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# Carbon storage and understory plant diversity in boreal *Larix gmelinii–Carex schmidtii* forested wetlands: A comparison of harvest, fire and draining disturbance

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FOREST MANAGEMENT

## ABSTRACT

**Background:** Forested wetlands are an important factor in carbon (C) sequestration. In this study, we compared the short-term effects (5 years) of three harvest intensities and two wildfire severities, and the mid-term effects (25 years) of four groundwater table depth (WTD) drainage for forestry on ecosystem C storage and understory vegetation structures in Daxing'anling, northeast of China.

**Results:** We found that: Low intensity harvest slightly enhanced ecosystem C storage, whereas moderate- and high-intensity harvest led to significant reductions (33.2-41.6%) in comparison with the control natural forested wetlands stand (274.54 t C·ha$^{-1}$), and light and heavy burn caused the ecosystem C storage significant decreases by 27.8% and 45.2%. As for the drainage for forestry, the ecosystem C storage was higher at the low WTD (316.78 t C·ha$^{-1}$), and diminished significantly by 24.1-28.1% with the increasing WTD on the forested wetland plantation transect. Compared with the control and high intensity harvest stands (8.28 t ha$^{-1}$ yr$^{-1}$, 5.08 t C·ha$^{-1}$ yr$^{-1}$ and 6.48 t ha$^{-1}$ yr$^{-1}$, 3.52 t C·ha$^{-1}$ yr$^{-1}$), significantly higher NPP (net primary productivity, defined by the biomass difference of two measurements) (69.1-83.2%) and annual C sequestration (52.0-78.7%) were observed in the low- and moderate-intensity harvest stands. Significant increases by 48.6% and decreases by 31.5% in NPP or by 52.9% in annual C sequestration were in light and heavy burn stands, respectively. In contrast, the NPP and annual C sequestration (3. 67-10. 34 t ha$^{-1}$ yr$^{-1}$ and 1. 59-4. 87 t C·ha$^{-1}$ yr$^{-1}$) showed a significant increasing trend with increasing WTD, respectively. The understory species diversity indices were generally lower in the harvest and burned stands than the control natural forested wetlands and more pioneer tree species regeneration occurred after the disturbances.

**Conclusion:** Therefore, it seems that low intensity harvest and wildfire could sustain the ecosystem C sink and drainage for forestry is an effect way to restore C sequestration for this forested wetland type.

**Keywords:** carbon sequestration; drainage for forestry; species diversity; selective harvest; wildfire; Daxing'anling

## HIGHLIGHTS

The effects of harvest, fire and drainage for forestry on C storage for forested wetlands of Daxing'anling were compared.
Low-intensity selective harvest caused an increase in total ecosystem C storage and C sequestration.
Drainage for forestry promoted NPP of the forested wetlands ecosystem.

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## INTRODUCTION

The carbon (C) storage of the wetland accounts for about 20% to 25% of the global terrestrial soil C storage, which directly affects the concentration of $CO_2$ in the atmosphere (Lal 2004, Sun 2021). Natural wetlands growing on organic soils are generally atmospheric $CO_2$ absorption sinks with greater standing biomass and productivity (Campbell et al., 2000), therefore wetlands have made an important contribution to global C absorption (Gorham, 1991; Wang et al., 2021). Since the industrial revolution, the global climate has become dry and warm due to the anthropogenic disturbances, such as the harvest, fire and drainage for forestry. Global wetlands loss were at least 33% as of 2009 (Hu et al., 2017), and it has led to net C emissions from global wetlands to the atmosphere (Maltby and Immirzi, 1993; Sun et al., 2011). This indicates the disturbance of anthropogenic activities can indeed have a substantial impact on wetland C sinks, but the extent of the impact and associated mechanisms are still not very clear.

In general, harvesting had a far great effect on ecosystem C due to its effect on the biomass and a weaker effect on soil C (Guo and Gifford, 2002). Harvesting is not primarily aimed at maximizing C sequestration and can increase the radial growth of the remaining trees at the expense of the total biomass (Sobachkin et al., 2005). A scheme of C dynamics after harvest shows the almost immediate C loss that is followed by a slow recovery of the C pool (Mu et al., 2013). Harvesting influences soil C in two contrasting ways: harvest residues left on the soil surface increase the C stock of forest floor and disturbance of the soil structure leads to soil C losses (Jandl et al., 2007). Although soil C changes were noted after harvesting, they diminished over time without a lasting effect. Soil C pools were similar to the uncut stand after 11 years harvesting in a northern forested wetland (Trettin et al., 2011). In the years following harvesting, soil C losses may exceed C gains in the aboveground biomass (Hu et al., 2015), that is, harvesting can turn forests into a C source because soil respiration is stimulated more than photosynthesis (Kowalski et al., 2004). This indicates that the losses of soil C in forested wetlands can be much more than that in upland forests after harvesting, but it can also be restored faster in wetlands than in upland forests.

Studies have noted that fire disturbance has a negative impact on forest C sinks (Pugh et al., 2019). After the fire disturbance, the wetlands may also be transformed from the original C sink into a C emission source (Kayranli et al., 2010). Forest wetlands with both the characteristics of forests and wetlands are one of the main body of the world's terrestrial upland wetlands. However, knowledge about the degree and mechanism of fire disturbance on its C sink is still lacking. Existing research mainly seek to the effect of fire disturbance on forest wetland C sinks and greenhouse gas emissions in the temperate Xiaoxing'anling wetland (Zhou et al., 2012; Wang et al., 2021), whereas fire disturbances on the impact of ecosystem C storage has not been hardly reported yet in the boreal Daxing'anling.

Existing findings have documented that the high groundwater table has severely restrained the tree growth in the peatland (Dearborn et al., 2021). Therefore, northern countries (e.g. Sweden, Finland, the Baltic countries and northwestern Russia) have long used drainage to increase the productivity of forest wetlands, and even drainage for forestry has become one of the main types of land use in these countries (Paavilainen and Päivänen, 1995). In recent years, some European scholars have successively carried out studies on the impact of drainage on the C balance and soil C storage of northern peatlands and their dynamics. The results show that the drainage for forestry can be converted into C emission sources or still maintain C sinks and mainly depends on the type of habitat and climatic conditions (Potapov et al., 2019). Wetland drainage practices have also been carried out in the northeast of China since the 1980s and the size of wetland drainage for forestry in the Daxing'anling is about 40,000 $km^2$ (Mu et al., 2007). Several studies have shown that wetland drainage can indeed increase the productivity and storage of forest stands (the middle and upper habitats of the environmental gradient); however, due to the drop in groundwater table depth and temperature rise after drainage, the decomposition process of soil peat is accelerated, and consequently the wetland peat layer has completely or partially disappeared (Mu et al., 2007; Sun et al., 2011). In terms of the ecosystem as a whole, it is still unclear whether the drainage afforestation plays a role of C sink or C source on a longer time scale.

In boreal ecosystems, understory communities are crucial both in terms of biodiversity and of ecosystems processes, for instance productivity, nutrient cycling, and soil microclimate regulation (Hart and Chen 2008; Jean et al., 2019). Other studies also documented that understory accounted for 14% of total NPP in forested wetlands (Campbell et al., 2000; Nelson et al., 2021). Studies found high severity fires consumed much of soil organic layer in comparison with low severity fires, and has been linked this phenomenon with understory community compositions (Préfontaine and Jutras, 2017). Whilst different harvest or fire intensities have great influences on tree regeneration, trees that remain in the forest may have been able to tolerate contexts associated with post-harvest conditions, such as the enhanced light and altered soil humidity, or remain protected in areas where trees have regenerated (Paquette et al., 2016). Given the comparatively low levels of ground level disturbed by harvest in relation to wildfire, post-harvest plots in general lack the suitable seedbeds for conifer species regeneration caused by fire (Lafleur et al., 2011). Early understory communities after harvest are composed of a variety of species, ranging from broad spectrum species or light demanding species which germinate from surviving belowground to species that have efficient long-distance dispersal strategies (Dyrness, 1973). On the contrary, mechanical disturbances associated with selective harvesting do not entirely remove understory shrub and herb, eliminate forest floor and saw dust, or expose large areas of mineral soil (Nguyen-Xuan et al., 2000; Lafleur et al., 2018). As time went by, initial differences in understory species composition between harvested and burned sites incline to disappear with the canopy closure since the species were mostly shade intolerant species (Rydgren et al., 2004; Jean et al., 2019). This assembly probably reflects that boreal understory communities are dominated by resilient species with reproductive strategies that enable them to survive through or recolonize following disturbances (Jean et al., 2019). However, the differential effects of harvest and wildfire on understory vegetation structural diversity and regeneration are less well known in boreal forested wetlands in Daxing'anling.

In this study, we compared the three types of disturbance, i.e., selective harvest (three harvest intensities), natural wildfire (two burned intensities) and drainage for forestry (four groundwater table depths) on C storage and early understory vegetation structure of forested wetlands in Daxing'anling, especially between the selective harvest and natural wildfire disturbance. Specifically, we evaluated whether C pool, NPP (net primary productivity) and understory species diversity significantly varied according to disturbance type and severity and we explored underlying causal mechanisms. We expect that low intensity harvest would increase the C storage and enrich the understory vegetation diversity because of the reduced stand density and more light intake in the stands.

## MATERIAL AND METHODS

### Site description

The study of selective harvest and wildfire effects was carried out in Nanwenghe National Nature Reserve, Daxing'anling, Heilongjiang Province, northeast China (51°05′-51°39′N, 125°07′-125°50′E). The location of the study area is shown in Figure.1. The altitude is 500-800 m above sea level. The soil type is predominently peatland soil and a dark brown forest soil. This region belongs to a continental monsoon climate with an average annual temperature of -3$^{o}$C and an average annual precipitation of 500 mm. The annual frost-free period is 90-100 days. The first frost starts in mid-September, and the second frost lasts until mid-May of the following year. The overstory tree species is dominanted by Dahurian larch (*Larix gmelinii*) and other tree species are white birch (*Betula platyphylla*), aspen (*Populus davidiana* Dole) and Scots pine (*Pinus sylvestris* L. var. *mongolica* Litv.). The understory and ground dominate species are blueberry (*Vaccinium angustifolium*), *Carex schmidtii*, *Betula fruticosa*. More detailed information can refer to our previous study (Mu et al., 2013).

The study of drainage for forestry effects was located in Guli Forest Farm, Songling Forestry Bureau of Heilongjiang Province, (51°09′-51°24′N, 123°29′-125°50′E) in the southeast of Daxing'anling, northeast China (Figure.1). It has the continental monsoon climate with an average annual rainfall of 600 mm. The zonal soil in this area is gray forest soil, and the low-lying land contains hidden meadow soil and swamp soil. The soil permafrost layer is distributed in island shape in some areas, while the seasonal frozen layer is widespread in the whole area. The zonal vegetation is cold-temperate coniferous forests. Many types of natural swamp wetlands are distributed in wide valleys. These wetlands follow the transitional environmental gradient from the typical grassy wetlands to the highland forests, and the micro-topography changes form a degree of accumulation of water. The water environment gradient in the transition zone gradually shortens the accumulation period, decreases the water level, and thins the peat layer. Based on the groundwater table depth gradient, there distributed different types of vegetation by typical herbaceous swamps, shrub swamps, and *Alnus sibiricavar. Hirsute* forested swamp, white birch forested wetlands and larch forest wetlands, respectively.

### Experimental design

Harvest: The size of 20 m×30 m plots were set up. The three selective harvest intensities were classified according to the volume percentage removed (25%, 35% or 50%) and were written as low intensity harvest, moderate intensity harvest, and high intensity harvest, respectively. Each harvest intensity treatment was replicated three times and in total 9 plots were established. The harvest activity took place in the autumn of 2006 and more harvest methods can be found in our previous study (Mu et al., 2013).

Fire: Three 20 m × 30 m plots of larch forested wetlands with light fire (ground fire, tree burned death rate was less than 30% of the total stand volume) and three 20 m × 30 m plots with heavy fire (crown fire, tree death rate was larger than 70% of the total stand volume) were established. The two types of burned plots in total 6 plots will be referred to be as lightly burned and heavily burned (Table 1). The fire naturally happened in 2006 and all the burned trees were left standing in the stands.

Drainage: Wetland drainage for forestry was conducted in the early 1980s, and *Larix gmelinii* (planting density with 3,300 trees ha$^{-1}$) was planted. The larch forested wetlands has approached 25 years of age when the study was conducted. The growth status of general stands was good, and the understory vegetation was relatively sparse due to the limited light transmitted from the fully stocked canopy. Along the increasing groundwater table depth (WTD) gradient, a 200 m × 400 m sample zone was set up in the transition zone of the larch forested wetland plantations formed by drainage afforestation, and 3 standard plots of 20 m × 30 m in each sample zone at intervals of 100 m and a total of 12 plots. The four groundwater table depth plots were 0-100 m in the lower part, 100-200 m in the middle-lower part, 200-300 m in the middle-upper part, and 300-400 m in the upper part, by distance to the drainage ditch, which were referred to as low WTD, low-medium WTD, medium WTD and high WTD, respectively (Table 1).

Control: Three undisturbed plots were established in the neighouring harvest and fire locations as control. The control stands, selective harvested and burned stands were all natural forested wetlands and undrained. The graphical experiment design of selective harvest, fire and drainage for forestry was illustrated in Figure 1. Their stand and plot information were shown in Table 1.

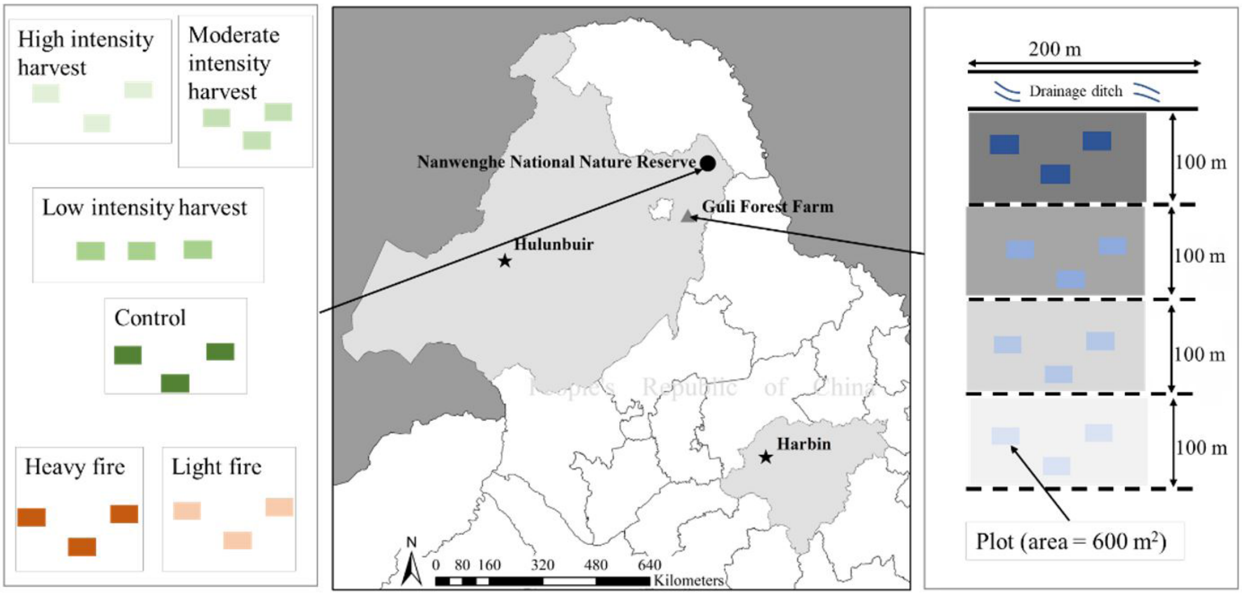


**Figure 1.** The location of study area relative to the city of Harbin, Heilongjiang Province, China. The graphical design of the three selective harvest intensities, two natural wildfire severities and drainage for forestry along the increasing groundwater table depth by distance to the drainage ditch.

**Table 1.** Stand and plot variables in harvest, fire and drainage for forestry treatments.

| Treatment | Tree species | Density (trees·ha$^{-1}$) | Basal area (m$^2$·ha$^{-1}$) | Mean d.b.h (cm) | d.b.h range (cm) | Overstory canopy cover (%) | Groundwater table depth (cm) |
|---|---|---|---|---|---|---|---|
| CK | Lg | 1753(210) | 26.1(4.6) | 12.5 | 4.8-27.7 | 80 | 40-50 |
| | Bp | 618(90) | 8.9(1.5) | 14.8 | 6.4-34.4 | | |
| LH | Lg | 1179(142) | 25.0(5.9) | 16.5 | 4.2-33.9 | 70 | 50-60 |
| | Bp | 406(63) | 3.3(0.5) | 11 | 5.2-18.8 | | |
| MH | Lg | 1107(98) | 18.9(4.8) | 13.3 | 5.1-34.9 | 60 | 50-60 |
| | Bp | 437(189) | 4.0(0.6) | 10.6 | 4.0-21.1 | | |
| HH | Lg | 750(153) | 17.5(7.6) | 15.3 | 5.2-35.8 | 50 | 50-60 |
| | Bp | 218(62) | 1.3(0.2) | 8.9 | 5.0-13.1 | | |
| LB | Lg | 1300(145.3) | 21.8(1.1) | 12.7 | 4.0-37.2 | 45 | 50-60 |
| | Bp | 355.6(111) | 7.0(3.3) | 13.1 | 4.5-25.9 | | |
| HB | Lg | 1438.9(386.3) | 25.7(3.6) | 14.1 | 4.0-37.1 | 10 | 50-60 |
| | Bp | 333.3(70.7) | 5.1(1.7) | 13.6 | 6.5-18.8 | | |
| Low WTD | Lg | 143(25) | 3.6(1.1) | 3.1 | 2.9-4.2 | 15 | 16-20 |
| | Bp | 1157(189) | 7.2(1.8) | 3.8 | 3.2-4.5 | | |
| Low-medium WTD | Lg | 2328(321) | 10.8(2.1) | 7.7 | 6.8-10.5 | 90 | 25-35 |
| | Bp | 72(8) | 1.9(0.2) | 7.4 | 7.1-8.9 | | |
| Medium WTD | Lg | 2744(287) | 3.5(1.1) | 11.2 | 10.1-16.8 | 95 | 40-45 |
| | Bp | 56(9) | 1.8(0.1) | 4.9 | 4.0-5.6 | | |
| High WTD | Lg | 2597(143) | 17.9(3.6) | 12.3 | 11.2-25.0 | 95 | 50-60 |
| | Bp | 53(10) | 1.1(0.3) | 6.5 | 5.6-7.1 | | |

CK: control; LH: low-intensity harvest; MH: moderate-intensity harvest; HH: high-intensity harvest; LB: lightly burned; HB: heavily burned; WTD: groundwater table depth; Lg: *Larix gmelinii*; Bp: *Betula platyphlla*; d.b.h: diameter at breast height at 1.3 m height. The data in the table are the mean and standard deviation in the parentheses.

### Field sampling

Vegetation: with regards to overstory vegetation in the three types of disturbances, the d.b.h of all trees were measured in each plot in May (at the start of the growing season) and October (at the end of the growing season), 2011, respectively. In August, 2 tree species, i.e., *Larix gmelinii*, *Betula platyphylla* were sampled when their biomass reached its maximum. This was done both in natural forested wetlands and forested wetland plantations. Biomass allometric equations for the components of each tree species were established by destructive stem analysis and the more detailed methods can be seen in the previous study (Mu et al., 2013). The standing biomass was estimated by the allometric equations and their NPP (net primary productivity) was obtained by comparing the biomass difference in May and October of 2011. As for the understory vegetations, within each 20 m×30 m plot, six 5 m×5 m shrub subplots and six 1 m×1 m herb quadrats per subplot were randomly surveyed. The shrubs were destructively harvested by separating into aboveground and belowground parts to determine its biomass. The herbs for each treatment were clipped at ground line. Forest floor litter was sampled using nine 0.5 m×0.5 m subplots randomly located within each 20 m×30 m plot (Mu et al., 2013). All samples were transported back to the laboratory and dried at 75°C to constant weight. Because all shrub species were harvested or burned in 2006, all current shrub biomass is 5 years old. NPP of the shrub layer was obtained by dividing the shrub biomass by its mean age (5 years) (Thormann and Bayley, 1997; Giese et al., 2003), whilst the NPP of the herb layer can be done directly through its biomass. Since there were hardly any shrubs grown in the forested wetland plantations, shrub C storage and NPP were not accounted in this study and the herb NPP was calculated from its biomass directly.

Soil: The soil sampling and process methods were the same as the previous study (Mu et al., 2013). Five points were systematically located in each plot. At each point, fifteen 100 $cm^3$ cores and fifteen soil samples (approximately 500 g each) were collected for determining soil bulk density and C contration from 0-10 cm, 10-20 cm, 20-30 cm, 30-40 cm, and 40-50 cm soil depth, respectively. The samples for measuring soil bulk density were dried for 24 hours, and the samples for measuring soil C were air-dried naturally. The biomass and soil samples were ground in a Wiley mill to pass through a #100 mesh screen and then their C concentration was measured with a Multi N/C 3000 analyzer with 1500 Solids Module (Analytik Jena AG, Germany) (Mu et al., 2013). The vegetation C storage was determined by biomass multiplied by their responding C concentrations. The soil organic C (SOC) storage was derived from the soil bulk density, SOC concentration and sampled depth (Guo and Gifford 2002), using equation [1].

$$C_t = \mathrm{SBD} \times C_c \times D_s \times 10 \qquad [1]$$

where SBD is the soil bulk density (g $cm^{-3}$), $C_c$ is the SOC concentration (g $kg^{-1}$), and $D_s$ is the soil sampled depth (cm).

Understory species diversity: Since the very limited number of understory shrub and herb species in drainage for forestry plots, the understory plant species diversity was only examined in selective harvest and fire stands. The shrub and herb species were identified, and their number as well as height and coverage were measured. To calculate the understory shrub and herb species diversity index, equations (2-6) are applied as follows:

Importance value of species ($P_i$) (Zheng et al., 2010)

$$P_i = (Ra + Rb + Rc)/3 \qquad [2]$$

Margalef richness index (Zheng et al., 2010)

$$\mathrm{Margalef} = (S\text{-}1)/\ \ln N \qquad [3]$$

Shannon-Wiener diversity index (Hill et al., 2003)

$$\text{Shannon-Wiener} = -\textstyle\sum_{i=1}^{s}(P_i \ln P_i) \qquad [4]$$

Pielou evenness index (Hill et al., 2003)

$$\mathrm{Pielou} = \mathrm{H}/\ln S \qquad [5]$$

Simpson dominance index (Hill et al., 2003)

$$\mathrm{Simpson} = 1\text{-}\textstyle\sum(P_i \ \ln P_i) \qquad [6]$$

where *Ra* is the relative abundance, *Rb* is the relative biomass, *Rc* is the relative coverage, *S* is the number of species in the sample, *N* is the sum of the individual numbers of all species in the sample.

### Statistical analysis

Statistical analyses and comparisons between the reference control, post-harvest, post-fire and drainage for forestry treatments were performed using SPSS Version 26 (SPSS Inc., Chicago, IL, USA) and Origin 2019 software. Pairwise comparisons among disturbances were performed using analysis of variance (ANOVA) followed by least-significant-difference tests. In all statistical analyses, the level of significance was set at $P < 0.05$.

## RESULTS

### Ecosystem C Pools

Selective harvest and fire caused significant decreases of the vegetation biomass by 8.7-34.0% and by 35.5-96.4% than in the control stand and these were largely attibuted to significant reductions of the tree biomass (Table 2). Both the vegation and tree biomass showed a decreasing tendency with increasing harvest and burned intensity. In contrast, drainage for forestry had significantly improved the vegetation biomass and showed an increasing trend with increasing WTD, and this mainly resulted from significant increase in tree biomass. Significant effects on shrub and herb biomass were seen only at moderate intensity harvest, however, the differences among the harvest and burned stands were not significant. In addition, the herb biomass decreased with the increasing WTD. The litter biomass was detected significantly lower in moderate intensity harvest and heavy fire stands than that of the 7.33 t·$ha^{-1}$ in the control stand, while the litter biomass showed an increasing tendency with the increasing WTD (Table 2).

**Table 2.** Biomass (t·ha⁻¹) of different components in *Larix gmelinii-Carex schmidtii* forested wetlands under different treatments.

| Treatment | Components | | | | |
|---|---|---|---|---|---|
| | Tree | Shrub | Herb | Vegetation | Litter |
| CK | 194.32(3.21)a | 1.29(1.08)a | 0.97(0.48)a | 204.71(1.71)a | 7.33(1.76)a |
| LH | 179.49(13.15)b | 0.61(0.22)a | 2.19(0.22)ab | 186.97(7.77)b | 4.68(1.81)ab |
| MH | 135.96(8.64)c | 4.83(1.44)b | 3.45(1.29)b | 148.62(3.51)c | 4.38(1.43)b |
| HH | 125.55(11.45)c | 2.01(0.65)a | 2.57(0.34)ab | 135.03(7.72)c | 4.90(0.64)ab |
| LB | 127.30(19.40)c | 1.10(0.50)a | 2.80(1.50)b | 132.10(20.30)c | 5.60(2.90)ab |
| HB | 1.80(0.60)d | 1.80(0.90)a | 3.70(0.80)b | 7.30(1.20)d | 3.50(1.50)b |
| Low WTD | 4.21(0.22)A | 9.54(3.04)A | 0.95(0.11)A | 14.70(3.05)A | 3.52(0.54)A |
| Low-medium WTD | 107.61(2.33)B | 0.00(0.00)B | 0.35(0.01)B | 107.96(2.36)B | 6.89(1.02)B |
| Medium WTD | 111.22(2.24)B | 0.00(0.00)B | 0.24(0.04)B | 111.46(2.21)B | 7.84(0.98)B |
| High WTD | 134.35(1.15)C | 0.00(0.00)B | 0.11(0.01)B | 134.45(1.14)C | 10.02(1.04)C |

CK: control; LH: low-intensity harvest; MH: moderate-intensity harvest; HH: high-intensity harvest; LB: lightly burned; HB: heavily burned; WTD: groundwater table depth. The data in the table are the mean and standard deviation in the parentheses. Regarding each component, different lowercase letters indicate significant differences between treatments at α=0.05 based on the least-significant-difference tests; different uppercase letters indicate significant differences between treatments among different groundwater table depth at α=0.05 based on the least-significant-difference tests.

After biomass was converted to C storage, C storage in tree, shrub, herb and vegetation biomass in harvested and burned plots showed a consistent pattern with their respective biomass (Table 3). Comparised with 274.54 t C·ha$^{-1}$ of the ecosystem C pools in the control reference, low intensity harvest promoted the ecosystem C pools slightly by 6.7%, while the other two harvest and burned intensities reduced the ecosystem C pools by 33.2-41.6% and 19.7-39.1%, respectively (Figure 2). Soil C pools accounted for the largest proportion of ecosystem C pools for each treatment (56.2-97.6%), followed by tree C pools (27.6-40.2%, and 0.4% in heavily burned stands), whereas both litter (0.7-1.3%) and understory C pools (0.4-2.3%) were very little. Litter C storage significantly reduced only in heavily burned stands and no significant difference was documented between harvested and burned plots. This was due to the significant decline of mineral soil C and tree pools in moderate- and high-intensity harvest and light- and heavy-burn stands, thereby the ecosystem C pools reduced significantly 5 years following harvest and fire.

Drainage afforestation had significantly improved the vegetation and litter C pools and exhibited an increasing tendency with increasing WTD, while the soil C and ecosystem C pools showed an opposite trend. Strikingly, no significance was detected between the low-medium, medium and high WTD in soil and ecosystem C pools (Figure.2). Hence, the decline of the ecosystem storage was mostly driven by the decrease of soil C storage which comprised 71.8-97.5% of the ecosystem C storage in the forested wetland plantations.

## NPP and C sequestration capacity

The NPP and annual C sequestration (ACS) were significantly higher with the low-, and moderate-intensity harvest and lightly burned stands, relative to the high-intensity harvest and control stands. However, the NPP and ACS only significantly declined in the heavily burned stands 5 years following fire, which was attributed to the significant decrease in tree. Drainage for forestry had significantly improved the NPP and ACS and showed an increasing trend with the increasing WTD, and this mainly resulted from significant increase in NPP and ACS in trees (Figure 3). There was no significance between the low-medium and medium, and between the medium and high WTD. Hence, drainage for forestry only had significant impacts on the low but not medium or high WTD habitats.

NPP or ACS of tree, shrub and herb showed slight differences among three selective harvest and two fire treatments. NPP or ACS of tree in low intensity harvest stands was detected significantly different from that 5.25 t·ha$^{-1}$·yr$^{-1}$ or 3.00 t C·ha$^{-1}$·yr$^{-1}$ in the control stand. NPP or ACS of shrub increased with moderate intensity harvest relative to the control stand (0.26 t·ha$^{-1}$·yr$^{-1}$ or 0.12 t C·ha-1·yr$^{-1}$). However, NPP or ACS of herb were found significant increases in moderate- and high-intensity harvest and light- and heavy-burn stands in comparison with the control (0.97 t·ha$^{-1}$·yr$^{-1}$ or 0.40 t C·ha$^{-1}$·yr$^{-1}$). Thus, the increase in NPP and ACS was largely due to a rise in tree with low intensity harvest and in understory shrub and herb with moderate intensity harvest, respectively.

**Table 3.** Carbon storage (t C·ha$^{-1}$) in various biomass components of *Larix gmelinii-Carex schmidtii* forested wetland with different treatments.

| Treatment | Component | | | | | | |
|---|---|---|---|---|---|---|---|
| | Tree | Shrub | Herb | Vegetation | Litter | Soil | Total |
| CK | 95.14(1.59)a | 0.62(0.42)a | 0.39(0.16)a | 99.61(1.47)a | 3.46(0.79)a | 174.93(37.19)a | 274.54(39.70)a |
| LH | 81.02(5.98)b | 0.27(0.09)a | 0.88(0.08)ab | 84.21(1.90)b | 2.04(0.84)ab | 208.82(26.28)a | 292.93(29.34)a |
| MH | 64.42(4.12)c | 2.29(0.70)b | 1.46(0.60)b | 70.18(0.78)c | 2.01(0.66)ab | 90.14(59.02)b | 161.98(55.04)b |
| HH | 57.03(5.29)c | 0.92(0.29)a | 1.06(0.12)ab | 61.16(0.67)d | 2.15(0.19)ab | 122.25(42.56)b | 183.39(46.26)b |
| LB | 62.42(10.32)c | 0.51(0.20)a | 1.01(0.62)b | 63.54(8.32)cd | 2.35(1.21)ab | 154.62(1.23)a | 220.41(15.3)c |
| HB | 0.72(0.31)d | 0.81(0.40)a | 1.32(0.81)b | 2.65(0.61)e | 1.50(0.71)b | 163.35(2.86)a | 167.45(22.7)b |
| Low WTD | 1.99(0.35)A | 3.25(0.86)A | 1.25(0.91)A | 6.49(1.35)A | 1.61(0.54)A | 308.68(10.35)A | 316.78(8.49)A |
| Low-medium WTD | 46.73(5.34)B | 0.00(0.00)B | 1.78(0.09)B | 48.51(2.56)B | 3.21(1.02)AB | 188.91(2.56)B | 240.16(5.24)B |
| Medium WTD | 50.35(4.36)B | 0.00(0.00)B | 0.31(0.05)B | 50.66(2.85)B | 3.62(0.98)B | 176.87(3.21)B | 229.41(4.75)B |
| High WTD | 59.39(6.32)C | 0.00(0.00)B | 0.56(0.02)B | 59.95(0.51)C | 4.69(1.04)C | 163.03(2.41)B | 227.68(2.63)B |

CK: control; LH: low-intensity harvest; MH: moderate-intensity harvest; HH: high-intensity harvest; LB: lightly burned; HB: heavily burned; WTD: groundwater table depth. Data are means followed by standard deviations in the parentheses. For each component, values with the different small letters denote significant difference among control, harvest and fire treatments at α=0.05 based on the least-significant-difference tests; values with the different capital letters denote significant difference among different groundwater table depth treatments at α=0.05 based on the least-significant-difference tests.

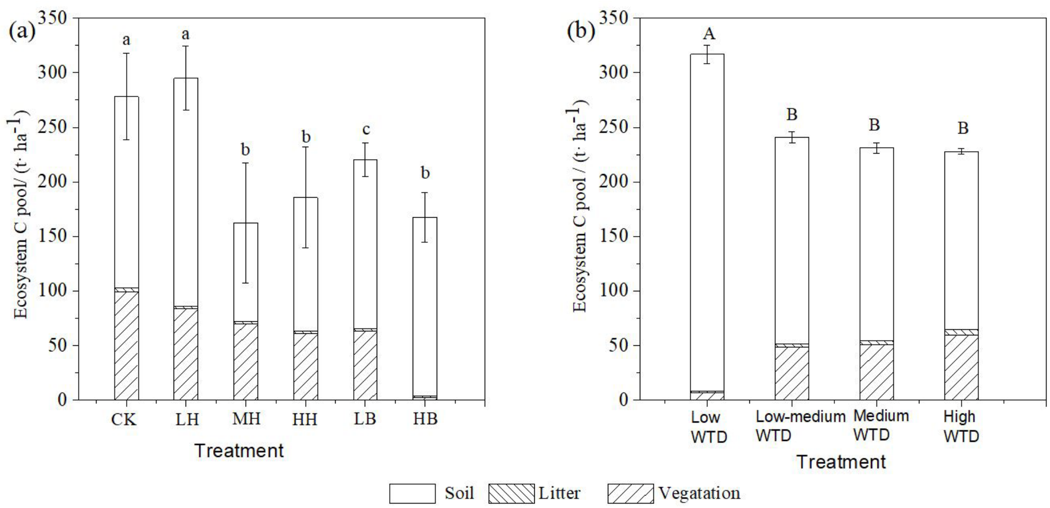


**Figure 2.** Ecosystem carbon pools in *Larix gmelinii-Carex schmidtii* forested wetland with control, harvest, fire and drainage for forestry treatments. The carbon pool and component (a) by control, harvest and fire treatments and (b) by four groundwater table depth (WTD) drainage for forestry treatments. Different lowercase letters indicate significant differences among control, harvest and fire treatments at α=0.05 based on the least-significant-difference tests; different uppercase letters indicate significant differences among different WTD treatments at α=0.05 based on the least-significant-difference tests. The error bars represent standard deviation. The legend "Vegetation" refers to the sum of tree and understoy shrub and herb.

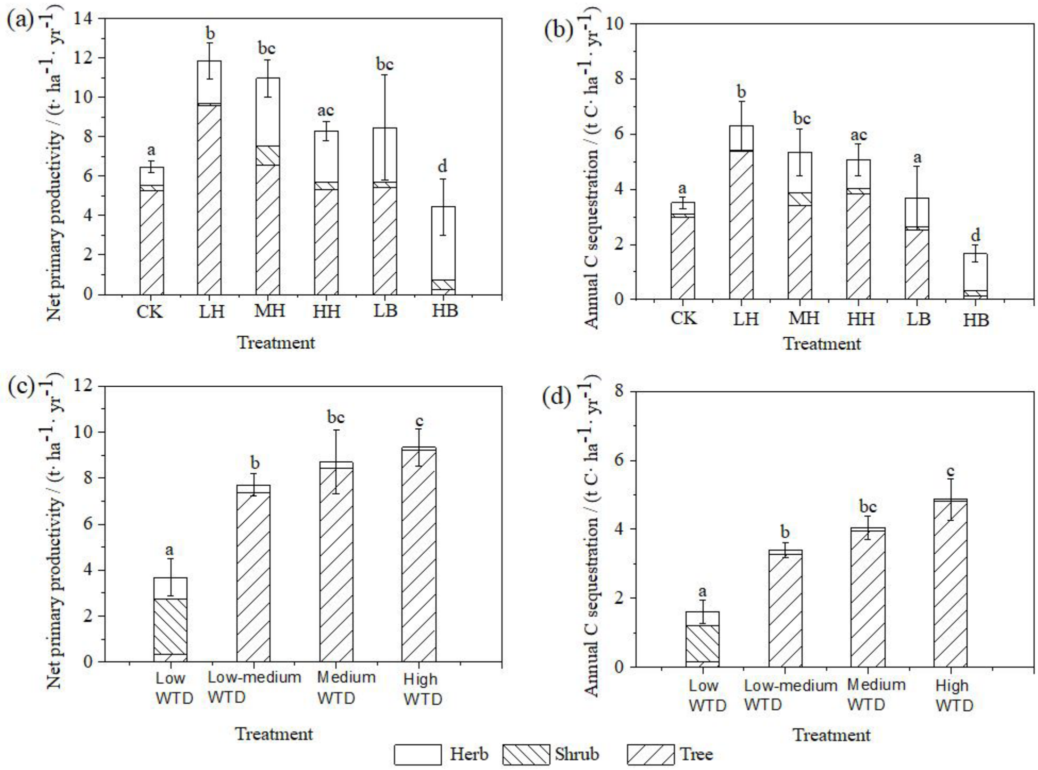


**Figure 3.** The net primary productivity (NPP) and annual carbon sequestration at control, harvest, fire and drainage for forestry treatment. (a) NPP of various components at control, harvest and fire treatment plots. (b) ACS of different components in herb, shrub and tree layers at control, harvest and fire treatment plots. (c) NPP of various components at drainage for forestry treatment plots. (d) ACS of various components in vegetation at drainage for forestry treatment plots. Values with the different letters demonstrate significant difference among treatments at α=0.05 based on the least-significant-difference tests. The error bars represent standard deviation.

### Understory species diversity and regeneration

Some differences were observed in understory species diversity among control, harvested and burned stands. The species diversity indices were generally lower in the harvest and burned stands than the control natural forested wetlands (Table 4). With respect to the Margalef and Shannon-Weiner, the shrub layer significantly decreased in low and moderate-intensity harvest, but not Simpson and Pielou. The herb layer species diversity decreased in harvest and wildfire stands, and especially Margalef and Pielou reduced significantly in moderate intensity harvest stands. In contrast, Pielou of the shrub layer increased significantly in low and high-intensity harvest stands, however, there were no significant differences between the harvest plots. The species regeneration and its number increased with the harvest and burn intensity. More pioneer light demanding tree species (*Salix raddeana* and *Populus davidiana*) occurred in the burned stands than in harvest stands.

## DISCUSSION

### Ecosystem C storage

In the low intensity harvest stands, the ecosystem C storage showed a slight increase by 6.7%, which was mostly caused by increases in the soil C storage. By contrast, the ecosystem C storage declined significantly by 33.2-41.6% with moderate- and high-intensity harvest and this was mainly driven by both vegetation and soil C storage. The result is in line with the findings that that the ecosystem C storage generally decreased (21.0-57.1%) with increasing thinning intensity in northern hardwoods (Powers et al., 2011). This indicates that low intensity harvest is more probably to raise or maintain the ecosystem C storage in relation with the other two harvest intensities for *Larix gmelinii–Carex schmidtii* forested wetlands. Like the moderate- and high-intensity harvest, both of the two fire severities significantly reduced the ecosystem C storage and the reduction increased with the fire severity. This result is similar to the study of fire severity effect on C pools in the same area (Hu et al., 2015). The main reason is due to the significant reduction of the largest fraction of C storage of tree since the fire disturbance burns most of the trees and significantly reduces its C storage. As a result, its vegetation C storage was significantly reduced. One study found the ecosystem C pools recovered to the pre-fire state after 10 years in Alaska (Houle et al., 2018), but another simulation study in the same geographic area suggested that ecosystem C storage was significantly reduced by fire and harvest and the long-term (60–150 years) effects of fire and harvest on C stocks were greater than the short-term (0–20 years) effects (Huang et al., 2018). Given the inherently variables and stochastic nature of disturbances and vegetation recovery over long time periods, the long-term effect is needed to track the recovery status in the harvested and burned stands.

**Table 4.** The understory shrub and herb species diversity index and species regeneration of in *Larix gmelinii-Carex schmidtii* forested wetlands with harvest and burn treatments.

| Treatment | Margalef species richness index | Shannon-Weiner diversity index | Simpson dominant index | Pielou evenness index | Species regeneration (species and number, stems plot$^{-1}$) |
|---|---|---|---|---|---|
| Shrub layer | | | | | |
| CK | 0.71(0.04)a | 0.91(0.05)a | 0.55(0.06)ab | 0.82(0.08)a | Bp 6, Lg 1 |
| LH | 0.37(0.08)b | 0.66(0.08)bc | 0.47(0.05)a | 0.95(0.15)b | Bp 8, Qm 1 |
| MH | 0.31(0.05)b | 0.61(0.05)c | 0.42(0.07)a | 0.88(0.08)ab | Sr 1, Bp 12 |
| HH | 0.59(0.09)ac | 1.08(0.21)a | 0.66(0.20)b | 0.98(0.09)b | Sr 15, Bp 22 |
| LB | 0.54(0.07)c | 0.99(0.22)a | 0.60(0.05)b | 0.89(0.05)ab | Lg 7, Bp 34, Qm 3, Pd 22, Sr 3 |
| HB | 0.68(0.08)ac | 1.02(0.16)a | 0.62(0.04)b | 0.93(0.03)b | Lg 10, Bp 71, Qm 3, Pd 24, Sr 16 |
| Herb layer | | | | | |
| CK | 1.29(0.20)a | 1.56(0.26)a | 0.78(0.03)a | 0.97(0.11)a | |
| LH | 1.17(0.15)a | 1.49(0.20)a | 0.76(0.05)a | 0.93(0.10)ab | |
| MH | 0.98(0.14)b | 1.43(0.15)a | 0.72(0.07)a | 0.89(0.04)b | |
| HH | 1.20(0.05)a | 1.53(0.12)a | 0.74(0.15)a | 0.86(0.10)b | |
| LB | 0.86(0.07)b | 1.23(0.13)b | 0.69(0.06)a | 0.89(0.08)b | |
| HB | 1.20(0.11)a | 1.53(0.05)a | 0.74(0.05)a | 0.86(0.07)b | |

CK: control; LH: low-intensity harvest; MH: moderate-intensity harvest; HH: high-intensity harvest; LB: lightly burned; HB: heavily burned. The data in the table are the mean and standard deviation in the parentheses. Lg: *Larix gmelinii*; Bp: *Betula platyphlla*; Pd: *Populus davidiana*; Sr: *Salix raddeana*; Qm: *Quercus mongolica*. Different lowercase letters indicate significant differences among control, harvest and fire treatments at α=0.05 based on the least-significant-difference tests.

The ecosystem C storage after drainage for forestry showed a decreasing trend with increasing the WTD. This is consistent with the existing results that drainage for forestry may turn northern peatlands into C emission sources (Mayer et al., 2020). The reason is that after drainage for forestry the degree of flooding is reduced, the soil physical and chemical properties have changed greatly, and the decomposition rate of peat and organic matter has accelerated (Zhang et al., 1996; Mu et al., 2007). Apart from that, leaching losses or lateral transport of C from the ecosystem to the draining ditch water would lead to the reduction of C after drainage (Nieminen et al., 2017). All of these processes significantly reduced the dominant position of the the ecosystem C storage (24.2-28.1%), although the vegetation C storage has increased with the increasing WTD. Thus it is necessary to take dissolved organic C exports from drained peatlands into account in the future study. Considering soil C storage accounts for the largest fraction of the ecosystem C pools (71.6-97.5%), so drainage for forestry after 25 years generally reduces the C storage. Compared with the average C storage of forest ecosystems in China (258.83 t C ha$^{-1}$) (Guohua et al., 2000), the ecosystem C storage of the forested wetland plantations after 25 years is slightly lower except for the low WTD (316.78 t C ha$^{-1}$) habitat. Therefore, in the Daxing'anling forested wetland plantations, drainage for forestry in the medium and high WTD habitats can reduce C storage but can still maintain a relatively high level, while the lower WTD habitats should maintain its natural grass wetland state to play its role as a C sink.

The understory shrub and herb C storage (96.0-271.3%) significantly improved with moderate- and high-intensity harvest and two fire severities in the forested wetlands studied, which is similar to the research that clear cutting enhanced the understory vegetation C storage in northern forested wetlands (Gale et al., 1998; Trettin et al., 2011). This could be explained by the increased availability and use of light, soil moisture and nutrients in the understory following harvest and fire (Jean et al., 2019). Taken together, these results suggest that understory vegetation plays a critical role in maintaining nutrients in the early stage of stand development (Wang et al., 2021). The litter C pool exhibited a decreasing tendency with the harvest and burned intensity. The two main reasons are as follows: first, harvest and burn reduced the litterfall inputs to forest floor and consequently the litter C storage decreased; second, harvest and burn raised air and soil temperature, thus promoting the litter decomposition process (Trettin et al., 1996; Kimble et al., 2002). Since the burned dead trees were left standing rather than taken away from the forest, they could increase the litter input and return to the nutrient cycling in the long run.

After drainage for forestry, the vegetation C storage along the WTD showed a significant increase. This may be attributed to that the lower WTD still maintains a high water level due to the low terrain, water accumulation is more serious resulting in the slow growth of larch, and its litter C storage is the lowest. As the terrain gradually rises, the WTD and accumulation of water amount gradually reduces and the temperature gently rises, thus allowing the habitat more suitable for the rapid growth of larch (Zhang et al., 1996; Mu et al., 2007). In the middle and upper WTD habitats of the transect, the terrain is further elevated, and the drainage effect reduces the degree of flooding (Stenberg et al., 2018). Accordingly, the growth of larch is accelerated and the amount of litter produced is further increased. Thus, the litter C storage increased significantly along the WTD and this could be attributed to more aboveground tree biomass and annual defoliation of larch. Another reason is that no forest management in the past several years, thus leading to the low light environments under the canopy and limiting the appearance of shrubs and herbs.

Soil C ranging from 50 to 1300 t C $ha^{-1}$ comprises the biggest C storage in northern forested wetlands (Armentano and Menges 1986). Timber harvest for wood products or natural fire could fundamentally determine soil C pools (James and Harrison 2016; Mayer et al., 2020). Our findings suggest that low intensity harvest helps to improve or maintain its soil C storage, while the moderate- and high harvest decline the soil C storage. Significant reductions were also noted in forested wetland soil C 2-5 years after harvest (Trettin et al., 1992; Gutenberg et al., 2019). This could result from increased mineralization of organic matter due to changes in soil temperature, moisture and aeration caused by harvesting (Trettin and Jurgensen, 2002; Gutenberg et al., 2019). But soil C storage would accumulate again with increasing litter input and recover within 11 years in post-harvest forest wetlands (Trettin et al., 2011). This is seen in two burned stands that soil C storage had recovered with no significant difference with the control stands, and the reason could be that the litter was burned and returned to the soil C storage.

Drainage for forestry not only changed the distribution pattern of soil C storage in the forested wetland plantations along the WTD transect, but also significantly reduced the soil C storage. This coincides in the conclusions that drainage for forestry or drainage cultivation reduces soil C storage (Gutenberg et al., 2019; Mayer et al., 2020). It may be that drainage for forestry has shortened the period and amount of water accumulation and improved the micro-topography leading to increase in soil temperature, humidity and aeration conditions, consequently enhancing the decomposition of microorganisms and the decomposition process of peat and litter (Mu et al., 2007). The mineralization process of soil organic matter gradually transforms the peat layer into a soil layer (Jenkinson et al., 1991; Zhang et al., 1996). Lastly, all the processes above mentioned would promote the emissions of greeenhouse gases which have a high value of the global warming potential, thus drainage for forestry would cause the temperature increase from this point of view. Compared with the similar latitude drainage disturbance in northeast China, drainage reclamation caused the loss of soil organic C in the Sanjiang Plain wetlands by more than 90% (Song et al., 2012), while drainage for forestry in the Daxing'anling reduced the soil C storage of this forested wetland by only 15.1% to 43.4%, indicating that the impact of drainage for forestry on soil C storage is weaker than that of agricultural drainage and reclamation.

Overall, our result suggests that low harvest intensity has the potential to accelerate the ecosystem C storage and drainage for forestry which is primarily aimed at standing biomass lowers the ecosystem C storage at the expense of soil C loss. On low WTD, the ecosystem C storage was slightly higher that control natural forested wetlands, since the forested wetland plantations with low WTD poss the largest soil C pools. This result is consistent with our study in lower latitude forested wetlands of Xiaoxing'anling, northeast China that higher C pools with more water accumulations (Wang et al., 2021).

## NPP and C sequestration

The NPP and ACS significantly increased with low- and moderate-intensity harvest owing to the significant increase in tree and understory, respectively. These could be related to several reasons: first, more number of trees were left in the low intensity harvest stands than the other two harvest intensity plots (Table 1); second, low intensity harvest diminished stand density, favored dominant trees, and stimulated the remaining trees radial growth; third, moderate intensity harvest could create more available light, nutrients, and water for understory (Beaudet et al., 2004). This finding was in line with those of other studies that harvesting was one of the best strategies to increase upland forest productivity and develop optimum C sequestration in managed upland forest ecosystems (Sayer et al., 2004; Nilsen and Strand, 2008). The NPP was significantly accelerated with light burn and was not significantly different from any of the harvesting treatments. Analyzing the reasons, it may be mainly due to the interference of mild ground fire accelerating the nutrient return process of forest land and changing the microenvironment, such as improved the light, temperature and moisture analogous to harvested stands. Additionally, the relative damage to the tree layer is slight, thereby increasing in the NPP and ACS as a result of the increase in the NPP and ACS of the herb layer. Heavy burn disturbance largely caused the forest structure severely damaged, especially most of the trees have been burned to death, thus resulting in significant reductions in NPP and ACS. Although a significant increase in the herb layer, it only accounted for little of the NPP and ACS and is of secondary importance. As a result, severe fire interference will inevitably lead to a decrease in the NPP and ACS of vegetation.

Drainage for forestry altered the distribution pattern of the NPP and ACS with a significantly increasing trend with the increasing WTD. This concides with those studies that tree growth was released after drainage (Préfontaine and Jutras 2017; Potapov et al., 2019). This may be due to the fact that drainage for forestry further aggravated the accumulation of water in the lower habitat of the transition zone, which severely restricted the growth of larch. Additionally, drainage for forestry gradually reduced the accumulation of water in the medium and high WTD habitats of the transition zone, which elevated the rapid growth of larch. At the same time, in the lower WTD habitat of the transect, drainage for forestry reduced the NPP and ACS of the herb layer by 88.2% and 88.3% compared with the natural grass swamp herb layer. The productivity and C sequestration are only equivalent to about one third of the natural grass swamp herb layer, which cannot offset the loss of its herb layer. As a result, the NPP and ACS of the low WTD habitat area declined. In the medium and high WTD habitats of the transect, the increase in NPP and ACS of the tree layer can compensate the loss of the shrub and herbaceous layer. Compared with the ACS of global wetlands (0.5-13.5 t C $ha^{-1}$ $yr^{-1}$) (Waddington and Roulet, 2000), the ACS of peatlands in the northern hemisphere (0.2-0.5 t C $ha^{-1}$ $yr^{-1}$) (Tolonen et al., 1992) and the ACS of the forest wetlands in the Xiaoxing'anling (1.61-2.73 t C $ha^{-1}$ $yr^{-1}$) (Wang et al., 2021), the medium and high WTD larch forested wetland of the drainage for forestry has higher ACS. It seems that drainage for forestry should be carried out in the medium and high WTD of the Daxing'anling wetland to obtain relatively high vegetation C sequestration capacity.

On the whole, our result demonstrates that that low to moderate intensity harvest and light burn promoted the stand NPP. Drainage for forestry is not comparable with harvest, which is due to several uncertainties in our study. On one hand, the stand stage of the main forest layer was not clear in harvest and burn plots and it could differ from the age of 25 year in the drainage for forestry plots. On the other hand, there was no silviculture in the drainage for forestry in recent years and self-thinning stage was on-going, thereby less growing space in the canopy hindering the tree growth. Consequently, from the ecosystem C and NPP point of view, low intensity harvest should be adopted as a permanent solution for maintaining C sinks for *Larix gmelinii–Carex schmidtii* forested wetlands.

### Understory species diversity

Our results showed the understory shrub and herb species diversity were generally lower in the harvest and burned stands than the control natural forested wetlands. The similarity between post-harvest and post-fire communities may be attributed to several reasons. First, the simplification of the complex hierarchical structure of the forest after harvesting or fire may result in the increased light, wet biochemistry of the habitat, and thus the reduction of some shade-tolerant and mesophyte plant groups or an alter in the composition and structure of vegetation (Ni et al., 2007; Lafleur et al., 2016). Second, the recovery time after harvesting or fire is still short (five years), and the forest stands are in the stage of pioneer succession. Third, the soil, such as increased soil bulk density, and understory species were affected by mechanized harvest operation and fire disturbance. All of them may play a part in the decline in species richness. Other than that, small differences in species diversity were found between harvest and fire sites with a relatively high value in the latter one and this could be due to higher temperature in the forest floor leading to more the seed germination after fire. This pattern is usually due to the greater impact of fire on the forest floor compared with harvest operations (Lafleur et al., 2018). Understory communities in sites originating from fire and harvest disturbances have been documented to converge in other parts of the boreal forest 40 years later after harvest and fire (Renard et al., 2016; Jean et al., 2019). Future investigations will be required to evaluate the successional trajectories of stands recovering following harvest operations and the fire disturbances in the study area.

Compared with undisturbed natural forested wetland stands, there were willow, aspen and birch mainly originated from the sprouts in early post-harvest and postfire sites. This observation was consistent with the study that documented forested wetland birch often respounts quickly after disturbances and thus has a competition advantage over other plants that establish from seed (Dyrness 1973; Rowe et al., 2017). Aspen is known for its great distances seed dispersal ability, thus its presence is not surprising in the study areas, since it is a common species in the nearby upland forests. We observed an increse in larch seedling regeneration in burned areas relative to harvests and this result reflected an influx of larch seed released from semi-serotinous cones after fire (Rowe et al., 2017). The lower abundance of larch regeneration in selective harvest plots was in agreement with the study which has reported reduced seed supply and lack of suitable microsites limites regenetation in these forested wetlands (Greene et al., 2007). Post-harvest understory communities are more similar to pre-harvest communities, with the exception of late successional shade intolerant species that do not survive stand opening caused by harvesting (Faivre et al., 2016). Additionally, large diameter trees of larch have not been burned to death, but most of birch trees died in the heavy fire, suggesting large larch is more fire-resistant than birch.

## CONCLUSIONS

In this study, low intensity harvest resulted in a mild increase in ecosystem C storage while moderate- and high-intensity harvest led to significant reductions (33.2-41.6%) compared with the control natural forested wetlands stand (274.54 t C·$ha^{-1}$), and light- and heavy-intensity burn caused the ecosystem C storage decreases by 27. 8% and 45. 2%. As for the drainage for forestry, the ecosystem C storage was higher at the low WTD (316.78 t C·$ha^{-1}$), and diminished significantly by 24.1-28.1% with the increasing WTD on the forested wetland plantation transect.

Low- and moderate-intensity harvest elevated significantly NPP (69.1-83.2%) and annual C sequestration (52.0-78.7%) in comparison with the high intensity harvest and control (8.28 t $ha^{-1}$ $yr^{-1}$, 5.08 t C·$ha^{-1}$ $yr^{-1}$ and 6.48 t $ha^{-1}$ $yr^{-1}$, 3.52 t C·$ha^{-1}$ $yr^{-1}$). Increases by 48.6% and 35.8% and decreases by 22.1% and 38.8% in NPP and annual C sequestration were in light- and heavy-intensity burn stands, respectively, while both the NPP and annual C sequestration (3. 67-10. 34 t $ha^{-1}$ $yr^{-1}$ and 1. 59-4. 87 t C·$ha^{-1}$ $yr^{-1}$) showed a significant increasing trend with increasing WTD. In general, the species diversity indices were lower in the harvest and burned stands than the control natural forested wetlands and more pioneer light demanding tree species occurred in the burned stands than in harvest stands.

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## REFERENCES

Armentano, T., and E. Menges. Patterns of change in the carbon balance of organic soil-wetlands of the temperate zone. The Journal of Ecology: p.755-774, 1986.

Beaudet, M., C. Messier, and A. Leduc. Understorey light profiles in temperate deciduous forests: recovery process following selection cutting. Journal of Ecology v.92: p.328-338, 2004.

Campbell, C., D. Vitt, L. Halsey, I. Campbell, M. Thormann, and S. Bayley. Net primary production and standing biomass in northern continental wetlands. Information Report-Northern Forestry Centre, Canadian Forest Service, 2000.

Dearborn, K. D., C. A. Wallace, R. Patankar, and J. L. Baltzer. Permafrost thaw in boreal peatlands is rapidly altering forest community composition. Journal of Ecology v.109: p.1452-1467, 2021.

Dyrness, C. Early stages of plant succession following logging and burning in the western Cascades of Oregon. Ecology v.54: p.57-69, 1973.

Faivre, N., C. Boudreault, S. Renard, N. J. Fenton, S. Gauthier, and Y. Bergeron. Prescribed burning of harvested boreal black spruce forests in eastern Canada: effect on understory vegetation. Canadian Journal of Forest Research v.46: p.876-884, 2016.

Gale, M. R., J. W. McLaughlin, M. F. Jurgensen, C. C. Trettin, T. Soelsepp, and P. O. Lydon.. Plant community responses to harvesting and post-harvest manipulations in a Picea-Larix-Pinus wetland with a mineral substrate. Wetlands v.18: p.150-159, 1998.

Giese, L. A., W. Aust, R. K. Kolka, and C. C. Trettin. Biomass and carbon pools of disturbed riparian forests. Forest Ecology and Management v.180: p.493-508, 2003.

Gorham, E. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecological Applications v.1: p.182-195, 1991.

Greene, D. F., S. E. Macdonald, S. Haeussler, S. Domenicano, J. Noel, K. Jayen, I. Charron, S. Gauthier, S. Hunt, and E. T. Gielau. The reduction of organic-layer depth by wildfire in the North American boreal forest and its effect on tree recruitment by seed. Canadian Journal of Forest Research. v.37: p.1012-1023, 2007.

Guo, L. B., and R. M. Gifford. Soil carbon stocks and land use change: a meta analysis. Global Change Biology. v.8: p.345-360, 2002.
Guohua, L., F. Bojie, and F. Jingyun. Carbon dynamics of Chinese forests and its contribution to global carbon balance. Acta Ecologica Sinica. v.20: p.732-740, 2000.

Gutenberg, L., K. W. Krauss, J. J. Qu, C. Ahn, and C. Xu.. Carbon Dioxide Emissions and Methane Flux from Forested Wetland Soils of the Great Dismal Swamp, USA. Environmental management. v.64, 2019.

Hart, S. A., and H. Y. Chen. Fire, logging, and overstory affect understory abundance, diversity, and composition in boreal forest. Ecological Monographs. v.78: p.123-140, 2008.

Hill, T. C., K. A. Walsh, J. A. Harris, and B. F. Moffett. Using ecological diversity measures with bacterial communities. FEMS microbiology ecology. v.43: p.1-11, 2003.

Houle, G. P., E. S. Kane, E. S. Kasischke, C. M. Gibson, and M. R. Turetsky. Recovery of carbon pools a decade after wildfire in black spruce forests of interior Alaska: effects of soil texture and landscape position. Canadian Journal of Forest Research. v.48: p.1-10, 2018.

Hu, S., Z. Niu, Y. Chen, L. Li, and H. Zhang. Global wetlands: Potential distribution, wetland loss, and status. Science of the total environment. v.586: p.319-327, 2017.

Hu, X., J. Zhu, C. Wang, T. Zheng, Q. Wu, H. Yao, and J. Fang. Impacts of fire severity and post-fire reforestation on carbon pools in boreal larch forests in Northeast China. Journal of Plant Ecology v.9: p.1-9, 2015.

Huang, C., H. S. He, Y. Liang, Z. Wu, T. J. Hawbaker, P. Gong, and Z. Zhu. Long-term effects of fire and harvest on carbon stocks of boreal forests in northeastern China. Annals of Forest Science 75: p.1-15, 2018.

James, J., and R. Harrison. The Effect of Harvest on Forest Soil Carbon: A Meta-Analysis. Forests 7: p.308, 2016.

Jandl, R., M. Lindner, L. Vesterdal, B. Bauwens, R. Baritz, F. Hagedorn, D. W. Johnson, K. Minkkinen, and K. A. Byrne. How strongly can forest management influence soil carbon sequestration? Geoderma 137: p.253-268, 2007.

Jean, M., B. Lafleur, N. J. Fenton, D. Paré, and Y. Bergeron. Influence of fire and harvest severity on understory plant communities. Forest Ecology and Management 436: p.88-104, 2019.

Jenkinson, D., D. Adams, and A. Wild.. Model estimates of CO 2 emissions from soil in response to global warming. Nature 351: p.304-306, 1991.

Kayranli, B., M. Scholz, A. Mustafa, and Å. Hedmark.. Carbon storage and fluxes within freshwater wetlands: a critical review. Wetlands 30: p.111-124, 2010.

Kimble, J. M., R. Lal, R. Birdsey, and L. S. Heath. The potential of US forest soils to sequester carbon and mitigate the greenhouse effect. CRC Press, 2002.

Kowalski, A. S., D. Loustau, P. Berbigier, G. Manca, V. Tedeschi, M. Borghetti, R. Valentini, P. Kolari, F. Berninger, and Ü. Rannik. Paired comparisons of carbon exchange between undisturbed and regenerating stands in four managed forests in Europe. Global Change Biology 10: p.1707-1723, 2004.

Lafleur, B., N. J. Fenton, M. Simard, A. Leduc, D. Paré, O. Valeria, and Y. Bergeron. Ecosystem management in paludified boreal forests: enhancing wood production, biodiversity, and carbon sequestration at the landscape level. Forest Ecosystems 5: p.1-14, 2018.

Lafleur, B., D. Paré, N. J. Fenton, and Y. Bergeron. Growth and nutrition of black spruce seedlings in response to disruption of Pleurozium and Sphagnum moss carpets in boreal forested peatlands. Plant and Soil 345: p.141-153, 2011.

Lafleur, B., S. Zouaoui, N. J. Fenton, P. Drapeau, and Y. Bergeron. Short-term response of Cladonia lichen communities to logging and fire in boreal forests. Forest Ecology and Management 372: p.44-52, 2016.

Lal, R.. Soil carbon sequestration to mitigate climate change. Geoderma 123: p.1-22, 2004.

Maltby, E., and P. Immirzi. Carbon dynamics in peatlands and other wetland soils regional and global perspectives. Chemosphere 27: p.999-1023, 1993.

Mayer, M., C. E. Prescott, W. E. Abaker, L. Augusto, L. Cécillon, G. W. Ferreira, J. James, R. Jandl, K. Katzensteiner, and J.-P. Laclau. Tamm Review: Influence of forest management activities on soil organic carbon stocks: A knowledge synthesis. Forest Ecology and Management 466: p.118-127, 2020.

Mu, C., H. Lu, B. Wang, X. Bao, and W. Cui. Short-term effects of harvesting on carbon storage of boreal *Larix gmelinii–Carex schmidtii* forested wetlands in Daxing'anling, northeast China. Forest Ecology and Management 293: p.140-148, 2013.

Mu, C. C., X. X. Sun, Z. Y. Ni, M. Yang, and N. Zhang. Comprehensive Evaluation of the Effects Planting in Swamp-Forest in Daxing'an Mountains. Scientia Silvae Sinicae 43: p.51-58, 2007.

Nelson, K., D. Thompson, C. Hopkinson, R. Petrone, and L. Chasmer. Peatland-fire interactions: A review of wildland fire feedbacks and interactions in Canadian boreal peatlands. Science of the total environment 769: p.145-212, 2021.

Nguyen-Xuan, T., Y. Bergeron, D. Simard, J. W. Fyles, and D. Paré. The importance of forest floor disturbance in the early regeneration patterns of the boreal forest of western and central Quebec: a wildfire versus logging comparison. Canadian Journal of Forest Research 30: p.1353-1364, 2000.

Ni, Z. Y., C. C. Mu, X. X. Sun, N. Zhang, and M. Yang. Effects of Different Restoration Approaches on Structure and Productivity of Forest-Swamp Communities in Daxing'an Mountain. Journal of Northeast Forestry University 35: p.24-27, 2007.

Nieminen, M., S. Sarkkola, and A. Laurén. Impacts of forest harvesting on nutrient, sediment and dissolved organic carbon exports from drained peatlands: A literature review, synthesis and suggestions for the future. Forest Ecology and Management 392: p.13-20, 2017.

Nilsen, P., and L. T. Strand. Thinning intensity effects on carbon and nitrogen stores and fluxes in a Norway spruce (Picea abies (L.) Karst.) stand after 33 years. Forest Ecology and Management 256: p.201-208, 2008.

Paavilainen, E., and J. Päivänen. Peatland forestry: ecology and principles. Springer Science & Business Media, 1995.

Paquette, M., C. Boudreault, N. Fenton, D. Pothier, and Y. Bergeron.. Bryophyte species assemblages in fire and clear-cut origin boreal forests. Forest Ecology and Management 359: p.99-108, 2016.

Potapov, A., S. Toomik, M. Yermokhin, J. Edvardsson, A. Lilleleht, A. Kiviste, T. Kaart, S. Metslaid, A. Järvet, and M. Hordo. Synchronous growth releases in peatland pine chronologies as an indicator for regional climate dynamics—A multi-site study including Estonia, Belarus and Sweden. Forests 10: p.1097, 2019.

Powers, M., R. Kolka, B. Palik, R. McDonald, and M. Jurgensen. Long-term management impacts on carbon storage in Lake States forests. Forest Ecology and Management 262: p.424-431, 2011.

Préfontaine, G., and S. Jutras. Variation in stand density, black spruce individual growth and plant community following 20 years of drainage in post-harvest boreal peatlands. Forest Ecology and Management 400: p.321-331, 2017.

Pugh, T. A., A. Arneth, M. Kautz, B. Poulter, and B. Smith. Important role of forest disturbances in the global biomass turnover and carbon sinks. Nature geoscience 12: p.730-735, 2019.

Renard, S. M., S. Gauthier, N. J. Fenton, B. Lafleur, and Y. Bergeron. Prescribed burning after clearcut limits paludification in black spruce boreal forest. Forest Ecology and Management 359: p.147-155, 2016.

Rowe, E. R., A. W. D'Amato, B. J. Palik, and J. C. Almendinger. Early response of ground layer plant communities to wildfire and harvesting disturbance in forested peatland ecosystems in northern Minnesota, USA. Forest Ecology and Management 398: p.140-152, 2017.

Rydgren, K., R. H. Økland, and G. Hestmark. Disturbance severity and community resilience in a boreal forest. Ecology 85: p.1906-1915, 2004.

Sayer, M. S., J. Goelz, J. L. Chambers, Z. Tang, T. Dean, J. D. Haywood, and D. J. Leduc.. Long-term trends in loblolly pine productivity and stand characteristics in response to thinning and fertilization in the West Gulf region. Forest Ecology and Management 192: p.71-96, 2004.

Sobachkin, R., D. Sobachkin, and A. Buzykin. The influence of stand density on growth of three conifer species. Tree species effects on soils: Implications for global change. Springer, p.247-255, 2005.

Song, Y., C. Song, G. Yang, Y. Miao, J. Wang, and Y. Guo.. Changes in labile organic carbon fractions and soil enzyme activities after marshland reclamation and restoration in the Sanjiang Plain in Northeast China. Environmental management 50: p.418-426, 2012.

Stenberg, L., K. Haahti, H. Hökkä, S. Launiainen, M. Nieminen, A. Laurén, and H. Koivusalo. Hydrology of drained peatland forest: Numerical experiment on the role of tree stand heterogeneity and management. Forests 9: p.645, 2018.

Sun, T.. Global Warming Effects on Mercury Cycling in Northern Peatlands, 2021.

Sun, X., C. Mu, and C. Song.. Seasonal and spatial variations of methane emissions from montane wetlands in Northeast China. Atmospheric Environment 45: p.1809-1816, 2011.

Thormann, M. N., and S. E. Bayley.. Aboveground net primary production along a bog-fen-marsh gradient in southern boreal Alberta, Canada. Ecoscience 4: p.374-384, 1997.

Tolonen, K., H. Vasander, A. Damman, and R. Clymo.. Rate of apparent and true carbon accumulation in boreal peatlands. Page 26 *in* Proceedings of the 9th International Peat Congress, Uppsala, Sweden, 1992.

Trettin, C. C., M. Davidian, M. Jurgensen, and R. Lea.. Organic matter decomposition following harvesting and site preparation of a forested wetland. Soil Science Society of America Journal Volume 60, no. 6, November-December 1996.

Trettin, C. C., M. R. Gale, M. F. Jurgensen, and J. W. McLaughlin.. Carbon storage response to harvesting and site preparation in a forested mire in northern Michigan, USA. Suo 43: p.281-284, 1992.

Trettin, C. C., and M. F. Jurgensen.. Carbon cycling in wetland forest soils. The potential of US forest soils to sequester carbon and mitigate the greenhouse effect. CRC Press, p.311-331, 2002.

Trettin, C. C., M. F. Jurgensen, M. R. Gale, and J. W. McLaughlin.. Recovery of carbon and nutrient pools in a northern forested wetland 11 years after harvesting and site preparation. Forest Ecology and Management 262: p.1826-1833, 2011.

Waddington, J., and N. Roulet.. Carbon balance of a boreal patterned peatland. Global Change Biology 6: p.87-97, 2000.

Wang, B., C. Mu, H. Lu, N. Li, Y. Zhang, and L. Ma.. Ecosystem carbon storage and sink/source of temperate forested wetlands in Xiaoxing'anling, northeast China. Journal of Forestry Research: p.1-11, 2021.

Zhang, W. W., X. Z. Ma, G. D. Ding, and X. X. Cui.. The effect of the improvement of fen land on soil and vegetation in Daxing'an Mountains. Journal of Northeast Forestry University 24: p.9-13, 1996.

Zheng, X. X., G. H. Liu, B. J. Fu, T. T. Jin, and Z. F. Liu.. Effects of biodiversity and plant community composition on productivity in semiarid grasslands of Hulunbeir, Inner Mongolia, China. Annals of the New York Academy of Sciences 1195:E52-E64, 2010.

Zhou, W., C. Mu, X. Liu, and H. Gu. Carbon sink in natural swamp forest ecosystems in Lesser Xing'an Mountains. Journal of Northeast Forestry University 40:p.71-1272012.