m., leaves) [104] than in the natural environment (described above).

Chromium. The adverse effect of chromium on the growth of plants is related to the disturbed metabolism of nutritional elements [105]. Concentrations of chromium in Lithuanian populations of *L. salicaria* were low (0.207–0.467 µg/g d. m., leaves), compared to several times' higher concentration of chromium in *L. salicaria* from the tidal wetlands of Belgium and The Netherlands (2.20 µg/g d. m., aboveground parts) [88] or to Rhodes Island in Greece (0922–4160 µg/g d. m., leaves) [72].

Cadmium. Cadmium is toxic to plants due to its ability to displace certain nutrients as components of enzymes. In addition, cadmium may impair nutrient uptake, causing a deficiency of calcium [106]. The cadmium concentrations in Lithuanian *L. salicaria* (0.012–0.028 µg/g d. m., leaves) were several times lower than those in Rhode Island (0.109–0.327 µg/g d. m., leaves) [72], in the tidal wetlands of Belgium and The Netherlands (0.173 µg/g d. m., leaves) [88], and in Lake Sevan in Armenia (number taken from figure, ~0.2 µg/g d. m., aboveground parts) [71]. According to the growth rate and the accumulation of Cd and other heavy metals (Zn, Cu, Pb), in a comparison of nine other Chinese plant species [43], *Lythrum salicaria* appeared to be the most resistant to pollutants and very good at absorbing and accumulating metals in stems and leaves.

4.4. Ionome-Environment Relationships

River basins. Biologists and agronomists are increasingly interested in the dependence of plant properties on environmental parameters [48,107]. Recent studies have shown that the elemental concentration profile of *Arabidopsis halleri* (L.) allowed discrimination depending on geographical location [108]. The classification of *Lythrum salicaria* populations studied by us into three groups according to the Nemunas, Seaside Rivers and Lielupė basins (Table 1) revealed statistically significant differences in element concentrations (Figure 3), which could be caused by both the natural environment and human influence. Higher sodium concentrations in *L. salicaria* populations located in the Seaside Rivers basin were probably related to the presence of sodium-containing aerosols near the Baltic Sea. Higher concentrations of N, Ni and Cr in *L. salicaria* populations from the Seaside Rivers basin may have resulted from very close residences, very intensive tourism and ornamental horticulture.

Land cover and use. Land cover and land use did not affect the concentrations of N, K, Na, Zn, Cu, Pb and Cd (Figure 4) for the groups of *L. salicaria* populations we studied (mostly belonging to agricultural and artificial areas) (Figure 4). Differences in land cover and use type were not reflected in leaf N concentrations of neighboring macrophyte species populations, either [77]. Such results could be caused by the reduced intensification of Lithuanian agriculture, transitioning to environmentally friendly farming, and the simultaneous increase in the load of the aforementioned elements in artificial territories. Growth of *Lythrum salicaria* in flooded or non-flooded soil cores from different land-use areas (agricultural and semi-natural grassland in the floodplain of the Beerze River in The Netherlands) also showed no significant differences in aboveground N concentration, but *L. salicaria* was more productive after winter flooding in agricultural areas [75]. An assessment of potential invasive effects on phosphorus metabolism in a waterlogged area in Minnesota with *Lythrum salicaria* displacing *Typha* sp. was inconclusive [70].

River regulation. After the Second World War, the intensification of Lithuanian agriculture was extremely important. More than 80% of the country's riverbeds have been restructured [60]. There is evidence of various damage to the landscape (habitat fragmentation, reduced macrophyte diversity) caused by river regulation [109]. Based on the data of present study, populations of *L. salicaria* near regulated riverbeds were characterized by significantly lower concentrations of Ca and Mg and significantly higher concentrations of N, K, Fe, Na, Ni, Cr and Cd (Figure 5). Fragments of regulated Lithuanian riverbeds can occur in soils that were previously used for agriculture and were enriched with N and heavy metals due to the use of fertilizers or pesticides. In parallel with *L. salicaria* ionomic transformations, significant differences in molecular diversity were recorded at AFLP loci [22] between the same population groups from natural and regulated riverbeds. Studies of other aquatic species (*Phalaris arundinacea*, *Batrachium* spp. and *Bidens* spp.) have also revealed significant changes in genetic diversity associated with river canalization [110–112].

4.5. Ionome–Genome Relationships

A assessment of AFLP loci in the same populations of *Lythrum salicaria* has shown that molecular diversity of *L. salicaria* populations in Lithuania varied significantly depending on the river basin, land cover and use type, and river regulation [22]. This was supported by the results of a significant 7% molecular variation of microsatellite loci of *Nuphar lutea* populations from the Nemunas Basin [113].

Until now, there have been few attempts to integrate plant ionomics and genomics [51,96,114,115]. Due to heavy metal exposure, isoenzymatic and cytological changes have been recorded in *Pinus sylvestris* populations in subsequent generations [115].

Analyses of fragmented amplified polymorphic sequences and microsatellite loci markers in Brassicaceae have led to the discovery of genes associated with heavy metal tolerance and/or hyperaccumulation [51]. Genome-wide association studies revealed polymorphisms (SNPs) affecting genomic variation in *Manihot esculenta* [116].

Present study examined the interrelationships between genetic and physiological parameters of *Lythrum salicaria* populations. The results showed that populations with a higher percentage of polymorphic loci had lower leaf concentrations of N, Na, Fe, Ni, Cr and Cd (Figure 6). Furthermore, the percentage of polymorphic AFLP loci and Fe and Cr concentrations were the most important factors contributing to population variability (Figure 7).

Leaf nutrient concentrations were within normal limits for growth and development, and heavy metal concentrations did not reach toxic levels. Our ionomic data show that the growth of perennial *L. salicaria* in environments more polluted with nitrogen or heavy metals may have negative consequences on the genetic structure. This assessment extended the ionomic data on leaf elemental concentrations in *L. salicaria* populations growing in their natural range. To confirm the results of this study, future assessments of *L. salicaria* should include more populations that differ in environmental characteristics and represent both native and invasive ranges of the species.

5. Conclusions

A comparison of the ionomic data on *Lythrum salicaria* populations with the amounts of elements defined for the species grown in constructed wetlands with artificial contaminants show that nitrogen or heavy metals pollution levels are not high in Lithuanian riparian habitats. Concentration ranges of Lithuanian *Lythrum salicaria* leaf elements further demonstrated the species' potential for indicatory and phytoremediation applications.

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