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Variation in the Biomass of *Phragmites australis* Across Community Types in the Aquatic Habitats of the Middle Volga Valley

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Abstract: Species composition and biomass are key indicators of vegetation performance. While *Phragmites australis* is extensively studied worldwide, data on its communities and biomass in natural habitats are limited in the European part of the Russian Federation. This study examines *P. australis*-dominated communities and their biomass in wetlands along the Middle Volga River. *P. australis* was either the dominant or co-dominant species in seven community types. Their seasonal maximum aboveground biomass correlated with plant projective cover, being highest in *Schoenoplecteto lacustris-Phragmitetum australis* (mean 1.7 kg m^{-2}), with nearly 100% cover, and lowest (0.5 kg m^{-2}) in *Spirodelo-Phragmitetum australis*, with 50% cover. Compared with communities dominated by *Glyceria maxima*, *Schoenoplectus lacustris*, and *Typha latifolia*, those of *P. australis* had the highest seasonal maximum aboveground biomass in running waters (mean 1.32 kg m^{-2}) but the lowest in standing waters of the Kuibyshev Reservoir (mean 0.70 kg m^{-2}), likely reflecting nutrient availability. A similar pattern was observed for the dominant species alone. The mean belowground biomass of *P. australis* was 1.9 kg m^{-2}, with a belowground/aboveground ratio of 1.5. Similar values were found for *S. lacustris* and *T. latifolia*. The community types and biomass values align with those found in other European regions with warm temperate climates.

Keywords: biomass; communities; *Glyceria maxima*; Middle Volga; *Phragmites australis*; river habitats; *Schoenoplectus lacustris*; *Typha angustifolia*; Kuibyshev Reservoir

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1. Introduction

The common reed (*Phragmites australis* [Cav.] Trin. ex Steud.) is a robust perennial grass frequently found in shallow waters and wetlands, with a nearly global distribution. In its native range [1], it is a dominant or co-dominant species in a wide variety of plant communities [2] and supports numerous invertebrate species and birds [1,3,4]. Moreover, it has been utilized by humans for centuries and provides a range of ecosystem services, both traditional and innovative [2,5].

In North America, native populations of *P. australis* (now classified as *P. australis* ssp. *americanus* [6]) are an integral part of wetlands, historically utilized by Indigenous peoples for various purposes [7]. However, some non-native lineages of *P. australis* [8] have become invasive in North America, significantly altering the structure and species composition of local communities due to their strong competitive ability, e.g., [9,10].

The optimum performance of *P. australis* is in stagnant to slowly flowing waters in mesotrophic to eutrophic conditions, where it forms dense monodominant communities with only a few other species occurring in low abundances. In addition, it tolerates a broad range of environmental conditions, including different climates (from boreal to warm), altitudes (up to 3600 m), hydrological regimes (stagnant to slow-flowing waters with depths of up to 2 m, and temporary droughts), nutrient availability (from oligotrophic to eutrophic), soil pH (from strongly acidic to slightly alkaline), and moderate salinity (reviewed by [1,11]). However, the species is sensitive to mechanical damage, irregular abrupt changes in water level, and highly reducing conditions in bottom sediments [1,11]. Toward the limits of its ecological tolerance, its productivity declines; however, the plant communities often become more diverse, supporting a higher number of co-existing plant species [1,2].

The ambiguous ecological role of *P. australis*, which can be beneficial in some wetland communities but a nuisance in others, has spurred intensive research into its genetic diversity, considering geographic distribution, population age, environmental conditions, and human impacts on habitats. Genetic differences occur among populations at both global and regional scales [12], as well as among clones within the same population, e.g., [13,14]. These variations often manifest in differences in plant morphology and productivity, not only under natural conditions [14], but also when the plants are grown under identical conditions in a controlled environment [15,16]. However, *P. australis* also exhibits considerable phenotypic plasticity, with its growth response being highly adaptable to varying environmental factors such as water regime and nutrient availability, e.g., [11,17,18].

In most studies, plant morphological traits and biomass production are the primary indicators of performance. However, these data are unevenly distributed across regions. While extensive research has been conducted in North America, Western and Central Europe, and East Asia, information on the performance of *P. australis* in the European part of the Russian Federation is limited in the English-language literature, despite numerous publications in Russian. This holds also for the Volga River Valley, where detailed reports on aquatic and wetland vegetation dominated by *P. australis* are limited to the Lower Volga [19,20].

The general purpose of this study is to fill the gap in knowledge regarding aquatic and wetland vegetation dominated by *P. australis* in the Middle Volga Valley. Its objectives are as follows:

1. To provide an overview of the species composition of plant communities dominated or co-dominated by *P. australis*, in relation to their aboveground biomass.
2. To assess the aboveground biomass of monodominant *P. australis* communities compared to other tall helophytes (*Glyceria maxima*, *Schoenoplectus lacustris*, and *Typha latifolia*), with separate analyses for running water habitats and standing water habitats exemplified by the littoral zones of the Kuibyshev Reservoir.
3. To compare the aboveground biomass of dominant tall helophytes in their monodominant communities, for both running and standing water habitats, with a particular focus on biomass in relation to projective cover, used as a proxy for shoot density.
4. To evaluate the belowground biomass and the belowground-to-aboveground biomass ratios for the four helophytes studied.

2. Materials and Methods

2.1. Study Area

The Middle Volga River is the middle course of the Volga River. It is bounded by the mouth of the Oka River (Nizhny Novgorod, 56°16.2′ N 44° 0.0′ E) and the mouth of the Kama River (Kamskoye Ustye, 55°12′ N 49°16′ E) (Figure 1). The riverbed has a length of approximately 815 km. Its valley extends across the eastern part of the East European Plain, covering a total area of 258,000 km^2. The landscape is predominantly flat to gently hilly, with altitudes ranging mostly between 100–200 m, and reaching up to 380 m at their highest points.

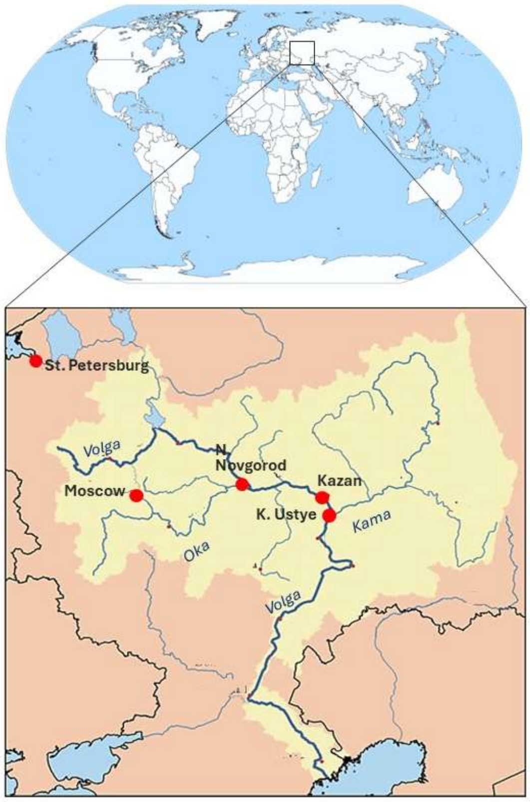

Figure 1. Map of the Volga River catchment.

The Middle Volga Valley lies within the temperate climatic zone, characterized by cold, snowy winters and warm, rather humid summers (classified as Dfb according to the Köppen and Geiger system). Minimum annual temperatures of −8 to −13 °C are recorded in January and maximum annual temperatures of 14–25 °C in July (1980–2016). The mean annual precipitation is between 690 and 630 mm.

The region's hydrological network is characterized by an intermediate density of rivers, a high density of man-made reservoirs, and a low incidence of wetlands and natural lakes. A notable water body is the Kuibyshev Reservoir, which extends on the Middle Volga and Lower Kama, covering a surface area of 6450 km^2.

2.2. Field Research Overview

The investigations were conducted through several extensive field campaigns carried out during the summer months of the 1980s and 1990s. Each campaign had specific objectives aligned with the aims of this paper. The study plots were distributed along the entire length of the riverbed (815 km) and included various wetland types: running waters, oxbows, littorals of lakes, and artificial reservoirs. The plant species composition and aboveground biomass were assessed in plant communities dominated or co-dominated by *P. australis*.

For comparison, the aboveground biomass was also estimated in monodominant communities of other common tall helophytes, i.e., *Glyceria maxima*, *Schoenoplectus lacustris*, and *Typha latifolia*. The aboveground biomass of the dominant species was assessed in a similar manner. Finally, the belowground biomass was estimated.

Overall, more than 500 plots were investigated, with each campaign including at least 100 samples. The exact numbers of samples are provided in the relevant tables in the Results section.

2.3. Vegetation Records

Aquatic vegetation dominated or co-dominated by *P. australis* was characterized by phytosociological relevés, which recorded the abundance and projective cover of the plant species [21] (referred to as cover in further text). The cover was estimated separately for emergent, floating-leaved, and submerged species on 4 × 4 m plots.

Based on the relevés, the plant assemblages were categorized into community types based on the presence of the dominant and co-dominant species. Plant nomenclature follows the WFO Plant list [22]. The nomenclature of the communities follows the European vegetation classification system [23].

2.4. Biomass Assessment

The aboveground biomass was estimated from the end of July to the end of August, when it reached its seasonal maximum. The samples were taken from 0.5 × 0.5 m^2 plots within the delineated communities. Rooted plants were cut at the soil level while lemnids were collected from the same area on the water surface. Fresh weight was determined on-site for each sample. Selected samples were then dried at 105 °C to a constant weight [24] and the fresh weight/dry weight ratio was calculated.

Belowground biomass was also assessed in a subset of samples of tall helophytes at the same time as aboveground biomass. The material was collected using a corer with a 0.2 m diameter, inserted into the soil to the rooting depth (typically no more than 0.6 m). The cores were extracted and washed on-site to remove sediment. After transport to the laboratory, the plant material was carefully rinsed with tap water, dried at 105 °C to a constant weight, and then weighed.

2.5. Statistical Evaluation

The data fits were made in MS Excel. The normality test was conducted using STATISTICA 12.0 (StatSoft, Inc., Tulsa, OK, USA). Although the data had approximately normal distribution, the data sets differed both in the sample sizes and variances. Therefore, multiple comparisons between data sets were performed using the Games–Howell procedure, following formulas published by Zar [25].

3. Results

3.1. Community Types Dominated or Co-Dominated by P. australis

P. australis dominated seven community types, distinguished by the co-dominant species (Table 1). The most prevalent was *Phragmitetum australis*, where *P. australis* was the only dominant. This type was found in both standing and running waters, natural and artificial. In most cases, *P. australis* had substantial cover (80–90%), resulting in a low incidence of accompanying species. A total of forty-nine other species were found in small quantities, indicating that they were not strictly associated with this community type. This type extended from the bank to depths of up to 150 cm, which was associated with a marked decrease in shoot cover (down to less than 10%).

The community type *Spirodelo-Phragmitetum australis* was also widespread. *P. australis* had a smaller cover (about 50%) than the type above, allowing for the co-dominance of *Spirodela polyrhiza* (30–90%). In standing waters, free-floating species occurred, including abundant *Lemna minor* and admixed *Hydrocharis morsus-ranae*. Among submerged species, *L. trisulca* was common (up to 90% cover) and *Ceratophyllum demersum* and *Utricularia vulgaris* were admixed. In river habitats (not shown in Table 1), the community was poorer in species, with *L. minor* present only in small quantities and no submerged vegetation.

The third common type was *Typheto angustifoliae-Phragmitetum australis*, found in all types of standing or slowly flowing waters (lakes, oxbow lakes, sheltered shallow parts of reservoirs, and large rivers). Four forms were distinguished based on the species present: (a) other species irregularly present in small quantities, (b) a form with marked development of *C. demersum*, *L. minor*, and *S. polyrhiza*, (c) a form with *Potamogeton lucens* and *P. perfoliatus*, and (d) a form with various hygrophytes in shoreline habitats.

The *Equiseto fluviatilis-Phragmitetum australis* type was commonly found in shallow-water habitats with strongly silted bottoms. Despite the high cover of *P. australis* (70–90%), there was still a substantial occurrence of *E. fluviatilis* in the undergrowth (cover 20–40%). *L. trisulca* was common in the water column and various hygrophytes were irregularly present in shallow depths near the shores.

Table 1. Community types dominated or co-dominated by *Phragmites australis* in aquatic habitats in the Middle Volga Valley; R—rivers, S—standing waters.

Community Type	Habitat Type	Soil	Depth (cm)	Plant Species	Projective Cover (%)
Phragmitetum australis	R, S	all types	0–150	*P. australis*	(10) 80–100
Spirodelo-Phragmitetum australis (standing waters)	R, S	fine-grained	40–80	*P. australis*	50
				Spirodela polyrhiza	30–90
				Lemna minor	(30) 50–80
				Lemna trisulca	(30) 50–90
				Hydrocharis morsus-ranae	1–5
				Ceratophyllum demersum	1–5
				Utricularia vulgaris	1–3 (5)
Typheto angustifoliae-Phragmitetum australis.	S	all types	20–100	*P. australis + Typha latifolia*	50–80
				Phalaris arundinacea	1–5 in some cases
				C. demersum	
				L. minor	
				S. polyrhiza	
				Potamogeton lucens	
				P. perfoliatus	
Equiseto-fluviatilis-Phragmitetum australis	R, S	silted	0–70	*P. australis*	70–90
	slow flow			*Equisetum fluviatilis*	20–40
				L. trisulca	70–95
				Carex acuta	1–10
Schoenoplecteto lacustris-Phragmitetum australis	R, S	clay	0–80	*Schoenoplectus lacustris*	40–50
				P. australis	50–60
Ceratophyllo-Phragmitetum australis	S	sandy, sandy-silt	1–90	*C. demersum*	average 70
				P. australis	50
				H. morsus-ranae	5–80
				S. polyrhiza	1–10
				L. minor	1
Nuphareto-Phragmitetum australis	R		0–140	*P. australis*	25–75
	strong currentrapid depth increase from the bank			*Nuphar lutea*	5–80
				H. morsus-ranae	5–80
				S. polyrhiza	40–80
				L. minor	20–30
				Sparganium erectum	1–20
				C. demersum	2–10
				Potamogeton pectinatus	1–5
				Sagittaria sagittifolia	1–3

Schoenoplectetum lacustris-Phragmitetum australis was rare, occurring on clayey bottoms at depths of 0–80 cm. Both co-dominant species had similar covers (50–60%). Other species were scarce.

Ceratophyllo-Phragmitetum australis type was recorded on the Sok River on sandy and sandy-silt soils at depths of up to 90 cm. *C. demersum* had a notably high cover (average

70%), surpassing *P. australis* (about 50%). *H. morsus-ranae* dominated the surface water layer (from 5 to 80%), with *S. polyrhiza* and *L. minor* present in small quantities.

A distinctive feature of the Sok River was also *Nuphareto-Phragmitetum australis*. This community formed 2–3 m wide strips in narrow channel sections characterized by strong currents and a rapid depth increase from the bank. Under such conditions, reed communities (cover 25–70%) with *Nuphar lutea* (cover from 5 to 80%) extended to a depth of 140 cm. The type was relatively rich in species, with abundant *H. morsus-ranae*, *S. polyrhiza*, and *L. minor* on the water surface and *Potamogeton pectinatus* and *C. demersum* in the water column. Emergent species typically included *Sparganium erectum* and *Sagittaria sagittifolia*. In some cases, other macrophyte species were present in small amounts.

3.2. Biomass Values

The seasonal maximum aboveground biomass ranged from 0.2 to 2.3 kg m^{-2} in the delineated communities dominated or co-dominated by *P. australis*, with mean values mostly close to 1.0 kg m^{-2} (Table 2). The values were highest in *Schoenoplecteto lacustris-Phragmitetum australis* (mean 1.7 kg m^{-2}) and lowest (0.5 kg m^{-2}) in *Spirodelo-Phragmitetum australis*.

Table 2. Seasonal maximum aboveground biomass in community types dominated or co-dominated by *Phragmites australis* in wetland and aquatic habitats in the Middle Volga Valley. Values denote means and ranges (in brackets).

Community Type	Biomass (kg Dry Weight m^{-2})
Phragmitetum australis	0.91 (0.43–1.78)
Spirodelo-Phragmitetum australis	0.46 (0.17–0.68)
Typheto angustifoliae-Phragmitetum australis	0.79
Schoenoplecteto lacustris-Phragmitetum australis	2.26 (0.80–1.66)
Ceratophyllo-Phragmitetum australis	1.14 (0.88–1.67)
Nuphareto-Phragmitetum australis	0.85 (0.62–1.30)

The biomass of the four community types dominated by tall helophytes differed between the river habitats and the Kuibyshev Reservoir (Table 3). In river habitats, all four community types had aboveground biomasses close to 1 kg m^{-2}, with *Phragmitetum* reaching the highest (1.3 kg m^{-2}) and *Schoenoplectetum* the lowest (0.7 kg m^{-2}). In the Kuibyshev Reservoir, three community types out of four had lower values than in rivers, with *Phragmitetum* and *Glycerietum* reaching only about 50% of their river biomass. Only *Schoenoplectetum* had a higher biomass in the Reservoir than in river habitats.

Table 3. Seasonal maximum total aboveground biomass (kg dry weight m^{-2}) of communities dominated by tall helophytes (*P. australis*, *G. maxima*, *S. lacustris*, and *T. latifolia*) in running water habitats of the Middle Volga Valley and littoral area of the Kuibyshev Reservoir. Means followed by the same letter are not significantly different among communities within a habitat type at $p \leq 0.05$. Asterisks (*) indicate significant differences for a community between habitat types at $p \leq 0.05$. *SE*—standard error, *n*—number of samples, *ns*—nonsignificant.

Community Type	Running Water Habitats		Kuibyshev Reservoir		
	Mean ± *SE*	*n*	Mean ± *SE*	*n*	
Phragmitetum australis	1.32 ± 0.07^{a}	38	0.70 ± 0.07^{ab}	19	*
Glycerietum maximae	1.16 ± 0.12^{a}	18	0.56 ± 0.03^{b}	41	*
Schoenoplectetum lacustris	0.70 ± 0.07^{b}	33	0.95 ± 0.07^{c}	19	*ns*
Typhetum angustifoliae	0.95 ± 0.04^{c}	62	0.78 ± 0.03^{ac}	115	*

The aboveground biomass of the dominant helophytes (Table 4) mirrored the total aboveground biomass patterns of their respective community types. Of the four helophytes, *P. australis* had the highest biomass in the running water habitats (mean 1.1 kg m^{-2}), while

S. lacustris reached its highest value in standing waters (mean 1.0 kg m^2). The aboveground biomass of each helophyte species was closely related to its cover (Figure 2). In running water habitats, the biomass doubled with each increase from one cover class to the next one. In *P. australis*, the aboveground biomass at a cover of 90–100% was even four times higher than at 60–90% cover.

Table 4. Seasonal maximum aboveground biomass (kg dry weight m^{-2}) of tall helophytes in their monodominant communities in running and standing water habitats in Middle Volga Valley. Means followed by the same letter are not significantly different among species within a habitat type at $p \leq 0.05$. Asterisks (*) indicate significant differences for a species between habitat types at $p \leq 0.05$. *SE*—standard error, *n*—number of samples, *ns*—nonsignificant.

Dominant Species	Running Water Habitats		Standing Water Habitats		
	Mean ± *SE*	*n*	Mean ± *SE*	*n*	
Phragmites australis	1.10 ± 0.16 [a]	54	0.63 ± 0.02 [a]	40	*
Glyceria maxima	0.73 ± 0.09 [b]	31	0.61 ± 0.07 [a]	20	*ns*
Schoenoplectus lacustris	0.61 ± 0.07 [c]	31	1.00 ± 0.11 [b]	23	*
Typha angustifolia	0.83 ± 0.05 [b]	66	0.91 ± 0.03 [b]	83	*ns*

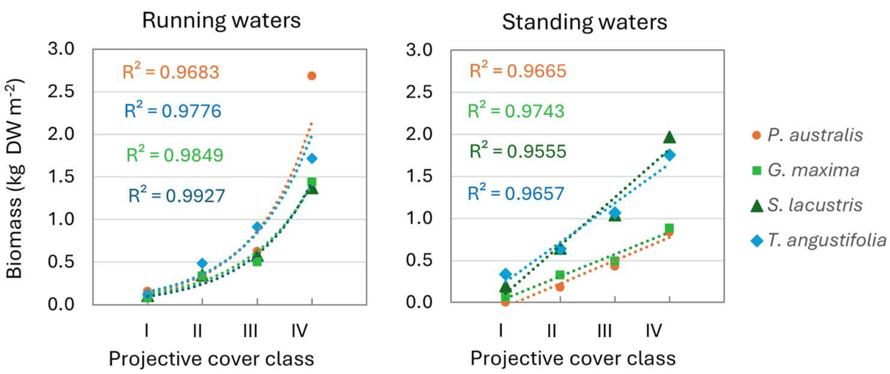

Figure 2. Seasonal maximum aboveground biomass of tall helophytes in running and standing water habitats in the Middle Volga Valley in different classes of projective cover (I: 0–30%, II: 30–60%, III: 60–90%, IV: 90–100%). R^2 denote determination coefficients for exponential and linear fits for species cover in running and standing water habitats, respectively. The colors of fits correspond to the colors for species given in the legend.

The mean belowground biomass in monodominant stands of *P. australis*, *T. angustifolia*, and *S. lacustris* ranged from 1.7 to 1.9 kg m^{-2}, corresponding to an aboveground to belowground biomass ratio of about 1.5. In comparison, the belowground biomass values were markedly lower for *G. maxima* (Table 5).

Table 5. Belowground biomass (kg dry weight m^{-2}) and belowground to aboveground biomass ratio (B/A) of tall helophytes, indicated by means ± standard error; *n*—number of samples. Means followed by the same letter within a column are not significantly different at $p \leq 0.05$.

Plant Species	Belowground Biomass	*B*/*A*	*n*
Phragmites australis	1.89 ± 0.18 [a]	1.54 ± 0.05 [a]	35
Glyceria maxima	0.70 ± 0.06 [b]	0.77 ± 0.02 [b]	15
Schoenoplectus lacustris	1.75 ± 0.33 [a]	1.41 ± 0.01 [a]	13
Typha angustifolia	1.68 ± 0.23 [a]	1.47 ± 0.02 [a]	38

4. Discussion

4.1. Vegetation Types

In the European vegetation classification system [23], community types dominated by tall helophytes fall under the alliance *Phragmition australis* Koch 1926. The four associations identified in this study align with those within this alliance: *Phragmitetum australis* Savič 1926, *Glycerietum maximae* Nowiński 1930 corr. Šumberová, Chytrý et Danihelka in Chytrý 2011, *Schoenoplectetum lacustris* Chouard 1924, and *Typhetum angustifoliae* Pignatti 1953. All of them are common in Europe [26], including its eastern regions [27,28].

This study describes seven community types within the *Phragmitetum australis* association, highlighting their species diversity and total aboveground biomass. Five types characterized by a co-dominant species may be considered transitional with other associations where that species is both dominant and diagnostic. In addition to the helophyte associations mentioned above, these include *Equisetetum fluviatilis* Nowiński 1930, *Ceratophylletum demersi* (Soó 1927) Eggler 1933, and *Nymphaeo albae-Nupharetum luteae* Nowiński 1927. *Spirodelo-Phragmitetum australis* may be regarded as a sub-type with a well-developed synusia of lemnids.

As shown in Table 1, the presence of a co-dominant species is facilitated by a limited cover of *P. australis*, usually below 50–70%. Raspopov [29] also describes communities with dominant *P. australis* and a co-dominant occurring in lakes of northwestern Russia. He identified several community types with various *Potamogeton* species, *N. lutea*, *E. fluviatile*, and *S. lacustris*, as well as other types not identified in this study.

4.2. Biomass and Its Relationship to Other Community Characteristics

The extensive research presented in this paper demonstrates that in communities dominated by *P. australis*, the total aboveground biomass is typically around 1 kg m^{-2} (Table 2). Variations among the community types were linked to the cover of *P. australis*, both alone and in combination with co-dominant species. This relationship is evident when comparing the projective cover in Table 1 with the aboveground biomass in Table 2. Specifically, the lowest total aboveground biomass was observed in the community type *Spirodelo-Phragmitetum australis*, where the *P. australis* cover is about 50%. On the other hand, the highest biomass was found in *Schoenoplecteto lacustris-Phragmitetum australis*, with a combined cover of *P. australis* and *S. lacustris* reaching about 100%.

The correlation between aboveground biomass and cover was also demonstrated for all four helophytes, studied separately in running water habitats and the littoral area of the Kuibyshev Reservoir (Figure 2). As expected, the total aboveground biomass of the community types closely correlated with the aboveground biomass of the dominant species. This is evident by comparing the values in Tables 3 and 4, despite the data in the two Tables coming from different field campaigns. Moreover, data for standing waters are not fully comparable because the community values (Table 3) refer only to the Kuibyshev Reservoir, while the species data (Table 4) include not only reservoirs but also other types of standing waters such as lakes and oxbow lakes.

The contrasting performance of the helophyte species between running water habitats and the Kuibyshev Reservoir (Table 4, Figure 2) deserves further consideration. The biomass might be affected by fluctuations in the water table level in the Kuibyshev Reservoir, which vary both seasonally and annually. However, this is likely not the main cause, as similar differences in species biomass were observed in Nizhnekamskoe Vodokhranilishche Reservoir, which maintains a constant water table level, compared to the river habitats of the Lower Kama River.

A more plausible explanation of this phenomenon is nutrient limitation, as all four helophytes thrive in nutrient-rich environments. The Ellenberg-type indicator value for nutrient requirements for *P. australis* in Europe is six out of nine [30], indicating its prosperity under intermediate to high nutrient availability. While *P. australis* can grow in low-nutrient conditions [1], numerous publications (reviewed by [11]) show that increased nutrient availability enhances its shoot growth. *S. lacustris* has a similar nutrient requirement to

P. australis (indicator value six), followed by *T. angustifolia* (indicator value seven). The highest nutrient requirement is seen in *G. maxima* (indicator value eight).

In the Middle Volga Valley, water mineralization, indicative of mineral nutrient availability, is considerably lower in lakes and reservoirs (100–500 mg L^{-1}) compared to rivers (400–900 mg L^{-1}). River habitats not only supply greater amounts of nutrients but also enhance their availability through water flow. For *P. australis*, this results in a pronounced edge effect, with the highest biomass values occurring toward the central part of the river. Under these conditions, *P. australis* achieves the greatest shoot densities, heights, and diameters (Papchenkov, unpublished data). This accounts for the extremely high biomass values at 90–100% cover as shown in Figure 2.

4.3. Biomass: Comparison with Other Parts of Europe

In the subsequent section, the biomass values observed in the aquatic habitats of the Middle Volga Valley are compared with data from European sites, excluding Southern Europe, which differs in climate and hosts specific genotypes [12,31] that tend to produce greater biomass (cf. [3] for Romania). The same reasons (i.e., different genotypes that may interact differently with the habitat conditions) apply to other continents, particularly North America, where *P. australis* of European origin is highly productive.

The mean aboveground biomass of *P. australis* in standing waters of the Middle Volga Valley (approximately 0.7 kg m^{-2}, Table 4) mostly falls within the ranges reported for standing waters in other regions of the Russian Federation [32–35] (Table 6). Higher values were found in limans in the Lower Volga Valley, which are habitats with standing or slowly flowing water and soft, nutrient-rich sediments [20].

Table 6. Seasonal maximum aboveground biomass (kg dry weight m^{-2}) of *P. australis* in standing waters of the Russian Federation with boreal to continental moderate climates. The values represent means followed by ranges (in brackets).

Habitat Type and Region	Biomass		Reference
	Mean	Range	
Oněga lake	0.35	0.1–1.1	[32]
Lakes of Karelia	0.78	0.1–2.0	[33,34]
Reservoirs of the Upper Volga Valley		0.3–0.6	[35]
Reservoirs in the Kuban Delta Region		0.3–0.8	[35]
The Kuban limans		0.3–7.5	[35]
Reservoirs in the Volga Delta		0.5–1.1	[35]
Lakes in the forest-steppe in Western Siberia		1.3–2.1	[35]
Lakes of the Novosibirsk Region		0.1–0.3	[35]
Reservoirs of the Baikal region		0.4–1.4	[35]

Extensive research has focused on the aboveground biomass and production of helophyte communities in Central and North-Western Europe. According to the overview of published data, minimum values of seasonal maximum aboveground biomass are about 300 g m^{-2} dry weight. Such low values typically reflect marginal growth conditions, which is not the subject of this study. Therefore, Table 7 [36–47] includes data from mesotrophic to eutrophic sites with closed, healthy-looking stands. In the lakes of North-Western Europe, typical values of seasonal maximum aboveground biomass are 0.7–1.1 kg m^{-2}, which is comparable to the results of this study. In fishpond littorals in the southern part of the Czech Republic (Central Europe), the mean values of *P. australis* aboveground biomass (about 1.5 kg m^{-2}, Table 7) are higher than in the standing waters of the Middle Volga Valley, but similar to those in the running waters there. The fishpond littorals are mostly sheltered habitats with shallow water (less than 0.5 m) and a high nutrient availability.

Table 7. Seasonal maximum aboveground and belowground biomass and B/A ratio (mean and range) in monospecific stands of tall helophytes in Europe (abbreviations in brackets denote states). The values represent means followed by ranges (in brackets).

Species	Site(s)	Aboveground Biomass (kg · m^{-2})	Belowground Biomass (kg · m^{-2})	B/A Ratio	Reference
P. australis	Lake Häljasjön (mesotrophic, SE)	0.9 (0.8–1.1)	0.7 (0.7–0.8)	1.0 (0.6–1.4)	[36]
	Lake Täkern, harvested stand (SE)	1.0			[37]
	Lake Ivösjön, harvested stand (SE)	0.7			[37]
	Lake Vänern, harvested stand (SE)	1.8			[37]
	Lake Võrtsjärv (eutrophic, EE)	(0.7–1.0)			[38]
	Branná sand pit (mesotrophic, CZ)	0.9	1.1	1.2	[39,40]
	Littoral of Rožmberk fishpond (eutrophic, CZ)	1.0 (0.8–1.4)	2.5 (2.2–3.4)	2.5 (1.7–4.1)	[39–43]
	Littoral of Opatovický fishpond (eutrophic, CZ)	1.8	5.1 (3.4–5.9)	2.9 (2.0–4.7)	[41,44]
	Kis–Balaton wetland, healthy stand (eutrophic, HU)	1.5	2.6	1.8	[45]
G. maxima	Fishponds littorals (CZ)	1.0 (0.6–2.6)	0.7–4.7	1.1–7.6	[46,47]
S. lacustris	Fishponds littorals (CZ	2.1 (0.8–3.0)	0.8–4.5	2.3–3.9	[47]
T. angustifolia	Fishponds littorals (CZ)	1.8 (1.0–3.0)	0.9–3.6	0.9–1.2	[47]

The data on belowground biomass are much scarcer than those on aboveground biomass because sampling is tedious and time-consuming. The data for tall helophyte communities in the Middle Volga Valley (Table 5) thus help fill the existing gap. The mean belowground biomass found for *P. australis* in this study is comparable to that of mesotrophic sites in North-Western and Central Europe but is lower than in eutrophic fishpond littorals (Table 7). The values for other tall helophytes overlap between the present study and the fishpond littorals.

5. Conclusions

P. australis-dominated community types showed variations in their seasonal maxima of total aboveground biomass depending on species composition, cover of *P. australis* and the co-dominant species, and habitat type. Among the four tall helophytes, *P. australis* achieved the highest aboveground biomass in river habitats and among the lowest in the Kuibyshev Reservoir, which was attributed to nutrient limitation.

The aboveground biomass of *P. australis* in the Kuibyshev Reservoir is comparable to the intermediate values found in other reservoirs in the Russian Federation and lakes in North-Western Europe. In contrast, the higher values observed in river habitats resemble the mean values of mesotrophic to eutrophic habitats of fishpond littorals in the Czech Republic.

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References

1. Packer, J.G.; Meyerson, L.A.; Skálová, H.; Pyšek, P.; Kueffer, C. Biological flora of the British Isles: *Phragmites australis*. *J. Ecol.* **2017**, *105*, 1123–1162. [CrossRef]
2. Čížková, H.; Kučera, T.; Poulin, B.; Květ, J. Ecological basis of ecosystem services and management of wetlands dominated by common reed (*Phragmites australis*): European perspective. *Diversity* **2023**, *15*, 629. [CrossRef]
3. Rodewald-Rudescu, L. *Das Schilfrohr, Phragmites Communis Trin*; Schweizerbart'scher Verlag: Stuttgart, Germany, 1974; p. 307.
4. Kiviat, E. Organisms using *Phragmites australis* are diverse and similar on three continents. *J. Nat. Hist.* **2019**, *53*, 1975–2010. [CrossRef]
5. Köbbing, J.F.; Thevs, N.; Zerbe, S. The utilisation of reed (*Phragmites australis*): A review. *Mires Peat* **2013**, *13*, 1–14.
6. Saltonstall, K.; Peterson, P.M.; Soreng, R.J. Recognition of *Phragmites australis* subsp. *americanus* (*Poaceae: Arundinoideae*) in North America: Evidence from morphological and genetic analyses. *SIDA Contrib. Bot.* **2004**, *21*, 683–692.
7. Kiviat, E.; Hamilton, E. Phragmites use by native North Americans. *Aquat. Bot.* **2001**, *69*, 341–357. [CrossRef]
8. Meyerson, L.A.; Lambert, A.M.; Saltonstall, K. A tale of three lineages: Expansion of common reed (*Phragmites australis*) in the US Southwest and Gulf Coast. *IPSM* **2010**, *3*, 515–520. [CrossRef]
9. Chambers, R.M.; Meyerson, L.A.; Saltonstall, K. Expansion of *Phragmites australis* into tidal wetlands of North America. *Aquat. Bot.* **1999**, *64*, 261–273. [CrossRef]
10. Kettenring, K.M.; de Blois, S.; Hauber, D.P. Moving from a regional to a continental perspective of *Phragmites australis* invasion in North America. *AoB Plants* **2012**, *2012*, pls040. [CrossRef]
11. Engloner, A.I. Structure, growth dynamics and biomass of reed (*Phragmites australis*)—A review. *Flora* **2009**, *204*, 331–346. [CrossRef]
12. Lambertini, C.; Gustafsson, M.H.G.; Frydenberg, J.; Lissner, J.; Speranza, M.; Brix, H. A phylogeographic study of the cosmopolitan genus *Phragmites* (*Poaceae*) based on AFLPs. *Plant Syst. Evol.* **2006**, *258*, 161–182. [CrossRef]
13. Neuhaus, D.; Kühl, H.; Kohl, J.G.; Dörfel, P.; Börner, T. Investigation on the genetic diversity of *Phragmites* stands using genomic fingerprinting. *Aquat. Bot.* **1993**, *45*, 357–364. [CrossRef]
14. Čurn, V.; Kubátová, B.; Vávřová, P.; Křiváčková-Suchá, O.; Čížková, H. Phenotypic and genotypic variation of *Phragmites australis*: Comparison of populations in two human-made lakes of different age and history. *Aquat. Bot.* **2007**, *86*, 321–330. [CrossRef]
15. Křiváčková-Suchá, O.; Vávřová, P.; Čížková, H.; Čurn, V.; Kubátová, B. Phenotypic and genotypic variation of *Phragmites australis*: A comparative study of clones originating from two populations of different age. *Aquat. Bot.* **2007**, *86*, 361–368. [CrossRef]
16. Eller, F.; Skálová, H.; Caplan, J.S.; Bhattarai, G.P.; Burger, M.K.; Cronin, J.T.; Guo, W.Y.; Guo, X.; Hazelton, E.L.; Kettenring, K.M.; et al. Cosmopolitan species as models for ecophysiological responses to global change: The common reed *Phragmites australis*. *Front. Plant Sci.* **2017**, *8*, 1833. [CrossRef]
17. Bastlová, D.; Čížková, H.; Bastl, M.; Květ, J. Growth of *Lythrum salicaria* and *Phragmites australis* plants originating from a wide geographical area: Response to nutrient and water supply. *Glob. Ecol. Biogeogr.* **2004**, *13*, 259–271. [CrossRef]
18. Bastlová, D.; Bastl, M.; Čížková, H.; Květ, J. Plasticity of *Lythrum salicaria* and *Phragmites australis* growth characteristics across a European geographical gradient. *Hydrobiologia* **2006**, *570*, 237–242. [CrossRef]
19. Golub, V.B.; Mirkin, B.M. Grasslands of the lower Volga valley. *Folia Geobot. Phytotax.* **1986**, *21*, 337–395. [CrossRef]
20. Golub, V.B.; Saveljeva, L.F. Vegetation of the lower Volga limans (basins without outflow). *Folia Geobot. Phytotax.* **1991**, *26*, 403–430. [CrossRef]
21. Dierschke, H. *Pflanzensoziologie*; Eugen Ulmer: Stuttgart, Germany, 1994.
22. WFO Plant List 2020. Available online: https://wfoplantlist.org/ (accessed on 29 September 2024).
23. Mucina, L.; Bültmann, H.; Dierßen, K.; Theurillat, J.P.; Raus, T.; Čarni, A.; Šumberová, K.; Willner, W.; Dengler, J.; García, R.G.; et al. Vegetation of Europe: Hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. *Appl. Veg. Sci.* **2016**, *19*, 3–264. [CrossRef]
24. Šesták, Z.; Čatský, J.; Jarvis, P.G. *Plant Photosynthetic Production. Manual of Methods*; Dr. W. Junk Publishers: The Hague, The Netherlands, 1971; 819p.
25. Zar, J.H. *Biostatistical Analysis*, 5th ed.; Prentice Hall: Upper Saddle River, NJ, USA, 2010; p. 944.
26. Hejný, S.; Husák, Š. Higher plant communities. In *Pond Littoral Ecosystems. Structure and Functioning. Ecological Studies 28*; Dykyjová, D., Květ, J., Eds.; Springer: Berlin, Germany, 1978; pp. 23–64.
27. Regel, C. The bogs and swamps of White Russia. *J. Ecol.* **1947**, *35*, 96–104. [CrossRef]
28. Dubyna, D.V.; Dziuba, T.P.; Iemelianova, S.M. Syntaxonomy of the *Phragmito-Magno-Caricetea* class in Ukraine. *Ukr. Bot. J.* **2014**, *71*, 263–274. [CrossRef]
29. Raspopov, I.M. *Vegetation of Higher Aquatic Plants in Large Lakes of Northwestern USSR*; Nauka: Leningrad, Russia, 1985; p. 199. (In Russian)
30. Tichý, L.; Axmanová, I.; Dengler, J.; Guarino, R.; Jansen, F.; Midolo, G.; Nobis, M.P.; Van Meerbeek, K.; Aćić, S.; Attorre, F.; et al. Ellenberg-type indicator values for European vascular plant species. *J. Veg. Sci.* **2022**, *34*, e13168. [CrossRef]
31. Lambertini, C.; Sorrell, B.K.; Riis, T.; Olesen, B.; Brix, H. Exploring the borders of European *Phragmites* within a cosmopolitan genus. *AoB Plants* **2012**, *2012*, pls020. [CrossRef] [PubMed]
32. Raspopov, I.M. Biomass of macrophyte groupings of Lake Ladoga and chemical composition of plants. *Proc. Karelian Branch GosNIIORKh* **1968**, *5*, 115–119. (In Russian)

33. Smirenskiy, A.A. *Aquatic Fodder and Protective Plants in Hunting and Fishing Farms*; Zagotizdat: Moscow, Russia, 1950; p. 136. (In Russian)
34. Katanskaya, V.M. Biomass of higher aquatic vegetation in the lakes of the Karelian Isthmus. *Proc. Lab. Lake Sci. USSR Acad. Sci.* **1954**, *3*, 102–117. (In Russian)
35. Ganetskaya, Z.G. Productivity of reed stands of inland water bodies of the USSR. In *Biological Productivity and Cycling of Chemical Elements in Plant Communities*; Nauka: Leningrad, Russia, 1971; pp. 91–113. (In Russian)
36. Vretare, V.; Weisner, S.E.; Strand, J.A.; Granéli, W. Phenotypic plasticity in *Phragmites australis* as a functional response to water depth. *Aquat. Bot.* **2001**, *69*, 127–145. [CrossRef]
37. Granéli, W. Reed *Phragmites australis* (Cav.) Trin. ex Steudel as an energy source in Sweden. *Biomass* **1984**, *4*, 183–208. [CrossRef]
38. Ksenofontova, T. Morphology, production and mineral contents in *Phragmites australis* in different waterbodies of the Estonian SSR. *Folia Geobot. Phytotax.* **1988**, *23*, 17–43. [CrossRef]
39. Čížková, H.; Pechar, L.; Husák, Š.; Květ, J.; Bauer, V.; Radová, J.; Edwards, K. Chemical characteristics of soils and pore waters of three wetland sites dominated by *Phragmites australis*: Relation to vegetation composition and reed performance. *Aquat. Bot.* **2001**, *69*, 235–249. [CrossRef]
40. Čížková, H.; Bauer, V. Rhizome respiration of *Phragmites australis*: Effect of rhizome age, temperature, and nutrient status of the habitat. *Aquat. Bot.* **1998**, *61*, 239–253. [CrossRef]
41. Fiala, K. Underground organs of *P. communis*, their growth, biomass and net production. *Folia Geobot. Phytotax.* **1976**, *11*, 225–259. [CrossRef]
42. Čížková, H. Work Package 2: Growth dynamics and ecophysiology of *Phragmites* in relation to the climatic conditions in boreal-Mediterranean and oceanic-continental gradients. In *Final Report of Project EUREED II: Dynamics and Stability of Reed-Dominated Ecosystems in Relation to Major Environmental Factors That Are Subject to Global and Regional Anthropogenically-Induced Changes*; Brix, H., Ed.; University of Aarhus: Aarhus, Denmark, 1999; pp. 45–52.
43. Šantrůčková, H.; Picek, T.; Šimek, M.; Bauer, V.; Kopecký, J.; Pechar, L.; Lukavská, J.; Čížková, H. Decomposition processes in soil of a healthy and a declining *Phragmites australis* stand. *Aquat. Bot.* **2001**, *69*, 217–234. [CrossRef]
44. Dykyjová, D.; Květ, J. Comparison of biomass production in reedswamp communities growing in South Bohemia and South Moravia. In *IBP PT-PP Report No. 1*; Czechoslovak Academy of Sciences: Praha, Czech Republic, 1970; pp. 71–79.
45. Čížková, H.; Istvánovics, V.; Bauer, V.; Balázs, L. Low levels of reserve carbohydrates in reed (*Phragmites australis*) stands of Kis-Balaton, Hungary. *Aquat. Bot.* **2001**, *69*, 209–216. [CrossRef]
46. Ondok, J.P.; Dykyjová, D. Assessment od shoot biomass of dominant reed-beds in Třeboň Basin. Methodical aspects. In *IBP/PT-PP Report No. 3: Ecosystem Study on Wetland Biome in Czechoslovakia*; Institute of Botany, Czech Academy of Sciences: Třeboň, Czech Republic, 1973; pp. 79–82.
47. Květ, J.; Husák, Š. Primary data on biomass and production estimates in typical stands of fishpond littoral plant communitites. In *Pond Littoral Ecosystems. Structure and Functioning. Ecological Studies 28*; Dykyjová, D., Květ, J., Eds.; Springer: Berlin, Germany, 1978; pp. 211–215.