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Carbon Sequestration as a Driver of Pine Forest Succession on Sandy Alluvium: Quantitative Assessment and Process Modeling

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Abstract

The biogenic organization of widespread valley pine ecosystems on sandy alluvium leads to an increase in soil fertility, productivity, and biodiversity through autogenic successions. Using our own stationary observations and literary data on the productivity of pine forests in Russia, Belarus, and Ukraine, we quantified the mechanism of autogenic forest successions associated with carbon sequestration and the influence of organic matter dynamics on the fertility and water retention of sandy soils. The low rate of organic matter turnover in primary succession leads to the intensive accumulation of thick (6–8 cm) forest litter and the formation of small humus-eluvial horizons with total carbon storage up to 50 Mg/ha. This soil structure retains 2–6 times more water and biophilic elements than in the original sandy alluvium. It is suitable for the settlement of more demanding broadleaf species and nemoral herbs with higher rates of litterfall, its decomposition and humification. As a result, simple pine forests on Arenosols and primitive Sod-podzolic soils are replaced by complex, more productive linden–oak–pine ecosystems on developed Cambisols with thick (up to 30 cm) humus horizons, carbon storage of 80–100 Mg/ha and higher (2–7 times compared to the previous soils) fertility and water-holding capacity. This mechanism is adequately described by a nonlinear process model with a trigger reaction of plant productivity to the storage and quality of soil organic matter, suitable for predicting long-term carbon sequestration during the succession of valley pine forests and the effectiveness of artificial afforestation.

Keywords: carbon cycle; pine forests; plant successions; soil fertility; soil water retention; biodegradation; long-term carbon sequestration; nonlinear modeling

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1. Introduction

Forest ecosystems, as the most perfect creation of our planet, play an extremely important role in its carbon balance, absorbing 3.6 ± 0.4 Pg C from the atmosphere annually, which is equivalent to almost half of current fossil fuel emissions (7.8 ± 0.4 Pg C yr^{-1} in 1990–2019, according to [1]). Carbon losses to the atmosphere due to deforestation and forest degradation with a total area of cut down forests of more than 100 Mha over the past 20 years are estimated at 44 ± 10 Pg C and are one of the most serious causes of anthropogenic imbalance in the global carbon cycle, along with man-made emissions [1–3].

Conversely, large-scale afforestation and reforestation appear to be the most effective for climate stabilization in the international Environment, Social, Governance (ESG) agenda [3–7]. A historical example of large-scale state and supranational actions in this area is the forest restoration program in Europe and Stalin's plan for the transformation of nature in the USSR after the Second World War. Modern examples include large-scale afforestation programs in China, Central Asian countries, Ethiopia, etc., as well as the Saudi and Middle East Green Initiatives aimed at planting tens of billions of trees [6–8]. At the same time, failures in the implementation of such programs indicate the main role of limiting edaphic factors, i.e., soil fertility, water-holding capacity and the amount of water available for the root water consumption of seedlings and germination of tree seeds, especially in the early stages of afforestation [9–13]. In particular, the world's largest Chinese plantation forests are generally of poor quality because of a series of environmental problems, such as decreased soil fertility [13–16]. Soil quality, along with topography, determine at least 50% of forest productivity and sustainability, according to a comprehensive analysis of the current state of pine ecosystems growing on the Loess Plateau in China [16]. The soil under natural forests or forest plantations and the associated factors of plant productivity are, however, not constant and are largely determined by the environment-forming function of forest biocenoses [17–21]. This function is especially clearly manifested during ecological successions on sandy alluvial and eolian–alluvial sediments with initially low fertility and water retention [22–25]. Pine forests on coarse-textured soils are widespread throughout the world and are intrazonal biomes, usually confined to river valleys, postglacial outwash landscapes and sandy deserts. Their contribution to the carbon budget of both natural forest associations and artificial pine plantations is greatest in the boreal ecosystems of Eurasia (Russian mixed pine–spruce–birch forests or European pine–hornbeam forests [26,27]), and in the vast pine plantations of North America, China, Korea, and some other countries [16,28,29]. Various species of pine are tolerant of poor soil fertility and coarse-textured substrates with low water retention and easily colonize them during primary psammophytic successions [22,24]. The further growth and development of pine in symbiosis with an equally unpretentious, usually moss–lichen and heather ground cover and a specific, predominantly fungal microbiocenosis are accompanied by the formation of primitive sandy forest soils (Arenosols, Podzols, Sod-podzols) [23,24,26,30]. Their topsoil, represented mainly by litter and small eluvial–humus mineral horizons with ephemeral soil aggregation through the accumulation of organo-metallic colloids, concentrate water and biophilic elements necessary for the sustainable functioning and reproduction of these ecosystems [23,24,31]. As unique bio-pumps, root systems collect rare biophilic elements dispersed in the thickness of the alluvium, accumulate them in their biomass, and after their death and litterfall—collect them in soil upper horizons in an accessible form for plants. That provides the current plants and their subsequent generations these elements. The main role in such deposition belongs to litter, which has a positive effect on water retention, the most significant factor limiting the afforestation of coarse-textured soils and sediments [32]. Further development with accumulation of organic carbon in the soil optimizes its quality to a level suitable for the settlement and survival of broad-leaved species (oak, linden, maple, hornbeam) and grass-shrubby ground cover, which demand more fertility and water nutrition [22,23,27]. This means a new turn in the successional development of the valley forest complex. Thus, in place of simple pine forests (SPFs), complex coniferous–broadleaf forests appear with higher biodiversity and productivity, intensive biological circulation with the large, long-term deposition of carbon in tree trunks and developed, full-profile forest soils [22,23]. According to [27,33], the increasing diversity of multi-aged populations with dense understory and ground cover ensures more efficient carbon sequestration and the stable functioning of complex ecosystems with mixed forest

stands. Such forests can apparently exist for a long time, reproducing in the process of natural development or secondary successions through the stages of small-leaved species (birch, aspen) after fires and forests cutting. Ultimately, oak forests usually become the dominant quasi-climax communities of the dune complex of river valleys [22].

Taking into account the importance of long-term carbon sequestration in natural pine forests and pine plantations, as well as the scarcity of study of its role in the mechanisms of successional dynamics of widespread pine ecosystems, the aim of this paper is the quantifying and modeling of autogenic successions of pine ecosystems on coarse-textured river alluvium in connection with the accumulation of organic matter. The main objectives of this study were as follows: 1. to quantify the storage of biophilic elements in different soil horizons, litter, and phytomass of the ground cover in the succession series of pine and complex coniferous–broadleaf forest ecosystems on river alluvium through their ecotones; 2. to quantify soil organic matter transformation in different successional series through litterfall input, decomposition, and humification; 3. to quantify and HYDRUS-1D model the effect of organic matter on the soil water retention capacity in different successional soils; 4. to develop a nonlinear trigger model of the "biocenosis–soil" dynamic system using Matlab-6 numerical implementation and application to predict long-term carbon sequestration during the autogenic succession of pine ecosystems on sandy alluvium.

Unlike most previous studies [11–16,19–21], our approach used the storage index for the content of organic carbon and biophilic elements instead of their mass concentrations in the soil, which allowed us to clearly assess their biogenic accumulation during the successional stages of pine forests. We also put forward and confirmed with field and laboratory experiments the hypothesis of the self-organization of pine ecosystems on sandy alluvium through the regulation of the kinetics of their organic matter transformation. In this case, the accumulation of organic carbon, as a material carrier of biogenic fertility and water retention of the soil, can be considered the driving force of autogenic successions. The trigger kinetic model using this hypothesis links successional changes with the accumulation of a critical level of organic carbon in the soil along with the introduction of a critical biomass of new, more productive, and soil fertility-demanding species. These critical levels of soil organic carbon and seedling biomass guarantee the start of succession series from SPFs to complex coniferous–broadleaf ecosystems on riverine sandy alluvium with the corresponding acceleration of the carbon cycle and carbon sequestration, which can be used both to explain the natural dynamics and sustainability of such biomes and for the smart bioengineering technologies of their successful restoration and afforestation.

2. Materials and Methods

The field research was conducted since the late 1990s in the Lokhin Island Nature Reserve (Moscow region, Krasnogorsk district; 55.776734 N, 37.273394 E) located in the middle reaches of the Moscow River opposite the estate-museum Arkhangelskoye. The island was formed in the second half of the 19th century due to the river breaking through the base of the bend during the straightening of the riverbed. The habitats of the studied valley pine ecosystems are associated with young alluvial sandy sediments of the ridge relief form, which rise above the level of the old floodplain by 4–6 m and represent riverbed ridges (dunes) shaped by flood waters. Macroclimatic conditions are generally characterized as moderately continental with an average annual precipitation of 550–700 mm, average January temperatures of −6 °C, July temperatures of 18 °C; however, the immediate proximity of the Moscow metropolis may have a local climatic impact, consisting of an increase in the amount of heat and precipitation. The flood regime of the Moscow River has been regulated since the 1930s. As a result, the soil and forest formation processes on young riverbed dunes and older floodplain terraces received a common zonal direction. This is

reflected in the evolution of simple boreal pine forests into complex pine–broadleaf ones accompanied by a change in primitive sandy surface–podzolic soils (Arenosols, Podzols) with a thick litter to full-profile soils (Sod-podzols, Cambisols) with thick mineral humus-accumulative horizons. Among SPFs occupying the river valleys, the primary stage of forest formation is represented by green moss–sheep fescue pine forests (Scots pine—*Pinus sylvestris* L.; green mosses: *Pleurozium schreberi* (Willd. ex Brid.) Mitt., *Dicranum polysetum* Sw., *Polytrichum juniperinum* Hedw., *Brachythecium starkei* (Brid.) Ignatov & Huttunen; sheep fescue—*Festuca ovina* L., and wood reed grass—*Calamagrostis arundinacea* (L.) Roth). The dominant composition of the vegetation ground cover and its dry biomass in different ecological parcels (top of the dune (DT), its slope (DS), and inter-dune depression (ID)) are shown in Tables S1 and S2 of the Supplementary Materials (SM). During autogenic successions, they are gradually replaced by complex pine forests (CPFs) under the influence of interbiogeocenotic connections with floodplain oak groves (English oak—*Quercus robur* L.) and linden forests (small-leaved linden—*Tilia cordata* Mill.) as foci of dissemination broadleaf species and nemoral herbs (yellow archangel—*Lamium galeobdolon* L., common goutweed—*Aegopodium podagraria* L., perennial wood anemone—*Mercurialis perennis* L.). Complex linden–oak–pine forests with nemoral ground cover are widespread on the ancient second and third terraces of the Moscow River and represent a more advanced stage of valley forest formation in the direction of zonal coniferous–broadleaf forest types on Sod-podzolic soils and Cambisols.

We used a generally accepted comparative-geographical approach for the quantitative analysis of the evolution of a simple green moss–reed–fescue pine forest into a complex linden–oak–pine forest with reed–fescue–yellow archangel ground cover on permanent trial plots, established in 1985 by the Institute of Forest Science of the Russian Academy of Sciences. Both compared types of pine forests, representing the initial link of the autogenous succession series on sandy alluvium, have the same initial forest growing conditions. Their adjacent sites are located on the top and slopes of sandy ridges with an absolute height of 138 and 137 m a.s.l. and a groundwater table deeper than 5 m. The parent rock in both cases is medium-grained homogeneous quartz sand poor in nutrients, with low specific surface area, water-holding and absorption capacity. Its physical and chemical characteristics are shown in Supplementary Materials Tables S3 and S4. The stand of SPFs is pure, single-tier, of III quality class; average trunks' diameter is 37 cm, height is 23 m, age is 100–120 years, sum of cross-sectional areas is 33 m^2/ha. The number of undergrowth (new generations of plants) is 20 thousand specimens/ha, composition formula: pine 80%, oak, birch, linden, spruce 20%. The shrub layer of undergrowth is not developed. The CPF has a mixed two-tier forest stand of the II quality class: 1st tier 90% pine, 10% oak + linden; age 120–130 years; the average diameter of pine is 39 cm, height 26 m, sum of cross-sectional areas is 38 m^2/ha, the average diameter of oak is 28 cm, height 23 m; 2nd tier 50% linden, 40% oak, 10% pine + birch + spruce + elm; average diameter 12–16 cm, height 12–15 m, age 70–85 years. The number of undergrowth is 33 thousand specimens/ha, composition 50% birch, 30% linden, 10% oak, 10% elm + pine. The shrub layer of the undergrowth is of medium (60%) density: warty euonymus—*Euonymus verrucosus* Scop., common honeysuckle—*Lonicera xylosteum* L., mountain ash—*Sorbus aucuparia* L., red elderberry—*Sambucus racemosa* L., bird cherry—*Prunus padus* L, common hazel—*Corylus avellana* (L.) H. Karst. The study took into account the small-scale parcel structure of forest associations with sampling by DT, DS, ID parcels, as well as ecotone zones (EZ) between SPF and CPF.

The research program included a year-round study of the organic matter input into the soil with plant litterfall (the weight control method on plastic litter nets with a cell size of 50 × 50 cm and a thickness of 2 mm), the rate of mineralization and humification of soil organic matter (see below), soil respiration (standard closed chamber method with

calculation of CO_2 emissions based on CO_2 growth trends, air temperature and barometric pressure, according to [34]) and the dynamics of the soil CO_2 profile by gas sampling from 5, 10, 20, 30, 50, 100 cm depths with subsequent analysis by a portable infrared gas analyzer PGA-7 (Electronstandart, St. Petersburg, Russia) [34]), weight analysis for storage of the phytomass of grass-shrub and moss covers at 100 × 100 cm^2 accounting areas, laboratory chemical analysis using the dichromate photocolorimetric method for organic carbon, the Kjeldahl method for nitrogen, the potentiometric method for the activity of hydrogen ions (pH), known agrochemical methods for assessing exchangeable soil cations, mobile forms of potassium and phosphorus, atomic absorption and emission spectroscopic methods for determining chemical elements in soils, phytomass, and necromass (litter) in accordance with the manuals [35–37]. Field and laboratory soil physical studies included gravimetric analysis of moisture, estimation of unsaturated hydraulic conductivity and gas diffusion coefficient in soil columns, gravity sedimentation analysis of particle size distribution after treatment with sodium pyrophosphate as a dispersant, soil bulk density assessment using a 100 cm^3 sampling auger, pycnometric analysis of soil particle density with subsequent calculation of porosity in accordance with known methods (see, e.g., [34,38]). The author's method of centrifugation was used for water retention curve analysis (WRC) [38]. The WRC after fitting by the standard Van Genuchten model together with the saturated hydraulic conductivity data was used for the HYDRUS modeling of water retention at the soil profile level [32,39].

Field monitoring of plant residue biodegradation, along with the well-known application method (see, e.g., [34]), used an original method of organic matter incubation on a calcined substrate. Organic material (fresh litterfall) was placed in an upside-down 100 cm^3 cylindrical glass funnel on a layer of calcined quartz sand with a geotextile backing. The funnel spout was sealed with a rubber hose. The funnels were installed in the soil for up to 1 year. The glass waterproof body of the funnel excluded leaching of the material by precipitation, and its moistening was carried out only by capillary feeding from the surrounding soil through the geotextile at the bottom of the funnel. Periodic gravimetric and carbon analysis of the loss of litter carbon and its gain in quartz sand provided a synchronous assessment of the intensity of biodegradation and humification during the observation period, and CO_2 monitoring by air sampling through a rubber hose provided information on the current intensity of biodegradation. Carbon loss data for a known time were processed using a standard exponential biodegradation model to calculate mineralization constants (k, $year^{-1}$), organic matter half-life ($T_{0.5} = \ln 2/k$), and 95% decomposition period ($T_{0.95} \approx 3/k$) according to [34]. An alternative indirect assessment of the kinetics of biodegradation of soil organic matter was based on monitoring soil respiration and CO_2 concentrations in the soil profile. We used a stationary approach [40] to calculate the soil CO_2 production (U_z, $gCO_2/(m^2 day)$) layer by layer from seasonally averaged (autumn, winter, spring, summer) soil CO_2 profiles (C, g/m^3), diffusion coefficients (D, m^2/day), and surface CO_2 emission data (U_0, $gCO_2/(m^2 day)$). Equation (1) shows the algorithm for layer-by-layer calculation of the U_z values.

$$U_1 = U_0 + K_1 (C_1 - C_2); U_2 = -K_1 C_1 + C_2(K_1 + K_2) - K_2 C_3; U_3 = -K_2 C_2 + C_3(K_2 + K_3) - K_3 C_4; \text{etc.}, \quad (1)$$

where $U_{1,2,3}$ are the U_z values for depths of 0–5, 5–10, 10–20 cm, etc., $C_{1,2,3}$ are the stationary CO_2 concentrations for these depths, $K_{1,2,3} = D_{1,2,3}/dz$ are the reduced coefficients of diffusion mass transfer (dz = 5, 10 cm, etc., are the corresponding thicknesses of the soil layer). After this, the average U_z values for the whole year as a function of soil depth were fitted by the well-known (see, e.g., [34,40]) exponential model for biogenic sources/sinks in soils: $U_z = U_f + a \times \exp(-bz)$, where U_f, a, b are empirical constants. Further calculation of the intensity of annual organic carbon mineralization used a simple

algorithm, assuming that 2/3 of soil CO_2 emission is heterotrophic (microbial) respiration. Since the emission conversion factor from $gCO_2/(m^2day)$ to MgC/(ha·year) is almost 1 ($365 \times 12/44/100 = 0.995$), it is possible to use the numerical values of U_z directly to calculate the annual mineralization of organic carbon based on its storage data (C_S) in Mg/ha. The percentage of carbon mineralization (%M) for a given soil layer is the ratio of annual C-CO_2 emission to the storage of organic carbon in this layer: $\%M = 2/3 \times 100 \times \int Uz\, dz/C_S$. Here $\int Uz$ is an integral production of CO_2 in the soil layer. For example, the empirical annual average U_z function for soils of an SPF is $U_z = 0.048 + 9.4 \times \exp(-0.495z)$, and the carbon stock in the 0–6 cm litter layer for the DT parcel is $C_S = 13.55$ Mg/ha. The integral annual emission for the 0–6 cm layer will be $\int Uz = \{0.048 \times 6 - (9.4/0.495) \times (\exp(-0.495 \times 6) - \exp(-0.495 \times 0))\}/6 = 3.05$ MgC /(ha·year). Then $\%M = 100 \times 2/3 \times 3.05/13.55 = 15\%$. This corresponds to the kinetic constant of biodegradation $k = \ln(100/(100 - 15)) = 0.1625$ year^{-1} or half-life values $T_{0.5} = \ln 2/0.1625 = 4.3$ years and $T_{0.95} \approx 3/0.1625 = 18.5$ years.

All field and laboratory experiments were carried out in at least triplicate with subsequent statistical and mathematical data processing, using MS Excel, Microsoft Office 2016 (Microsoft, Redmond, DC, USA), the R 3.5.3 computer software (RStudio PBC, Boston, MA, USA), and the S-Plot 11 program software with the "Regression Wizard" application for nonlinear regression (Systat Software GmbH, Erkrath, Germany). The process modeling used the HYDRUS-1D (PC-Progress, Riverside, CA, USA) and Matlab-6 (MathWorks, Natick, MA, USA) software for the numerical simulation of soil moisture dynamics and root water uptake under the influence of soil organic matter accumulation, as well as for the numerical implementation of a nonlinear trigger model for long-time carbon sequestration in plant biomass and soil during pine forest successions. To verify the model, along with our own experimental data, we used generalized literary data on the productivity of pine ecosystems and the fertility of sandy forest soils in Russia, Belarus, and Ukraine, published in monographs [41–55] of the USSR in Russian and poorly known in world forestry for this reason.

3. Results

3.1. Accumulation of Organic Carbon and Biogenic Organization of Soil During Successional Series

Pioneer vegetation transforms the alluvial landscape primarily by concentrating dispersed biophilic elements in its biomass, litter, and topsoil. Significant quantities of chemical elements previously scattered throughout the entire thickness of the parent rock are concentrated in the phytomass of grass–shrub and moss covers (see Supplementary Materials Tables S1 and S2). Only the phytomass of green mosses, reaching 200–300 g/m^2, contains 3.5–5.0 g/m^2 of nitrogen, 1–1.5 g/m^2 of phosphorus, 2–3 g/m^2 of potassium, 0.2–0.5 g/m^2 of calcium and magnesium, 0.5–0.7 g/m^2 of manganese and up to 3–4 g/m^2 of iron and aluminum. Annual litterfall of SPFs supplies the soil surface with 270 ± 25 g/m^2 of organic matter, containing 107 ± 10 g/m^2 of carbon, 3.5 ± 1.0 g/m^2 of calcium, 1.7 ± 0.3 g/m^2 of nitrogen, 0.3–0.6 g/m^2 of phosphorus, potassium, magnesium, and other chemical elements (Figure 1a).

The litterfall of coniferous and evergreen plants of SPFs, due to the large proportion of polyphenolic compounds, wax, resins, and other compounds resistant to biodegradation [34,56], decomposes quite slowly, contributing to the formation of large (up to 60–80 Mg/ha) litter storage (5–8 cm horizon "L") on the soil surface. A small 5–10 cm humus-eluvial horizon A1E" is formed under the litter. This biogenic soil structure (L + A1E) retains significantly more nutrients and water compared to the original alluvial sand, with a significant portion of the substances localized in the litter (Figure 1b,c). To-

gether, horizons L and A1E retain 1000–1500 kg/ha of biogenic nitrogen, 200–400 kg/ha of phosphorus, magnesium, and calcium, and about 1000 Mg/ha of available moisture, that is 2–6 times higher than similar characteristics for a layer of parent rock of the same thickness.

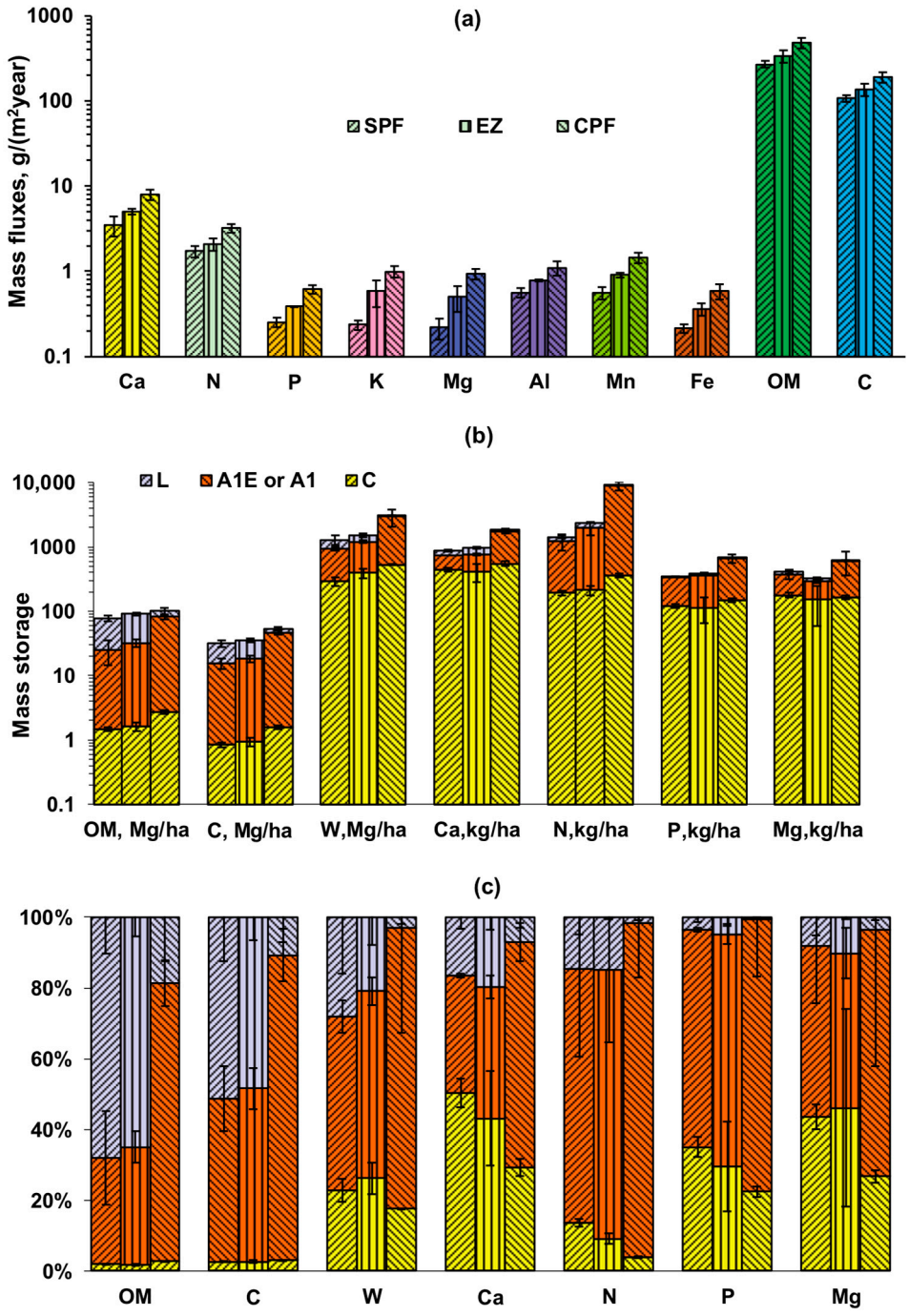

Figure 1. Biogenic organization of sandy soils in successional series of pine ecosystems: (**a**)—input of biophilic elements into soils with plant litter (mass flows in g/(m^{2}year)); (**b**)—deposition of organic matter (OM), soil water (W), and biophilic elements in litter (L), humus horizons (A1E, A1) and parent rock (C), mass storage per 1 ha; (**c**)—relative contribution (in %) of different soil horizons (L, A1, C) to deposition of organic matter, water, and biophilic elements. Hereafter bars indicate confidence intervals at $p = 0.05$.

The next stage of succession begins with the introduction of more demanding soil fertility broadleaf species (oak, linden) and nemoral components of the ground cover (yel-

low archangel, common goutweed, perennial wood anemone, etc.). This vegetation with rapidly decomposing mull and moder-mull litterfall, rich in biophilic elements, together with adapted microbial communities and zoocenoses contribute to the formation of more fertile soil with large (20–30 cm) humus-accumulative horizons "A1", and underlying eluvial-illuvial horizons "E" (10–15 cm and "$B_{h,fe}$" (up to 50 cm) with additional accumulation of carbon and biophilic elements relative to the sandy parent rock. During a new succession, the phytomass of inert wintergreen plants (mosses, berry bushes) decreases sharply (4–8 times, see, e.g., Supplementary Materials Table S1); however, large (150–200 kg/ha) storage of their biophilic elements is not lost, but is fixed in the phytomass of the new vegetation of the ground cover and forest stand with higher rates of organic matter turnover, annual growth, and litterfall. In comparison with SPFs, the total mass and organic carbon of annual litterfall increase by 1.6–2.2 times and contain 2–4 times or more biophilic elements, including nitrogen, phosphorus, potassium, etc. (Figure 1a). As a result, the total annual litterfall in CPFs reaches 480 $\pm$ 70 g/m^2 biomass, including 192 $\pm$ 27 g/m^2 of organic carbon, 8.0 $\pm$ 1.1 g/m^2 calcium, 3.2 $\pm$ 0.4 g/m^2 nitrogen, 0.6–1.5 g/m^2 of phosphorus, potassium, magnesium and other biophilic macro and micro elements. The new soil structure in the form of the L-A1-E-$B_{h,fe}$ horizon's system accumulates and retains 1.6–3 times more carbon, available moisture, calcium, phosphorus, magnesium, and up to 7 times more deficient nitrogen compared to the poorly differentiated soil of SPFs (Figure 1b). As before, the driver of biogenic organization is organic matter; however, the large (20–50%) contribution of forest litter to the deposition of carbon, available water, nitrogen, and other biophilic elements for SPFs gradually decreases and in CPFs the main significance for soil fertility and water retention belongs to powerful (20–30 cm) humus-accumulative horizons with maximum (50 Mg/ha and more) carbon storage (Figure 1c). An additional subsoil depot is formed in the subsoil illuvial–humus–iron horizons ($B_{h,fe}$), concentrating 27 $\pm$ 9 Mg/ha of organic carbon in the parcels of the complex pine ecosystem, i.e., about half of its storage is in the humus-accumulative layers of topsoil. In all cases, ecotone zones consistently occupy an intermediate position in the compared successional series in all quantitative indicators of biological circulation, reflecting the gradual evolution of simple communities into complex ones (Figure 1).

3.2. Kinetics of Organic Matter Input and Transformation in Successional Series

This part quantitatively examines our working hypothesis about the regulation of the biological cycle rate during successions as a biophysical mechanism of self-organization of the "biocenosis–soil" system in the initially unfavorable edaphic conditions of coarse-textured alluvium. Figure 2a,b illustrate the patterns of litterfall input into successional soils. This indicator varies significantly not only from year to year, but also during different seasons. The maximum litterfall occurs in the autumn months; however, even in the cold period from November to March, the input of organic matter continues, reaching half of the autumn litterfall. Therefore, simplified studies with an assessment of the amount of litterfall only in autumn lead to significant distortions in the quantification of this indicator in forest ecosystems. The amount of litterfall in the parcels of the CPF is 1.5–2.0 times greater than in the SPF and its average perennial value is 6.5 $\pm$ 1.2 Mg/ha. The maximum amount of annual litterfall in the parcels of the SPF reached 4.5 Mg/ha, and for the complex linden–oak pine forest—8.4 Mg/ha. The minimum values were 2.3 and 4.8 Mg/ha, respectively. In all cases, the ecotone site occupies an intermediate position between the SPF and the CPF (Figure 2a,b).

The qualitative (fractional) composition of litterfall of the two compared communities also differs significantly (Supplementary Materials see Table S5). The litterfall of an SPF consists of 85%–95% of hardly decomposable needles, branches, bark, and pinecones. In a

CPF, 30%–50% of the organic matter is represented by fractions of mull leaf litter, susceptible to biodegradation and rich in biophilic elements. Within the ecosystems, significant spatial variation in the input and fractional composition of organic matter is also noted for different parcels (Figure 2, Supplementary Materials Table S5).

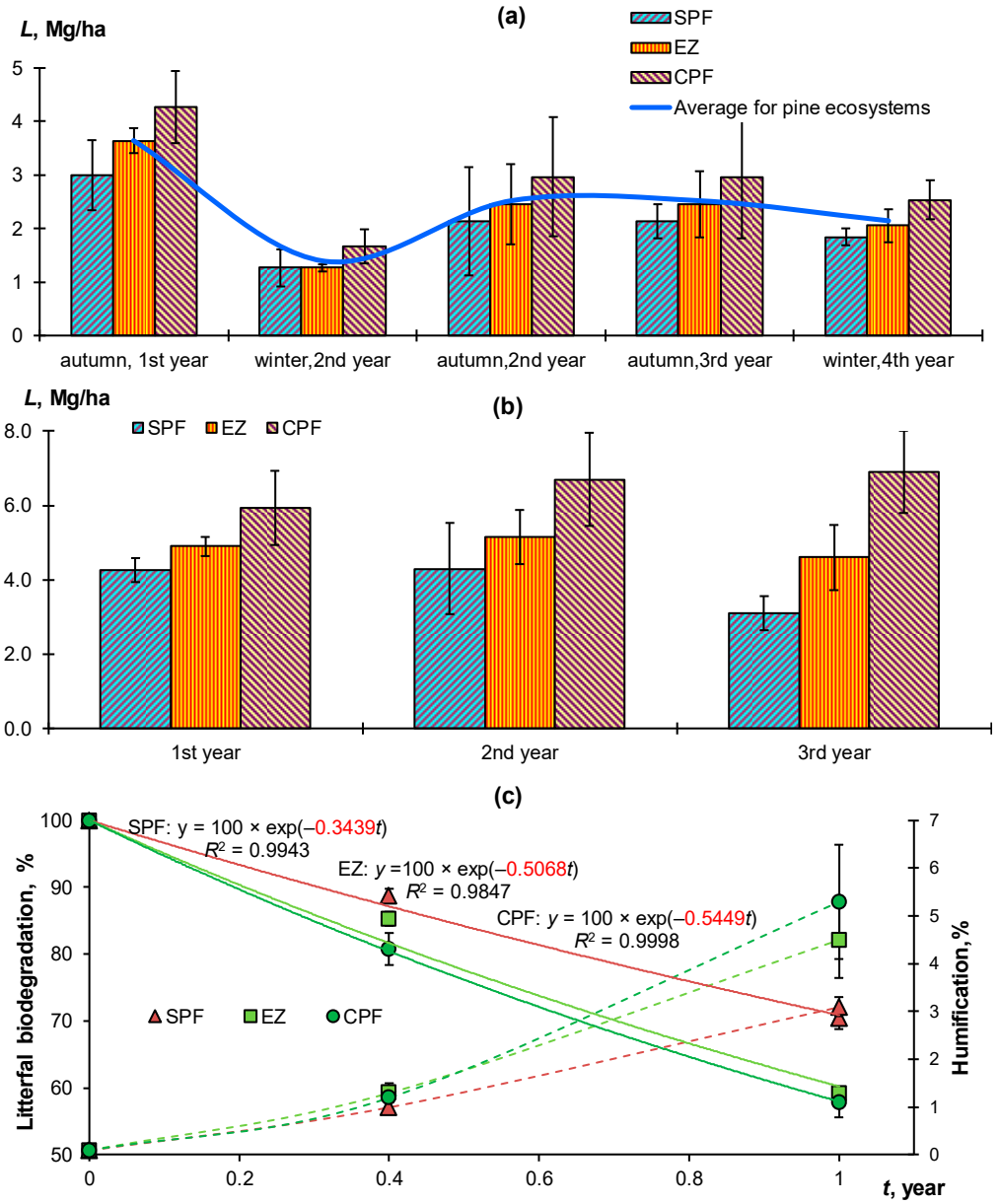

Figure 2. Kinetics of the input and transformation of organic matter in soils of a successional series: (**a**)—seasonal dynamics of litterfall (L, Mg/ha); (**b**)—annual dynamics of litterfall (L, Mg/ha); (**c**)—biodegradation (%wt), and humification (%wt) of litterfall.

The composition of the litterfall obviously determines the intensity of its biodestruction [34,56]. In the parcels of a CPF, the intensity of destruction of dead plant matter is 1.4–1.8 times higher than in a simple biocenosis and reaches 43%–44% of dry matter per year (Figure 2c, Table 1). In the parcels of the SPF, the litterfall of the "mor" type with a predominance of coniferous remains is more stable and its biodegradation rate does not exceed 30–31% per year. Ecotone zones continue to occupy a characteristic intermediate position, including this indicator. Note that both the traditional method of assessing biodegradation in nylon nets and the proposed modification with decomposition of litter in glass funnels with a permeable bottom gave similar results for assessing the

rates of the biodegradation (Table 1). Also noteworthy is the high contribution of winter biodegradation, which, as in the case of organic matter input, is no less than 1/3 of the total annual values. Fitting the data for the annual period of the experiment with a standard exponential model [34] allows us to estimate the kinetic constants (k) of litter decomposition (Figure 2c, Table 1). They regularly increase in the successional series "SPF-EZ-CPF" from 0.34 ± 0.3 to 0.55 ± 0.1 year^{-1}, i.e., by 1.6 times.

Table 1. Litterfall and transformation of organic matter in soils of pine ecosystems (Lokhin Island).

Parcels	* Litterfall, Mg/ha		3 November–29 March Next Year			3 November–3 November Next Year			Litter Storage, Mg/ha	k, Year^{-1}
	Winter	Annual	I D%	I H%	II D%	I D%	I H%	II D%		
					SPF					
DT	0.8 ± 0.1	3.4 ± 1.1	10.6 ± 0.6	0.9 ± 0.1	10.8 ± 0.9	30.0 ± 2.0	3.2 ± 0.2	27.8 ± 1.7	44.3 ± 16	0.08 ± 0.02
DS	1.1 ± 0.4	3.6 ± 0.9	12.5 ± 0.8	1.0 ± 0.1	nd	31.0 ± 2.3	2.9 ± 0.2	nd	61.2 ± 22.8	0.06 ± 0.02
					EZ					
DT	1.3 ± 0.1	5.1 ± 0.8	15.5 ± 1.4	1.1 ± 0.1	nd	40.0 ± 2.7	5.2 ± 0.3	nd	52 ± 34.4	0.10 ± 0.02
DS	1.4 ± 0.2	4.4 ± 0.4	15.0 ± 1.0	1.4 ± 0.2	13.6 ± 1.1	41.0 ± 3.1	3.7 ± 0.3	41.4 ± 2.6	66.4 ± 49.4	0.07 ± 0.01
					CPF					
DT	1.8 ± 0.1	6.9 ± 0.7	16.8 ± 1.2	1.1 ± 0.2	17.6 ± 1.3	39.5 ± 2.8	4.0 ± 0.6	42.5 ± 3.4	17.5 ± 12.4	0.39 ± 0.04
DS	2.1 ± 0.2	7.4 ± 0.9	19.2 ± 1.6	1.3 ± 0.1	21.5 ± 1.5	43.0 ± 4.2	6.6 ± 0.8	43.9 ± 3.1	27.5 ± 19.0	0.27 ± 0.03
					Statistical comparison criteria:					
LSD	0.46	1.60	2.69	0.33	4.55	5.78	1.62	8.10	29.3	0.08
					** Tukey p-values for multiply comparisons of means:					
EZ vs. SPF	0.171	0.235	0.031	0.250	0.269	0.009	0.243	0.026	0.403	*** 0.552
CPF vs. SPF	0.002	0.002	0.001	0.153	0.024	0.006	0.049	0.020	0.039	*** 0.042
CPF vs. EZ	0.037	0.020	0.106	0.937	0.078	0.954	0.562	0.858	0.049	*** 0.044

* Litterfall—average values for 4 years of observations are given; P%, H%—percentage of decomposed and humified OM from the initial mass of litter; I, II—experiment in glass funnels (I) and nylon nets (II). Hereafter "±" indicates confidence intervals at $p = 0.05$; ** parametric comparisons; *** nonparametric comparisons using p-values for Wilcoxon rank sum test.

An additional assessment using the so-called decomposition coefficient (the ratio of litterfall to litter storage, see, e.g., [57,58]) gives the lower values of k = 0.06–0.10 year^{-1} for an SPF and ecotone zones and k = 0.27–0.39 year^{-1} for a complex ecosystem (Table 1). Such strong discrepancies with the experimental assessment of biodegradation are most likely associated with the specious assumption for these ecosystems about their stationary state, which is the basis for calculating the decomposition coefficient [34,57]. However, this rough estimate also indicates an acceleration of organic matter input into soils during the transition from simple to complex pine ecosystems, with the 3–4 fold time overestimation of the k value.

All the above comparative results are statistically confirmed by ANOVA using the R 3.5.3 computer software. Preliminary tests of normality (Lilliefors (Kolmogorov–Smirnov) criteria) and homogeneity of variances (Bartlett's criterion) were passed for all parameters of Table 1, excluding the biodegradation constant (k), at p-values = 0.07–1 significantly higher than the reference p-value = 0.05. Therefore, for all parameters of Table 1, except k, we used the parametric ANOVA with LSD and Tukey comparison criteria. For the biodegradation constant k, the nonparametric Wilcoxon rank sum test was used. Regardless of the criterion (parametric, non-parametric ANOVA), the pairwise comparison of kinetic indicators for organic carbon transformation in SPFs and CPFs almost always gives statistically significant differences with a p-value less than 0.05 (see Table 1, second row from the bottom). Differences from the ecotone zone are not always statistically significant, which emphasizes the gradual nature of successional processes.

Information on the seasonal dynamics of CO_2 concentrations in funnel reservoirs containing decomposing litter indicates the oscillatory nature of the biodegradation process for parcels of both types of ecosystems (Figure 3). A significant decrease in CO_2 concentrations (down to background atmospheric values) occurs in mid-January. Subsequently, this

value gradually increases, indicating the activation of destructor organisms. The maximum biodegradation activity is observed in mid-spring, the second half of summer, and late autumn.

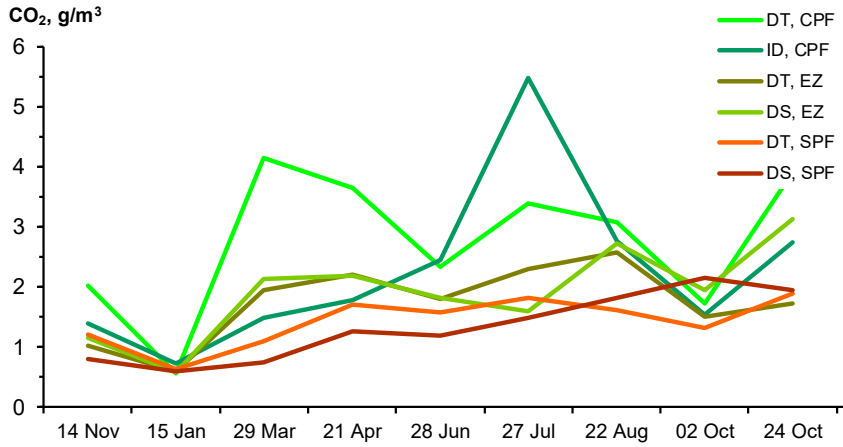

Figure 3. Seasonal dynamics of CO_2 concentrations in funnels with decomposing litterfall.

A complex field experiment in glass funnels also made it possible to estimate the intensity of litter humification (Figure 2c, Table 1). The results showed that humified substances made up on average 3.3% of the initial dry mass of litter in an SPF and 5.3% in a complex ecosystem. In general, the intensity of annual humification in the parcels of the CPF is 1.5–2.0 times higher than this value for a simple biocenosis. As in the case of biodegradation, the amount of humified matter for the period November–March reached 1/3 of the total mass transformed during the year (Table 1). Analysis of the gas monitoring results confirmed significant differences in biogenic carbon transformation for pine ecosystems in the compared successional series (Figure 4). The CO_2 concentration gradually increases with the soil depth; the highest values (0.15%–0.30%) are observed at 50–100 cm. The soils are automorphic and well aerated due to their coarse texture, so throughout the year the CO_2 content in the gas phase does not exceed 0.2–0.3% or 3–4 gCO_2/m^2 of its storage in the 0–100 cm layer. Maximum values of daily emissions in summer months rarely exceed 10–12 gCO_2/m^2. The difference in gas content and emission depending on type of biogeocenosis is clearly visible. More productive CPFs emit and concentrate 1.3–2 times more CO_2 than simple ones, which is in good agreement with the previously identified differences in the intensities of input and biodegradation of organic matter for these ecosystems. Ecotone areas, as before, occupy an intermediate position in terms of the characteristics under consideration.

Since the storage of CO_2 in well-aerated sandy soils is usually much less than the daily emission, we can consider this soil system to be quasi-steady state, assuming that the emission from the surface is practically identical to the gross production of CO_2 in the soil volume. Using this assumption and the methodology [40] based on it (see Equation (1) in Materials and Methods), we obtained stationary gas profiles for all four seasons and calculated the functions of gross CO_2 production in soil layers of different depths (Figure 5). In winter, CO_2 concentrations in the soil profile level out and approach its atmospheric content (0.035–0.05%). In spring, the soil begins to gradually fill with carbon dioxide. Maximum concentrations are formed in summer. Then, in autumn, they begin to gradually decrease (Figure 5a–c). Significant differences in gas profiles between seasons, reliable at the $p = 0.05$ level, also confirm the possibility of using the steady-state approach [40] in calculating the CO_2 gross production function. The effective diffusion coefficients of carbon dioxide used in the calculation varied slightly in the range of 100–140 cm^2/h and were higher for topsoil due to the lower bulk density of the soil compared to subsoil

(see the inset in Figure 5d). The estimated gross CO_2 production depending on soil depth was successfully (R^2 = 0.999, s = 0.02–0.05) fitted by an exponential model [34] with approximation parameters reliable at p = 0.001–0.05 (see Supplementary Materials Table S6). Using this model and data on carbon storage in different soil layers, we estimated the constants of organic carbon biodegradation for litter of the L horizon and for humus horizons in soils of the successional series (Table 2).

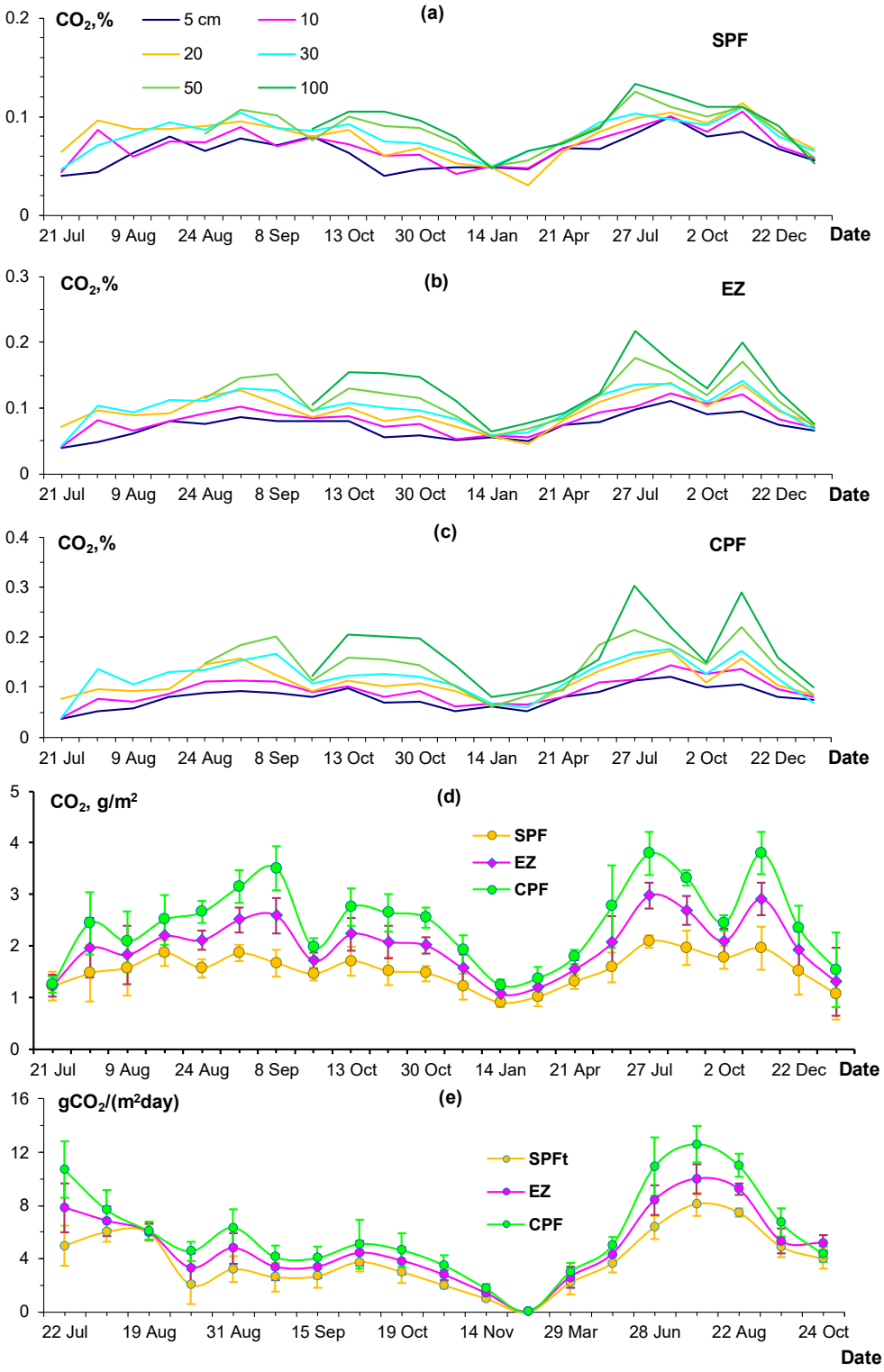

Figure 4. Seasonal dynamics of CO_2 content in soil air (**a**–**c**) its storage in the 0–100 cm layer (**d**) and CO_2 emission from the surface of successional soils (**e**) over a 2-year monitoring period.

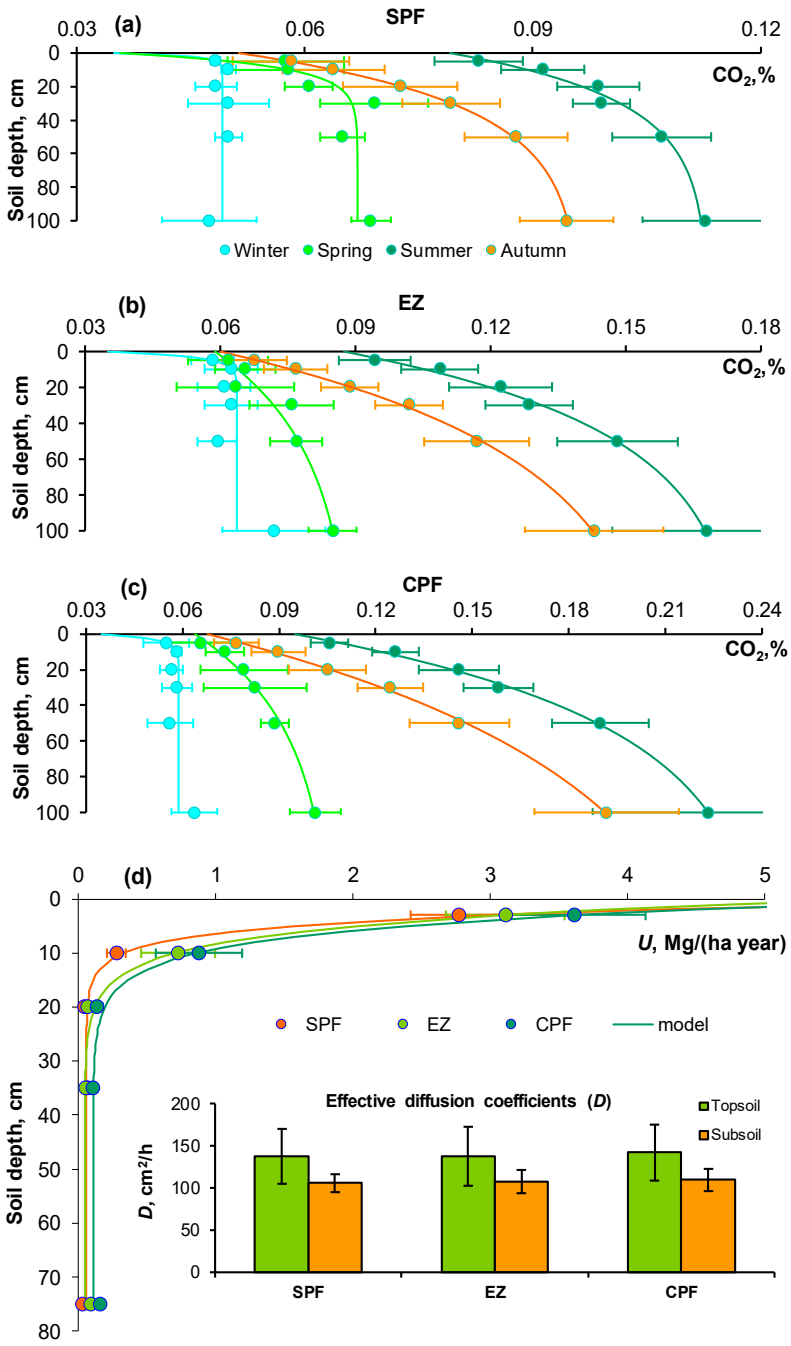

Figure 5. Steady-state seasonal carbon dioxide (CO_2,%) profiles (**a**–**c**) and estimated gross CO_2 production (U, Mg/ha) as a function of soil depth (**d**) together with diffusion coefficient data (inset).

Table 2. Estimation of carbon turnover parameters * for litter and humus of simple and complex pine ecosystems.

Organic Matter	Indirect Assessment by CO_2 Emissions			Direct Assessment by Incubation in Glass Funnels		
	k, Year^{-1}	$T_{0.5}$, Year	$T_{0.95}$, Year	k, Year^{-1}	$T_{0.5}$, Year	$T_{0.95}$, Year
			SPF			
Litter	0.177 ± 0.062	3.9 ± 1.6	17.0 ± 6.9	0.349 ± 0.025	2.0 ± 0.1	8.6 ± 0.6
Humus	0.026 ± 0.005	26.3 ± 5.1	113.6 ± 22.0	nd	nd	nd
			CPF			
Litter	0.427 ± 0.207	1.6 ± 1.1	7.0 ± 4.6	0.546 ± 0.017	1.3 ± 0.1	5.5 ± 0.2
Humus	0.021 ± 0.009	32.9 ± 17.6	142.7 ± 76.2	nd	nd	nd

* turnover parameters notation, see the "Materials and Methods" section.

For the litter of a complex ecosystem, the k value varied in the range of 0.2–0.6 year^{-1} and was 1.5–3.2 times higher than for parcels of the SPF (k = 0.10–0.23 year^{-1}). The half-life of litter organic carbon was estimated at 1–5 years, and complete biodegradation at 3–24 years. Direct assessment of the kinetics of biodegradation of litter yields slightly higher values of k = 0.32–0.55 year^{-1} and, accordingly, lower half-life ($T_{0.5}$ = 1.3–2.1 years) and total carbon turnover $T_{0.95}$ = 5.4–9.3 years (Figure 2, lower part, Table 2). However, the direct incubation assessment used fresh litterfall, whereas the indirect assessment dealt with data on the multiyear storage of forest litter and CO_2 emissions from it. It is obvious that stratified multi-year litter enriched with lignin and other poorly degradable compounds (see, e.g., [56]) will be more resistant to biodegradation than fresh litterfall, which explains the differences obtained.

The new approach also allowed us to estimate the turnover of humus carbon in the A1E and A1 topsoil horizons of the successional series (Table 2). For humus of both pine ecosystems, the biodegradation constants varied in the range of 0.01–0.03 year^{-1} with the corresponding half-life indicators of 20–50 years and $T_{0.95}$ = 90–220 years.

In general, the kinetics of the input and transformation of organic matter are completely determined by the specificity of the plant dominants of the stand and ground cover. In an SPF with a boreal ground cover, the rate of input of litterfall and its decomposition is relatively low, since the needles of conifers and foliage of winter-green plants do not die off annually and contain organic compounds that are resistant to biodegradation and inhibit the activity of microorganisms. The introduction of broadleaf species and nemoral herbs with annual dying off of foliage accelerates the input of litterfall and biodegradation of litter by 1.5–2 times or more, leading to a general intensification of the biological cycle in CPF.

3.3. Effect of Organic Matter on Soil Water Retention: Laboratory Experiment and Modeling

3.3.1. Laboratory Assessment of Soil Hydraulic Properties

Accumulation of organic matter significantly improves soil water retention as the main edaphic factor limiting the afforestation of coarse-textured alluvium. The original sandy alluvium, as shown in Figure 6, has low water retention, since a pressure head near 10 cm is sufficient to remove 70%–80% of the water from the total pore volume (water-saturated state). The estimated field capacity of the sandy alluvium of the Moscow River and the lower soil layers (C-horizons up to 200 cm deep), based on a pressure head of 330 cm, does not exceed 3%–4% (Table 3). The corresponding range of available water (AWR) varies from 1 to 2.5%, i.e., it is also very low. The hydraulic properties of sandy alluvium are also unfavorable for plants: very high (up to 1500–2000 cm/day) saturated hydraulic conductivity and a sharp decrease in unsaturated hydraulic conductivity to 0.01–0.001 cm/day at 100–1000 cm of suction, in accordance with the Campbell power model [59]. These hydraulic properties promote the strong leaching of nutrients during infiltration and a limited root water uptake during the drying of sand with low water conductivity at the border with the root, where water is still potentially available to plants with a pressure head of 100–1000 cm much less than the permanent wilting point (15,000 cm).

Accumulation of litter (L-horizon) sharply increases water retention, radically changing the unfavorable forest growing conditions of sandy alluvium. High total water capacity of litter increases the maximum water content almost twice to 90% and more compared to sandy alluvium. This water capacity remains almost unchanged at a pressure head up to 10–40 cm and only then begins to gradually decrease. As a result, the FC of litter is in the range of 30%–50%, and the AWR reaches 26%–32%, i.e., water retention increases by 15–20 times compared to sandy alluvium. The accumulation of humus also leads to a significant change in the water retention of sand, although less in comparison with the

litter. The FC of horizons A1E and A1 is on average 11%–18%, and the AWR is 6%–8%, or 3–6 times higher than similar parameters in alluvial sand. Along with increasing water retention, the accumulation of organic carbon reduces the saturated hydraulic conductivity of sandy soils by 1.5–2 times or more (see inset in Figure 6b). All together this creates good prerequisites for the optimization of forest vegetation edaphic properties; however, this effect can be fully assessed only at the level of the soil profile. For this purpose, in the next section we used HYDRUS-1D modeling (hysteresis in WRC is neglected) of water retention and root water uptake, simulating the situation of a complete water saturation of the soil at the initial moment (for example, after the spring flood) and the subsequent pore water redistribution for 1 month. All experimental WRC data were previously fitted by the standard Van Genuchten (VG) model with high coefficients of determination (R^2 = 0.9855–0.9998) and acceptable standard errors (s = 0.4–2.0%) at the level of variation in experimental WRC data in the centrifugation method (Table 3).

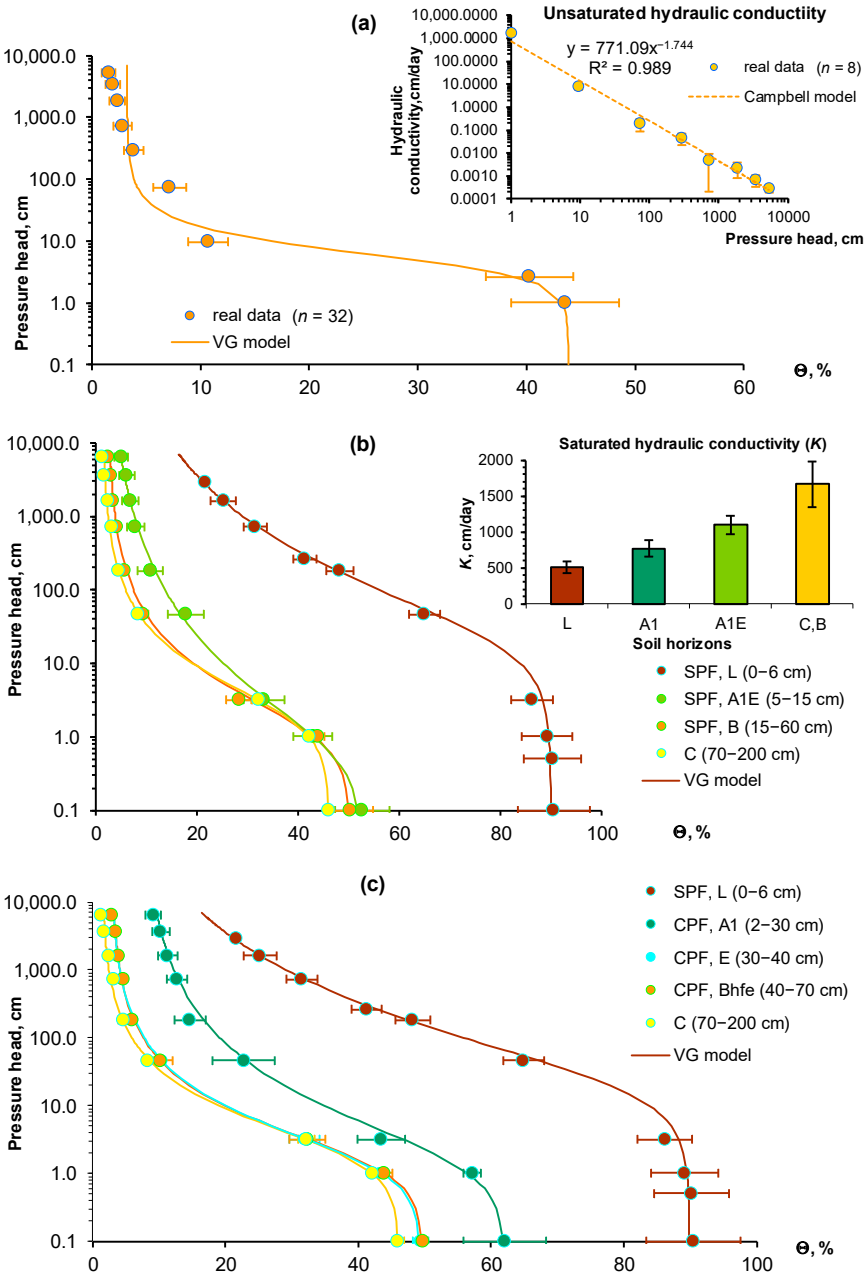

Figure 6. Water retention curves (**a**–**c**), unsaturated (insert (**a**)) and saturated (insert (**b**)) hydraulic conductivity of different soil horizons in a successional series; VG—the Van Genuchten model.

Table 3. Approximation parameters of the VG model, field capacity, and AVR for assessing water retention in different soil horizons.

Soil Horizons	Θ_r, %	Θ_s, %	α, cm^{-1}	n	R^2	s, %	* FC, %	** AWR, %
SPF								
A1E (5–15 cm)	1.2 ± 0.8	52.6 ± 5.3	1.38 ± 0.83	1.29 ± 0.04	0.9973	0.784	11.3 ± 6.1	6.3 ± 2.7
B (15–60 cm)	2.3 ± 0.5	50.2 ± 4.5	0.71 ± 0.34	1.52 ± 0.05	0.9986	0.611	5.5 ± 2.4	2.7 ± 1.5
CPF								
A1 (2–30 cm)	7.2 ± 1.7	62.1 ± 6.2	0.58 ± 0.51	1.38 ± 0.06	0.9996	1.289	18.3 ± 10.9	8.0 ± 6.2
E (30–40 cm)	2.6 ± 0.3	49.4 ± 1.1	0.60 ± 0.07	1.54 ± 0.03	0.9997	0.391	5.3 ± 0.9	2.4 ± 0.5
Bhfe (40–70 cm)	2.7 ± 0.2	49.7 ± 0.7	0.58 ± 0.04	1.56 ± 0.02	0.9998	0.257	5.2 ± 0.6	2.2 ± 0.3
Common to both ecosystems								
L (0–6 cm)	0.0 ± 1.0	89.9 ± 0.88	0.05 ± 0.03	1.30 ± 0.02	0.9981	1.435	39.9 ± 10.6	26.5 ± 5.8
C (70–200 cm)	1.3 ± 0.3	46.0 ± 0.8	0.44 ± 0.04	1.60 ± 0.03	0.9997	0.390	3.6 ± 0.8	2.1 ± 0.4
Alluvium	3.2 ± 0.8	43.8 ± 2.2	0.21 ± 0.04	2.37 ± 0.64	0.9855	2.031	3.4 ± 1.6	1.7 ± 0.9

* FC is the field capacity determined by the WRC at a pressure head of 330 cm. ** AWR is the range of available water; AWR = FC − WP, where WP is the wilting point at a pressure head of 15,000 cm.

3.3.2. HYDRUS-1D Modeling of Hydrological Dynamics at the Soil Profile Level

Our HYDRUS-1D model considered the dynamics of volumetric soil water content and root water uptake for small pine seedlings with a root system up to 20 cm after a complete soil saturation with boundary conditions of 3 mm/day evapotranspiration and free drainage (Figure 7). The parameters of the Feddes model for root water uptake (P_0 = 0 cm; P_{0pt} = 0 cm; P_{2H} = −5100 cm; P_{2L} = −12,800 cm; P_3 = −21500 cm; r_2h = 0.5 cm/day; r_{2L} = 0.1 cm/day) were taken from [60]. The experimental input information included VG parameters for WRC and unsaturated hydraulic conductivity of sandy alluvium and different horizons for soils of the succession series (Table 3, Figure 6). The output information compared soil water content, root water uptake, and cumulative drainage in the soils of simple, CPF, and initial alluvium. As expected, the original alluvium lost the main amount of water through drainage within 12–24 h, with a sharp decrease in the moisture content of the topsoils to 15%–20% (Figure 7a). As a result, pine seedlings maintained potential evapotranspiration for no more than 5 days, after which it dropped sharply to a critical level of 1 mm/day in less than a week. The accumulation of detritus in the form of 6 cm litter and humus in the A1E horizon doubled the initial moisture content of topsoil and increased (up to 30%–40%) the residual moisture content after 15 days of drainage. As a result, the potential root water uptake was prolonged threefold (up to 15 days), and the critical evapotranspiration level of 1 cm/day for pine seedlings was reached only on the 25–27th day. Obviously, over such a long period the probability of a new water charge of topsoil by rain is very high, i.e., the seedlings take root and subsequently develop successfully. Similar dynamics are observed in the case of a complex pine ecosystem, where the reduction in the litter layer is compensated by thick (30 cm) humus horizons with high water retention (Figure 7c). In general, both biogenic mechanisms (accumulation of litter and humus) successfully optimize the unfavorable hydrophysical properties of sandy alluvium by increasing the water retention of topsoil and the period of active root water uptake by 2–3 times, along with a 15%–20% reduction in cumulative drainage.

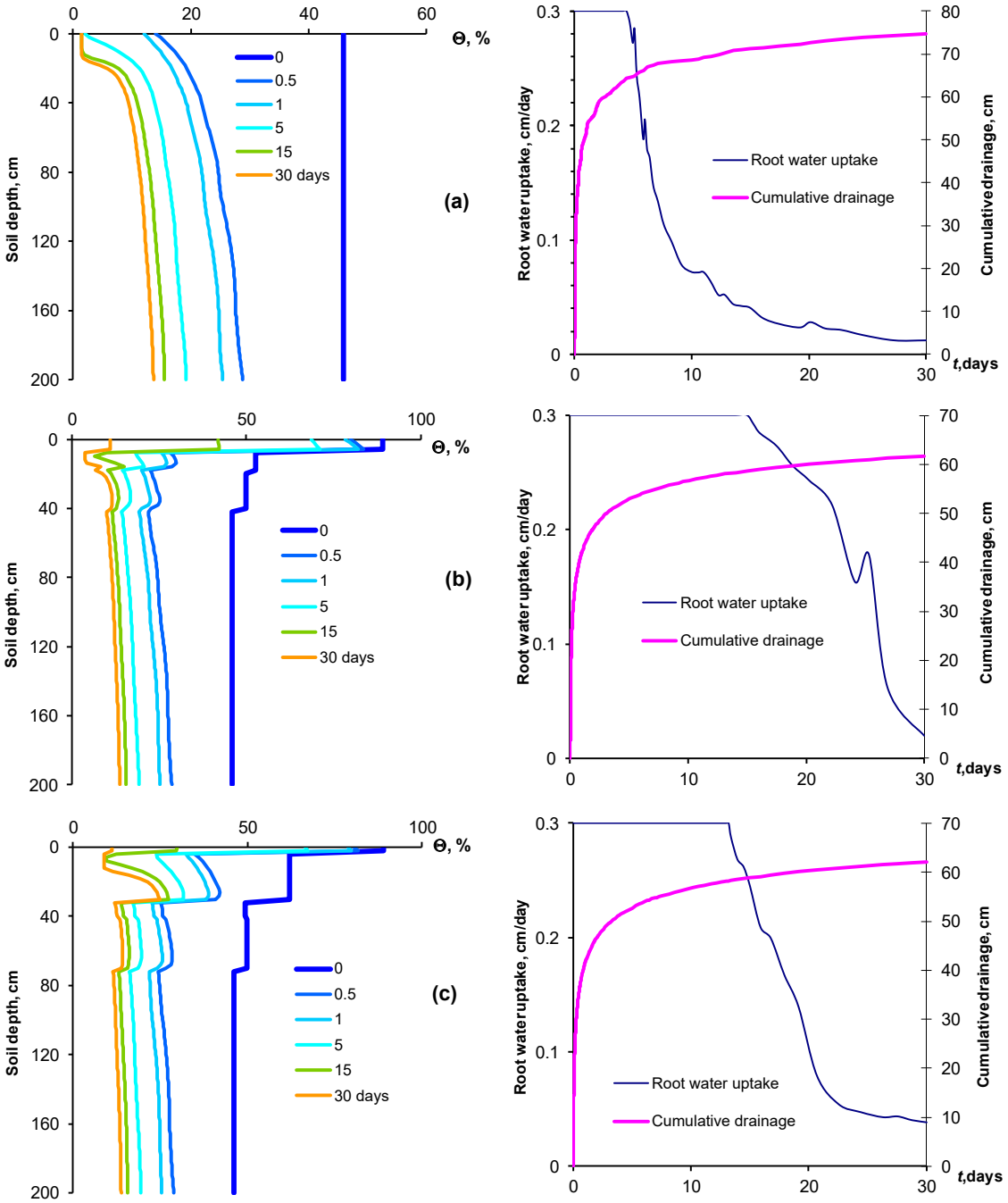

Figure 7. HYDRUS-1D modeling of volumetric water content (Θ,%), root water uptake, and drainage in homogeneous sandy alluvium (**a**), in soils of SPF (**b**), and a complex pine ecosystem (**c**) as a function of litter and humus accumulation.

3.4. Trigger Model of Successional Dynamics of Pine Forests Under the Influence of Soil Organic Matter Accumulation

3.4.1. Theoretical Basis and Formulation of the Model

Previous experimental studies have shown the importance of biogenic accumulation of organic matter as a driver of autogenic successions of pine forests on sandy alluvium. In this regard, we attempted to present the mechanism of successional dynamics of pine forests on sands in the form of a nonlinear process model with a trigger reaction of tree stand growth to the accumulation of soil organic matter. The model includes direct (environment-forming function of biocenosis) and feedback (biogenic fertility) links. The growth of the forest stand is described by a modified Verhulst–Pearl equation with quadratic nonlinearity of

growth and its additional regulation by the level of soil fertility (storage of organic matter) by the nonlinear Michaelis–Menten function. The influx of organic matter into the soil in the form of litter is assumed to be proportional to the phytomass. The basic model consists of a system of two nonlinear coupled ordinary differential equations:

$$\begin{array}{l} \frac{dB}{dt} = rB\frac{X}{\alpha_M + X} - k_1 B - k_1 \frac{B^2}{K} \\ \frac{dX}{dt} = k_2 B - \gamma X \end{array}, \quad (2)$$

with steady state equations

$$\begin{array}{l} \overline{B}_1 = 0;\ \overline{B}_{2,3} = \frac{m \pm \sqrt{m^2 - 4KS}}{2};\ \overline{X}_{1,2,3} = \frac{k_2 \overline{B}}{\gamma}; \\ S = \alpha_M \gamma / k_2,\ m = \frac{rK}{k_1} - K - S \end{array}, \quad (3)$$

under Lyapunov stability conditions

$$B_0 > \overline{B}_3;\ X_0 > \overline{X}_3, \quad (4)$$

where $B(t)$, $X(t)$, are the storage of phytomass and soil organic matter in Mg/ha, entering the soil with intensities $k_2 B$, t/(ha year), and decomposing with a specific rate γ, year^{-1}; soil organic matter controls phytomass growth according to Michaelis–Menten kinetics (α_M is the Michaelis constant, Mg/ha), and a modified Verhulst–Pearl equation with a Malthusian growth parameter r, year^{-1} and the environmental capacity for phytomass K, Mg/ha. Along with synthesis, the growth equation includes dissimilation losses of phytomass ($-k_1 B$), and self-limitation ($-k_1 B^2/K$). B_0, X_0 are the initial contents of phytomass and soil organic matter, Mg/ha. The upper bars in Equations (3) and (4) designates the steady-state limits.

The trigger mode is set by conditions (4). If the initial storage of phytomass and soil organic matter (B_0, X_0) is less than critical, then the zero value is stable ($\overline{B}$, $\overline{X}$ = 0), i.e., the ecosystem perishes. If the storage of seedlings and soil carbon is higher than the critical values, the growth of the forest stand continues with a new carbon accumulated in the soil. The additional linear sub-model (5) divides the block of soil organic matter into litter (L) and humus (H) with corresponding kinetic turnover constants (k_3, k_4, k_5, year^{-1}):

$$\begin{array}{l} \frac{dL}{dt} = k_2 B - k_3 L \\ \frac{dH}{dt} = k_4 L - k_5 H \end{array}, \quad (5)$$

where $L + H = X$.

3.4.2. Validation of the Model Using Experimental Data

In assessing the parameters of the model, we used, along with our own experimental data (Tables 1 and 3, Figures 2 and 3), numerous literature sources on the bioproductivity of pine forests on sandy soils in Russia, Belarus, and Ukraine [41–55]. In particular, Figure 8a shows the growth dynamics of pine stands of different ecosystems according to the basic Verhulst–Pearl equation in the following form: $B = K_0/(1 + (K_0 - B_0) \times \exp(-r_0 t)/B_0)$, where r_0, K_0, B_0 are the approximation parameters of the model. This equation allows us to estimate the parameters of the growth rate (r_0, year^{-1}), environmental capacity or maximum biomass of the ecosystem (K_0, Mg/ha), and initial biomass (B_0, Mg/ha) using the real data from long-term stationary studies of the pine ecosystem dynamics. The preliminary Malthusian growth parameter (r_0) in pine forests of different types varied within the range of 0.04–0.10 year^{-1}. Taking into account the modification of the Verhulst–Pearl equation in the model (2) by introducing Michaelis–Menten kinetics and the constant of phytomass mortality-respiration ($k_1 \approx (0.3–0.5) \times r$), the final Malthusian parameter

for this model, calculated as $r = (2–3) \times r_0/\beta$; $(0.8 \leq \beta = 1/(1 + \alpha_M/\overline{X}) \leq 1)$, was in the range of 0.10–0.35 year^{-1}. The maximum environmental capacity (K_0) of pine ecosystems varies from 120 to 330 Mg/ha, and the initial phytomass (B_0 as an analog of seedling density)—from 2 to 18 Mg/ha. The indicator of environmental capacity (K) in model (2) is lower than K_0 in most cases and with a ratio of r/k_1 = 2–3 its approximate estimate is $K \approx (0.5 - 1) \times K_0 - \delta$, where $2 \leq \delta \leq 12$ Mg/ha.

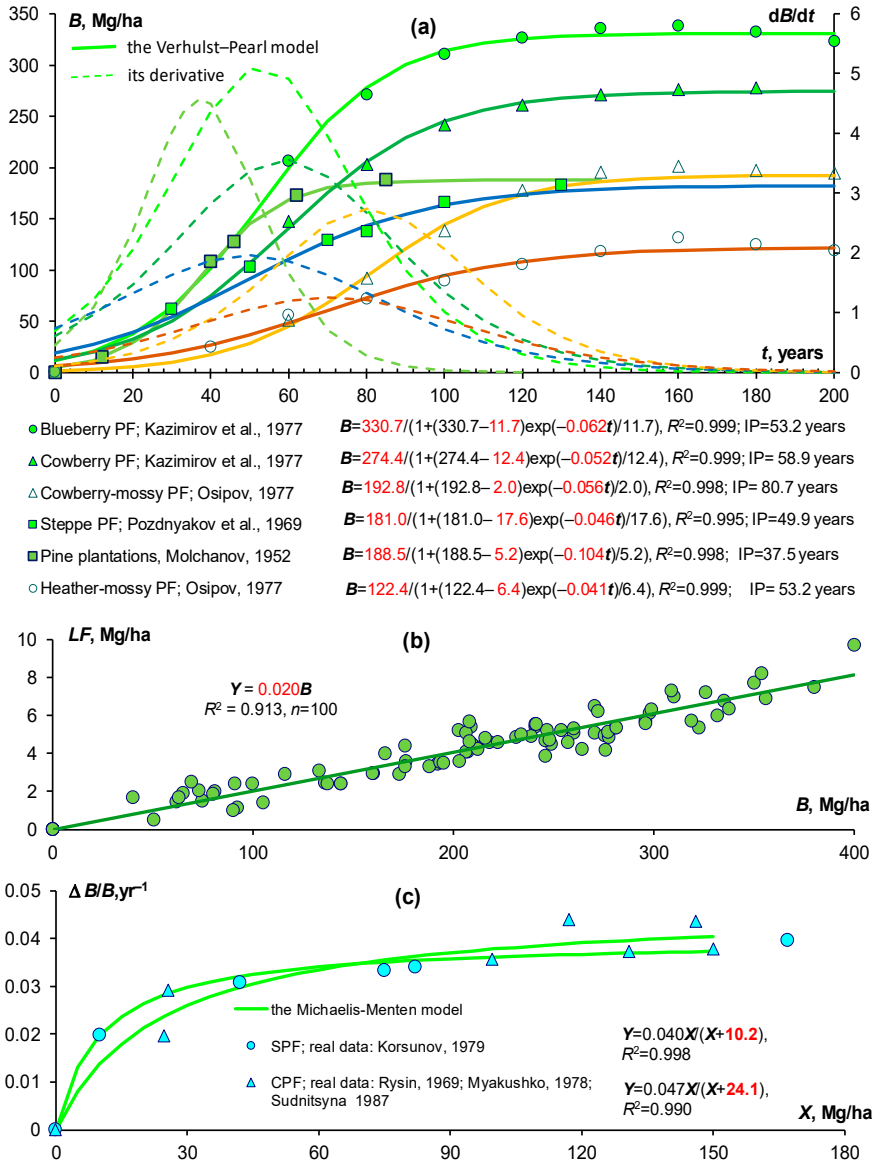

Figure 8. Assessment of the parameters of the model (5) using literature data [41–55]: (**a**)—assessment of the Malthusian parameter based on the growth trend of pine stands according to the data razimirov et al., 1977 [43], Osipov, 1977 [52], Pozdnyakov et al., 1969 [51], Molchanov, 1952, [45]; (**b**)—determination of the litterfall constant (k_2) using the generalized dependence of litterfall (LF) and phytomass of pine ecosystems (B) according to the data [41,43–50,54,55]; (**c**)—determination of the Michaelis constant based on the relationship between the specific growth of pine forests ($\Delta B/B$) and soil organic matter storage (X) according to the data Korsunov, 1979 [44], Rysin, 1969 [53]; Myakushko, 1978 [49]; Sudnitsyna 1987 [41,43–50,54,55]; the required parameters are highlighted in red; IP is an inflection point of growth curves.

The inflection point (IP) of pine forest growth curves is of interest for the theoretical assessment of their age with the maximum efficiency of carbon sequestration. The analytical determination of the inflection point for the Verhulst–Pearl model is

IP = $\ln(r_0) \times B_0/(K_0 - B_0)$. As Figure 8a shows, the IP of pine forests typically varies within 40–80 years. After this age, the growth rate and, consequently, the efficiency of carbon sequestration gradually decreases and by the age of 150–200 years, these ecosystems reach a steady state.

The litterfall constant (k_2) for numerous (n = 100) pairs of litterfall–phytomass data for pine ecosystems in Russia, Belarus, and Ukraine was found to be equal to 0.020 ± 0.008 year^{-1} (Figure 8b). An assessment of the Michaelis constant (α_M) based on the dependence of pine forest growth per unit of biomass gave a range from 10 ± 4 Mg/ha (SPF) to 24 ± 6 Mg/ha in complex pine ecosystems (Figure 8c). The remaining constants of the models (2)–(5) were estimated based on the experimental data of this study, taking into account the 1.5–2-fold acceleration of the rates of input and transformation of soil organic matter identified in Section 3.2.

3.4.3. Matlab-6 Numerical Modeling of Long-Term Carbon Sequestration During Successional Series of Pine Forests

The results of numerical simulation of autogenous successions of pine forests on sandy alluvium using models (2)–(5) are presented in Figure 9. The first illustrations (Figure 9a,b) show positive successional dynamics in the case of stability of the nonlinear trigger system "biocenosis–soil" when the initial reserves of phytomass and soil organic matter exceed their critical values. The growth of a pioneer pine community begins with a critical storage of soil organic matter of no less than 4–6 Mg/ha. A steady-state level of phytomass is formed after 150–200 years with a final storage of 120–130 Mg/ha. The total final amount of soil organic matter reaches 60 Mg/ha with similar amounts of litter and humus. The growth of the phytocenosis and accumulation of soil carbon create conditions for the renewal of the second generation with the replacement of the lichen–moss ground cover with a shrub–green moss cover and the formation of a mixed forest stand of higher quality. The critical level of soil organic matter that triggers this succession is 10–12 Mg/ha. Finally, the accumulation of an even greater amount of soil organic matter (from 30 to 40 Mg/ha and higher) allows the introduction of broadleaf species, nemoral species of ground cover, more demanding of soil trophism (α_M = 24 ± 6 Mg/ha), and with more intensive rates of soil carbon transformation (k_2 = 0.03, γ = 0.05 year^{-1}). This succession over the next 100–150 years leads to the formation of highly productive complex ecosystems with a final phytomass of more than 250 Mg/ha and soil organic matter of more than 150 Mg/ha with a predominance of humus (75%) over litter (25%). Since the stability of humus (turnover time of 100–150 years or more, see Table 2) is significantly higher than that of litter (turnover time of 7–25 years), these ecosystems are obviously more effective in long-term carbon sequestration. In general, the formation of a stationary storage of soil organic matter under a forest occurs over a period of time comparable to the growth period of the phytocenosis, which corresponds to data on the successional dynamics of forest ecosystems on coastal dunes [23,42,61,62].

If the soil organic matter storage and initial seedling density are below the critical values predicted by the system stability conditions (4), the ecosystem is doomed to failure (Figure 9c). From a formal point of view, in this case, steady states with zero phytomass and soil organic matter content become stable. Therefore, at $B_0, X_0 < B_{cr}, X_{cr}$, the curves of the biomass dynamics gradually tend to zero in accordance with their turnover times—first phytomass, then litter, then soil humus (Figure 9c). In general, the trigger mode of the new process model can successfully describe both the long-term sequestration of organic carbon by the "biocenosis–soil" system and the failures of natural or artificial afforestation of sandy substrates with low soil fertility.

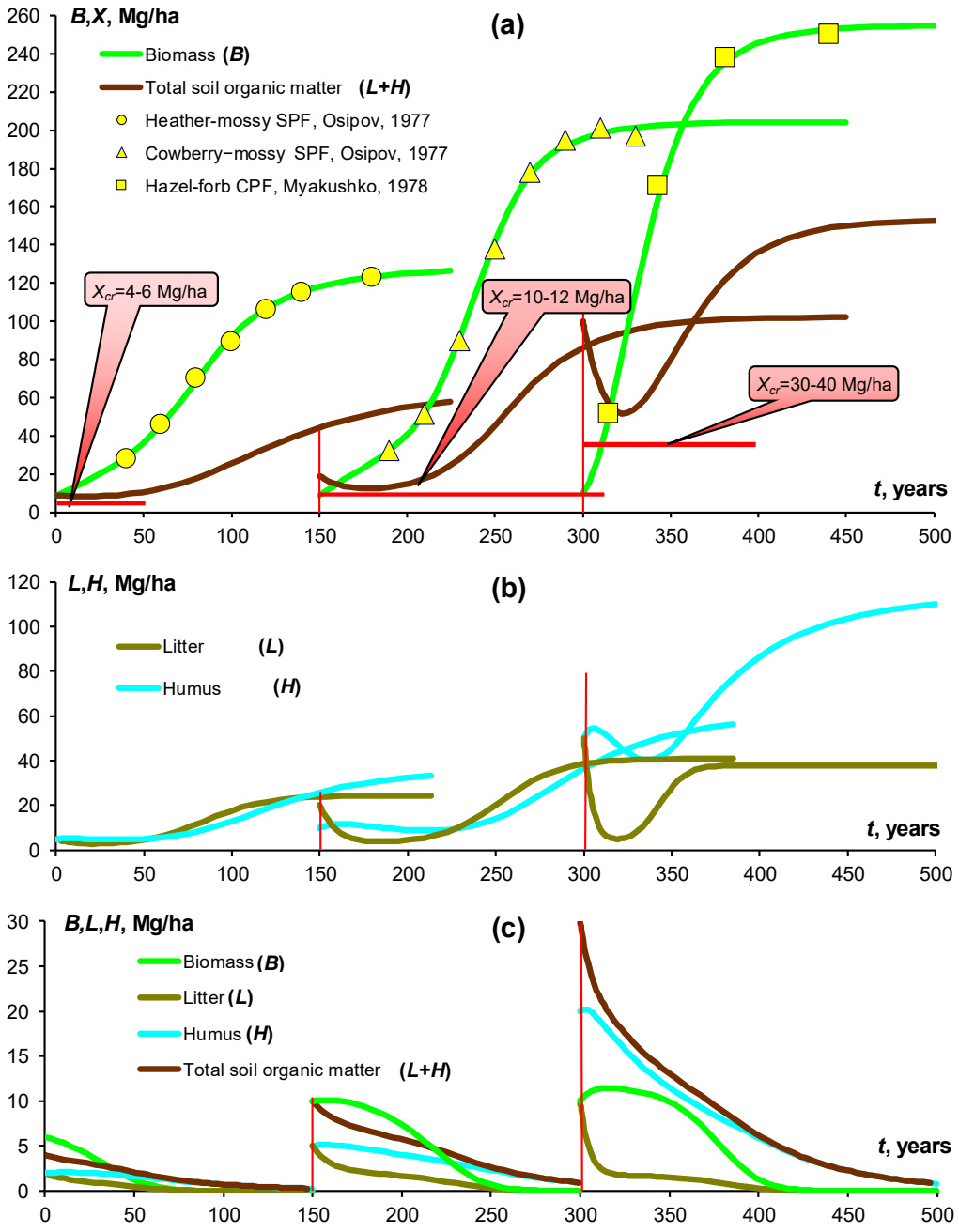

Figure 9. Matlab-6 triggers numerical modeling of organic matter dynamics during autogenic successions of pine ecosystems on sandy alluvium: (**a**)—dynamics of phytomass (B) and total soil organic matter (X) in the case of $B_0,X_0 > B_{cr},X_{cr}$; model parameters: primary succession (heather-mossy pine forest)—$r = 0.25$, $k_1 = 0.1$, $k_2 = 0.01$, $\gamma = 0.02$ year^{-1}, $\alpha_M = 6$, $K = 100$, B_0, $X_0 = 9$ Mg/ha; second generation (cowberry-mossy pine forest)—$r = 0.25$, $k_1 = 0.1$, $k_2 = 0.02$, $\gamma = 0.04$ year^{-1}, $\alpha_M = 10$, $K = 160$, $B_0 = 9$, $X_0 = 19$ Mg/ha; succession of SPF to complex pine ecosystem—$r = 0.30$, $k_1 = 0.1$, $k_2 = 0.03$, $\gamma = 0.05$ year^{-1}, $\alpha_M = 24$, $K = 160$, $B_0 = 10$, $X_0 = 100$ Mg/ha; (**b**)—dynamics of soil organic matter divided into litter (L) and humus (H) by sub-model (5) $_r$; model parameters: primary succession—$r = 0.18$, $k_1 = 0.1$, $k_2 = 0.02$, $k_3 = 0.1$, $k_4 = 0.03$, $k_5 = 0.02$ year^{-1}, $\alpha_M = 7$, $K = 170$, $B_0 = 10$, L_0, $H_0 = 5$ Mg/ha; second generation—$r = 0.18$, $k_1 = 0.1$, $k_2 = 0.02$, $k_3 = 0.1$, $k_4 = 0.03$, $k_5 = 0.02$ year^{-1}, $\alpha_M = 10$, $K = 280$, B_0,$H_0 = 10$, $L_0 = 20$ Mg/ha; succession of SPF to CPF—$r = 0.30$, $k_1 = 0.1$, $k_2 = 0.03$, $k_3 = 0.2$, $k_4 = 0.06$, $k_5 = 0.02$ year^{-1}, $\alpha_M = 24$, $K = 143$, $B_0 = 10$, L_0, $H_0 = 50$ Mg/ha; (**c**)—negative trigger of phytomass, soil litter, and humus in case of ecosystem instability due to a lack of initial fertility and seedlings: $B_0,X_0 < B_{cr},X_{cr}$, i.e., critical values of soil organic matter and biomass (see Section 3.4.1). Real data sources: [50,52].

4. Discussion

4.1. Kinetic Mechanism of Biogenic Self-Organization for Pine Ecosystems on Sandy Alluvium in Relation to Carbon Sequestration

The studied succession series, as already stated in the Introduction, is typical for widespread pine ecosystems on sandy alluvium. However, previous studies of such successions were mainly descriptive [22,24–26,62]. Our research is one of the few attempts to identify the succession mechanism at a quantitative level. It assumes that the kinetics of transformation for ecosystem organic carbon is in full compliance with the requirements of self-organization and sustainable functioning of the considered bio-inert systems [17]. The sustainable development of SPFs on poor, highly drained alluvial sands dictates the need for low rates of organic matter transformation. Evergreen conifers and the accompanying winter-green ground cover (mosses, heather, berry bushes, lichens, etc.) are characterized by a low rate of carbon turnover, since their vegetative elements do not die off annually. For example, pine needles remain on the branches for 2–4 years or more (up to 6–7 years) [48,63,64]. As a result, the rate of litterfall in SPF is 1.5–2 times lower than in complex coniferous–broadleaf ecosystems (Table 1, Figure 2). The kinetic constants of litter biodegradation in SPF do not exceed 0.3 year^{-1} with an annual litterfall of 3–4 Mg/ha, and a share of humified substances of 3%–3.5%, lead to the accumulation of organic matter in the form of a thick litter (40–60 Mg/ha) and "mor"-type humus in the A1E horizon (10–20 Mg/ha). The resulting biogenic soil structure effectively (2–6 times more in comparison with sandy alluvium) retains deficient biophilic elements and precipitation water in topsoil, supplying the root systems of plants. High water retention of soil organic matter, especially litter [32] and moss [46], contributes to a twofold prolongation of normal root water uptake, increasing the survival rate of seedlings (Figure 7). The succession trigger, as shown by process modeling (Figure 9), occurs with the accumulation of 30–40 Mg/ha of soil organic matter, creating favorable conditions for the introduction of broadleaf species and the accompanying herb ground cover with the annual death of foliage.

The replacement of SPFs by complex coniferous–broadleaf ecosystems is accompanied by a 1.5–2-fold increase in the rates of input and transformation of organic matter (litterfall: 6–6.5 Mg/ha, humification: 5–6%, litter biodegradation constant: 0.5–0.6 year^{-1}). This leads to a gradual decomposition and humification of litter and the formation of a differentiated system of mineral soil horizons A1-E-$B_{h,fe}$ with a total humus content exceeding 100 Mg/ha. The new soil structure is not inferior to the previous one in water-holding capacity and satisfaction of the root water supply (Figure 7), and significantly (2–7 times or more) exceeds it in the accumulation of biophilic elements, especially deficient nitrogen (Figure 1). Similar quantitative estimates of biogenic accumulation in the litters of sandy soils under three coniferous and one broadleaf species, as well as litter turnover, are given in [57]: the litter dry mass from 32 to 82 Mg/ha, litterfall rate from 1.4 to 4 Mg/ha per year, input of biophilic elements (kg/ha per year) between 240 and 914 for N, 15 and 56 for P, 40 and 113 for K, 99 and 507 for Ca and Mg, litter lifespan from 17 to 32 years.

It should be noted that the main pool of biophilic elements in the litter as part of its biomass is low-mobility and accessible compared to the exchangeable pool in mineral humus-accumulative horizons, where the elements are adsorbed or bound by ionic interactions with the specific surface of soil particles. A study of the soil aggregate structure [23], using water vapor sorption isotherms for soils of the SPF and CPF, shows a 3–9-fold increase in specific surface area under the influence of carbon accumulation compared to the sandy alluvium of rivers (Moscow River, Oka) in the Moscow region. Artificial dehumification by means of calcination at 500 °C brings the specific surface of humus-accumulative horizons to the level of the parent rock (sandy alluvium), i.e., confirms its complete biogeneity [23]. In general, the productivity, stable functioning, and reproduction of forest ecosystems on

sands are determined mainly by biogenic fertility, accumulation of organic carbon for the retention of scarce nutrients and water in root-inhabited topsoil, which is also confirmed by other researchers [42,44,45,62,65]. At the same time, as [11,33] correctly note, the cycle of soil carbon, nitrogen, and other biophiles varies among different types of plants, and high plant diversity (complex ecosystems) can contribute to the more intensive accumulation of soil carbon and nutrient exchange. This important fact should be taken into account in afforestation with increased carbon sequestration and soil improvement, as, for example, in the proposal [13] for the development of mixed plantations, either by creating a mixture with broadleaf trees or by introducing understory vegetation (herbs and shrubs) as an inexpensive and effective way to prevent soil degradation in purely coniferous plantations.

It is also interesting to note that despite the narrowing of the C/N ratio and the increase in pH (see Supplementary Materials Table S4), the humus stability in the complex coniferous–broadleaf ecosystem was only slightly higher than in the simple pine forest, without statistically significant differences (Table 2). We agree with the point of view of our anonymous reviewer that this may be a specificity of coarse-textured soils without strong interactions of organic polymers with the mineral soil matrix. In this case, the main result of the succession of simple pine forests into complex coniferous–broadleaf ecosystems is an increase in the sequestration of soil humus, as a more biochemically stable organic matter compared to forest litter (Tables 1 and 2, Figure 9).

4.2. Is Successional Series a Dynamic or a Spatial Variation?

The indicators of ecotone zones almost always occupied an intermediate position between a simple and a complex ecosystem (Figures 1, 2, 4 and 5; Table 1). This result confirms the sequence of changes in vegetation and soil in the considered successional series. However, the comparative-geographical method [22–25,54,62], which is widely used in studies of successional series, becomes most convincing if it is confirmed by real observations of long-term successional dynamics. For this purpose, we analyze data [23] from a 70-year primary succession at the site of a forest sand quarry for the construction of a railroad on the II terrace of the Moscow River near the "Rublevo" settlement in the Western Administrative District (55.767099, 37.344238), where a simple fescue–green moss pine forest and primitive sandy soil (Arenosol) spontaneously formed in the middle of the last century (Figure 10). The soil structure is represented by a system of horizons L (0–3 cm), A1E (3–8 cm), B (8–15 cm), and parent rock C (15–100 cm and deeper) in the form of sandy alluvium (Figure 10, Supplementary Materials Tables S3 and S4). During the primary succession, 50 ± 12 Mg/ha of carbon, 920 ± 126 kg/ha of nitrogen, and 170 ± 26 kg/ha of phosphorus, 340–570 kg/ha of exchangeable calcium and magnesium accumulate in the biogenic soil horizons, which is 2–8 times greater than the initial properties of the parent rock. The specific surface area of topsoils increases just as strongly under the influence of biogenic carbon accumulation (Figure 10), ensuring effective water retention, sorption, and exchange capacity of the soil. Generally, studies of the actual successional dynamics of pine forests over a 70-year period fully confirm the previous results of the biogenic organization of pine ecosystems on sandy alluvium.

One important circumstance must be taken into account in the correct studies of forest successions by the comparative-geographical method. This is preliminary evidence of initially identical forest conditions, i.e., the similarity of time, climate, topography, and soil-forming parent rock, as, in particular, in our succession series from an SPF to a complex coniferous–broadleaf ecosystem (see "Materials and Methods"). Otherwise, the results may be completely different, and the conclusions will not be consistent with the known expertise in forest science. For example, the results of the study [66] of carbon sequestration by sandy soils in western Russia reveal the same (within one climate zone) or increased (up

to 1.5–2.7 times) carbon storage in the soils of SPF as compared to complex ecosystems. This contradicts not only our results, but also numerous studies of the input and transformation of soil carbon in sands under different types of forests [11,13,42,45,50,53–55,57]. It is obvious that in [66] only one factor (a sandy parent rock) was relatively the same, but others (age, climate, pine forest quality class, relief, groundwater position, etc.) vary significantly. In particular, based on the data on the content and profile distribution of soil carbon, it can be assumed that the soils under the CPF of the Bryansk Opolye from [66] are younger and have not yet reached a steady state corresponding to a more productive coniferous–broadleaf vegetation. This assumption, and possibly also the differences in relief positions, fire susceptibility, and anthropogenic impacts (deforestation, plowing for agricultural crops) explain the atypical results of low carbon stock in the soils of complex pine ecosystems.

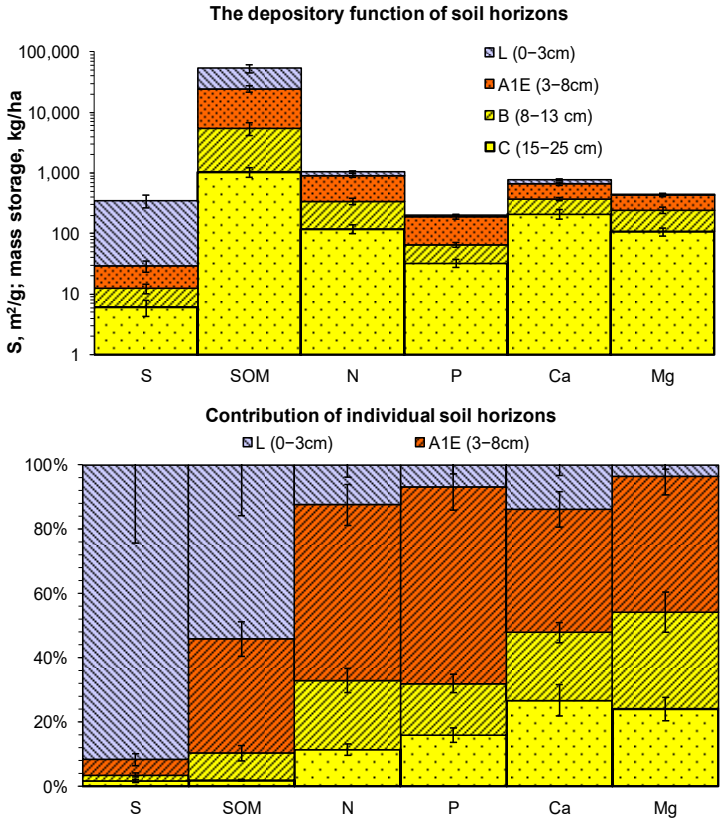

Figure 10. Biogenic accumulation of biophilic elements and increase in specific surface area in different horizons of Arenosol during 70 years of primary succession. S (m^2/g) is the specific surface area of the soil, SOM (kg/ha) is the soil organic matter storage.

4.3. Trigger Process Model of Long-Term Carbon Sequestration: Advantages, Disadvantages, and Prospects for Further Improvement

An important part of our study is an attempt to model the successional dynamics of pine ecosystems on sands with a trigger response to the accumulation of soil carbon. The problem of the mathematical modeling of the ontogenetic development of individual forest species and the successional dynamics of forest ecosystems as a whole is widely discussed in the scientific literature in connection with the forecast of the response of forest ecosystems to global climate change, as well as the applied aspects of afforestation and reforestation [67–77]. The most common are empirical models of individual biomass growth or individual stand parameters (trees' height, diameter) using sigmoid growth functions, such as the Mitscherlich, the Chapman–Richards, the Weibull, the Hossfeld, the Korf, the logistic function, and their modifications, as well as models based on artificial intelligence (see, e.g., [67–72]). In our case, for the primary processing of biomass dynamics

data for different types of pine forests, the logistic function, more precisely, the Verhulst–Pearl equation (Figure 8a), close to the model [70], was successfully applied. Its difference from [70] was in the introduction of the initial biomass parameter, as well as the analytical evaluation of the inflection point. This gave us the opportunity to estimate the minimum biomass of seedlings for the successful afforestation of sands, as well as the age of the most effective carbon sequestration by stands of different pine forest types (Figure 8a).

However, another type of model should be recognized as the most promising in the field of long-term carbon sequestration forecasting. The process-based models like CENTURY, ROMUL, Forest-DNDC, Biome-BGC, etc., with different compartments (plant, soil, climate, etc.) and spatial modeling scales were evaluated to estimate the potential effect of climate change on carbon sequestration by forests or/and their soils (see, e.g., [74–77]). Analysis of the structure of these models, usually represented by a set of ordinary differential equations or their difference analogs with numerical computer simulation, shows that in most cases their disadvantage is quasi-linearity, i.e., over-simplistic forecast of the dynamics in the vicinity of stable (quasi-equilibrium) attractors (stationary states) [73]. This leads to an overestimation of external factors in the management of these systems and an underestimation of the internal mechanisms of their stability through self-organization in flows of substances and energy with complex (trigger, oscillatory, etc.) functioning regimes [73]. Our nonlinear model (3)–(5) is one of the few attempts to take into account such self-organization based on the trigger reaction of phytomass growth to soil fertility. Unlike most known process models of organic carbon dynamics in the "biocenosis–soil" system, when the fertility level decreases, it does not smoothly reduce productivity and carbon sequestration to lower values, but rather abruptly switches to a new regime—reaching zero values. This is a more realistic behavior, since in nature, a lack of soil fertility, and therefore water storage, leads to the death of seedlings or existing tree stands, for example, in the case of unfavorable climatic changes. The trigger model allowed us to identify critical levels of soil fertility (organic matter reserves) and seedlings that guarantee a successional start and long-term carbon sequestration during the successional series from SPFs to complex coniferous–broadleaf ecosystems (Figure 9). This result is interesting not only for theoretical environmental science, but also for the practice of afforestation and reforestation on sands, which is often unsuccessful due to the failure to take into account soil fertility factors (see, e.g., [11,13]).

The new model is certainly greatly simplified compared to the known process models of organic matter dynamics in the "biocenosis–soil" system [74–77]. In particular, such a simplification is the use of constant kinetic parameters for organic matter transformation, whereas in more realistic models they depend on climatic factors. In principle, it is acceptable in forecasting the long-term dynamics of carbon sequestration, since seasonal fluctuations in carbon pools due to unstable weather conditions are smoothed out as the system reaches a quasi-stationary state [73]. However, for predicting the response to global climate change, the model should of course be equipped with variable kinetic parameters depending on humidity and temperature, and this modification is easily implemented in Matlab-6 (see, e.g., [34]). In the future, the introduction of a trigger reaction to precipitation and temperature in conjunction with a climate block, by analogy with [76], as well as the connection of GIS technology with upscaling to the region level seems to be the most promising approach for a more adequate forecast of long-term carbon sequestration during the succession of pine ecosystems in the context of global climate change.

5. Conclusions

This study quantifies and models the biophysical mechanism of self-organization in pine ecosystems on sandy alluvium during autogenous succession series. The driver of

successions is the accumulation of organic carbon in the soil as a material carrier of its biogenic fertility, optimizing the unfavorable forest-growing properties of sandy alluvium (low water retention and lack of biophilic elements). The process of carbon sequestration is determined by the kinetics of the input and transformation of soil organic matter. In turn, the rates of litterfall, its biodegradation and humification largely depend on the biomass and biochemical composition of vegetation, specific for different tree species and ground vegetation cover. The success of primary succession, i.e., the colonization of sandy alluvium by SPF with evergreen lichen–moss and berry–shrub ground vegetation cover, is determined by the low turnover of evergreen plant biomass and soil organic matter, mainly in the form of difficult-to-decompose coniferous litter. This makes it possible to effectively capture and protect deficient biophilic elements in the phytomass itself and organogenic horizons of the sandy upper soil layer from leaching. One or two generations of the SPF are enough to form soil fertility and water-holding capacity, satisfying the needs of more demanding broadleaf species and nemoral herbs cover with the annual dying off of the vegetative mass. The trigger of a new succession of the SPF into complex coniferous–broad-leaved ecosystems is accompanied by a 1.5–2-fold acceleration of litterfall and transformation of soil organic matter. As a result, one generation of a complex pine ecosystem is sufficient to form carbon storage in phytomass and soil up to two times higher than in previous SPFs and with a longer deposition time. The process trigger model adequately describes this natural mechanism, allowing to estimate long-term carbon sequestration in pine ecosystems on sands, as well as the critical storage of soil organic matter and seedlings, which guarantee a successful successional start. In this regard, the study is of interest for forest management aimed at effective carbon sequestration through the afforestation of sands and subsequent formation of complex coniferous–broadleaf systems with higher biodiversity and sequestration potential.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/f16091482/s1, Table S1: Aboveground phytomass (g/m^2) of ground cover plants (Lokhin Island); Table S2: Chemical composition of dry phytomass of ground cover plants (Lokhin Island); Table S3: Particle size distributions and physical properties of sandy soils in the studied pine ecosystems; Table S4: Some chemical properties of sandy soils of the studied pine ecosystems; Table S5: Dry mass and fractional composition of autumn litterfall of pine ecosystems; Table S6: Approximation parameters of the exponential model [34] for carbon dioxide gross production as a function of soil depth.

Author Contributions: Conceptualization, A.S.; methodology, A.S.; software, A.S. and A.K.; validation, A.S., and N.S.; formal analysis, A.S.; investigation, A.S., N.S. and E.B.; data curation, N.S.; writing—original draft preparation, A.S.; writing—review and editing, A.K.; visualization, N.S. and E.B.; project administration, M.S.; funding acquisition, A.S. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data presented in this study are available on request from the corresponding author. The data, with the exception of the Tables in the article and Supplementary Materials, are not yet publicly available due to privacy until the end of the scientific project.

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Abbreviations and Terminology

The following abbreviations and terminology are used in this manuscript:

ESG	Environment, Social, Governance
DT	Top of the dune
DS	Slop of the dune
ID	Inter-dune depression
EZ	Ecotone zone
SPF	Simple pine forest
CPF	Complex pine forest
SOM	Soil organic matter
WRC	Water retention curve
Trigger model	The model simulating the nonlinear trigger regime (reaction) of an ecosystem to an environmental factor, in particular, the change in forest growth and development to its death with a lack of soil fertility and water supply (see, e.g., [73]).
Self-organization of ecosystems	The result of the creative activity of living organisms, aimed at forming favorable conditions for their development and reproduction in the immediate environment (see, e.g., [73]). A clear example is soil formation through biogenic accumulation of carbon and other biophilic elements, as well as improving the water-holding, absorption, and ion-exchange capacity of the original parent rock (see, e.g., [17]).
Bio-pump	The ecological function of absorption by plants of biophilic elements scattered in the environment, with their subsequent concentration in their biomass and the upper soil layer.

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