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Cutaway Peatland Fertilisation With Wood Ash Leads to More Than a Tenfold Increase in Plant Biomass Accumulation

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ABSTRACT

Afforestation is one of the widely used methods of reclamation in cutaway peatlands where spontaneous revegetation is not feasible, but fertilization or liming is usually required to encourage the development of vegetation cover. Wood ash application increases planted tree biomass, but the role of spontaneously incoming species in early-stage biomass accumulation is lesser known. The amount of below-and aboveground biomass accumulation was evaluated in relation to the drainage ditch position (2 or 9 m from the ditch edge) and the amount of wood ash applied (0, 5, 10, or 15 megagrams ha^{-1}) three years after fertilization. The biomass accumulation, species richness, and plant carbon and nitrogen ratio were positively impacted by wood ash treatment, but biomass allocation was species dependent: for all tree and herbaceous species with individual root systems, the proportion of biomass accumulated in roots was higher in the unfertilized group, but for *Phragmites australis* with a clonal root system, it was contrariwise. The application of 10 Mg ha^{-1} wood ash was the most productive, with an average of 485.0 g/m^2 total plant dry biomass accumulation next to and 301.3 g/m^2 further from the drainage ditch, compared to the unfertilized 36.8 g/m^2 (2 m from ditch) and 13.9 g/m^2 (9 m from ditch). During the initial vegetation establishment, herbaceous species comprised the majority of the biomass, primarily graminoids.

1 | Introduction

Peat has long been recognized as a valuable natural resource and has been extracted for energy, horticulture, and other applications. Prior to peat extraction, peatlands are drained to ensure technical accessibility, resulting in severe ecosystem alteration and degradation (Word et al. 2022). Thus, in many countries, management of extracted peatlands is now legally required to minimize environmental risks (Triisberg et al. 2013; European Commission 2020). In Latvia, the national legislation also determines that after the extraction of natural resources, the area must be recultivated within the time limit specified in the permit or license, covering the costs oneself (Law: On Subterranean Depths 1996). Using the previously developed guidelines, a full evaluation of the area from geological, economic, climatic and biological aspects should be carried out before peat extraction, thus choosing the purpose and type of further use of each territory, from the recommended ones: restoration, afforestation, establishment of arable land, cultivation of cranberries and blueberries, establishment of perennial grasses, creation of water reservoirs or establishment of paludiculture a.k.a. farming with high water table (Priede and Gancone 2019). However, a large proportion of extracted peatlands had already been abandoned before the regulations were introduced—around 18,000 ha in Latvia are degraded areas subject to recultivation (Priede and Gancone 2019).

Although peatland ecosystem restoration is the most profitable solution from an ecological perspective, it can be problematic due to the high costs of restoration activities and site-specific properties limiting the potential of restoration, including changed peat chemical structure and too thin peat layer (Glenk and Martin-Ortega 2018). Besides restoration, peatlands may continue to be used for economic gains by implementing agriculture, paludiculture, or forestry practices (Räsänen et al. 2023). After peat extraction, landowners usually turn to afforestation (Laasasenaho et al. 2017, 2023).

The primary limiting factor for natural revegetation in restored and unmanaged cutaway peatland is low water availability, but if the area is reclaimed with afforestation method, peatland rewetting is not suitable (Orru et al. 2016). Regeneration of vegetation in drained extracted peatlands is slow and sparse due to unfavourable soil conditions—high soil acidity limits nutrient uptake, with initially low soil phosphorus and potassium levels (Orru et al. 2016). Liming and soil fertilization are practised to create conditions suitable for afforestation and vegetation development (Derome et al. 2000; Huotari et al. 2008; Ots et al. 2024; Renou-Wilson et al. 2008; Silvan and Hytönen 2016). Liming mitigates the adverse effects of acidity (Hytönen 2005), increases nutrient availability (Arshad et al. 2012), and promotes the establishment of forest vegetation cover (Zuševica et al. 2022). Applying wood-ash, a by-product from cogeneration stations, provides cost-effective liming and supports circular economy principles. Additionally, wood ash serves as a source of minerals (Demeyer et al. 2001). Revegetation induced by liming can mitigate soil erosion (Campbell et al. 2002; Huotari et al. 2007), stabilize the water regime (Price et al. 2003), and promote carbon assimilation in afforested areas (Aguraijuja et al. 2015).

In the long term, woody species invest more in carbon storage than herbaceous species in the dominated ecosystem (Hytönen and Saarsalmi 2009). Therefore, afforestation and regeneration research often focus on trees as carbon stores, but herbaceous plants can also have a significant role in early ecosystem recovery and carbon accumulation (Huotari et al. 2009). Additionally, species accumulate biomass at different rates (Hytönen and Saarsalmi 2009) and have different allocation proportions between the aboveground and belowground parts (Laganière et al. 2015). Woody species store most of the carbon in the perennial parts; however, depending on the species, a significant proportion can be accumulated in the foliage (Laganière et al. 2015; Klein et al. 2016). Herbaceous species tend to store more biomass in roots, but this is influenced by plant form (e.g., annual species invest more in above-ground biomass), habitat, and nutrient availability (in poor growth conditions, plants allocate more biomass in roots) and competition (which enhance the above-ground growth) (Gross et al. 1983). Nevertheless, these patterns can shift depending on the specific ecological strategy of the species.

This study evaluates biomass accumulation of spontaneous revegetation in cutaway peatland treated with wood ash in doses of control (0), 5, 10, and 15 Mg ha^{-1}. We address the following research questions: (1) How do doses of wood ash and the distance from the drainage ditch affect the total accumulated biomass in vascular plants? (2) Does the allocation of biomass, carbon and nitrogen in dominant woody and herbaceous species change after fertilisation of wood ash? We hypothesized that increasing the dose of wood ash fertilizer would increase the production of biomass and accumulated carbon. Since the water regime is a growth limiting factor in cutaway peatlands, we expected to find a difference in biomass accumulation depending on the distance from a drainage ditch (Gagnon et al. 2018). We also hypothesized that three years after the application of fertilizer, herbaceous plants would accumulate more carbon per unit area compared to woody plants.

2 | Methods

2.1 | Study Site and Experimental Design

The experimental field site, with a total area of 8 ha with 0.96 ha of natural revegetation, is located in central Latvia (N 56°43′41.35″ E 23°34′39.61″) and was established within "LIFE Restore" project (LIFE14 CCM/LV/001103) (Priede and Gancone 2019) (Figure S1). It was established in a cutaway peatland with acidic (pH 3.5) *Sphagnum* peat, where restoration was hindered by active peat extraction, long-term drainage, and unsuitable primary habitat prior to anthropogenic distribution. The area was an undrained peatland forest until at least 1963, with the first record of drainage within 500 m starting before 1986 when peat extraction also began at this site. Active peat extraction ended and drainage was not actively maintained any longer in 2014 with at least 0.5 m of peat layer left. During the first three years after peat extraction, natural revegetation was very slow and formed sparsely (Figure S2). In spring 2017, vegetation was removed and contour ditches cleaned to ensure stable hydrological conditions and optimal groundwater level for afforestation (20–40 cm). Wood ash was applied and tilled into the upper layer of the topsoil (< 20 cm) in three replications of 20 × 245 m plots in the following doses: 0 (control), 5, 10, and 15 megagrams (Mg) ha^{-1}. Each plot was divided into five 20 × 45 m subplots for afforestation with multiple tree species, with one subplot left for natural regeneration (Figure S1). Wood ash doses were chosen based on suitable tree fertilization doses in this region (Kikamägi et al. 2013). Windborne dispersion of wood ash was prevented by mixing with water prior to application. Dry wood ash contained 6.6 g phosphorus, 24.7 g potassium, 18.2 g magnesium, and 120.4 g calcium per kg. All fertiliser application doses were separated by drainage ditches. In each natural revegetation subplots, two sampling plots of 2 × 2 m were established, together 24 sampling plots. One was placed beside the drainage ditch, with its centre 2 m from the ditch centre, and the other was located 9 m away from the ditch (Figure 1). Meteorological data during the study period was obtained from the nearest meteorology station, 12 km from the study site (Figures S3–S5) (Data from nearest meteorological station "Jelgava", (*Source:* VSIA "Latvijas Vides, ģeoloģijas un meteoroloģijas centrs" (2024) https://videscentrs.lvgmc.lv/)).

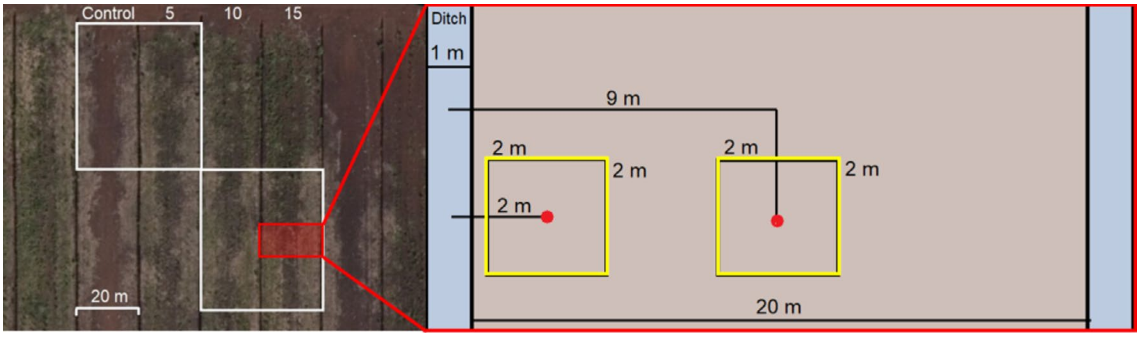

FIGURE 1 | Aerial photo of study site design, showing one replicate of natural revegetation (white rectangles) after wood ash treatment (Control (0), 5, 10, or 15 Mg ha^{-1}) and the location of sample plots (yellow square) in relation to drainage ditches (LGIA 2019). [Colour figure can be viewed at wileyonlinelibrary.com]

2.2 | Plant Parameters Sampling

Woody and herbaceous plants that had naturally recolonized the area were counted and collected from each sampling plot in August 2019, two years after fertilisation. Plant species were determined by botanist using a species identification guide from Latvian plant species (Priedītis 2014). Number of individuals per species was counted, and plants were separated into: aboveground and belowground parts for herbaceous plants and stem (including branches), root, and foliage for woody plants. Fresh and dry biomass was weighed (0.01 g precision). Before weighing fresh biomass, roots were carefully cleaned from peat, washed, and dried with paper towels. Prior to weighing dry mass, all plants were oven-dried at 40°C until a constant weight. Samples were milled, and the nitrogen and carbon contents were measured using an 'Elementar El Cube' elemental analyser (Elementar, Langenselbold, Germany) according to LVS ISO 10694 (2006) and LVS ISO 13878 (1998). All Woody species parts were combined together for chemical analyse. The five most abundant herbaceous species [*Calamagrostis epigejos* (L.) Roth, *Carex cinerea* Pollich (syn. *C. canescens* L.), *Eupatorium cannabinum* L., *Phragmites australis* (Cav.) Trin. ex Steud., and *Carex vesicaria* L.] were analysed separately, but others were analysed from a composite sample. Due to the low number of individuals and biomass of some species, plants from three replicates were combined to obtain the minimum sample weight required for the chemical analysis (this resulted in a maximum of 16 samples per species: four treatments, two distances, and separate samples for above and belowground parts). Plant chemical composition was analysed only in one replicate.

2.3 | Soil Properties

The remaining peat layer after extraction comprised acidic, moderately decomposed raised bog peat. Soil sampling was conducted at the end of the 2018 and 2019 growing seasons, two and three growing seasons after wood ash application. In 2018, three soil samples were collected per wood ash treatment ata depth of 0–10 cm in three repetitions. In the 2019 soil sampling, the distance from the drainage ditch was considered, with samples taken from each plot at soil layers of 5–10, 15–20, 25–30, 35–40, and 45–50 cm. The soil samples were collected using a soil core sampler with a volume of 100 cm^3 for collecting undisturbed core samples. Samples were prepared for analyses according to the Latvian Standard (LVS) ISO 11464 (2005) standard. The fine fraction of soil (D < 2 mm) was used for chemical analyses. The dry soil bulk density was determined according to LVS ISO 11272 (2017), and the soil pH was determined according to LVS ISO 10390 (2002) L/NAC:2005L. The total carbon (C) and nitrogen (N) contents were determined with an elemental analyser according to LVS ISO 10694 (2006) and LVS ISO 13878 (1998); the HNO_3 extractable potassium (K), magnesium (Mg), and calcium (Ca) contents were determined by inductively coupled plasma optical emission spectrometry according to LVS European Standard (EN) ISO 11885 (1997), and phosphorus (P) content was determined using spectrophotometry according to LVS EN 14672 (2006).

2.4 | Data Analyses

Data analysis and visualization (ggplot2 package) were conducted using R version 4.3.2 (Core Team 2023). Species richness differences between treatments was tested using ANOVA, as data did not differ significantly from normal distribution ($p = 0.279$). The sample size per treatment was low ($n = 3$), but a large plot size was used to limit possible type 1 error. Non-parametric methods were applied to data that differed significantly from normal distribution, which could be due to the small sample size. A Kruskal-Wallis test (stats package) followed by Dunnett's test (DescTools package) was applied to assess significant differences in accumulated plant biomass between treatment groups.

Linear mixed-effects models (lmer) (lme4 package) were used to assess the effect of treatment on biomass partitioning between plant parts (woody plants: stem, roots, foliage, herbaceous: aboveground, belowground) ($n = 6$). Biomass investment percentage was calculated for each plant part of individual plants, and mean values were then determined. Percentage biomass investment was a response variable, with repetition as a random factor. Based on Akaike information criterion (AIC; stats package) values, we selected a model with wood ash treatment and plant part as fixed factors, excluding distance from the drainage ditch. Although residuals from the lmer model significantly differed from normal distribution ($p = 0.007$), only one value (total n of data points = 162) fell outside of the 95% confidence interval, and data was homogeneously dispersed (Figures S6–S8). We created separate models for conifers (pine) and deciduous (aspen, birch,

TABLE 1 | Number of species by ash treatment and distance from the ditch.

Treatment ($Mg\,ha^{-1}$)	0		5		10		15	
Distance from drainage ditch	**2 m**	**9 m**	**2 m**	**9 m**	**2 m**	**9 m**	**2 m**	**9 m**
Herbaceous species	10	1	14	11	15	7	13	13
Woody species	4	1	4	4	4	4	5	4
Total per treatment	15		22		20		23	

willow) species due to their different biomass allocation trade-offs. Lmer was also used to analyze the C:N ratio in plant aboveground and belowground parts, with location and wood ash treatment as fixed effects and species as random effects, due to the insufficient representation of each species in fertilization groups. The analyses focused on C:N ratio and total accumulated biomass (AIC values: both treatments = 127.4, only distance = 146.2, only wood ash application = 130.1).

Multiple linear regression was used to determine the relationship between soil parameters (pH, soil bulk density, and K and P contents) at different soil depths (5–10, 15–20, 25–30, 35–40, and 45–50 cm) and the accumulated total, herbaceous, and woody plant biomass. The multicollinearity was assessed using the variance inflation factor (VIF) (car package). Since the pH was strongly correlated with the soil P and K contents, we selected best-fitting models based on the AIC values, comparing different fixed factor combinations (pH, P, K). Assumptions were assessed by plotting quantile-quantile (Q–Q) plots, residuals versus fitted values, scale location, and Cook's distances. All analyses were performed at a significance level of 0.05. Although the study design limits full randomization, the plot structure with large fertilized areas (20 × 245 m), separated by drainage ditches under similar conditions (peat layer depth, water table level), helps mitigate confounding effects related to fertilization.

3 | Results

3.1 | Biomass Accumulation

Willow (*Salix* spp.), Eurasian aspen (*Populus tremula*), birch (*Betula pendula* and *Betula pubescens*), Scots pine (*Pinus sylvestris*), and Norway spruce (*Picea abies*) were the naturally regenerating woody species in the study area. The woody species richness and abundance were significantly lower in the control plot (ANOVA results ($n = 6$)—Species richness control vs. 5 $Mg\,ha^{-1}$ $p = 0.001$, control vs. 10 $Mg\,ha^{-1}$ $p = 0.001$, control vs. 15 $Mg\,ha^{-1}$ $p < 0.001$; Abundance control vs. 5 $Mg\,ha^{-1}$ $p = 0.037$). Willow was the most abundant tree species in wood ash treatment, while pine dominated the control plots. Herbaceous species diversity was higher, with a total of 30 species in the sampling plots, including the most abundant *Calamagrostis epigejos*, *Phragmites australis*, and *Carex vesicaria* (Table 1).

Among the woody species, willow and aspen accumulated the most biomass, with willow accumulating 0.3, 71.9, 48.2, and 42.5 g/m^2 and aspen accumulating < 0.01, 37.7, 4.2, and 58.0 g/m^2 of biomass under control, 5, 10, and 15 $Mg\,ha^{-1}$ wood ash treatment, respectively. Total woody species biomass per unit

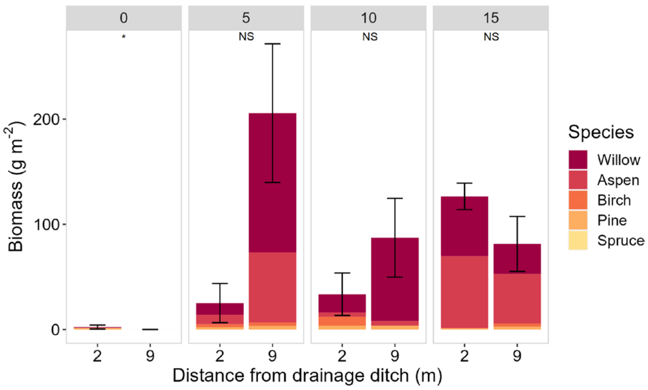

FIGURE 2 | Average plant biomass accumulated by woody species per unit area depending on the wood ash treatment dose (0 (control), 5, 10, 15 $Mg\,ha^{-1}$) and sampling plot location in relation to drainage ditch. Error bars represent standard error (SE) for total woody biomass ($n = 3$). [Colour figure can be viewed at wileyonlinelibrary.com]

area was significantly higher under all wood ash treatment doses: 117.6 g/m^2 more in 5 $Mg\,ha^{-1}$ ($p = 0.002$), 94.8 g/m^2 more in 10 $Mg\,ha^{-1}$ ($p = 0.018$), and 137.6 g/m^2 more in 15 $Mg\,ha^{-1}$ ($p = 0.003$) compared to the control group. No significant differences were found in accumulated woody biomass between distances from the ditch, although mean values suggested greater biomass accumulation under 5 $Mg\,ha^{-1}$ further from the ditch (Figure 2).

Only the 10 $Mg\,ha^{-1}$ treatment resulted in significantly higher herbaceous biomass accumulation (Dunn's test: $p = 0.001$) compared to the control. Under this treatment, *Calamagrostis epigejos* produced 179.3 g/m^{-2}, *Phragmites australis* 61.2 g/m^{-2}, *Carex vesicaria* 58.3 g/m^{-2}, *Carex canescens* 3.1 g/m^{-2}, and *Eupatorium cannabinum* 6.6 g/m^{-2} of dry biomass (Figure 3). Contrary to woody species, herbaceous species were more abundant and productive near the ditch, except at the highest wood ash dose. Most of the biomass in sampling plots was from herbaceous species, with woody species having a smaller investment. This pattern is more applicable with smaller wood-ash doses (5 and 10 $Mg\,ha^{-1}$) and closer to the drainage ditch (Table A1). Total plant accumulated biomass was 12.3 times higher in 5 $Mg\,ha^{-1}$, 15.8 times higher in 10 $Mg\,ha^{-1}$, and 9.6 times higher in 15 $Mg\,ha^{-1}$ treatment compared to the control.

3.2 | Biomass Allocation

Based on AIC values, the model explaining biomass allocation under different doses was better than the model based on distance from the ditch (AIC values: wood-ash fertiliser 787.64, distance from the drainage ditch 817.44). For deciduous trees, biomass allocation to roots was higher in the control compared to fertilised groups, though the difference was not statistically significant when species were analysed separately (lmer test—control vs. $5\,\mathrm{Mg\,ha^{-1}}$, $p=0.050$; control vs. $10\,\mathrm{Mg\,ha^{-1}}$, $p=0.088$; control vs. $15\,\mathrm{Mg\,ha^{-1}}$, $p=0.042$) (Figure 4). Willow had the smallest proportion of biomass in foliage and showed a significant difference between root and foliage proportion ($p=0.004$), but aspen ($p=0.006$) and birch ($p=0.003$) stored significantly more biomass in root than in stem. Wood ash application did not affect biomass partitioning for pine, but in all groups, biomass in foliage was significantly greater than in stem ($p<0.001$) or roots ($p<0.001$, Figure 4).

The allocation was species-dependent, therefore, species were analysed separately. Both *Carex* species (except *Carex vesicaria* in the control plots), located most biomass to the aboveground parts (lmer results: *C. canescens* $p=0.022$, *C. vesicaria* $P=\mathrm{NS}$), whereas *Eupatorium cannabinum* located more biomass to belowground parts (lmer results: *E. cannabinum* $p=0.002$). The only significant fertilisation impact was observed for *C. vesicaria*, which allocated significantly higher biomass proportion to roots in the control compared to the fertilised groups (lmer results—control (0) vs. $5\,\mathrm{Mg\,ha^{-1}}$ $p=0.001$, control (0) vs. $10\,\mathrm{Mg\,ha^{-1}}$ $p=0.003$, control (0) vs. $15\,\mathrm{Mg\,ha^{-1}}$ $p=0.012$) (Figure 5).

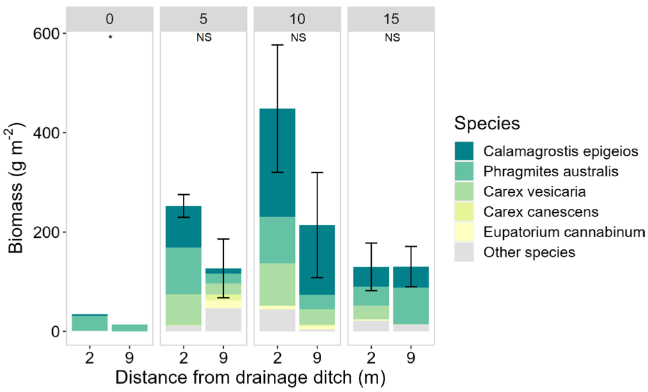

FIGURE 3 | Average biomass accumulated by herbaceous species per unit area depending on wood ash treatment dose (0 (control), 5, 10, $15\,\mathrm{Mg\,ha^{-1}}$) and sampling plot distance from drainage ditch. Error bars represent standard error between a sum of all woody biomass in three repetitions ($n=3$). [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | C and N Content

The moisture content of all woody species was significantly higher ($p<0.001$) in plots treated with the highest ($15\,\mathrm{Mg\,ha^{-1}}$) fertilizer dose (7.5% SE = 1.57 in $0\,\mathrm{Mg\,ha^{-1}}$, 35.7% SE = 1.82 in $5\,\mathrm{Mg\,ha^{-1}}$, 34.1% SE = 3.5 in $10\,\mathrm{Mg\,ha^{-1}}$, 52.6% SE = 0.81 in $15\,\mathrm{Mg\,ha^{-1}}$). Distance from the drainage ditch did not significantly affect the macronutrient content of woody species. However, the C and N contents in dry woody biomass decreased with increasing wood ash dose (Table A2). Treatment dose also increased the C:N ratio in aboveground plant parts under all doses compared to the control (lmer results—control vs. $5\,\mathrm{Mg\,ha^{-1}}$ $p=0.013$, SE = 4.82; control vs. $10\,\mathrm{Mg\,ha^{-1}}$ $p=0.001$, SE = 5.15; control vs. $15\,\mathrm{Mg\,ha^{-1}}$ $p=0.002$, SE = 4.93; Table A3). Belowground parts did not differ from the control at 5 and $10\,\mathrm{Mg\,ha^{-1}}$ doses, but the $15\,\mathrm{Mg\,ha^{-1}}$ dose significantly increased the C:N ratio compared to the control and other treatment doses (lmer results—$p=0.016$, SE = 11.87). These results have limitations; due to the sparsity of vegetation in the sample plots, the treatment effect was analyzed on all woody species biomass combined.

Also in herbaceous species, the treatment significantly increased the C:N ratio (lmer results—control vs. $5\,\mathrm{Mg\,ha^{-1}}$, $p<0.001$; control vs. $10\,\mathrm{Mg\,ha^{-1}}$, $p<0.001$; control vs. $15\,\mathrm{Mg\,ha^{-1}}$, $p=0.001$), but negatively affected the N content (lmer results—control vs. $5\,\mathrm{Mg\,ha^{-1}}$, $p<0.001$; control vs. $10\,\mathrm{Mg\,ha^{-1}}$, $p<0.001$; control vs. $15\,\mathrm{Mg\,ha^{-1}}$, $p<0.001$; Table A4). The effect on the C content was significant only in the aboveground parts, where plants growing under 10 and $15\,\mathrm{Mg\,ha^{-1}}$ treatments stored relatively less C (lmer results—control vs. $10\,\mathrm{Mg\,ha^{-1}}$, $p=0.004$; control vs. $15\,\mathrm{Mg\,ha^{-1}}$, $p<0.001$) (Table A5). Neither the C and N storage nor the C:N ratio was significantly affected by the distance from the drainage ditch, and the differences between belowground and aboveground parts were also not significant.

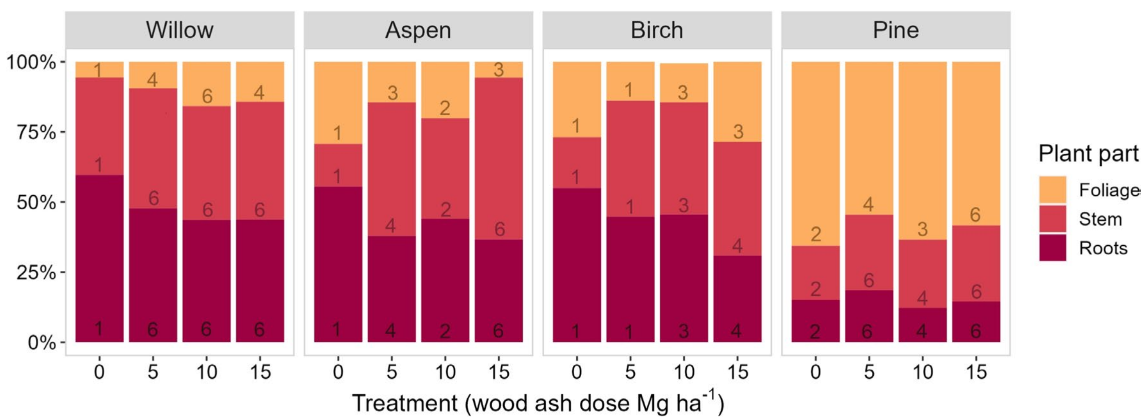

FIGURE 4 | Relative distribution of accumulated biomass in woody plant parts depending on treatment, distance from drainage ditch, and species. $n_{max}=6$, the numbers in stacked bar charts indicate the number of sample plots. [Colour figure can be viewed at wileyonlinelibrary.com]

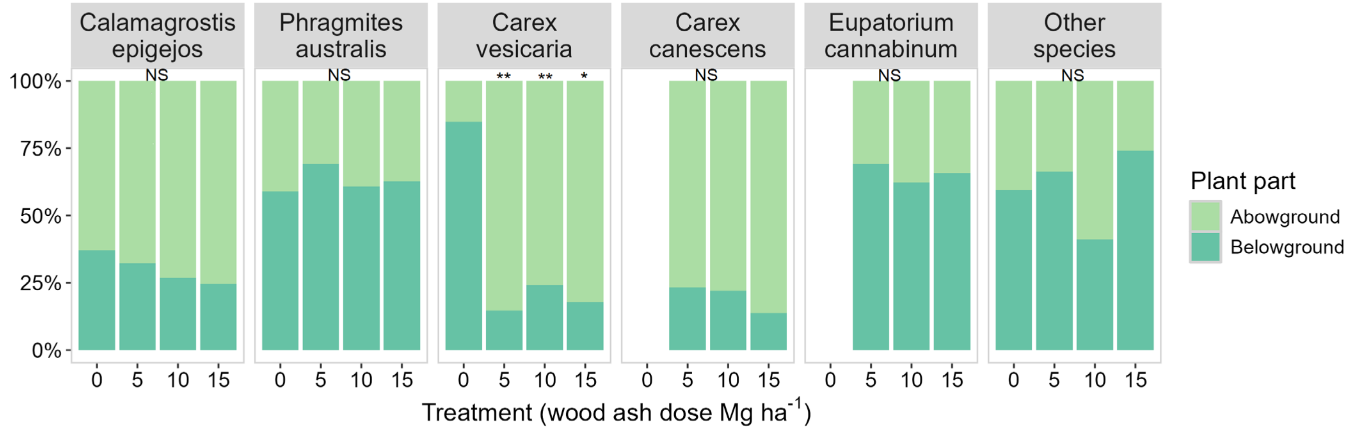

FIGURE 5 | Relative distribution of accumulated above and below ground biomass in herbaceous plant parts depending on treatment and species. $n_{\max}=6$, the numbers in stacked bar charts indicate the number of sample plots. [Colour figure can be viewed at wileyonlinelibrary.com]

3.4 | Soil Properties

Wood ash application decreased soil C and N, but increased the pH and other nutrient content (Table 2). The highest doses (10 and 15 Mg ha^{-1}) also increased soil bulk density. There were no correlations between woody species biomass and soil K and P contents, pH and bulk density (K, $R=0.11$; P, $R=-0.06$), and the relationship strength decreased with depth (AIC values of models: 0 cm AIC = 341.65, 20 cm AIC = 358.95).

The total biomass accumulation was best explained by the K content (multiple $R^2=0.26$, $P=0.01$, F-statistic = 7.46 on 1 and 21 DF), which was also true for herbaceous biomass (multiple $R^2=0.33$, $p<0.01$, F-statistic = 10.46) (Figure 6). The relationship was stronger at 0–20 cm soil depth and decreased with increasing depth. P content did not significantly affect biomass accumulation.

4 | Discussion

4.1 | Biomass Accumulation

Following wood ash application, a rapid increase of woody and herbaceous biomass accumulation was observed in all fertilised groups. Conversely, the control group exhibited a sparse, uneven growth of low-productivity plants, with extensive open peat areas. Even after three years, the peat surface remains susceptible to strong wind erosion and solar radiation. The dominant herbaceous species—*Calamagrostis epigejos*, *Phragmites australis*, and *Carex vesicaria*—were the same across all treatments and locations. Thus, the total biomass was mainly determined by the species abundance and individual plant biomass, both significantly affected by the wood ash application. The highest biomass accumulation in woody species was observed in willow and aspen, which primarily occurred with wood ash fertilization. This suggests that wood ash doses ranging from 5 to 15 Mg ha^{-1} are sufficient to support the initial development of these species. Successful aspen and willow plantations have been achieved earlier on cutaway peatlands with proper drainage and adequate soil fertilisation for selected planted species (Hytönen and Saarsalmi 2009). This study shows that at an early stage, cutaway peatland left to natural revegetation accumulates more biomass in herb species than in woody species. Therefore, when assessing the impact of cutaway peatland natural afforestation on climate and ecology, understory vegetation development and biomass, especially in the early stages, must be included in the calculations (Huotari et al. 2009).

Woody species allocate most biomass to their perennial parts, serving as a long-term carbon store both above and belowground. However, most aboveground and some belowground biomass of herbaceous plants turns into necromass at the end of the growing season. It continues to interact with the environment, promoting vegetation cover development by enriching topsoil with nutrients, supporting microbial development, mitigating wind erosion, providing shade, and limiting water evaporation (Campbell et al. 2002; Huotari et al. 2011; Leung et al. 2015). In this study, biomass allocation was more affected by wood ash treatment and species. A difference existed between pine and deciduous tree species, with pine allocating more biomass to foliage under all treatments. Other studies have also found that conifers have greater relative foliar biomass than deciduous species (Grote 2002; Weigt 2010); however, the foliar proportion decreases with age (Hu et al. 2020). Herbaceous plant biomass partitioning was mainly species-specific.

4.2 | Response to Wood Ash Treatment

The wood ash treatment promoted vegetation cover development in the first three growing seasons, but it is unclear whether the growth will be sustained in the long term. Our results confirm previous researches (Silvan and Hytönen 2016; Ots et al. 2024), that wood-ash-treated plots produced more biomass and had higher species richness and abundance than untreated cutaway peatland. Kikamägi et al. (2013), applying the same dose of wood ash to planted silver birches in cutaway peatlands, concluded that the highest biomass could be obtained with either 10 or 15 Mg ha^{-1} treatment. In earlier studies conducted at the same experimental site, we concluded that the wood-ash doses (5, 10, and 15 Mg ha^{-1}) accelerated the ecosystem development by providing optimal conditions for greater species richness (Zuševica et al. 2022). This study indicated that the most productive wood ash dose from ecological, economic, and climate perspectives is 10 Mg ha^{-1}.

TABLE 2 | Soil properties two and three years after wood ash treatment, depending on application dose (Control (0), 5, 10, or 15 Mg ha^{-1}) and sampling plot location (distance: 2 or 9 m from the drainage ditch; values present average ± standard error).

	Treatment (Mg ha^{-1})	0		5		10		15	
Years after treatment	**Distance from drainage ditch**	**2 m**	**9 m**	**2 m**	**9 m**	**2 m**	**9 m**	**2 m**	**9 m**
Two	pH_{CaCl2}	3.5 ± 0.01		4.2 ± 0.03		4.8 ± 0.04		5.9 ± 0.04	
	P, mg kg^{-1}	237.0 ± 8.1		258.5 ± 7.6		452.7 ± 58.0		791.9 ± 40.0	
	K, mg kg^{-1}	72.0 ± 5.8		331.8 ± 6.2		694.7 ± 74.4		1703.0 ± 115.7	
	Mg, mg kg^{-1}	1037.2 ± 10.6		1450.5 ± 2.1		2068.6 ± 10.6		2807.8 ± 7.5	
	Ca, mg kg^{-1}	1111.9 ± 14.8		1346.1 ± 26.0		1867.8 ± 113.7		2493.1 ± 69.8	
Three	pH_{KCl}	3.6 ± 0.1	3.3 ± 0.1	3.8 ± 0.1	3.9 ± 0.2	4.5 ± 0.5	4.0 ± 0.2	4.7 ± 0.5	4.1 ± 0.2
	P, mg kg^{-1}	288.1 ± 50.0	247.1 ± 28.2	444.5 ± 44.7	440.9 ± 84.0	588.8 ± 220.0	306.1 ± 60.3	550.4 ± 160.4	430.7 ± 34.1
	K, mg kg^{-1}	133.7 ± 17.0	123.2 ± 24.9	253.9 ± 52.9	321.5 ± 66.0	986.6 ± 266.8	477.8 ± 69.1	624.4 ± 164.8	462.3 ± 88.8
	Bulk density, g ml^{-1}	172.4 ± 9.6	170.8 ± 24.7	216.8 ± 15.3	225.4 ± 17.9	213.1 ± 9.8	228.3 ± 15.9	281.8 ± 35.6	221.0 ± 14.6

4.3 | Effect of Drainage Ditch

The importance of drainage ditches in vegetation patterns has long been recognized, as they influence moisture distribution (Fisher et al. 1996; Jutras et al. 2006; Sarkkola et al. 2010; Sinclair et al. 2020). A limitation of this study is the lack of water table data, which is speculated to vary with the distance from the ditch and precipitation, as the ditch can shift between influent (gaining water from groundwater) and effluent (loss water to groundwater; Winter et al. 1998). The distance from the drainage ditch minimally affected the vegetation development, probably due to relatively dry summers when water was absent from the ditches for most of the growing season. It is also known that vegetation affects the moisture content of the soil by evapotranspiration (Sarkkola et al. 2010). While denser vegetation cover reduces evaporation from the soil surface, it promotes water loss through evapotranspiration (Fay and Lavoie 2009).

4.4 | C and N Content

The total carbon accumulation per unit area was also higher in plots treated with 10 Mg ha^{-1}. Given that the carbon content in both woody and herbaceous plants was 42%–53%, herbaceous plants sequestrate more carbon. At the plant level, the proportional carbon and nitrogen content was higher in plants growing under control. Additionally, access to other elements was limited, affecting the relative chemical composition of the plants. Subsequently, the C:N ratio was lower in these plots. Biomass mainly comprises carbon (C), oxygen (O), and hydrogen (H) (Sánchez et al. 2019; Vassilev et al. 2010), and these nutrients are mainly absorbed from water and air (Mahler 2004). Low C:N ratios have been found in plants growing in drier areas (Zhang et al. 2020). The N content contributes to regulating stomatal conductance as a mechanism to improve water use efficiency (Mata and Lamattina 2001; Zangani et al. 2021). Thus, a low C:N ratio could result from limited water uptake caused by a lack of soil moisture or possibly short roots and dense root tissue (Comas et al. 2013; Verelst et al. 2013). This coincides with our findings of higher plant moisture contents under higher treatment doses. The soil C and N contents two years after fertilisation were highest in the control plots, decreasing with higher wood ash doses, indicating that wood ash addition and vegetation development enhanced decomposition processes, increasing C and N lability. Increasing pH has been shown to reduce methane (CH_4) emission (Putkinen et al. 2018); however, raising the soil pH can initially increase CO_2 emissions by creating more favourable conditions for microorganisms and vegetation growth, which promotes the decomposition of organic material and CO_2 release from respiration (Lazcano et al. 2020; Mäkiranta et al. 2007; Silvan and Hytönen 2016; Waddington and Warner 2001).

4.5 | Soil Properties

The difference in vegetation cover between the control and treated plots confirms that the lack of plant emergence in the control plots is not due to a lack of seeds or propagules, but rather unfavorable germination conditions (Salonen 1994; Salonen and Laaksonen 1994). Although fertilization affected overall herbaceous species emergence, no difference was found between the applied wood ash doses. This suggests that in the control plots,

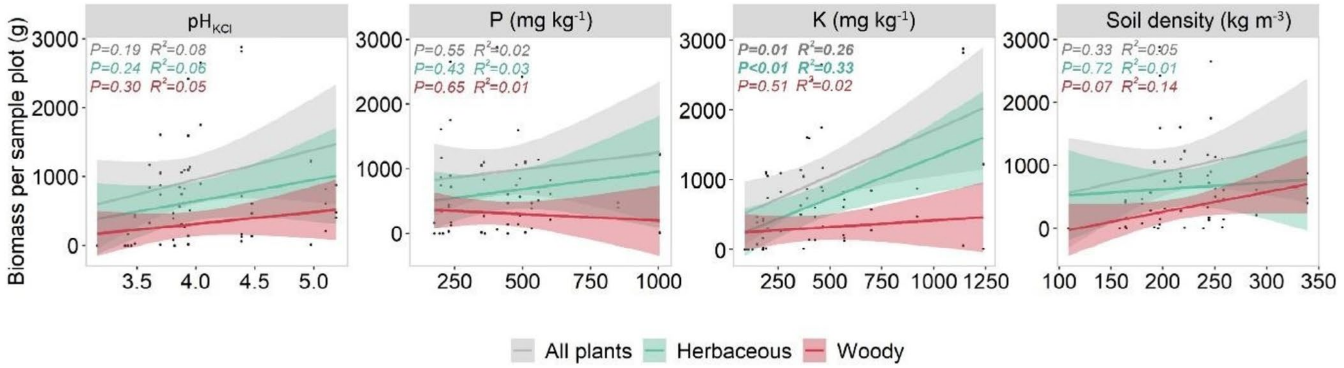

FIGURE 6 | Relationship between soil factors at 0–20 cm depth and accumulated total, herbaceous, and woody biomass. [Colour figure can be viewed at wileyonlinelibrary.com]

nutrient availability was below the critical level required for seed germination and early plant development. Other studies have found that mineral fertilizer has an inconsistent effect on species occurrence (Triisberg et al. 2013); thus, the higher number of species in treated plots may have been primarily due to the changes in soil pH rather than the soil nutrient status. However, the strongest relationship between herbaceous plant biomass accumulation and soil K content suggests that K is the main factor affecting plant growth. Fertilizers rich in K could be applied to enhance herbaceous species productivity, as K contributes to only around 0.3%–5% of plants dry weight, and has a crucial role in stress resistance (Amtmann and Rubio 2012; Pandey and Mahiwal 2020; Sánchez et al. 2019; Trolldenier 1971). Under K-limited conditions, plant growth is restricted, and cell size is reduced, particularly in the aboveground parts, which could explain the higher root-to-shoot ratios observed in the control of this study (Amtmann and Rubio 2012; Padan and Landau 2016). Interestingly, soil P did exhibit a significant linear relationship with plant biomass accumulation. The decreases in soil P and K contents between two and three years after fertilization were small and inconsistent, suggesting limited plant uptake and leaching. Under similar conditions, soil fertilization with P, PK, and wood ash increased accumulated biomass of silver birch and Scots pine (Aro et al. 2020; Hytönen and Aro 2012; Ots et al. 2017).

5 | Conclusions

Wood ash application aids natural vegetation recovery on cutaway peatlands, supplying nutrients and pH for initial growth. However, its long-term effects and influence on species composition are unclear. In the early years of recultivated cutaway peatlands, herbaceous species dominate biomass accumulation and carbon assimilation, driven by the performance and abundance of *Calamagrostis epigejos*, *Phragmites australis*, and *Carex vesicaria*. Biomass allocation in herbaceous species varies by species, while woody plants primarily allocate biomass to perennial parts, acting as long-term carbon stores and contributing more in later ecosystem stages. No clear patterns were observed in plant biomass accumulation, allocation, C and N contents, or C:N ratio based on the distance from the drainage ditch. Differences in plant moisture, C and N contents, and C:N ratio under wood ash treatments suggest these parameters are influenced more by species- and nutrient-driven water use efficiency than soil moisture availability. This research shows, that during the initial vegetation development, herbaceous species comprised the majority of the biomass, compared to woody species.

Author Contributions

All the authors contributed to the study conception and design. Data collection was performed by S.N.-Š. and A.Z. Material preparation was performed by S.N.-Š, A.Z., and V.V. Data visualization and analyses were performed by S.C., S.N.-Š, and A.Z. The first draft of the manuscript was written by S.C., and all authors commented on, reviewed, and edited previous versions of the manuscript. Supervision, project coordination, and funding acquisition were performed by D.L. All the authors read and approved the final manuscript.

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Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

Aguraijuja, K., J. Klõšeiko, K. Ots, and A. Lukjanova. 2015. "Effect of Wood Ash on Leaf and Shoot Anatomy, Photosynthesis and Carbohydrate Concentrations in Birch on a Cutaway Peatland." *Environmental Monitoring and Assessment* 187, no. 7: 444. https://doi.org/10.1007/s10661-015-4681-5.

Amtmann, A., and F. Rubio. 2012. *Potassium in Plants*, 1–10. ELS. https://doi.org/10.1002/9780470015902.a0023737.

Aro, L., A. Ahtikoski, and J. Hytönen. 2020. "Profitability of Growing Scots Pine on Cutaway Peatlands." *Silva Fennica* 54, no. 3: 10273.

Arshad, M. A., Y. K. Soon, R. H. Azooz, N. Z. Lupwayi, and S. X. Chang. 2012. "Soil and Crop Response to Wood Ash and Lime Application in Acidic Soils." *Agronomy, Soils & Environmental Quality* 103, no. 3: 715–721. https://doi.org/10.2134/agronj2011.0355.

Campbell, D. R., C. Lavoie, and L. Rochefort. 2002. “Wind Erosion and Surface Stability in Abandoned Milled Peatlands.” *Canadian Journal of Soil Science* 82, no. 1: 85–95. https://doi.org/10.4141/S00-089.

Comas, L. H., S. R. Becker, V. M. V. Cruz, P. F. Byrne, and D. A. Dierig. 2013. “Root Traits Contributing to Plant Productivity Under Drought.” *Frontiers in Plant Science* 4, no. 442: 1–16. https://doi.org/10.3389/fpls.2013.00442.

Core Team, R. 2023. *R: A Language and Environment*. R Foundation for Statistical Computing.

Demeyer, A., J. C. Voundi Nkana, and M. G. Verloo. 2001. “Characteristics of Wood Ash and Influence on Soil Properties and Nutrient Uptake: An Overview.” *Bioresource Technology* 77, no. 3: 287–295. https://doi.org/10.1016/S0960-8524(00)00043-2.

Derome, J., M. Kukkola, A. Smolander, and T. Lehto. 2000. “Liming of Forest Soils.” In *Forest Condition in a Changing Environment. Forestry Sciences*, edited by E. Mälkönen, vol. 65. Springer. https://doi.org/10.1007/978-94-015-9373-1_39.

European Commission. 2020. “Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions. *EU Biodiversity Strategy for 2030. Bringing Nature Back into Our Lives*.” 1–22.

Fay, E., and C. Lavoie. 2009. “The Impact of Birch Seedlings on Evapotranspiration From a Mined Peatland: An Experimental Study in Southern Quebec, Canada.” *Mires and Peat* 5, no. 3: 1–7.

Fisher, A. S., G. S. Podniesinski, and D. J. Leopold. 1996. “Effects of Drainage Ditches on Vegetation Patterns in Abandoned Agricultural Peatlands in Central New York.” *Wetlands* 16, no. 4: 397–409. https://doi.org/10.1007/BF03161329.

Gagnon, F., L. Rochefort, and C. Lavoie. 2018. “Spontaneous Revegetation of a Peatland in Manitoba After Peat Extraction: Diversity of Plant Assemblages and Restoration Perspectives.” *Botany* 96, no. 11: 779–791. https://doi.org/10.1139/cjb-2018-0109.

Glenk, K., and J. Martin-Ortega. 2018. “The Economics of Peatland Restoration.” *Journal of Environmental Economics and Policy* 7, no. 4: 345–362. https://doi.org/10.1080/21606544.2018.1434562.

Gross, K. L., T. Berner, E. Marschall, and C. Tomcko. 1983. “Patterns of Resource Allocation Among Five Herbaceous Perennials.” *Bulletin of the Torrey Botanical Club* 110, no. 3: 345–352.

Grote, R. 2002. “Foliage and Branch Biomass Estimation of Coniferous and Deciduous Tree Species.” *Silva Fennica* 36, no. 4: 779–788. https://doi.org/10.14214/sf.520.

Hu, M., A. Lehtonen, F. Minunno, and A. Mäkelä. 2020. “Age Effect on Tree Structure and Biomass Allocation in Scots Pine (*Pinus sylvestris* L.) and Norway Spruce (*Picea abies* [L.] Karst.).” *Annals of Forest Science* 77, no. 3: 90. https://doi.org/10.1007/s13595-020-00988-4.

Huotari, N., E. Tillman-Sutela, A. Kauppi, and E. Kubin. 2007. “Fertilization Ensures Rapid Formation of Ground Vegetation on Cut-Away Peatlands.” *Canadian Journal of Forest Research* 37, no. 5: 874–883. https://doi.org/10.1139/X06-292.

Huotari, N., E. Tillman-Sutela, and E. Kubin. 2009. “Ground Vegetation Exceeds Tree Seedlings in Early Biomass Production and Carbon Stock on an Ash-Fertilized Cut-Away Peatland.” *Biomass and Bioenergy* 33, no. 9: 1108–1115. https://doi.org/10.1016/j.biombioe.2009.05.009.

Huotari, N., E. Tillman-Sutela, and E. Kubin. 2011. “Ground Vegetation Has a Major Role in Element Dynamics in an Ash-FertilizedCut-Away Peatland.” *Forest Ecology and Management* 261: 2081–2088.

Huotari, N., E. Tillman-Sutela, J. Pasanen, and E. Kubin. 2008. “Ash-Fertilization Improves Germination and Early Establishment of Birch (*Betula pubescens* Ehrh.) Seedlings on a Cut-Away Peatland.” *Forest Ecology and Management* 255, no. 7: 2870–2875. https://doi.org/10.1016/j.foreco.2008.01.062.

Hytönen, J. 2005. “Effects of Liming on the Growth Birch and Willow on Two Cut- Away Peat Substrates in Greenhouse.” *Baltic Forestry* 11, no. 2: 68–74.

Hytönen, J., and L. Aro. 2012. “Biomass and Nutrition of Naturally Regenerated and Coppiced Birch on Cutaway Peatland During 37 Years.” *Silva Fennica* 46, no. 3: 377–394. https://doi.org/10.14214/sf.48.

Hytönen, J., and A. Saarsalmi. 2009. “Long-Term Biomass Production and Nutrient Uptake of Birch, Alder and Willow Plantations on Cut-Away Peatland.” *Biomass and Bioenergy* 33, no. 9: 1197–1211. https://doi.org/10.1016/j.biombioe.2009.05.014.

Jutras, S., H. Hökkä, J. Bégin, and A. P. Plamondon. 2006. “Beneficial Influence of Plant Neighbours on Tree Growth in Drained Forested Peatlands: A Case Study.” *Canadian Journal of Forest Research* 36, no. 9: 2341–2350. https://doi.org/10.1139/X06-134.

Kikamägi, K., O. K. Katri, and T. Kuznetsova. 2013. “Effect of Wood Ash on the Biomass Production and Nutrient Status of Young Silver Birch (*Betula pendula* Roth) Trees on Cutaway Peatlands in Estonia.” *Ecological Engineering* 58: 17–25. https://doi.org/10.1016/j.ecoleng.2013.06.014.

Klein, T., Y. Vitasse, and G. Hoch. 2016. “Coordination Between Growth, Phenology and Carbon Storage in Three Coexisting Deciduous Tree Species in a Temperate Forest.” *Tree Physiology* 36, no. 7: 847–855. https://doi.org/10.1093/treephys/tpw030.

Laasasenaho, K., R. Lauhanen, A. Räsänen, et al. 2023. “After-Use of Cutover Peatland From the Perspective of Landowners: Future Effects on the National Greenhouse Gas Budget in Finland.” *Land Use Policy* 134: 1–13. https://doi.org/10.1016/j.landusepol.2023.106926.

Laasasenaho, K., A. Lensu, J. Rintala, and R. Lauhanen. 2017. “Landowners' Willingness to Promote Bioenergy Production on Wasteland – Future Impact on Land Use of Cutaway Peatlands.” *Land Use Policy* 69: 167–175. https://doi.org/10.1016/j.landusepol.2017.09.010.

Laganière, J., X. Cavard, B. W. Brassard, D. Paré, Y. Bergeron, and H. Y. H. Chen. 2015. “The Influence of Boreal Tree Species Mixtures on Ecosystem Carbon Storage and Fluxes.” *Forest Ecology and Management* 354: 119–129. https://doi.org/10.1016/j.foreco.2015.06.029.

Latvian Geospatial Information Agency (LGIA). 2019. “Ortho-photo map of cycle 7 of Latvia.”

Law: On Subterranean Depths. 1996. “Latvijas Vēstnesis, 87, 21.05.1996.” https://likumi.lv/ta/en/en/id/40249.

Lazcano, C., A. S. Deol, M. E. Brummell, and M. Strack. 2020. “Interactive Effects of Vegetation and Water Table Depth on Belowground C and N Mobilization and Greenhouse Gas Emissions in a Restored Peatland.” *Plant and Soil* 448, no. 1–2: 299–313. https://doi.org/10.1007/s11104-020-04434-2.

Leung, A. K., A. Garg, J. L. Coo, C. W. W. Ng, and B. C. H. Hau. 2015. “Effects of the Roots of Cynodon Dactylon and Schefflera Heptaphylla on Water Infiltration Rate and Soil Hydraulic Conductivity.” *Hydrological Processes* 29: 3342–3354. https://doi.org/10.1002/hyp.10452.

LVS EN 14672:2006. 2006. “Foodstuffs – Determination of phosphorus content by spectrophotometry. Latvian Standard.”

LVS EN ISO 11885:1997. 1997. “Water quality – Determination of selected elements by inductively coupled plasma optical emission spectrometry (ICP-OES). Latvian Standard.”

LVS ISO 10390:2002. 2002. “L/NAC:2005 L 2002 Soil quality – Determination of pH. Latvian Standard.”

LVS ISO 10694:2006. 2006. “Soil quality – Determination of organic and total carbon after dry combustion (elementary analysis). Latvian Standard.”

LVS ISO 11272:2017. 2017. “Soil quality – Determination of dry bulk density. Latvian Standard.”

LVS ISO 11464:2005. 2005. “Soil quality – Pretreatment of samples for physico-chemical analyses. Latvian Standard.”

LVS ISO 13878:1998. 1998. “Soil quality – Determination of total nitrogen content by dry combustion (elementary analysis). Latvian Standard.”

Mahler, R. L. 2004. “Nutrients plants require for growth. University of Idaho. College of Agricultural and Life Sciences, CIS 1124.” 1–4.

Mäkiranta, P., J. Hytönen, L. Aro, et al. 2007. “Soil Greenhouse Gas Emissions From Afforested Organic Soil Croplands and Cutaway Peatlands.” *Boreal Environment Research* 12, no. 2: 159–175.

Mata, C. G., and L. Lamattina. 2001. “Nitric Oxide Induces Stomatal Closure and Enhances the Adaptive Plant Responses Against Drought Stress.” *Plant Physiology* 126, no. 3: 1196–1204. https://doi.org/10.1104/pp.126.3.1196.

Orru, M., K. Ots, and H. Orru. 2016. “Re-Vegetation Processes in Cutaway Peat Production Fields in Estonia in Relation to Peat Quality and Water Regime.” *Environmental Monitoring and Assessment* 188, no. 12: 655. https://doi.org/10.1007/s10661-016-5669-5.

Ots, K., M. Tilk, and K. Aguraijuja. 2017. “The Effect of Oil Shale Ash and Mixtures of Wood Ash and Oil Shale Ash on the Above- and Belowground Biomass Formation of Silver Birch and Scots Pine Seedlings on a Cutaway Peatland.” *Ecological Engineering* 108: 296–306. https://doi.org/10.1016/j.ecoleng.2017.09.002.

Ots, K., T. Tullus, M. Sild, et al. 2024. “Ash Treatment Promotes the Revegetation of Abandoned Extracted Peatlands.” *Land* 13: 1623. https://doi.org/10.3390/land13101623.

Padan, E., and M. Landau. 2016. “Sodium-Proton (Na+/H+) Antiporters: Properties and Roles in Health and Disease.” *Metal Ions in Life Sciences* 16: 391–458. https://doi.org/10.1007/978-3-319-21756-7-12.

Pandey, G. K., and S. Mahiwal. 2020. “Role of Potassium in Plants.” In *SpringerBriefs in Plant Science*, vol. 81. Springer Nature Switzerland AG. https://doi.org/10.1007/978-3-030-45953-6.

Price, J. S., A. L. Heathwaite, and A. J. Baird. 2003. “Hydrological Processes in Abandoned and Restored Peatlands: An Overview of Management Approaches.” *Wetlands Ecology and Management* 11, no. 1–2: 65–83. https://doi.org/10.1023/A:10220464094852003.

Priede, A., and A. Gancone. 2019. “Sustainable and responsible after-use of peat extraction areas. Baltijas krasti, Riga.”

Priedītis, N. 2014. “Latvijas augi [Plants of Latvia]. Gandrs poligrāfija, Rīga.” 888.

Putkinen, A., E. S. Tuittila, H. M. P. Siljanen, L. Bodrossy, and H. Fritze. 2018. “Recovery of Methane Turnover and the Associated Microbial Communities in Restored Cutover Peatlands Is Strongly Linked With Increasing Sphagnum Abundance.” *Soil Biology and Biochemistry* 116: 110–119. https://doi.org/10.1016/j.soilbio.2017.10.005.

Räsänen, A., E. Albrecht, M. Annala, et al. 2023. “After-Use of Peat Extraction Sites – A Systematic Review of Biodiversity, Climate, Hydrological and Social Impacts.” *Science of the Total Environment* 882: 163583. https://doi.org/10.1016/j.scitotenv.2023.163583.

Renou-Wilson, F., M. Keane, G. McNally, J. O. Sullivan, and E. P. Farrell. 2008. “Developing a forest resource on industrial cutaway peatland. The BOGFOR programme, COFORD, Dublin.”

Salonen, V. 1994. “Revegetation of Harvested Peat Surfaces in Relation to Substrate Quality.” *Journal of Vegetation Science* 5: 403–408. https://doi.org/10.2307/3235863.

Salonen, V., and M. Laaksonen. 1994. “Effects of Fertilization, Liming, Watering and Tillage on Plant Colonization of Bare Peat Surfaces.” *Annales Botanici Fennici* 31: 29–36.

Sánchez, J., M. D. Curt, N. Robert, and J. Fernández. 2019. “Biomass Resources.” In *The Role of Bioenergy in the Bioeconomy: Resources, Technologies, Sustainability and Policy*, edited by C. Lago, N. Caldés, and Y. Lechón, 25–111. Academic Press. https://doi.org/10.1016/B978-0-12-813056-8.00002-9.

Sarkkola, S., M. Nieminen, E. Ahti, et al. 2010. “Role of Tree Stand Evapotranspiration in Maintaining Satisfactory Drainage Conditions in Drained Peatlands.” *Canadian Journal of Forest Research* 40, no. 8: 1485–1496. https://doi.org/10.1139/X10-084.

Silvan, N., and J. Hytönen. 2016. “Impact of Ash-Fertilization and Soil Preparation on Soil Respiration and Vegetation Colonization on Cutaway Peatlands.” *American Journal of Climate Change* 5, no. 2: 178–192. https://doi.org/10.4236/ajcc.2016.52017.

Sinclair, A. L., L. L. B. Graham, E. I. Putra, et al. 2020. “Effects of Distance From Canal and Degradation History on Peat Bulk Density in a Degraded Tropical Peatland.” *Science of the Total Environment* 699: 134199. https://doi.org/10.1016/j.scitotenv.2019.134199.

Triisberg, T., E. Karofeld, and J. Paal. 2013. “Factors Affecting the Re-Vegetation of Abandoned Extracted Peatlands in Estonia: A Synthesis From Field and Greenhouse Studies.” *Estonian Journal of Ecology* 62, no. 3: 192–211. https://doi.org/10.3176/eco.2013.3.02.

Trolldenier, G. 1971. “Recent Aspects of the Influence of Potassium on Stomatal Opening and Closing. Potassium in Biochemistry and Physiology.” 130–133. https://doi.org/10.1097/00010694-197503000-00015.

Vassilev, S. V., D. Baxter, L. K. Andersen, and C. G. Vassileva. 2010. “An Overview of the Chemical Composition of Biomass.” *Fuel* 89, no. 5: 913–933. https://doi.org/10.1016/j.fuel.2009.10.022.

Verelst, W., E. Bertolini, S. De Bodt, et al. 2013. “Molecular and Physiological Analysis of Growth-Limiting Drought Stress in Drachypodium Distachyon Leaves.” *Molecular Plant* 6, no. 2: 311–322. https://doi.org/10.1093/mp/sss098.

VSIA “Latvijas Vides, ģeoloģijas un meteoroloģijas centrs”. 2024. “Meteorological data from the nearest station Jelgava.” https://videscentrs.lvgmc.lv/.

Waddington, J. M., and K. D. Warner. 2001. “Atmospheric CO2 Sequestration in Restored Mined Peatlends.” *Ecoscience* 8, no. 3: 359–368. https://doi.org/10.1080/11956860.2001.11682664.

Weigt, R. B. 2010. “Effects of elevated ground-level ozone on nitrogen acquisition of mature European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) trees. Technische Universität München, Lehrstuhl für Ökophysiologie der Pflanzen [Chair of Ecophysiology of Plants, Technical University of Munich] (in German).”

Winter, T. C., J. W. Harvey, O. L. Franke, and W. M. Alley. 1998. “Ground Water and Surface Water: a Single Resource. U.S. Geological Survey Circular.” https://doi.org/10.3133/cir1139.

Word, C. S., D. L. McLaughlin, B. D. Strahm, et al. 2022. “Peatland Drainage Alters Soil Structure and Water Retention Properties: Implications for Ecosystem Function and Management.” *Hydrological Processes* 36, no. 3: 1–13. https://doi.org/10.1002/hyp.14533.

Zangani, E., K. Afsahi, F. Shekari, E. M. Sweeney, and A. Mastinu. 2021. “Nitrogen and Phosphorus Addition to Soil Improves Seed Yield, Foliar Stomatal Conductance, and the Photosynthetic Response of Rapeseed (Brassica Napus l.).” *Agriculture* 11, no. 6: 1–10. https://doi.org/10.3390/agriculture11060483.

Zhang, J., N. He, C. Liu, et al. 2020. “Variation and Evolution of C:N Ratio Among Different Organs Enable Plants to Adapt to N-Limited Environments.” *Global Change Biology* 26, no. 4: 2534–2543. https://doi.org/10.1111/gcb.14973.

Zuševica, A., S. Celma, S. Neimane, M. von Cossel, and D. Lazdina. 2022. “Wood-Ash Fertiliser and Distance From Drainage Ditch Affect the Succession and Biodiversity of Vascular Plant Species in Tree Plantings on Marginal Organic Soil.” *Agronomy* 12: 421. https://doi.org/10.3390/agronomy12020421.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1.** Supporting Information.

Appendix A

TABLE A1 | Biomass (g per m^2, ±standard error) accumulated in woody and herbaceous species depending on wood ash treatment (0 (control), 5, 10, and 15 Mg ha^{-1}) and distance from the drainage ditch (N = 3).

Treatment (Mg ha^{-1})	0		5		10		15	
Distance from drainage ditch	**2 m**	**9 m**	**2 m**	**9 m**	**2 m**	**9 m**	**2 m**	**9 m**
Herbaceous species	34.5 ± 34.5	13.8 ± 13.8	231.9 ± 22.8	123.3 ± 59.0	451.5 ± 128.3	214.1 ± 105.8	129.9 ± 47.9	130.4 ± 40.5
Woody species	2.3 ± 1.9	0.04 ± 0.03	25.1 ± 18.6	205.7 ± 65.9	33.5 ± 20.2	87.2 ± 37.4	126.5 ± 12.6	81.3 ± 26.13
Total	36.8	13.9	257.1 ± 3.0	329.0 ± 137.9	485.0 ± 125.1	301.3 ± 68.3	256.4 ± 44.1	211.7 ± 36.3

TABLE A2 | Proportional mean N and C contents in woody plant aboveground and belowground parts depending on the wood ash treatment (0 (control), 5, 10, and 15 Mg ha^{-1}), values present average ± standard error, sample size in parentheses.

	N %				C %			
Treatment	**0**	**5**	**10**	**15**	**0**	**5**	**10**	**15**
Aboveground	2.0 ± 0.2 (2)	1.4 ± 0.3 (7)	1.3 ± 0.2 (5)	1.2 ± 0.2 (2)	51.6 ± 2.0 (2)	50.9 ± 1.3 (7)	50.5 ± 1.6 (5)	49.7 ± 1.6 (7)
Aspen		1.3 ± 0.5 (2)	1.3 (1)	1.0 ± 0.1 (2)		49.7 ± 0.2 (2)	49.2 (1)	49.1 ± 0.4 (2)
Birch		1.5 (1)	1.4 (1)	1.4 (1)		52.1 (1)	52.4	50.4 (1)
Pine	2.1 (1)	1.7 ± 0.2 (2)	1.4 (1)	1.4 ± 0.1 (2)	53.1 (1)	52.3 ± 0.5 (2)	51.9 (1)	51.5 ± 0.2 (2)
Willow	1.9 (1)	1.1 ± 0.1 (2)	1.1 ± 0.1 (2)	1.0 ± 0.4 (2)	50.2 (1)	50.0 ± 6 (2)	49.5 ± 0.9 (2)	48.2 ± 1.4 (2)
Belowground	1.4 ± 0.1 (2)	1.0 ± 0.2 (7)	1.1 ± 0.4 (5)	0.8 ± 0.3 (7)	50.3 ± 2.1 (2)	49.1 ± 1.7 (7)	48.4 ± 1.5 (5)	48.9 ± 1.8 (7)
Aspen		0.8 ± 0.1 (2)	0.7 (1)	0.6 ± 0.1 (2)		47.6 ± 0.8 (2)	47.0 (1)	47.1 ± 1.2 (2)
Birch		1.17 (1)	1.8 (1)	0.6 (1)		50.2 (1)	49.1 (1)	49.6 (1)
Pine	1.37 (1)	1.2 ± 0.1 (2)	0.9 (1)	0.9 ± 0.1 (2)	51.8 (1)	51.2 ± 0.6 (2)	50.7 (1)	50.9 ± 0.4 (2)
Willow	1.43 (1)	0.8 ± 0.1 (2)	1.0 ± 0.1 (2)	1.0 ± 0.4 (2)	48.8 (1)	48.1 ± 0.1 (2)	47.7 ± 0.3 (2)	48.3 ± 1.4 (2)
Whole woody biomass	1.7 ± 0.4 (4)	1.2 ± 0.4 (14)	1.2 ± 0.3 (10)	0.98 ± 0.3 (14)	51.0 ± 1.9 (4)	50.0 ± 1.7 (14)	49.5 ± 1.8 (10)	49.31 ± 1.7 (14)

TABLE A3 | C:N ratios in different woody species depending on wood ash treatment (0 (control), 5, 10, and 15 Mg ha^{-1}), values present average ± standard error, sample size in parentheses.

Treatment (Mg ha^{-1})	C:N ratio			
	0	5	10	15
Aboveground				
Aspen	—	34 ± 7 (2)	37 (1)	49 ± 0.1 (2)
Birch	—	35 (1)	37 (1)	36 (1)
Pine	25 (1)	32 ± 2 (2)	37 (1)	36 ± 1 (2)
Willow	27 (1)	44 ± 3 (2)	44 ± 1 (2)	47 ± 5 (2)
Belowground				
Aspen	—	59 ± 1 (2)	71 (1)	88 ± 10 (2)
Birch	—	43 (1)	28 (1)	78 (1)
Pine	38 (1)	43 ± 1 (2)	59 (1)	58 ± 1 (2)
Willow	34 (1)	66 ± 2 (2)	48 ± 2 (2)	61 ± 12 (2)

TABLE A4 | C:N ratios in different herbaceous species depending on wood ash treatment (0 (control), 5, 10, and 15 Mg ha^{-1}), values present average ± standard error, sample size in parentheses.

Treatment (Mg ha^{-1})	C:N ratio			
	0	5	10	15
Aboveground				
Calamagrostis epigejos	35 (1)	52 ± 4 (2)	63 ± 0.4 (2)	46 ± 14 (2)
Phragmites australis	29 ± 2 (2)	44 ± 3 (2)	44 ± 1 (2)	32 (1)
Carex vesicaria	—	53 ± 1 (2)	45 ± 2 (2)	47 (1)
Carex canescens	—	43 ± 6 (2)	38 (1)	33 (1)
Eupatorium cannabinum	—	44 (1)	47 ± 13 (2)	40 (1)
Other species	28 (1)	48 ± 3 (2)	54 (1)	40 ± 11 (2)
Belowground				
Calamagrostis epigejos	29 (1)	50 ± 6 (2)	55 ± 8 (2)	56 ± 5 (2)
Phragmites australis	27 ± 2 (2)	39 ± 1 (2)	35 ± 1 (2)	42 (1)
Carex vesicaria	—	39 ± 2 (2)	43 ± 3 (2)	53 (1)
Carex canescens	—	36 ± 1 (2)	32 (1)	40 (1)
Eupatorium cannabinum	—	62 (1)	42 ± 3 (2)	56 (1)
Other species	22 (1)	45 ± 7 (2)	86 (1)	55 ± 1 (2)

TABLE A5 | Proportional N and C contents in herbaceous plant aboveground and belowground parts depending on wood ash treatment (0 (control), 5, 10, and 15 Mg ha^{-1}), values present average ± standard error, sample size in parentheses.

Treatment (Mg ha^{-1})	N %				C %			
	0	5	10	15	0	5	10	15
Aboveground	1.6 ± 0.2 (4)	1.0 ± 0.1 (11)	1.0±	1.2±	49.3 ± 0.7 (4)	48.3 ± 0.7 (11)	47.5±	46 ± 2
Calamagrostis epigejos	1.4 (1)	0.9 ± 0.1 (2)	0.7 ± 0.1 (2)	1.1 ± 0.4 (2)	49.28 (1)	47.9 ± 0.8 (2)	46.9 ± 1.1 (2)	46.5 ± 1.5 (2)
Phragmites australis	1.7 ± 0.1 (2)	1.1 ± 0.1 (2)	1.1 ± 0.1 (2)	1.5 (1)	49.8 ± 0.1 (2)	49.4 ± 0.7 (2)	48.6 ± 1.3 (2)	48.3 (1)
Carex vesicaria		0.9 ± 0.1 (2)	1.1 ± 0.1 (2)	1.0 (1)		48.0 ± 0.3 (2)	46.9 ± 1.0 (2)	46.0 (1)
Carex canescens		1.2 ± 0.2 (2)	1.3 (1)	1.4 (1)		48.2 ± 0.4 (2)	48.0 (1)	47.7 (1)
Eupatorium cannabinum		1.1 (1)	1.0 ± 0.3 (2)	1.1 (1)		48.1 (1)	48.0 ± 0.1 (2)	45.1 (1)
Other species	1.7 (1)	1.0 ± 0.1 (2)	0.9 (1)	1.2 ± 0.4 (2)	48.38 (1)	48.3 ± 0.5 (2)	46.2 (1)	44.6 ± 3.1 (2)
Belowground	1.9 ± 0.2 (4)	1.1 ± 0.2 (11)	1.1 ± 0.3 (11)	1.0 ± 0.2 (9)	48.3 ± 1.7 (4)	48.4 ± 1.7 (11)	46.8 ± 1.7 (11)	47.4 ± 1.4 (9)
Calamagrostis epigejos	1.7 (1)	1.0 ± 0.1 (2)	0.9 ± 0.2 (2)	0.9 ± 0.1 (2)	49.5	48.5 ± 0.2 (2)	48.1 ± 0.3 (2)	48.2 ± 0.3 (2)
Phragmites australis	1.8 ± 0.2 (2)	1.3 ± 0.1 (2)	1.3 ± 0.1 (2)	1.2 ± 0.1 (1)	48.9 ± 0.5 (2)	49.2 ± 0.8 (2)	47.6 ± 0.3 (2)	48.2 ± 0.2 (2)
Carex vesicaria		1.2 ± 0.1 (2)	1.1 ± 0.2 (2)	0.9 (1)		48.3 ± 1.0 (2)	45.8 ± 4.2 (2)	48.3 (1)
Carex canescens		1.4 ± 0.1 (2)	1.5 (1)	1.2 (1)		50.6 ± 1.9 (2)	47.7 (1)	48.8 (1)
Eupatorium cannabinum		0.7 (1)	1.1 ± 0.1 (2)	0.8 (1)		45.5 (1)	45.9 ± 0.8 (2)	46.2 (2)
Other species	2.1 (1)	1.0 ± 0.2 (2)	0.9 ± 0.5 (2)	0.8 ± 0.1 (2)	45.9 (2)	46.8 ± 0.8 (2)	46.3 ± 0.2 (2)	45.4 ± 0.6 (2)
Whole herbaceous biomass	1.8 ± 0.2 (4)	1.1 ± 0.2 (11)	1.1 ± 0.3 (11)	1.1 ± 0.2 (9)	48.8 ± 1.7 (4)	48.4 ± 1.7 (11)	47.1 ± 1.7 (11)	46.8 ± 1.4 (9)