

Article

Carbon Stock in Coastal Ecosystems of Tombolos of the White and Baltic Seas

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Abstract: “Blue carbon”, apart from marine humus, includes the carbon (C) stock of coastal ecosystems such as mangroves, saltmarshes, and seagrass meadows, which have been overlooked until recently. Information about the role of coastal wetlands in C sequestration and providing other ecosystem services is still insufficient. In the present study, we assessed the C reserves of soils and vegetation biomass in two complex coastal landscapes (tombolos) located on the coasts of the White and Baltic seas. The soil and plant C stocks were slightly higher at the plot on the Baltic Sea (93.4 ± 46.7 Mg C·ha^{−1} and 5.22 ± 2.51 Mg C·ha^{−1}, respectively) than at the plot on the White Sea (71.4 ± 38.2 Mg C·ha^{−1} and 3.95 ± 2.42 Mg C·ha^{−1}, respectively). We attributed the higher values of the C reserved to a warmer climate and less saline water at the plot on the Baltic Sea. Both soil and plant C showed high heterogeneity due to geomorphological complexity and differences in vegetative communities. The *Phragmites australis* community showed the highest plant biomass and, in some places, high soil C reserves. Allochthonous C contributed to the soil C stock at the site on the White Sea. Though *P. australis* sequestered more C than other communities, its effect on ecosystem services was mostly negative because the invasion of reeds reduced the biological diversity of the marshes.

Keywords: “blue carbon”; carbon sequestration; marsh; wetland; soil carbon stock; plant biomass carbon stock; *Phragmites australis*



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1. Introduction

An increase in the average concentration of carbon dioxide (CO₂) and other greenhouse gases in the atmosphere is considered one of the causes of global warming and climate change [1]. It is of great importance not only to reduce anthropogenic emissions of climatically active gases but also to protect natural carbon (C) depots and promote C sequestration in natural landscapes [2,3]. The World Ocean, which is the largest carbon pool on the planet, thereby makes a huge contribution to the global carbon cycle [1]. All C that is captured by marine and coastal ecosystems and stored in their components is called “blue carbon” [4]. The capture and accumulation of blue carbon by coastal ecosystems such as mangroves, marshes, and seagrass meadows have been overlooked until recently [2]. Apart from C sequestration, coastal landscapes provide a number of other ecosystem services, including playing an important role in biogeochemical cycles, granting a habitat for many organisms, acting as a natural filter for water, and protecting soils from coastal erosion. The area occupied by coastal ecosystems has been rapidly decreasing in recent decades due to anthropogenic pressure [5].

Coastal landscapes are characterized by high rates of C accumulation in sediments and soils [2,5]. The predicted total global carbon burial for mangroves, saltmarshes, and

seagrass beds is 31–34 teragrams (Tg) $\text{C}\cdot\text{yr}^{-1}$, 5–87 Tg $\text{C}\cdot\text{yr}^{-1}$ and 48–112 Tg $\text{C}\cdot\text{yr}^{-1}$, respectively [2]. Comparable to terrestrial forest types, these worldwide C burial rates are 53.0 Tg $\text{C}\cdot\text{yr}^{-1}$ for temperate forests, 78.5 Tg $\text{C}\cdot\text{yr}^{-1}$ for tropical forests, and 49.3 Tg $\text{C}\cdot\text{yr}^{-1}$ for boreal forests [2]. A recent review found that restored coastal marshes accumulate carbon at an average rate of 4.41 Mg $\text{C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ [6]. The amount of stored soil C per unit area in coastal ecosystems is greater than in terrestrial landscapes: for saltmarshes, global estimates vary from 1.8 to 6.2 Pg [3]. In some cases, organic deposits on the shores can reach a thickness of tens of meters, which is associated with regular flooding with seawater and the dominance of anaerobic conditions in soils [3,7]. Low rates of organic matter decomposition make coastal wetlands similar to freshwater bogs and swamps [7,8]. However, tidal ecosystems have an advantage as a C pool over inland peatlands. Due to their position on the border of land and sea, coastal ecosystems receive allochthonous organic matter both with terrestrial runoff and with particles of marine humus, which is fixed by coastal vegetation, settles in the tidal zone, and replenishes blue carbon reserves on the shores [7,9]. In some cases, the share of allochthonous C in total reserves may exceed the share of autochthonous C [2]. Freshwater runoff and tidal waves also introduce mineral particles that may bury the incoming organic material and thus contribute to the long-term preservation of blue carbon stocks [3]. Though allochthonous organic matter is important for C balance on the seacoast, vegetation composition and productivity are of crucial importance. It is noteworthy that in coastal plant communities, the underground biomass is several times higher than the terrestrial one, and a major part of organic deposits in coastal sediments consists of dead underground plant organs [10].

Coastal ecosystems, as a rule, are characterized by a mosaic of habitats and a variety of environmental conditions, which leads to different rates of C accumulation in different parts of the landscape. For example, the rate and capacity of accumulation of organic residues in mangroves and marshes will be the highest in the part that is flooded daily at high tide [11]. The accumulation of blue carbon is influenced by multiple factors, such as climatic conditions, hydrology, seawater salinity, topography, sedimentation rate, texture of coastal sediments, plant biomass, species composition, fauna activity, etc. [2,12].

The most important factor influencing the accumulation of blue carbon is soil salinity [13]. The degree of salinity depends on the geomorphology of the coast, climate, season, and thalassogenic conditions and can vary significantly within the boundaries of one ecosystem [14,15]. Soil salinity does not always increase with proximity to the sea in coastal ecosystems. In some places, the highest salinity values are found in areas relatively remote from the sea [16]. This may be due to hot and dry weather conditions that lead to the evaporation of seawater and the accumulation of salts [15,17]. Also, a high degree of salinization can depend on soil texture because water lingers longer on clay soils than on sandy ones; therefore, clay soils are more saturated with salts [14]. The degree of salinity of the substrate significantly affects the species composition of plant communities on the shores and the distribution of species across the ecosystem [15,18]. Under increased salinization, plants experience salt stress, which leads to inhibition of their vital activity and, consequently, reduced rates of carbon sequestration [13,19]. Even halophytic species achieve the best growth parameters under low concentrations of salts [20]. The highest species diversity, the largest primary production, and, in general, the largest blue carbon reserves are observed in the part of the coastal ecosystem with the lowest level of salinity [13,18,21]. Organic residues of plants growing in the most saline areas have fewer stable substances such as lignin, cellulose, and hemicellulose, which increases the rate of their mineralization [21].

Soil texture has both indirect and direct effects on the accumulation of blue carbon. Apart from its effect on soil salinity, texture affects soil aeration. Clay soils are less saturated with oxygen and have a higher water retention capacity than sandy soils, which leads to reduced rates of microbiological decomposition of organic residues and favors C accumulation in heavy-textured soils [22]. Also, organic substances form strong bonds with clay particles rather than with sand, which also contributes to the preservation of soil carbon reserves in clayey soils [23].

The soil reaction somewhat intersects with substrate salinity. The largest carbon reserves are found in parts of the coastal ecosystem where soil pH values are close to neutral. Along the gradient to acidic or alkaline soils, the biomass of plants decreases, and consequently, carbon stocks are also lower. Sidorova et al. [24] showed that organic C concentration increases with distance from the sea and decreasing pH values. The more often seawater impacts vegetation, the less C accumulates. Coastal areas flooded only in syzygy store several times more C than those flooded daily [25]. Syzygy is an astronomic phase in which three or more celestial bodies are arranged in a straight line. On Earth, syzygy is related to the full and new moons. Tidal forces are maximized during this period, which causes so-called spring tides—the highest ones.

The diversity of geomorphological positions, sediments, water regime, soils, and vegetation in the coastal areas is the highest on tombolos, deposition landforms connecting islands to the mainland. According to our hypothesis, this diversity might lead to a complex spatial distribution of C incorporated into biomass in soil organic matter. Though an extensive body of literature on C reserves on saltmarshes exists, little is still known about the dependence of soil C and biomass on the geomorphological type of the coast [3]. Though global overviews of C sequestration in coastal wetlands were published recently [6], the variation in the obtained results is still high, and there are many gaps in our knowledge of how the climate, tidal regime, and geomorphology regulate the amount of C sequestered in plant biomass and soil organic matter. Data on C accumulation on tombolos are practically absent in the literature. In the present study, our objective was to access and compare organic C stocks on two tombolos formed on the coasts of two northern European seas: the Baltic and the White Sea. We attempted to relate C reserves to environmental variables and soil properties where possible. Also, we discussed the importance of coastal soils and vegetation for ecosystem services in the region.

2. Materials and Methods

2.1. Study Area

We conducted our research on the Pomor coast of the White Sea, near the village of Kolezhma (Figure 1) and in the southern part of the Gulf of Finland, the Baltic Sea, near the village of Gakkovo. Both study sites are tombolos connecting the mainland with small islands with a linear size of less than 500 m. The environmental conditions, groundwater salinity, soil texture, and acidity, as well as the description of vegetation, are available in our previous publication [26].

The White and Baltic Seas differ significantly from each other, and the coastal ecosystems at the Kolezhma site and the Gakkovo site are fundamentally different. The climatic conditions at the experimental plots were different: the Gakkovo plot was warmer and more humid than the Kolezhma plot (Figure 2). At the Gakkovo site, the mean annual temperature was 6 °C and the annual precipitation was 723 mm, while at the Kolezhma site, the mean annual temperature was 1 °C and the annual precipitation was 435 mm. Also, the salinity of the water in the Baltic Sea is much lower than in the White Sea (4‰ in the southern waters of the Gulf of Finland versus 26‰ in the Onega Bay of the White Sea), and tidal activity is much weaker (the average height of a tidal wave in the Baltic Sea is 0.2 m, while in the Onega Bay it is 3.4 m). At the Gakkovo site (the Baltic Sea), the sea has minimal impact on the coastal ecosystem. The vegetative cover on this tombolo is represented by the communities of the euryhaline species *Phragmites australis* Cav. (*communis* (Trin.)), forming dense thickets both in the narrow tidal zone and in the central part of the tombolo, and the communities of hygrophytic zonal species (Figure 3). The soils had sandy and loamy sand textures; in most soil profiles, the water was fresh or absent; and the soil pH values were higher than in zonal soils [26]. The soils were classified as Arenosols and Gleysols [27]. In contrast, the ecosystem of the Kolezhma site (the White Sea) is a developed marsh ecosystem. Based on the dominant species in the composition of plant communities, we allocated lower and middle levels of coastal meadows. Lower-level marshes are flooded daily or at high tide with salty seawater. The soils (Stagnosols and Gleysols [27]) at the

lower level mostly have a silty loam texture, the pH values of the soils are close to neutral, and groundwater salinity is high. As a result, halophytic species constitute the majority of vegetative cover: *Juncus gerardii* L., *Salicornia europaea* L., *Carex salina* Wahlenb., *Bolboschoenus maritimus* L., *Puccinellia coarctata* Parl., and *Eleocharis uniglumis* Link. There are also salt puddles practically devoid of vegetation on the lower level; the water lingers longer in wet and cool periods and dries faster in hot and dry periods. As a result, the salinity values here are the highest at this site. The vegetation is represented by the community of *Salicornia europaea* L., a pioneer type of marsh that can survive under extreme salinity.



Figure 1. The location of the study plots: Gakkovo (59°40′ N 28°01′ E) and Kolehmma (64°13′ N 35°55′ E).

2.2. Soil Sample Collection and Analysis

We collected the samples at the Kolehmma site between 21 and 24 July 2022 and at the Gakkovo site between 24 and 30 July 2022. The reserves of soil and plant C were estimated according to the formulas presented in the UNESCO methodological manual [28], and the results are presented in $\text{Mg C} \cdot \text{ha}^{-1}$. In total, 33 control points were established at the Kolehmma site and 20 at the Gakkovo site. The bulk density of the soil was determined using the cylinder method. Soil samples were collected from each soil horizon. Each soil sample was put into an individual zip-bag. In the laboratory, soil samples were dried to a constant weight in an oven for 6 h at 105°. Then, soil dry bulk density was calculated by dividing the mass of dry soil (g) by the original volume sampled (cm^3 , 100 cm^3 in our case). Further soil samples were homogenized by manually grinding the dried soils and sieving them through a 1 mm sieve. In the laboratory, we determined C content via dry combustion using the analyzer CN 802 8020 (VELP Scientifica Srl, Usmate, Italy). C stock was calculated for the upper 30 cm of soil using the equation:

$$C_{\text{total}} = 10 \cdot h \cdot C \cdot d, \quad (1)$$

where C_{total} is C stock in $\text{Mg C} \cdot \text{ha}^{-1}$, d is dry bulk density ($\text{g} \cdot \text{cm}^{-3}$), C is organic carbon density ($\text{g} \cdot \text{kg}^{-1}$), h is soil layer depth (m), and 10 is the coefficient to convert the stock from $\text{g} \cdot \text{m}^2$ to $\text{Mg C} \cdot \text{ha}^{-1}$. If more than one soil horizon was present within the 30 cm topsoil, the stock was calculated for each soil horizon separately, and then the values were summed up for, e.g., the A horizon (0–10 cm) and Bg horizon (10–30 cm) because the density of C and bulk density differed in these soil layers.

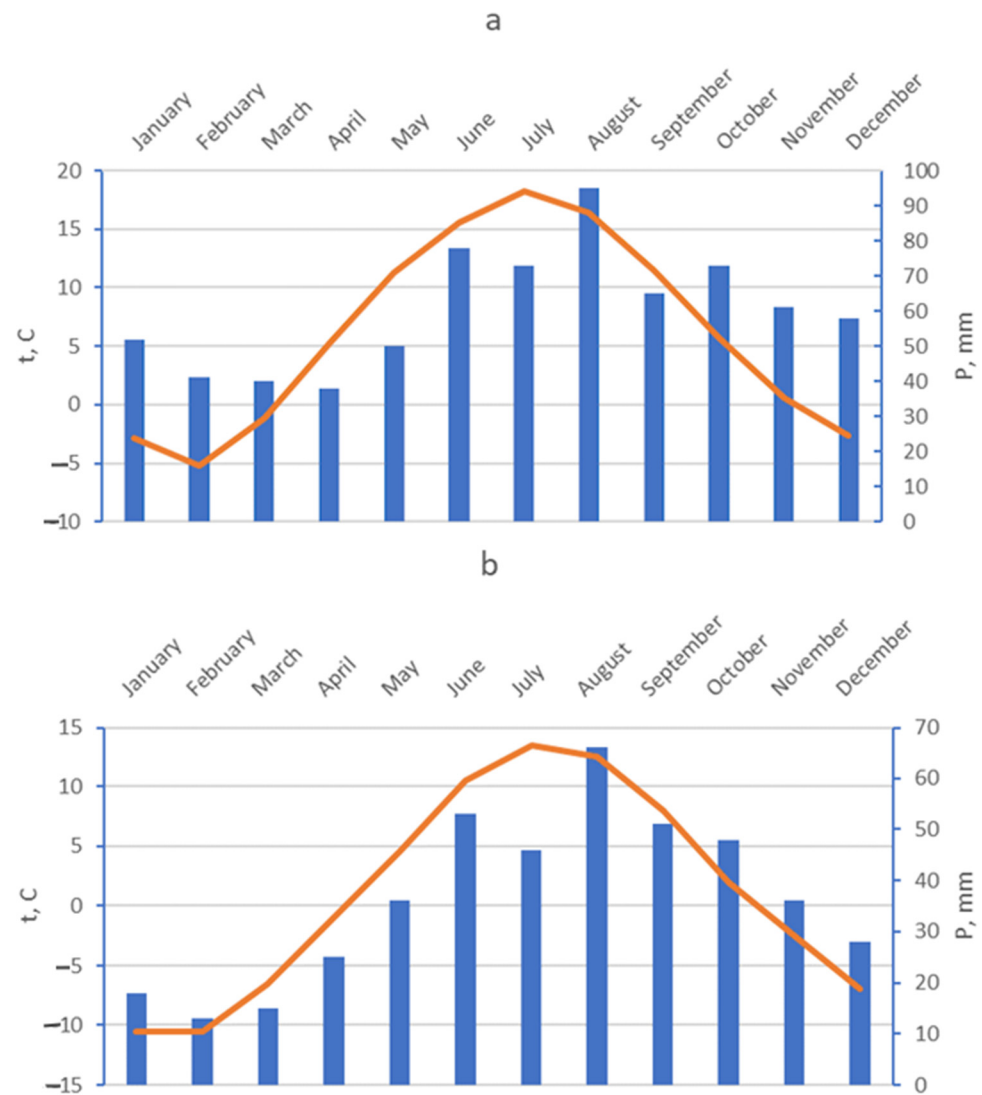
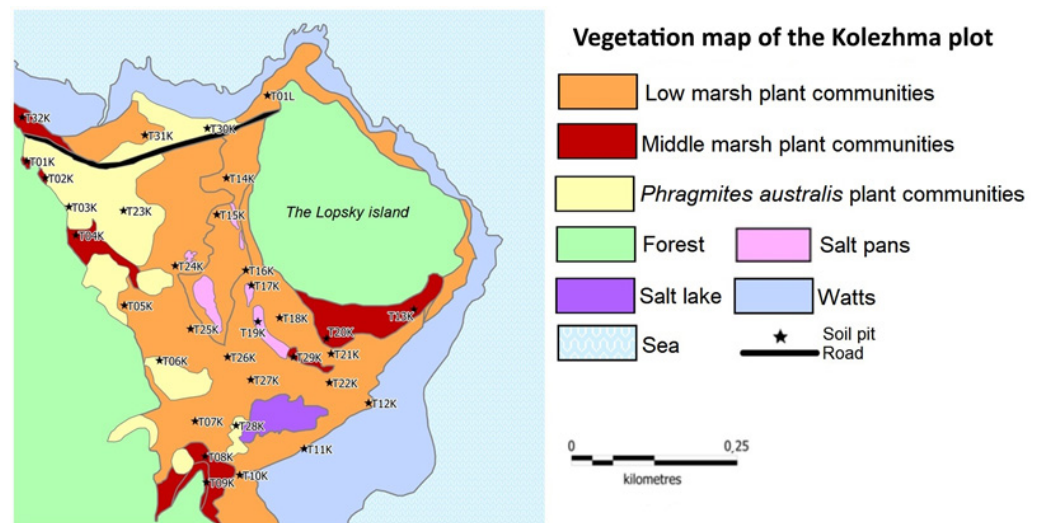


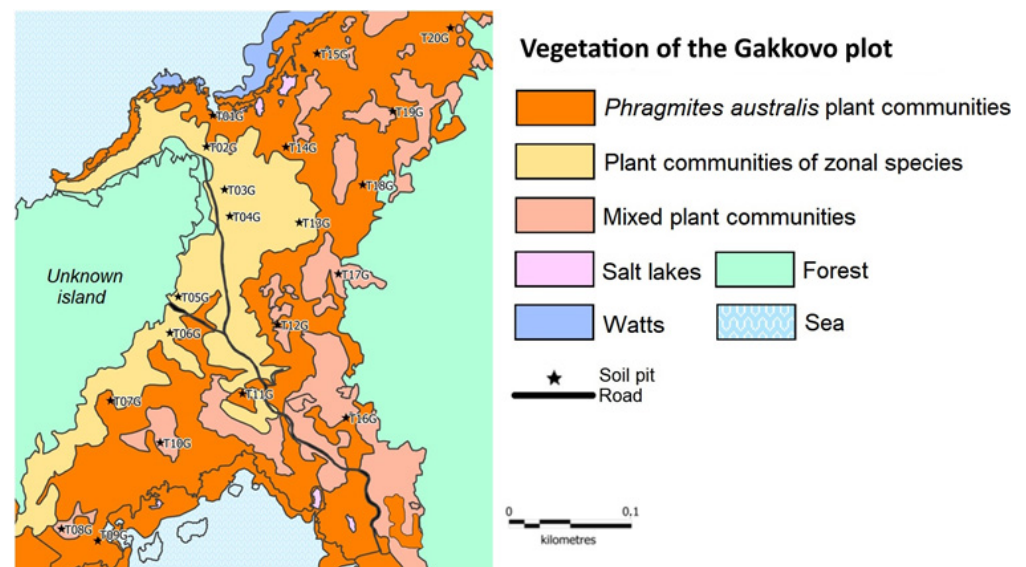
Figure 2. Climatic diagrams of the study sites: (a) Gakkovo, (b) Kolezhma. Columns show monthly precipitation; lines show mean monthly temperatures.

2.3. Vegetation Collection and Analysis

Sampling points for vegetative biomass assessment were selected with reference to plant communities. The collection of plants was performed on the same dates as soil sampling. At the first site, on the tombolo near Kolezhma, 11 sampling points were selected; at the second site, on the tombolo near Gakkovo, 6 sampling points were selected. At each point, we laid out three sample squares with an area of 0.25 m² each for collecting the aboveground biomass of plants. Only above-ground biomass was collected. Plant biomass was determined by drying collected samples to a constant weight in an oven for 72 h at 60 °C. The biomass of individual species has not been determined. We determined the mass of the entire mowing, the total of all species that fell into the sample square.



(a)



(b)

Figure 3. Vegetative communities of the studied tombolos, with the indication of sampling sites: (a) Kolehmma plot; (b) Gakkovo plot. Modified after [24] with permission.

Of the 11 vegetation sampling points at the first site (Figure 3), 1 point was located in the thickets of *P. australis* (T23K), 4 in the marsh on the middle level (T01K, T04K, T09K, T01L), and the rest in the marsh on the lower level (T11K, T12K, T14K, T17K, T21K, T27K).

On the tombolo in the Gakkovo area, sites T03G and T05G were located under a meadow–swamp community. At T09 and T14, *P. australis* dominated the composition of plant communities. The two remaining sites, T17G and T10G, were located in transitional communities. For each vegetation type, we made a vegetation description at five test sites, where the species composition and the projective cover of each species were evaluated.

The determination of carbon reserves in vegetation biomass was carried out according to the methodology proposed in the methodological manual on the assessment of “blue carbon” reserves [26]. Within the framework of this methodology, the first stage is the C content in vegetation:

$$CGC = B \cdot C_{\text{coef}} \cdot S^{-1} \quad (2)$$

where CGC is the C in the grass component, $\text{kg} \cdot \text{C} \cdot \text{m}^{-2}$; B is the biomass of vegetation on the test site, kg; C_{coef} is the carbon conversion coefficient, equal to 0.45; and S is the area of the test site, m^2 . C reserves in vegetation ($\text{Mg C} \cdot \text{ha}^{-1}$) are as follows:

$$C_{\text{veg}} = \text{CGC} \cdot 1000 \text{ kg}^{-1} \cdot 10,000 \text{ m}^{-2} \quad (3)$$

2.4. Statistical Processing and Mapping

Next is the mean value of carbon stocks among the three test sites. The results are presented taking the standard deviation into account. Statistical processing of the results (finding the mean value and standard deviation) took place in the Microsoft Excel 2016 program. Based on the received and processed data, cartograms were built in the MapInfo Pro 15.2. program using open-source remote sensing data (Google Earth Pro 7.3.6.9345). Inverse Distance Weighing (IDW) was used to construct cartograms.

3. Results

3.1. C Stock at the Kolezhma Plot (the White Sea)

3.1.1. Soil C Reserves

Soils and vegetative cover near the village of Kolezhma resembled soils and plant communities previously described on the other shores of the White Sea [29,30]. Soil C content in the majority of profiles decreased with depth, sharply or gradually. In the soil profiles T02K and T07K, there were deep layers with slightly higher C concentration (Table A1). It is a typical feature for Tidalic Fluvisols, where organic matter-enriched layers indicate buried soils or sediments with allochthonous humus accumulation [27]. Though the highest C density corresponded to the upper organic horizons, the highest C reserves were found in the mineral humus-enriched layer, where the bulk density values were much higher than in the organic topsoil. The C stock in the soils on the tombolo strongly varied (Figure 4a). The minimum values were recorded at the T17K control point located in the central part of the tombolo ($9.63 \text{ Mg C} \cdot \text{ha}^{-1}$). This locality was associated with salt puddles formed in the depression in the middle of the tombolo. This area was almost free of vegetation (see Figure 5a) and thus did not receive organic debris. Also, the continental runoff did not reach here, and all the organic material carried by the tidal wave settled closer to the coastline. The highest values were detected in the southern parts of the plot, especially near the root coast, where forest with arboreal vegetation and a dense moss–shrub layer representing zonal vegetation were close to the coastline: the highest value was recorded at the sampling point T01K— $144.3 \text{ Mg C} \cdot \text{ha}^{-1}$. On average, soil carbon reserves for the study plot amounted to $71.4 \pm 38.2 \text{ Mg C} \cdot \text{ha}^{-1}$.

Other points with the biggest C reserves were located in areas close to the water edge, where soil salinity was the highest. Elevated C stock in the southern part of the tombolo could result from the influx of allochthonous organic matter from the sea and/or from the continental runoff. A tidal wave might bring particles of marine humus and algae, as observed at point T11K. Combined with the reduced rates of microbiological decomposition of organic residues, this could lead to increased soil C accumulation. However, the C reserves at the neighboring points were much lower (Figure 4a). The phenomenon shows that the augmentation of organic matter is strongly dependent on the geomorphological position. Point T12K was located along the route of tidal flux, while point T11K corresponded to an accumulative position.

3.1.2. Above-Ground Plant Biomass C Reserves

The average reserves of plant C equaled $3.95 \pm 2.42 \text{ Mg C} \cdot \text{ha}^{-1}$ at the Kolezhma plot (Table A3, Figure 5a). The highest stocks of C in plant biomass were confined to the territories occupied by *P. australis*: $6.9 \pm 6.3 \text{ Mg C} \cdot \text{ha}^{-1}$. At the lower and middle levels of the marshes, the reserves were comparable, with a small difference in favor of the lower level: $3.8 \pm 1.6 \text{ Mg C} \cdot \text{ha}^{-1}$ and $3.6 \pm 1.3 \text{ Mg C} \cdot \text{ha}^{-1}$, respectively.

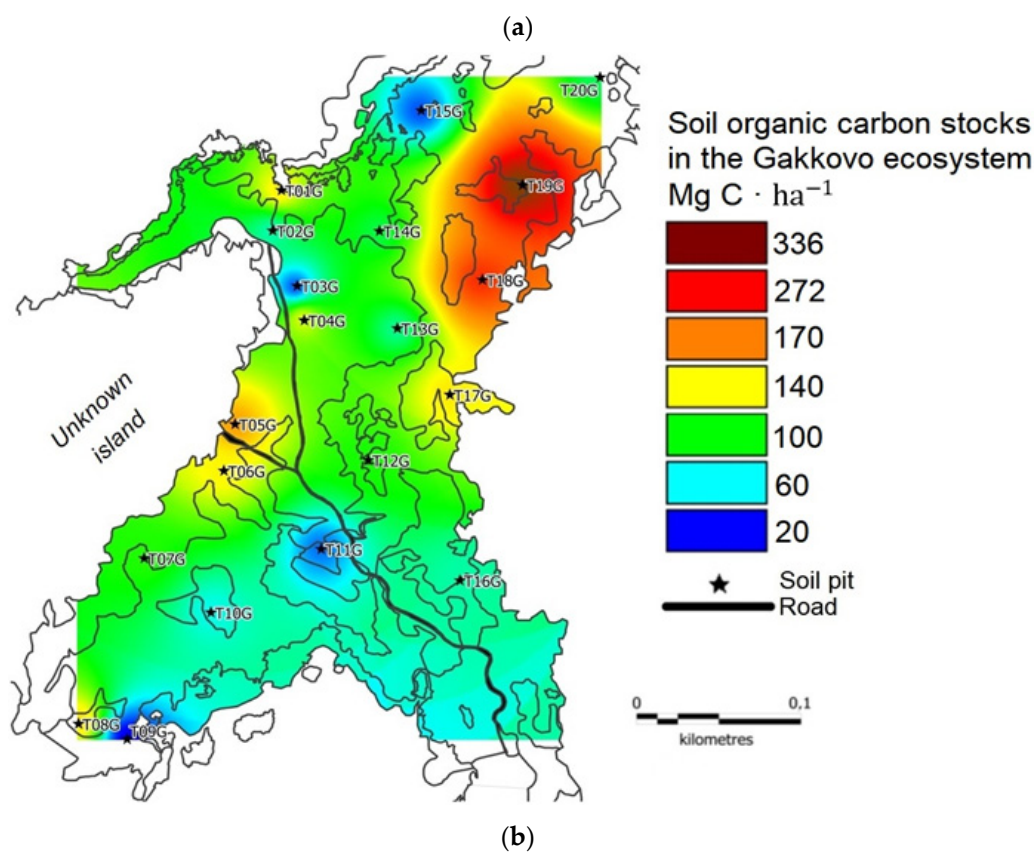
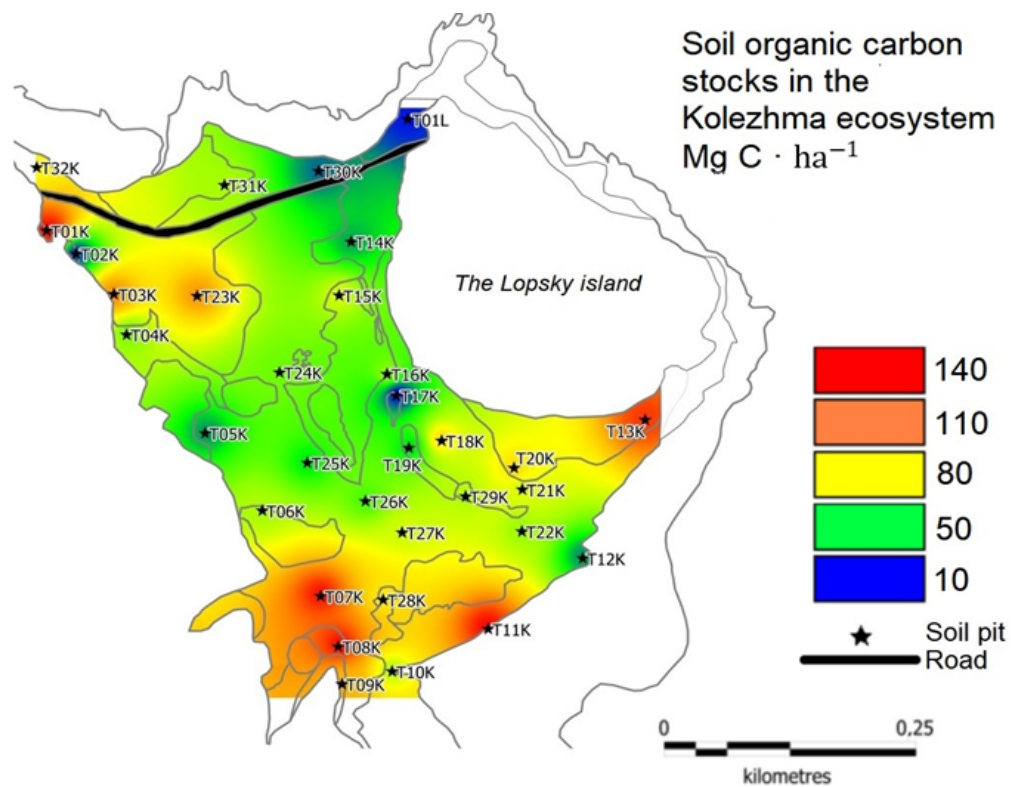


Figure 4. C stock in soils, $\text{Mg C} \cdot \text{ha}^{-1}$: (a) Kolehmma plot; (b) Gakkovo plot.

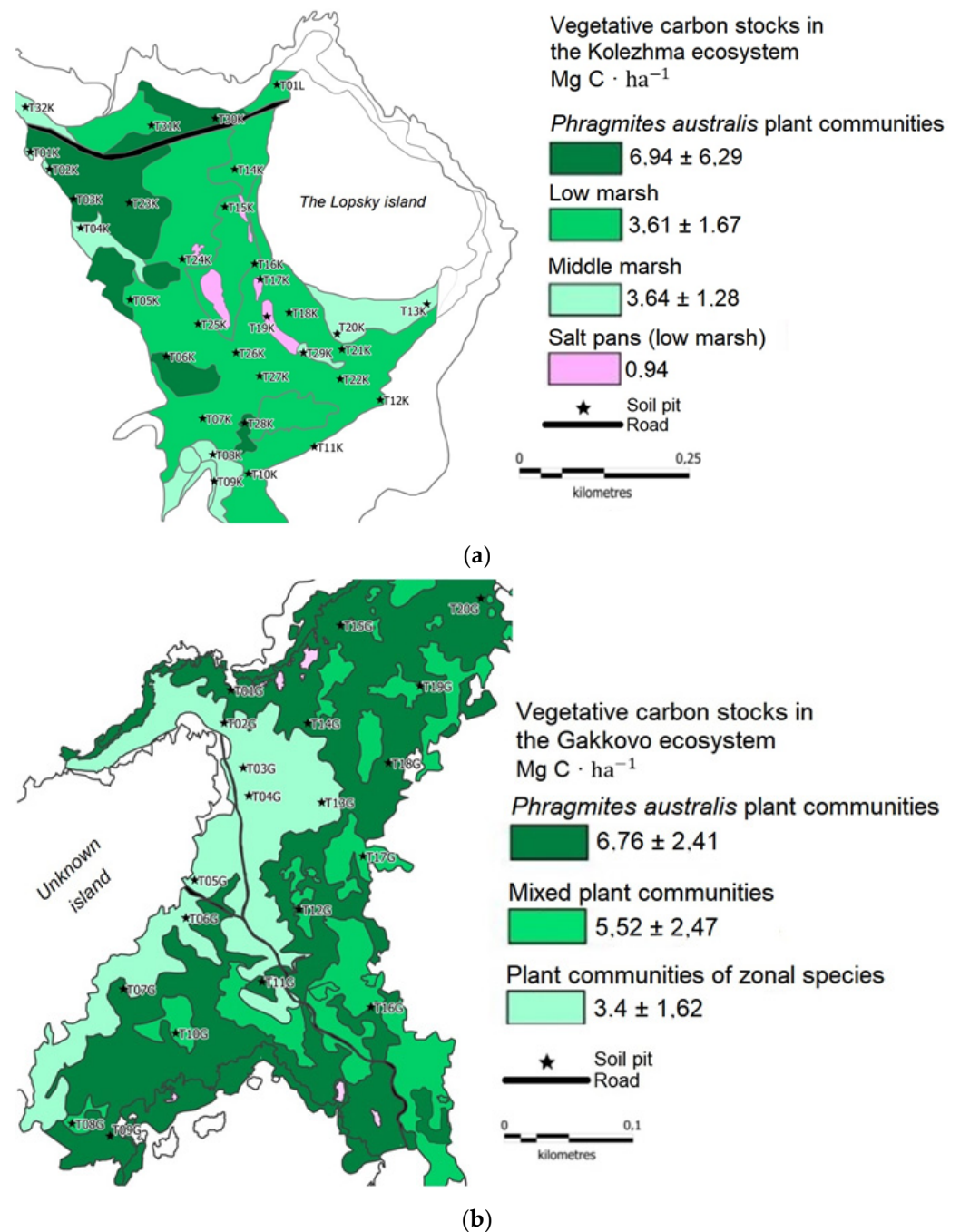


Figure 5. C stock in plant biomass, Mg C·ha⁻¹: (a) Kolehmma plot; (b) Gakkovo plot.

The reserves of plant C at points T11K and T12K were on average among the highest, excluding reeds, at the Kolehmma site, amounting to 4.1 ± 2 and 4.4 ± 2.1 Mg C·ha⁻¹, correspondingly. The phenomenon was ascribed to the low salinity values here: 10‰ in T11K and 8‰ in T12K against 11‰ on average for the Kolehmma site. Most likely, the low salinity was due to the fact that this area was affected by freshwater continental runoff, which flowed into the sea through a network of creeks; their role for the marshes of the White Sea has been described previously [31].

The lowest C stock at the Kolehmma plot was confined to the central part of the tombolo, to the territory where salt puddles were common. At the point T17K, the reserves of plant C were 0.94 Mg C·ha⁻¹, which was the absolute minimum for the Kolehmma plot.

3.2. C Stock at the Gakkovo Plot (the Baltic Sea)

3.2.1. Soil C Reserves

At the Gakkovo plot, most soil profiles had a normal distribution of C density with gradual decrease with depth (Table A2). However, several profiles had evident buried soils (T02G and T03G), and some others had irregular vertical distribution of organic matter (T06G, T07G, and T16G). In the lack of tidal activity, the phenomenon was explained by aeolian accumulation of sediments. The average C reserves were $93.4 \pm 46.7 \text{ Mg C} \cdot \text{ha}^{-1}$, which exceeded those at the Kolezhma plot. The highest reserves were found at point T19G ($335.97 \text{ Mg C} \cdot \text{ha}^{-1}$), and the smallest C reserves at points located in a narrow tidal zone, T09G ($16.8 \text{ Mg C} \cdot \text{ha}^{-1}$) and T15G ($33.3 \text{ Mg C} \cdot \text{ha}^{-1}$). Elevated C stock was confined to the central part of the tombolo (or to the territory near the tidal zone (Figure 4b).

3.2.2. Plant Biomass C Reserves

The reserves of plant C in the Gakkovo ecosystem are higher than in the Kolezhma vegetation (Table A4, Figure 5b): the mean values of plant C stock were $5.22 \pm 2.51 \text{ Mg C} \cdot \text{ha}^{-1}$. The major part of plant C is stored on the territories occupied by communities of *P. australis*— $6.8 \pm 2.4 \text{ Mg C} \cdot \text{ha}^{-1}$. The lowest C reserves were recorded in hygrophytic meadows: $3.4 \pm 1.6 \text{ Mg C} \cdot \text{ha}^{-1}$. In the areas with communities of transitional botanical composition, the C stock in plants was $5.5 \pm 2.5 \text{ Mg C} \cdot \text{ha}^{-1}$. It is noteworthy that the reserves of plant carbon were also lower in the tidal zone than at a distance from the shoreline: T09G— $5.7 \pm 2 \text{ Mg C} \cdot \text{ha}^{-1}$, T14G— $7.8 \pm 2.7 \text{ Mg C} \cdot \text{ha}^{-1}$. Despite the fact that dense thickets of reeds were common throughout almost the entire territory of the tombolo, *P. australis* gained the best growth parameters at a distance from the sea.

The mean stock of plant C on the tombolo near the village of Gakkovo exceeded the reserves on the tombolo near the village of Kolezhma. In almost the entire territory of the tombolo near Gakkovo, and especially in the areas close to the tidal zone, for example, at points T01G and T14G, the reed reached about three meters in height. The environmental conditions there were suitable for the growth of hydrophilic species because the territory was moistened and flooded with slightly saline water. Soil reaction varied from slightly acidic to slightly alkaline, which was higher than in zonal soils due to proximity to the sea. All this caused a high biomass at the tombolo.

4. Discussion

4.1. C Stocks of Coastal Ecosystems

According to various estimates, the average global reserves of soil C for marsh ecosystems vary from $162 \text{ Mg C} \cdot \text{ha}^{-1}$ [8] to $226 \text{ Mg C} \cdot \text{ha}^{-1}$ [1] for the upper meter of the soil profile. A recent global overview of the soil C stock in saltmarshes reported much higher values for Europe ($342.10 \pm 223.45 \text{ Mg C} \cdot \text{ha}^{-1}$) [6], but the results are difficult to compare. Most probably, the cited paper might overestimate soil C stock because the authors assumed linear distribution of organic C in the upper meter of sediments, while in the majority of soils, C concentration is the highest in the topsoil and decreases with depth. At the tombolo near the village of Kolezhma, the average values of soil C reserves were significantly lower ($71.4 \pm 38.2 \text{ Mg C} \cdot \text{ha}^{-1}$), as well as at the Gakkovo plot ($93.4 \pm 46.7 \text{ Mg C} \cdot \text{ha}^{-1}$). However, few of the profiles at the experimental plots reached one meter depth in the present study, mostly due to the close groundwater table. We decided to limit the estimation of C reserves to 30 cm, like in many other studies of grasslands [32]. The presence of buried organic matter-enriched layers has also been previously reported for the marshes on the coast of the Barents Sea [33], and thus, it was not possible to extrapolate the C stock at the depth below the groundwater level. To avoid unreliable estimates, we accepted the assessment of C stock in the 0–30 cm layer for our study. Recent results found for temperate marshes are comparable with those for the current study: $80.6 \pm 43.8 \text{ Mg C} \cdot \text{ha}^{-1}$ in the northwestern USA [34] and $85 \pm 19 \text{ Mg C} \cdot \text{ha}^{-1}$ on the Pacific coast of Canada [35]. The soils of temperate inland grassland ecosystems and meadows are reported to contain approximately $55\text{--}75 \text{ Mg C} \cdot \text{ha}^{-1}$ in the upper 30 cm, i.e., are somewhat poorer in C than marsh soils [36].

The reserves of C incorporated in vegetative biomass varied depending on the plant communities. *P. australis* is one of the most common invasive species worldwide [37]. The maximum reserves of plant C at both the Kolezhma and Gakkovo plots were found precisely in the territories occupied by reeds: $6.94 \pm 6.3 \text{ Mg C} \cdot \text{ha}^{-1}$ at the Kolezhma plot and $6.76 \pm 2.41 \text{ Mg C} \cdot \text{ha}^{-1}$ at the Gakkovo plot. The high value of the standard deviation for the Kolezhma object is due to the fact that some individual reeds reached a height of more than 2 m, and some plants were only 30–50 cm in height. The obtained values were much lower than those reported for the marshes in New Jersey [38], where the biomass of reeds turned out to be $17 \text{ Mg C} \cdot \text{ha}^{-1}$. Most probably, the difference is due to much warmer climatic conditions on the Atlantic coast of the USA than on the coasts of the Baltic and White seas. C reserves in other plant associations, except for communities of *P. australis*, turned out to be less than the average global carbon reserves on the marshes, but of the same order— $4.3 \pm 0.10 \text{ Mg C} \cdot \text{ha}^{-1}$ [39]. Also, plant communities affected soil C reserves. On the other hand, it is known that emergent plants can influence the movements and deposition of water and nutrients across ecosystems, with the effects varying between different plant species [2].

On most of the Gakkovo site, hygrophytic meadows have formed; only a narrow strip of land near the water's edge is flooded with brackish sea water. Consequently, the wetland ecosystem occupies an extremely small fraction of the area of the plot. In our case, taking into account the very large biomass and significant moisture content of the territory, soil C reserves are high, even despite the light texture of the soils.

4.2. The Difference in C Stocks between the Coasts of the White and Baltic Seas

The average soil C reserves at the Gakkovo plot were $93.4 \pm 46.7 \text{ Mg C} \cdot \text{ha}^{-1}$, which exceeded those at the Kolezhma plot at $71.4 \pm 38.2 \text{ Mg C} \cdot \text{ha}^{-1}$. The difference in soil C stock was ascribed mainly to the difference in the vegetative biomass and biological productivity. The average reserves of plant C on the tombolo near the village of Gakkovo ($5.22 \pm 2.51 \text{ Mg C} \cdot \text{ha}^{-1}$) exceed the reserves on the tombolo near the village of Kolezhma ($3.95 \pm 2.42 \text{ Mg C} \cdot \text{ha}^{-1}$). This is due to the fact that thalassogenic factors have minimal impact on the Gakkovo ecosystem. The fact that the climate in the Baltic is milder than in the White Sea also plays a role. This is expressed, in particular, in higher air temperatures on the southern shores of the Gulf of Finland, compared with temperatures on the Pomor coast of the White Sea (see Figure 2). As a result, the most favorable conditions for the recruitment of biomass by vegetation are formed on the Gakkovo plot. For the tombolo near the village of Gakkovo, the less the impact of the sea on the territory, the higher the soil C reserves. Paradoxically, the largest reserves were noted in the territory where zonal hygrophytic plant communities were common, despite the fact that zonal species did not gain as much biomass as reeds. We attributed the phenomenon to the fact that the bulk density of topsoil was high under zonal vegetation because the roots of herbaceous species are less voluminous than the roots of reeds. As a result, topsoil with high bulk density formed in the uplifted areas, while under the reeds, the topsoil contained massive roots, which decreased the bulk density of the soil and, as a result, C stock. According to the previous studies, the large *Phragmites* rhizomes might both increase soil C stock and expand soil layers [40].

In general, reed, being an intrazonal hygrophytic species, introduces uncertainty into the assessment of carbon reserves in plant biomass and soil. Its expansion somewhat negates the differences that could be in carbon reserves due to differences in salinity, heat availability, and other biogeographic patterns. It is important to note that the distribution of *P. australis* is very dynamic. When we returned to the same plots for additional sampling three years after the beginning of the research, reeds had invaded a significant part of the tombolos, replacing other meadow plant communities. Maybe the quick distribution of this species does not allow us to establish a clear relation between soil C and plant biomass.

4.3. The Role of Allochthonous C

Organic matter introduced via terrigenous runoff and tidal waves plays an important role in the C cycle of the tombolo ecosystem near the village of Kolezhma. At the Gakkovo plot, the tidal activity was low, and consequently, the contribution of allochthonous material was less significant. Allochthonous organic material coming from the continent, as a rule, is more stable and mineralizes more slowly than autochthonous organic material [41]. There are studies that show that the organic C content is significantly higher in the marshes where fresh continental runoff enters because of a higher content of slowly decomposing allochthonous organic matter [42].

Creeks contribute to the distribution of water and solid material on marshes [14,31]. Through the creeks, a tidal wave can penetrate territories remote from the sea while carrying a certain amount of mineral and organic material. This material settles along the way, thereby replenishing carbon reserves in adjacent territories. At the same time, creeks also contribute to the leaching of mineral and autochthonous organic substances from the nearby soil, as well as leading to soil erosion and the volatilization of CO₂ from the substrate; that is, their contribution to the carbon cycle is quite twofold [43]. The vegetation also has a secondary effect on organic matter redistribution, as emergent plants influence the movements and deposition of water and nutrients across ecosystems, with the effects varying between different plant species.

In our case, the contribution of allochthonous organic matter is quite evident at the Kolezhma plot, where the distribution of soil organic C followed the main direction of the tidal wave.

4.4. Ecosystem Services of Coastal Wetlands

The assessment of the ecosystem services for marshes turns out to be a complicated task because of the lack of uniform methodology [44]. The accumulation of C in biomass and soil organic matter seems to be an evident measure of the services provided by these ecosystems. Marshes overgrown with *P. australis* are the most promising C pool because reeds, as a rule, gain much more biomass than herbaceous species. In general, according to other studies, the reserves of not only plant but also soil carbon increase with the invasion of marshes by reeds [45]. The results obtained in the course of this study demonstrate that the reserves of plant carbon are indeed greater in reed beds than in meadows of native species. Reeds are gaining huge terrestrial and underground biomass, and their organic residues are characterized by slow rates of mineralization, which favors an increase in carbon reserves [45].

However, the invasion of *P. australis* in the marshes causes concern, since reeds lead to the removal of native coastal species from their habitat. The contribution to maintaining biodiversity is one of the most important services provided by wetlands [42]. The assessment of ecosystem services through C sequestration is popular because it allows a simple transfer to monetary value, while the contribution of biodiversity to the natural capital is difficult to evaluate [46]. However, an increase in biomass on the account of species diversity can hardly be considered to be beneficial. Also, the results of the current study do not show an increase in soil carbon reserves, especially in the areas with a strong impact of the sea on reeds.

5. Conclusions

The assessment of C stock in soil and in aboveground biomass on two tombolos located on the coasts of the White and Baltic seas showed that the mean values fitted the range reported previously for northern saltmarshes. We found that most soil profiles have normal distribution of organic C density, decreasing with depth, but in some soils, we detected irregular distribution, which has been ascribed to continuous sediment accumulation in the coastal zone. Thus, mere linear extrapolation might overestimate real C stock in coastal soils, and simple spline might underestimate it. We used real data for the 30 cm layer with

no extrapolation in the present study, and we recommend using soil pits with a 100 cm depth for studies that require precise assessment of C reserved in the first meter of soil.

The tombolo is a unique object in coastal landscapes with extreme heterogeneity of sediments, soils, and vegetation. This heterogeneity results in non-uniform distribution of soil C reserves, which may differ more than 10-fold within a few dozens of meters. The density of sampling should be higher on complex costal elements such as tombolos than on simple flat saltmarshes.

On a regional scale, soil C stock depends on vegetative biomass. However, on a large scale, soil and plant C do not completely correspond. We ascribed the phenomenon to the dynamics of vegetative communities on saltmarshes, especially to the action of invasive species such as reeds. Also, the invasion of *P. australis* may affect important ecosystem services of coastal wetlands, such as the maintenance of biodiversity.

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Data Availability Statement: The data presented in this study are available on request from the corresponding author. The data are not publicly available until the finalization of the project.

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Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Table A1. Soil C stock in the upper 30 cm at the Kolezhma site (the White Sea).

Soil Horizon, Depth (cm)	C, g·kg ^{−1}	BD *, g·cm ^{−3}	C Stock per Layer, Mg C·ha ^{−1}	C Stock 0–30 cm, Mg C·ha ^{−1}
		T01K		
Oe (0–5)	231.5	0.34	38.94	144.29
A (5–15)	164.5	0.62	101.99	
Eg (15–20)	2.1	0.83	0.87	
Bg (20–30)	2.0	1.25	2.49	
BC (30–40)	2.3	2.12	4.88	
		T02K		
Oa (0–5)	53.4	0.14	3.64	16.90
ABeg (5–15)	17.2	0.62	10.66	
Bl (15–35)	1.0	1.73	3.46	
BCl (35–50)	2.0	1.68	5.05	
Cl (35–70)	3.5	1.21	14.80	
		T01L		
A (0–15)	5.6	1.09	9.18	13.29
Cl (15–30)	1.9	1.44	4.10	
2Cl (30–60)	1.0	1.25	3.76	
3Cl (60–70)	0.8	1.50	1.20	

Table A1. *Cont.*

Soil Horizon, Depth (cm)	C, g·kg ^{−1}	BD *, g·cm ^{−3}	C Stock per Layer, Mg C·ha ^{−1}	C Stock 0–30 cm, Mg C·ha ^{−1}
		T03K		
Oe (0–10)	100.5	0.30	29.90	107.86
C (10–30)	29.0	1.34	77.96	
2C (30–40)	4.0	1.41	5.65	
2Cg (40–60)	1.6	1.70	5.44	
		T04K		
Oi (0–10)	100.5	0.11	11.02	59.77
C (10–20)	31.2	1.33	41.44	
2C (20–40)	5.4	1.35	14.62	
2Cl (40–50)	3.1	1.65	5.11	
		T05K		
Oi (0–6 (12))	100.9	0.13	16.20	31.26
Aeg (6 (12)–42)	5.1	1.64	20.08	
BCg (42–60)	1.0	1.37	2.46	
		T06K		
Oi (0–7)	223.0	0.30	46.77	66.76
B (7–37)	6.2	1.40	26.08	
BCg (37–50)	1.2	1.70	4.68	
BC (50–60)	2.2	1.29	2.83	
		T07K		
Oi (0–10)	254.0	0.38	96.52	140.15
AB (10–50)	15.9	1.37	87.27	
Bg (50–60)	20.4	1.77	36.04	
		T08K		
Oa (0–7)	67.3	0.42	19.97	139.99
ABg (7–15)	60.4	1.72	82.94	
Bg (15–35)	27.9	0.89	49.44	
BCg (35–60)	0.3	1.88	1.41	
		T09K		
Oi (0–10 (15))	200.5	0.28	84.12	96.22
Ag (10 (15)–50)	4.9	1.65	28.24	
B (50–60)	2.0	1.74	3.47	
		T10K		
Oa (0–11)	65.0	0.40	28.44	68.48
AB (11–38)	49.1	0.43	56.90	
C (38–60)	17.2	0.85	32.27	
2C (60–80)	11.6	1.33	30.96	
		T11K		
Oa (0–7)	267.5	0.46	85.59	142.05
Ag (7–13)	38.2	0.92	28.15	
B (13–32)	13.1	1.27	31.64	
BC (32–38)	4.0	1.56	3.75	
		T12K		
A (0–5)	21.6	1.09	11.81	29.80
AB (5–20)	10.1	1.03	15.61	
BC (20–30)	1.9	1.25	2.38	
2BC (30–50)	1.2	1.88	4.50	
3BC (50–60)	1.7	1.92	3.27	
		T13K		
Oi (0–9)	112.0	0.15	14.99	130.27
B (9–45)	34.1	1.61	197.62	
Cl (45–60)	3.4	1.99	10.13	

Table A1. Cont.

Soil Horizon, Depth (cm)	C, g·kg ^{−1}	BD *, g·cm ^{−3}	C Stock per Layer, Mg C·ha ^{−1}	C Stock 0–30 cm, Mg C·ha ^{−1}
		T14K		
Oi (0–9)	105.0	0.21	19.56	33.09
ABl (9–20)	7.4	1.44	11.72	
BCl (20–60)	1.0	1.80	7.22	
Cl (60–70)	2.3	1.93	4.45	
		T15K		
O (0–7)	111.5	0.33	25.83	71.71
B (7–30)	14.6	1.37	45.89	
Bl (30–40)	2.9	1.74	5.04	
		T16K		
Oe (0–7 (10))	169.0	0.36	61.16	69.86
ABg (7 (10)–50)	3.0	1.45	17.40	
Cg (50–70)	2.0	1.25	5.02	
		T17K		
ABl (0–10)	2.0	1.70	3.41	9.63
Bl (10–26)	2.1	1.62	5.45	
BCl (26–55)	1.2	1.59	5.55	
Cl (55–70)	3.3	1.54	7.63	
		T18K		
Oi (0–9)	239.0	0.25	53.88	83.89
Bg (9–35)	9.9	1.44	37.15	
BCg (35–55)	2.3	1.60	7.36	
		T19K		
Ah (0–3)	8.1	0.46	1.11	38.56
Bwg (3–30)	8.7	1.59	37.45	
Cg (30–40)	1.6	0.33	0.53	
2Cl (40–50)	1.5	1.54	2.31	
		T20K		
Oi (0–7)	289.0	0.20	40.01	85.71
ABeg (7–40)	16.9	1.18	65.56	
Cg (40–50)	0.8	1.64	1.31	
2Cl (50–75)	1.6	1.72	6.89	
		T21K		
Oe (0–10 (15))	179.0	0.17	60.36	72.25
Bg (10 (15)–35)	14.7	1.22	26.98	
2Bl2 (35–45)	1.2	1.65	1.98	
3Bl3 (45–55)	1.9	1.44	2.73	
		T22K		
Bhl (0–30)	18.8	1.14	64.44	64.44
Cl (30–50)	17.7	0.33	11.83	
		T23K		
Oe (0–12)	138.0	0.30	50.14	104.43
Bh (12–40)	35.2	0.86	84.45	
Cl (40–50)	18.3	1.21	22.12	
		T24K		
Oe (0–13)	117.5	0.11	16.96	58.40
AB (13–40)	15.6	1.56	65.83	
BC (40–50)	1.5	1.39	2.08	
Cl (50–60)	1.6	1.79	2.86	

Table A1. Cont.

Soil Horizon, Depth (cm)	C, g·kg ^{−1}	BD *, g·cm ^{−3}	C Stock per Layer, Mg C·ha ^{−1}	C Stock 0–30 cm, Mg C·ha ^{−1}
		T25K		
Oe (0–10)	126.0	0.14	17.01	40.96
ABg (10–25)	9.2	1.41	19.51	
Bg (25–40)	6.7	1.32	13.29	
BC (40–50)	1.5	1.39	2.08	
Cl (50–60)	3.7	1.66	6.15	
		T26K		
Oe (0–7 (10))	68.5	0.30	20.71	39.50
AB (7 (10)–40)	8.1	1.16	28.19	
Cg (40–50)	2.4	1.73	4.15	
		T27K		
Oa (0–16)	73.5	0.30	35.55	71.44
BC (16–40)	22.1	1.16	61.53	
C (40–50)	14.2	1.73	24.54	
		T28K		
Oe (0–13)	107.5	0.21	28.87	82.76
AB (13–30)	36.8	0.86	85.58	
Cl (30–40)	27.4	1.18	32.24	
		T29K		
Oi (0–5)	80.0	0.31	12.21	66.88
BCl (5–40)	13.7	1.60	76.53	
2Cl (40–50)	2.3	1.29	2.96	
		T30K		
Agh (0–5)	13.7	0.70	4.78	24.13
Bh (5–30)	5.6	1.38	19.35	
Cl (30–60)	1.7	1.18	6.01	
		T31K		
O (0–11 (19))	60.5	0.33	37.76	66.16
Bl (11 (19)–25)	23.1	1.85	25.63	
2Cl (25–30)	3.0	1.85	2.77	
		T32K		
O (0–11)	110.5	0.33	39.93	79.24
ABg (11–40)	20.0	1.03	60.00	
BC (40–50)	14.2	1.73	24.54	
Cl (50–60)	2.0	1.85	3.70	

* BD—bulk density.

Table A2. Soil C stock in the upper 30 cm at the Gakkovo site (the Baltic Sea).

Soil Horizon, Depth (cm)	C, g·kg ^{−1}	BD *, g·cm ^{−3}	C Stock per Layer, Mg C·ha ^{−1}	C Stock 0–30 cm, Mg C·ha ^{−1}
		T01G		
Oi (0–50)	240.0	0.19	229.56	137.74
Bl (50–60)	4.9	1.09	5.32	
Cl (60–70)	1.4	1.34	1.88	

Table A2. *Cont.*

Soil Horizon, Depth (cm)	C, g·kg ^{−1}	BD *, g·cm ^{−3}	C Stock per Layer, Mg C·ha ^{−1}	C Stock 0–30 cm, Mg C·ha ^{−1}
T02G				
Oi (0–5)	258.0	0.08	10.22	73.29
Oe (5–15)	123.2	0.23	27.99	
Oi (15–25)	108.0	0.32	34.37	
Ch (25–30)	2.8	0.51	0.72	
2Ahb (30–44)	2.9	1.33	5.41	
2Clb1 (44–75)	8.6	1.26	33.54	
2Clb2 (75–80)	1.5	2.07	1.55	
T03G				
Oi (0–7)	240.5	0.16	26.82	34.48
C (7–30)	2.1	1.59	7.66	
2Agb (30–41)	59.0	1.33	86.06	
2Gb (41–49)	32.0	0.87	22.34	
3Agb (49–56)	76.8	0.85	45.57	
4C (56–69)	3.3	0.61	2.60	
4C2 (69–80)	0.9	1.40	1.39	
4C3 (80–95)	0.9	1.56	2.11	
T04G				
Oi (0–10)	309.0	0.13	40.94	133.62
Ap (10–40)	53.1	0.87	139.02	
C (40–59)	1.3	1.79	4.43	
2Cl1 (59–80)	0.8	1.57	2.63	
3Cl2 (80–90)	0.8	1.77	1.41	
T05G				
Oi (0–14)	216.0	0.19	57.52	174.44
Ah (14–35)	47.0	1.55	153.47	
Cl1 (35–71)	1.7	1.47	9.00	
2Cl2 (71–80)	0.8	1.58	1.14	
T06G				
Oi (0–9)	253.0	0.23	53.44	143.11
Ah (9–35)	47.8	0.89	111.02	
Agb (35–56)	40.8	0.87	74.30	
Cg1 (56–63)	1.5	1.54	1.62	
Cg2 (63–81)	7.0	1.59	8.93	
T07G				
Oi (0–16)	197.0	0.16	49.05	105.48
Ap (16–34)	65.6	0.61	72.56	
A (34–53)	21.4	0.87	35.55	
Cg1 (53–72)	3.0	1.51	8.59	
Cg2 (72–94)	0.8	1.47	2.59	
Cg3 (94–105)	2.3	1.99	5.03	
T08G				
Oi (0–15)	268.5	0.21	85.34	150.21
Ag (15–26)	87.2	0.66	62.85	
C1 (26–80)	3.3	1.53	27.30	
2Cl2 (80–90)	2.7	1.99	5.37	
T09G				
Oi (0–50)	103.0	0.05	28.07	16.84
Cl (50–60)	7.1	1.34	9.50	
T10G				
Oi (0–31)	270.0	0.08	64.87	62.78
Cl (31–75)	1.2	1.62	8.55	

Table A2. *Cont.*

Soil Horizon, Depth (cm)	C, g·kg ^{−1}	BD *, g·cm ^{−3}	C Stock per Layer, Mg C·ha ^{−1}	C Stock 0–30 cm, Mg C·ha ^{−1}
		T11G		
Oa (0–20)	44.5	0.15	13.47	
Ap (20–45)	45.0	0.54	60.89	37.82
C (45–95)	0.9	1.48	6.67	
		T12G		
Oh (0–9)	270.5	0.22	54.24	
Ap (9–26)	34.5	0.82	48.18	103.20
C (26–63)	1.4	1.40	7.23	
Cl (63–100)	0.6	1.42	3.15	
		T13G		
Oi (0–11)	161.5	0.19	33.72	
Ah (11–25)	21.6	0.83	25.15	77.49
A (25–35)	58.3	0.64	37.23	
Cl1 (35–65)	0.7	1.41	2.97	
Cl2 (65–84)	0.7	1.41	1.88	
C3 (84–90)	0.4	1.35	0.32	
		T14G		
Oi (0–11)	238.0	0.11	29.69	
Ah (11–42)	135.2	0.23	97.74	89.59
Cl (42–75)	1.2	0.50	1.99	
		T15G		
Oi (0–25)	159.0	0.08	31.84	
Cg (25–50)	1.9	1.50	1.42	33.26
		T16G		
Oi (0–7)	177.0	0.14	17.79	
A (7–27)	68.1	0.41	55.54	73.99
E (27–41)	1.7	1.29	3.06	
Bw (41–54)	0.9	1.56	1.83	
Cl (54–61)	2.3	1.58	2.55	
		T17G		
Oi (0–26)	309.5	0.28	103.55	
A (26–49)	36.7	0.69	42.84	146.48
Cl1 (49–70)	0.7	1.32	2.49	
Cl2 (70–80)	0.4	1.63	0.59	
		T18G		
Oi (0–26)	218.5	0.37	208.15	
C1 (26–49)	147.2	0.63	211.90	245.00
2Cl2 (49–70)	1.3	1.54	4.19	
3Cl3 (70–80)	2.8	1.94	5.42	
		T19G		
Oe (0–24)	197.5	0.60	286.01	
C1 (24–45)	48.3	1.72	174.87	335.97
2C2 (45–50)	2.6	1.88	2.44	
		T20G		
Oi (0–15)	344.5	0.11	54.88	
Oe (15–50)	171.5	0.12	74.49	86.80
Cl (50–69)	2.9	1.44	7.93	
2Cl (69–75)	2.8	1.84	3.09	

* BD—bulk density.

Table A3. C stock in aboveground vegetative biomass at the Kolezhma site (the White Sea).

Phytocenosis	Sampling Point	Dry Biomass, g	Vegetative C Stocks, Mg C·ha ^{−1}
Low marsh plant communities	T01L1	34.4	2.48
	T01L2	45.0	3.24
	T01L2	40.2	2.89
	T11K1	86.8	6.25
	T11K3	30.6	2.20
	T11K1	53.6	3.86
	T12K1	44.3	3.19
	T12K3	43.7	3.15
	T12K2	93.5	6.73
	T14K1	53.4	3.84
	T14K2	24.9	1.79
	T14K3	34.4	2.48
	T17K	13.0	0.94
	T21K2	77.6	5.59
	T21K3	21.9	1.58
	T21K1	45.9	3.30
	T27K1	88.7	6.39
	T27K3	57.8	4.16
	T27K2	63.7	4.59
Middle marsh plant communities	T01K1	57.1	4.11
	T01K2	52.3	3.77
	T01K3	57.2	4.12
	T04K2	55.9	4.02
	T04K3	49.1	3.54
	T09K3	23.4	1.68
	T09K1	80.3	5.78
	T09K2	28.6	2.06
<i>P. australis</i> communities	T23K3	195.0	14.04
	T23K1	65.6	4.72
	T23K2	28.6	2.06

Table A4. C stock in aboveground vegetative biomass at the Gakkovo site (the Baltic Sea).

Phytocenosis	Sampling Point	Dry Biomass, g	Vegetative C Stocks, Mg C·ha ^{−1}
Hygrophytic plant communities of zonal species	T03G 1	45.2	3.25
	T03G 2	92.3	6.65
	T03G 3	37.7	2.71
	T05G 1	38.7	2.78
	T05G 2	34.9	2.51
	T05G 3	34.4	2.48
<i>P. australis</i> communities	T09G 1	47.8	3.44
	T09G 2	89.5	6.44
	T09G 3	99.2	7.14
	T14G 1	107.8	7.76
	T14G 2	72.4	5.21
	T14G 3	146.5	10.55
Mixed plant communities	T10G 1	64.3	4.63
	T10G 2	44.1	3.18
	T10G 3	61.9	4.46
	T17G 1	142.2	10.24
	T17G 2	81.2	5.85
	T17G 3	65.8	4.74

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