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Research article

Effects of stand age, tree species, and climate on water table fluctuations and estimated evapotranspiration in managed peatland forests

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ABSTRACT

Lowland conifer forests dominated by black spruce (*Picea mariana*) and tamarack (*Larix laricina*) typically occur in peatlands in the boreal North American forest with near-surface water tables throughout the year. These forests are ecologically and economically important resources that may be impacted by climate change. However, information characterizing effects of forest disturbance, such as even-aged harvest on water table dynamics is needed to evaluate which forest tree species cover types are most hydrologically susceptible to even-aged harvest and changes in precipitation. We used a chronosequence approach to evaluate water table fluctuations and evapotranspiration across four stand age classes (<10, 15–30, 40–80, and >100-years old) and three distinct forest cover types (productive black spruce, stagnant black spruce, and tamarack) for a period of three years in Minnesota, USA. In general, there is limited evidence for elevated water tables in the younger age classes; the <10-year age class had no significant difference in mean weekly water table depth compared to the older age classes across all cover types. Estimated actual daily evapotranspiration (ET) generally agreed with the water table observations, with the exception of the tamarack cover type where ET was significantly lower in the <10-year age class. Productive black spruce sites that are 40–80-years old had higher evapotranspiration, and lower water table, possibly reflecting increased transpiration associated with the stem exclusion stage of stand development. Tamarack in the 40-80-year age class had higher water tables but no difference in ET compared to all other age classes, indicating that other external factors are driving higher water tables in that age class. To evaluate susceptibility to changing climate, we also assessed the sensitivity and response of water table dynamics to pronounced differences in growing season precipitation that occurred across study years. In general, tamarack forests are more sensitive to changes in precipitation compared to the two black spruce forest cover types. These findings can inform expected responses of site hydrology for a range of precipitation scenarios that may occur under future climate and be used by forest managers to evaluate hydrologic impacts of forest management activities across lowland conifer forest cover types.

1. Introduction

Lowland conifer forests of black spruce, (*Picea mariana* (Mill) BSP), and tamarack (*Larix laricina* (Du Roi) K. Koch), are ecologically and economically important ecosystems. Lowland conifer forests encompass the range of the boreal forest ecosystem in North America, spanning the Canadian shield, the northeastern states in the United States, and reach its western edge in the Lake States (Michigan, Minnesota, Wisconsin, USA and Ontario, Canada) (Viereck et al., 1990). Lowland conifer ecosystems are actively managed to meet multiple ecological and economic objectives including provision of wildlife habitat and conventional wood products (McKee et al., 2022; Skay et al., 2021). These forests commonly grow in *Sphagnum* moss-dominated peatlands (Boelter and Verry, 1977; Perala, 1971; Viereck et al., 1990); ecosystems with high water tables (WT) that prevent decomposition (Clymo and Fogg, 1984), resulting in the accumulation of deep organic peat and the storage of a large amount

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of carbon (C) (Heinselman, 1963). While peatlands cover only 2.8% of the global land surface, these ecosystems store large proportions of terrestrial C with an estimated 600–1000 Gt of C (Nichols and Peteet, 2019; Page and Baird, 2016; Yu et al., 2010). Hydrology plays a key role in peatland carbon sequestration, resulting from ecohydrological feedbacks (Waddington et al., 2015) that influence plant species composition (Dunn et al., 2007; Holden, 2006; Magnan et al., 2020). For example, hydrologic change (e.g., change in hydroperiod, seasonal WT dynamics, net outflow, etc.) can alter plant species composition, ultimately affecting ecosystem functions such as carbon storage (Harden et al., 1997; Munir et al., 2014; Strilesky and Humphreys, 2012) and other benefits described above.

Although lowland conifer forests are extensively managed throughout Canada and the USA, there is continued uncertainty regarding how conventional forest management practices such as harvesting influence site hydrology. One of the foremost concerns is for a potential 'watering-up' effect, where after a clearcut regeneration harvest, WTs rise because of a reduction in transpiration associated with tree removal (Dubé et al., 1995; Morris, 1997). Such an effect can result in a change in ecosystem type toward ericaceous plants and more nutrient-poor conditions that promote the process of paludification and limits the regrowth of productive black spruce stands (Dussart and Payette, 2002; Thiffault et al., 2013). Although several studies have observed WT rise following harvesting (Lavoie et al., 2005; Pothier et al., 2003; Slesak et al., 2014), other studies have not observed such an effect. For example, Verry (1986) noted that average WT level did not change following a clearcut in a black spruce peatland, which was attributed to offsetting effects of increased near surface evaporation following canopy removal. In a study evaluating WT change following a clearcut harvest in Canada, Dubé et al. (1995) found that the response was most pronounced in mineral soils and where the WT was initially deep; sites with near surface WTs had smaller responses or even a lowering of WT. In addition, peat depth, which can vary according to peatland type, is associated with differences in ecosystem productivity that are likely driven by WT depth (Hökkä and Groot, 1999), and may indicate potential post-harvest water table rise. Most studies assessing water table response to harvest are limited in scope and occurred decades ago, underlying a need to quantify the response across a range of conditions common to lowland forest cover types subject to contemporary forest management practices.

Because climate change creates unique challenges for peatland ecosystems (Dieleman et al., 2015; Waddington et al., 2015), lowland conifer forests occurring in peatlands may be particularly susceptible to future warming. For example, climate change is projected to adversely affect peatlands, with changes to surface and subsurface flows impacting critical processes that influence forest structure and the ability of the ecosystem to store carbon (Holden, 2005). Currently, high WTs inhibit carbon mineralization, but future changes in hydroclimate and site water budgets could put these carbon stocks at risk of decomposition, leading to carbon emissions (Bridgham et al., 2008; Moore and Dalva, 1993; Turetsky et al., 2002). Some studies predict WTs to decrease in response to increased ET due to warming (Helbig et al., 2020; Shi et al., 2015), but overall precipitation in the region is expected to increase (Peltier et al., 2018), with an increase in high-intensity but low frequency storms (Giorgi et al., 2019), which may offset any reduction in WTs associated with increased ET.

Lastly, biological feedback to the ecohydrological system may also be of concern; for example tamarack in areas of north America is at threat from eastern larch beetle (*Dendroctonus simplex* (LeConte)) invasion that has affected at least 666,000 ha of tamarack in Minnesota (DNR, 2019), and climate change may increase populations and infestation outbreaks (McKee and Aukema, 2015; Ward and Aukema, 2019), possibly modifying the ET-WT dynamics in this forest type. Although there is much uncertainty regarding the hydrologic response to changing climate, assessing the sensitivity and response of lowland conifer forests WTs to changes in precipitation may allow us to improve predictions under future conditions.

Our study region is focused on Minnesota, USA in the Great Lakes Region of North America. Minnesota contains nearly 2.4 million ha of peatlands (Xu et al., 2018), with many covered by lowland conifer forests. In Minnesota there are approximately 446,000 ha of tamarack with removals via harvesting of 54,000 cords annually and 553,000 ha of black spruce forests with annual removals of 279,000 cords (DNR, 2019). Both black spruce and tamarack are conventionally managed using even-aged silvicultural treatments, mainly clearcut regeneration harvests with rotations varying between 60 and 100 years based on site quality (but see Anderson et al. (2020) for a full description of potential alternative regeneration harvests). Lowland conifer forests in Minnesota are also at the southern edge of their current range, thus may be more susceptible to the effects of climate change in the near term.

We used a chronosequence approach to evaluate the effects of stand age on WT dynamics across a range of sites that encompassed three distinct lowland conifer forest cover types in Minnesota USA: productive black spruce, stagnant black spruce, and tamarack dominated forests. The over-arching goal of our study is to better understand how stand age influences WT dynamics and ecohydrological feedbacks within these forest cover types over time. Furthermore, we were interested in understanding the range of response to precipitation variability across cover types and age classes to determine those most susceptible to future changes in precipitation. Our specific objectives are to; 1) quantify the influence of stand age on WT response dynamics and ET and any differences in the response among the three forest cover-types of interest and 2) characterize the relationship between WT depth and precipitation and how it may vary by cover-type and stand age. Our intent of this study is to provide a framework for forest managers and stakeholders to better understand the response of the hydrologic conditions of lowland conifer forests to consider ecosystem resilience in the face of a changing climate.

2. Methods

2.1. Environmental setting of study site lowland conifer stands

The study was conducted over a large geographic region of northern Minnesota in the Laurentian mixed forest ecological province and across two ecological regions: the Northern Minnesota and Ontario Peatlands and the Northern Minnesota Drift and Lake Plains (Hanson and Hargrave, 1996). The study area spans from 25 km north of Mille Lacs Lake (46.6°N) to 5 km south of Lake of the Woods (48.9°N) over 2° latitude (Fig. 1). Geologically the region is post-glacial, with deep till on top of bedrock, and histosols (acidic organic soil) that can be meters thick (Glaser, 1987; Viereck et al., 1990).

Climate in the region is continental. The meteorological record from the centrally located Marcell Experimental Forest shows average annual air temperature of 3 °C, with cold and dry winters with average January temperature of −15 °C (Fig. 2), and humid and warm summers average July air temperature of 19 °C (Sebestyen et al., 2020). Monthly precipitation in the region from 1961 to 2021 was greatest in the summer months, averaging about 400 mm cumulative from June through September (Fig. 2) or approximately 51% of the annual 787 mm of precipitation (Sebestyen et al., 2022).

2.2. Experimental design and measurements

We used a chronosequence approach to develop a factorial design with two factors. Factor 1 was lowland conifer forest cover type (productive black spruce, stagnant black spruce, or tamarack) determined using Minnesota's Ecological Classification System (ECS (DNR, 2003),) and site index (SI: measured as the height of dominant and co-dominant trees in a stand at 50 years post-harvest (Viereck et al., 1990),); where an SI $<$ 7 m at 50 years is considered "stagnant black spruce" and an SI $>$ 7.1 m at 50 years is considered "productive black spruce". In our study

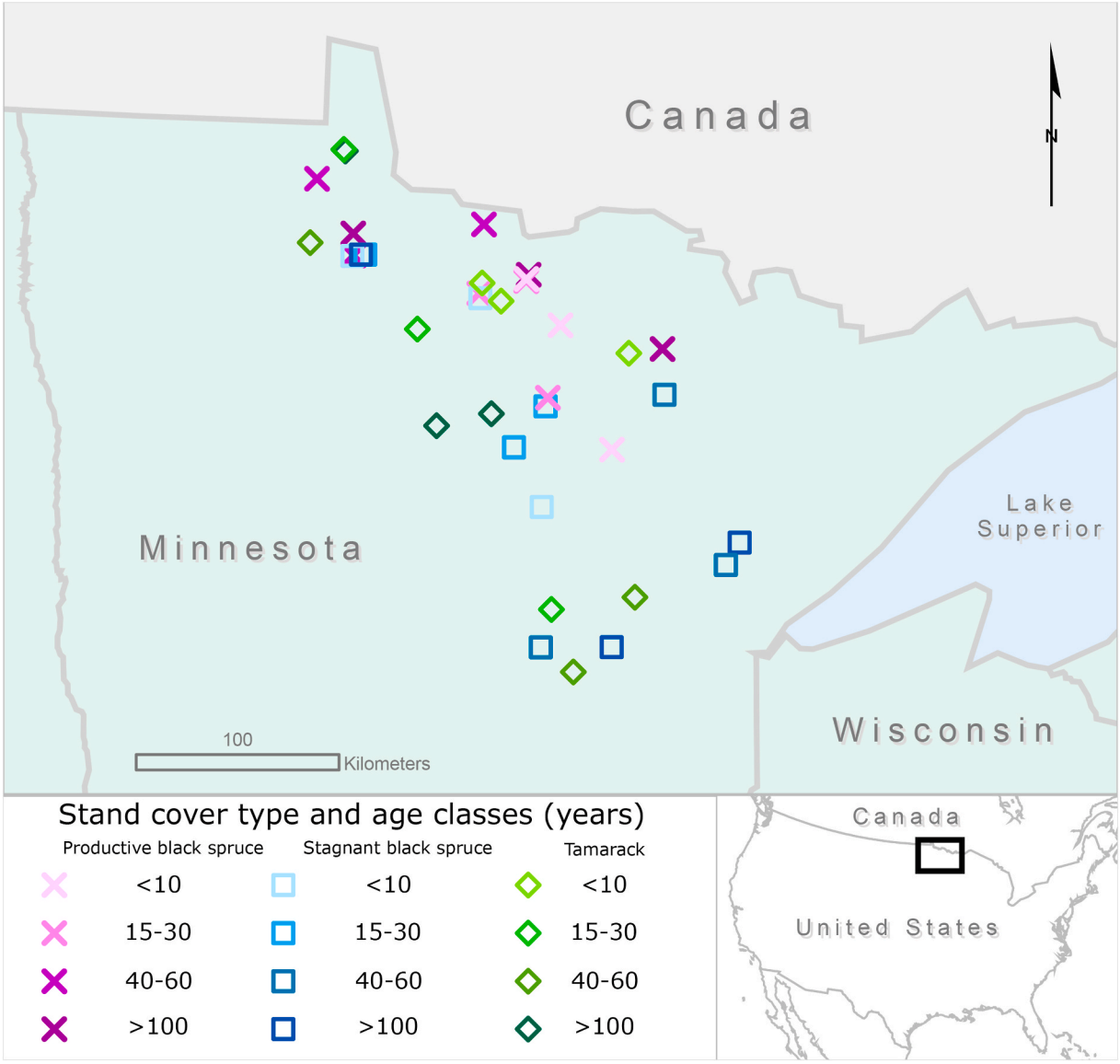

Fig. 1. Regional map showing study area. Sites were located where state forest lands containing targeted cover types and age classes (in years since stand replacement). Stagnant black spruce and tamarack age categories are distributed throughout the study area; however, productive black spruce sites are only found in the northern 2/3 of the study area.

area, the differences in productive and stagnant black spruce stands are generally attributed to the nutrient-poor, acidic soil conditions compared to productive black spruce stands that generally occur on peat substrates that are poor in nutrients but are influenced by mineral-rich groundwater. Tamarack stands were not subdivided and included sites that were dominated by tamarack. Factor 2 was age class as determined using a combination of inventory records and assessment from representative tree cores (Rueling, unpublished data). Stand age was divided into four classes: <10, 15–30, 40–80, and >100 years. We are confident that for the two youngest classes (<10, 15–30 years) the stand replacing disturbance was prescribed even-aged regeneration harvest. Due to age and lack of consistent records, we are unable to determine the initiating event of the two oldest age classes (40–80 years and >100 years). The two oldest age classes may have regenerated after a human caused disturbance (clear-cut harvest) or through another natural stand replacing event (e.g., wind or fire). For this reason, we refer to stand age throughout the manuscript rather than time since harvest. Final sites were selected after field validation of inventory records and based on site accessibility; each treatment combination was replicated three times for a total of 36 sites (Fig. 1).

WT dynamics were assessed with a shallow groundwater monitoring well located near the center of each site. Wells were constructed of 5 cm slotted PVC and installed in the fall of 2018 to a depth of ~1 m using augers with the same diameter. Water levels were recorded using pressure transducers located near the bottom of each well that logged at 15-min intervals (HOBO Model U20-L-04, Onset Corporation, MA, USA); monitoring was conducted from ~May–Sept. in 2019–2021. We also placed dry wells within close proximity of grouped sites to measure temperature-buffered barometric pressure for barometric pressure compensation (see below (McLaughlin and Cohen, 2014),). Tipping bucket rain gauges (HOBO Model RG3) were also installed at each site; in some instances, sites in close proximity had only one common rain gauge associated with them (7 sites total).

Peat depth was estimated at each site at six locations systematically located within a site and at the well location. At each of the six within-site locations, three measurements of peat depth were collected using a peat probe and averaged. For each measurement, the probe was pushed through the peat profile using constant force until mineral soil was

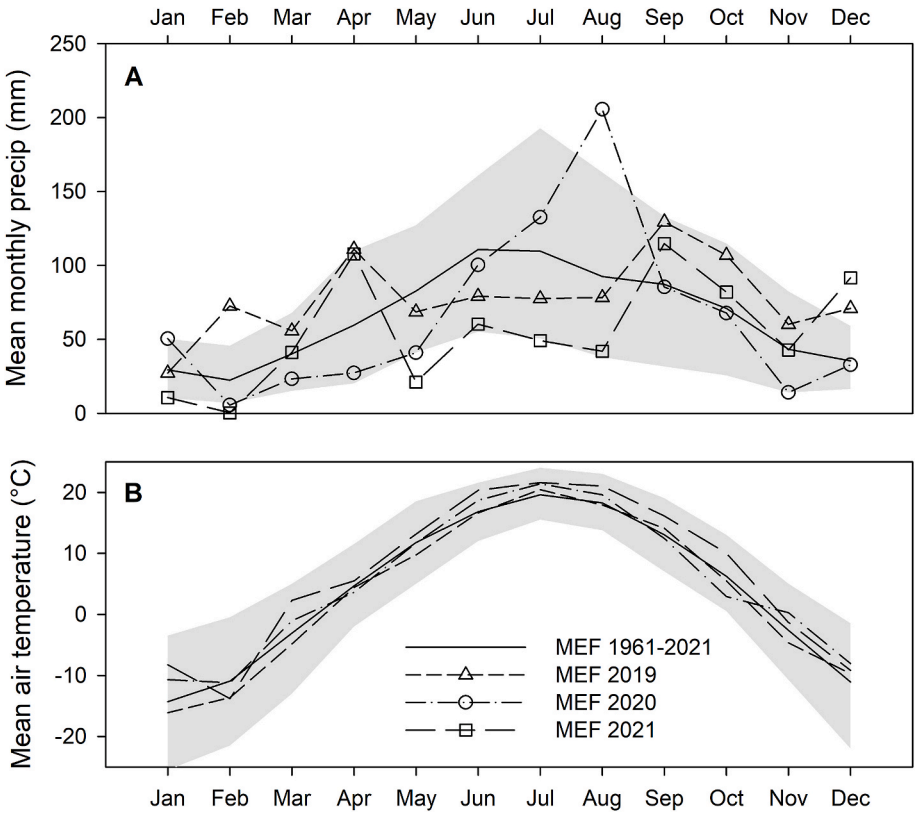

Fig. 2. Regionally representative climate from a centrally located weather station at Marcell Experimental Forest (MEF). This long-term environmental record of precipitation and air temperature since 1961 shows A) the mean monthly (black line with grey shading: 10th-90th percentile) cumulative precipitation (mm) from 1961 to 2021, relative to the cumulative precipitation for years 2019–2021 (dashed lines), and B) mean monthly air temperature (°C) 1961–2019 (black line with grey shading: 10th-90th percentile).

reached as determined by the change in resistance. When obvious obstructions were encountered (coarse wood or roots), the probe was offset, and another measurement was taken.

2.3. Evapotranspiration estimation and data processing

For general WT response, water level readings were first averaged by day and then by week prior to analysis. For estimated ET we first needed to determine net groundwater inflow and specific yield using established methods outlined in previous studies (Cianciolo et al., 2021; Diamond et al., 2018; Loheide II, 2008). We estimated ET by application of the modified White (1932) method:

$$S_y \frac{dWT}{dt} = r(t) - ET(t) \quad (1)$$

Where the rate of change over time (t) of groundwater storage near the well is represented by the water table rate of change (dWT/dt) scaled for specific yield (Sy) and is equal to the net inflow of groundwater (r) into and from the soil near the well, minus the consumption rate of groundwater due to evapotranspiration (ET). At night, when ET is assumed to be negligible, this can be simplified to estimate net inflow:

$$S_y \frac{dWT}{dt} = r(t) \quad (2)$$

However, due to differences in hydraulic head at differing elevations, the net inflow is calculated in as small a period as possible, from the day prior to the ET estimate, through the day after the ET estimate. For this 3-day sliding window of the inflow is estimated from detrended water table depth (WT_{DT}) using equation (3):

$$WT_{DT}(t) = WT(t) - m_T \times t - b_T \quad (3)$$

Where detrended water table depth is calculated by subtracting the trend slope (m_T) and the intercept (b_T) of the linear regression of the 3-day period. Therefore, after rearranging equation (1) we are able to use 15-min WT depths at each site during the growing season (approx. June–Sept) using the following equation (Cianciolo et al., 2021; Diamond et al., 2018):

$$ET = Sy * [r - S] \quad (4)$$

Where ET = daily evapotranspiration, Sy = specific yield as a function of WT depth, r = net groundwater inflow as a function of detrended WT, and S = 24-hr change in storage (change in daily WT). The net inflow (r) is a result of all flows into or out of the region near the wells at night (when ET is assumed to be negligible), and was estimated from the rate of change with respect to WT elevation as a function of 3-day sliding window detrended from WT depth (Loheide II, 2008; Loheide II et al., 2005), and specific yield (Sy) was estimated using an empirically derived relationship between rain to WT rise to construct depth-Sy relationships at each site (McLaughlin and Cohen, 2014).

Daily ET for each site was calculated using eq. (4) on days without rainfall, which were then used to calculate weekly mean daily ET. We focused on the growing season of each year as this is the time period when WT is most likely to be influenced by precipitation and ET. Due to timing differences in sensor deployment from year-to-year, the time period analyzed each year varied; in 2019 Jun 3-Sept 15, in 2020 May 11 – Sept 13, and in 2021 May 10- Oct 10. Our WT fluctuation measurements yielded 8750 ET event-days over the 36 sites and the three years, or an average of 83 ET event days per site per year. We used this information to estimate weekly means of ET for the growing season which provided estimating a mean daily ET for each week during the months Jun–Sept.

2.4. Data analysis

Treatment effects (cover type and age) on WT and ET were assessed using a mixed effects repeated measures ANOVA analysis with the *nlme* package (Pinheiro et al., 2021) on yearly growing season mean (WT only) and weekly mean values (WT and ET). We used an AR (1)

correlation matrix to account for temporal correlation. The variables forest cover type (productive black spruce, stagnant black spruce, or tamarack), stand age (<10, 15–30, 40–80, >100 years), measurement period (yearly growing season or weekly), and their interactions were modeled as fixed effects and site was modeled as a random effect. Each year was run independently for the weekly WT and ET models; all years were included in the yearly growing season mean model. Mean peat depth was included as a covariate in models when significant. Prior to statistical analysis, all data was tested for outliers using the rstatix package. Within sites, we eliminated ET and WT outliers as any value greater than the 75th percentile value + 1.5 times the inter quartile range, or less than the 25th percentile – 1.5 times the inner quartile range (Kassambara, 2021). The outliers removed using this process were <3% of the total dataset. When F statistics indicated significant effects, we conducted multiple comparisons using post-hoc pairwise analysis with a Bonferonni correction using the *emmeans* package (Lenth, 2022) to identify which treatments were significantly different from each other. ET was not normally distributed, so we applied a log transformation by site and back calculated the response variable using the chain rule, and standard errors are estimated via the delta method (Lenth, 2016). All statistical analyses were carried out in R (R Core Team, 2021).

We evaluated effects of precipitation on WT dynamics using comparisons of linear regression relationships between cumulative growing season precipitation and mean weekly WT height that were developed for each site, cover type, and year. Regression line comparisons were conducted to compare slopes and intercepts among forest cover type classes, and within forest cover classes among age classes using the dummy variable method in base R. For sites with shared precipitation gauges and years when precipitation gauges were faulty, we acquired unique precipitation estimates for the site using the Parameter-elevation Regressions on Independent Slopes Model data (PRISM, 2014) from Oregon State University. We used an alpha level of 0.1 in all analysis because of the low replication and high variability of the response variables, which increase the likelihood of a Type 2 error.

3. Results

3.1. Peat depth by species cover type

Mean peat depths for the three cover classes were 1.10 m (±0.2 m) for productive black spruce, 1.76 m (±0.2 m) m for stagnant black spruce, and 1.24 m (±0.2 m) m for tamarack. There was a significant difference in mean peat depth by species cover class, where stagnant black spruce was significantly deeper than the productive black spruce cover type (estimated difference of 0.66±0.27 m). Tamarack was not significantly different in peat depth from either black spruce cover class (Supplemental Tables 1 and 2).

3.2. Effects of cover type and age class on mean WT depth

Across all age classes, there were similar patterns of mean weekly WT depth among the cover types and within a year (Fig. 3). Water tables are highest in the spring, with slight drawdowns during the growing season in years with typical precipitation (i.e., 2019 and 2020). On the other hand, in 2021 which experienced a severe drought, the growing season WT drawdown was much more pronounced.

The repeated measures ANOVA model of yearly growing season mean WT depth indicated significant interactions between cover type and year and stand age and cover type (Table 1).

For the cover type-year interaction, in years 2019 and 2020 mean WT was lowest in productive black spruce, intermediate in stagnant black spruce, and highest in tamarack; however, mean comparisons failed to identify any significant differences among the cover types in either year (Fig. 4A). In 2021, WTs were very similar and much lower across all cover types. When comparing the stand age -cover type means, there was no clear pattern in response among the treatment combinations, but tamarack stands within the 40–80 age class had the highest WT that was significantly different from most of the other treatment combinations (Fig. 4B).

There were significant effects of age class and interaction between age class and week on weekly mean WTs depending on cover type and year (Supplementary Table 3). In general, treatment effects of age or the age-week interaction were significant in some years for both productive black spruce and tamarack cover types, but there was no effect in the stagnant black spruce cover type (Fig. 5).

For productive black spruce, the 40–80-year-old class had significantly lower WT elevations in weeks 32–37 of 2020 and weeks 26–33 weeks of 2021 compared to the other age classes. For tamarack in 2019, the 40–80 years old class had significantly higher WTs than all of the

Table 1
F-statistics and associated p-values for repeated measures analysis of yearly growing season mean WT elevation (WT) with peat depth as covariate.

WT All Sites	Num DF	F-value	p-value
(Intercept)	1	336.94	<0.01*
Age	3	2.54	0.06*
cover type	2	2.73	0.07*
Year	2	157.35	<0.01*
Peat depth	1	15.17	<0.01*
Age* cover type	6	4.48	<0.01*
Age*Year	6	1.33	0.26
cover type*Year	4	2.23	0.07*
Age* cover type*Year	12	1.40	0.19

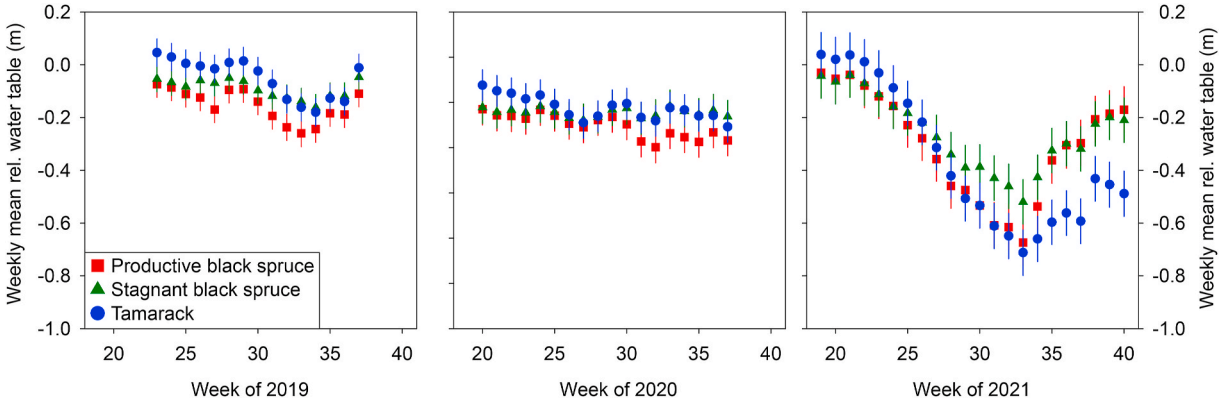

Fig. 3. Time series plots of weekly mean WT elevation by cover type for all 36 sites for years 2019–2020. This highlights the interannual variability of WT fluctuation and timing of drawdown. Error bars represent the 90% CI.

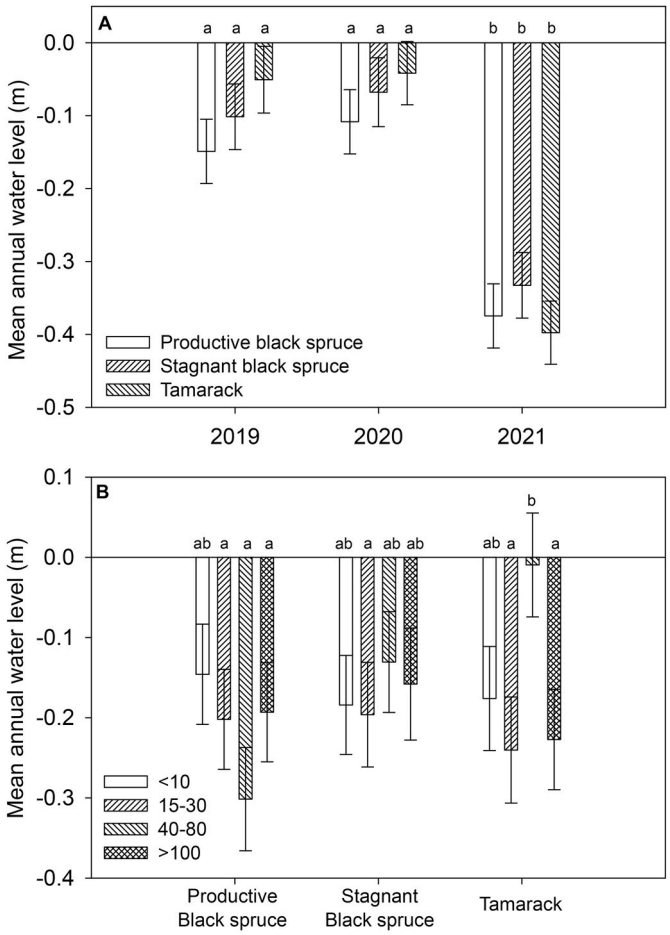

Fig. 4. Yearly growing season least-squares mean WT depth from repeated measures ANOVA, by A) cover type X year, and B) age X cover type. Treatments containing different letters are significantly different. Error bars are the standard error of the mean.

other age categories, with a similar response observed in 2021 (significant differences from week 27 through 40).

3.3. ET in response to stand age

Across all sites, the weekly mean ET was 2.7 ± 1.4 (sd) mm/d. Within species cover types (and across all age classes), estimated mean weekly ET for productive black spruce was 2.6 ± 1.3 (sd) mm/d, 2.7 ± 1.2 (sd) mm/d for stagnant black spruce, and 2.8 ± 1.3 (sd) mm/d for tamarack (data not shown).

There were significant effects of age class on mean weekly ET in some years for each of the cover types (Fig. 6; Supplemental Table 4). For the productive black spruce cover type in 2019, ET in the 40–80-year age class was 1.25 mm/d greater ($p = 0.09$) than >100-year age class. Similar response patterns were observed in 2020 and 2021, but effects were not significant in those years. In stagnant black spruce ET in the 15–30-year age class was 0.86 mm/d greater ($p = 0.04$) than the <10-year age class in 2019, and in 2020 the 40–80 year age class was 0.76 mm/d ($p = 0.03$) and 0.73 mm/d ($p = 0.03$) less than the <10 and the >100 year age classes, respectively. In the tamarack cover type, the <10-year-old forests had lower ET (1.1–1.5 mm/d) compared to all other age classes and was lower than the 15–30 year age class in 2020 by 1.3 mm/d ($p = 0.06$). There were no differences in estimated ET among age classes for any of the cover types in 2021.

3.4. WT response to precipitation

Growing season cumulative precipitation during the study period ranged from a maximum of 534 mm in 2019 to a minimum of 135 mm in 2021, with a median 307 mm. Additionally, across all sites, growing season mean WT elevation ranged from a maximum of 119 mm above the surface in 2019, to a minimum of 203 mm below the surface in 2021, with a median of 124 mm below the surface (data not shown). Of note, in 2021 northern Minnesota was experiencing severe drought until a series precipitation events at the end of growing season. A post-hoc comparison of precipitation means for the three years showed that there was no difference in precipitation between 2019 and 2020, but 2021 had ~135 mm less growing season precipitation than 2019, and ~150 mm less growing season precipitation than 2020.

Across all sites and years, the relationship between WT elevation and cumulative precipitation was significant ($p < 0.01$ and adj-$R^2 = 0.32$) with a slope coefficient of approximately 1 (Table 2). When comparing the species cover classes, productive black spruce and stagnant black spruce slope coefficients were 0.79 m/m and 0.89 m/m respectively, which were significantly lower ($p = 0.09$) than the estimated tamarack slope coefficient (1.43 m/m; Fig. 7). No significant differences in y-intercept were found among species cover class.

In addition, we compared differences in regression coefficients among age classes within each of the cover types. The relationship between precipitation and water level was not significant for productive black spruce 15–30 and 40–80, and stagnant black spruce 40–80 and > 100 years (Table 2; Fig. 7). All of the tamarack WT age classes were significantly correlated with cumulative precipitation. Comparison of the regression line slopes and intercepts among age classes within a cover type failed to identify any differences among any treatments where the regression was significant (data not shown).

4. Discussion

Interactions among climate change, forest management, and disturbance dynamics have potential to impact ecohydrological processes and change ecosystem functions (Holden, 2006; Waddington et al., 2015). Here, we compared three lowland conifer forest cover types of different age classes to evaluate the WT and ET dynamics for three years across a wide range of condition including differing amounts of growing season precipitation. A key finding is that we did not detect any evidence for a water table rise effect in the first 10 years after stand replacing disturbances (i.e., following clearcut harvest). We did observe differences in ET and WT response that varied by cover type and age class. These differences were largely associated with the 40–80-year age classes in both the productive spruce and tamarack cover types with no apparent differences among age classes in the stagnant spruce type. This study is one of the most comprehensive assessments documenting the associations of ET and WT in lowland conifer-peatland ecosystems, and our results demonstrate the potential for understanding response of hydrology to management in these important forest ecosystems.

The positive relationship between cumulative precipitation and WT depth we observed highlights the importance of variations in climate on ecohydrological processes in lowland conifer forests. Importantly, it appears that the WT-precipitation dynamics are variable by cover type and age class, suggesting different sensitivity and response depending on ecosystem parameters such as peat thickness and dominant cover type. Overall, the tamarack sites are more strongly influenced by variations in precipitation than either of the spruce cover types, and these dynamics have important implications in evaluating the resilience of these forested peatlands to future changes in climate.

4.1. General trends in WT and ET by species cover type

WTs across all study sites were drawn down throughout the growing season, with periodic rise in WTs that was associated with precipitation

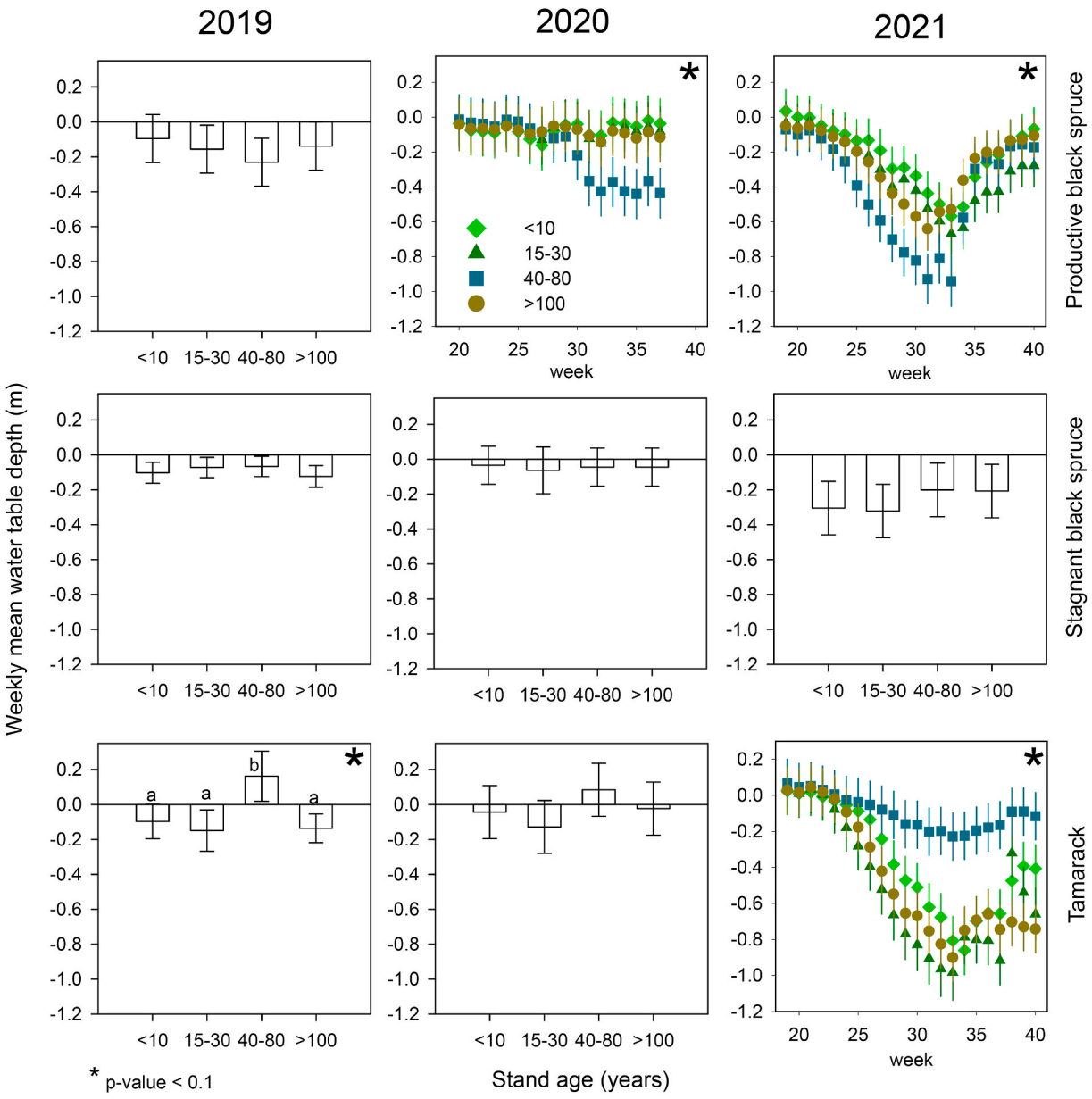

Fig. 5. Weekly least-squares mean WT from repeated measures ANOVA, within species and by year of measurement. Asterisks indicate a significant effect of age or the age-year interaction for a given cover type and year. Means with different letters with a cover type-year are significantly different. Error bars are the standard error of the mean. Note: plots displayed are based on statistical test; where time was not significant, we show the main effects of age class and cover type, when time was significant, we display the main effects by time period.

events. As there is a large heterogeneity and random distribution in the occurrence of precipitation events, these patterns varied among years and there is no general observed trend in timing of WT drawdown during the growing season by each forest cover type (see Fig. 3). Still, the general pattern of high WTs following winter snowmelt, followed by the gradual drawdown of WTs throughout the growing season is common in northern forested wetlands including hardwood swamps, riparian forests, and other forested wetlands (Mitsch and Gosselink, 2007).

Stagnant black spruce tended to have higher WTs than productive black spruce, but there were no significant differences in either yearly growing season mean WT trends or weekly comparisons. Tamarack had slightly higher WT mean than the two spruce cover types, but this was driven by a single age class, 40–80 years old (see Fig. 4). High WTs would not be unprecedented in tamarack; physiologically tamarack is better able to mitigate harmful effects of flooding than black spruce (Islam and Macdonald, 2004; Islam et al., 2003; Wolken et al., 2011) but the high water level pattern was not consistent across age classes. This finding may be anomalous due to limited site availability. Minnesota is currently experiencing a 20-year eastern larch beetle outbreak (DNR, 2019; Ward and Aukema, 2019) which likely impacted the availability of more productive stands for that age class (Crocker et al., 2016). According to our site selection criteria, forests where there was evidence of large amounts of infestation upon site feasibility inspection were not considered for study. Regardless, more monitoring is needed in these peatland types to determine if there are linkages between stand composition (and age) and WT dynamics.

ET was very similar in the three cover types, between 2.6 and 2.8 ± 1.3 mm/d, and this is within the range expected based on prior studies of black spruce or peatland ET using other methods such as Eddy Covariance (Arain et al., 2003; Humphreys et al., 2006; Moore et al., 2013), or closed chamber humidity observations (Kettridge et al., 2017). However, we found no significant difference between the three forest cover

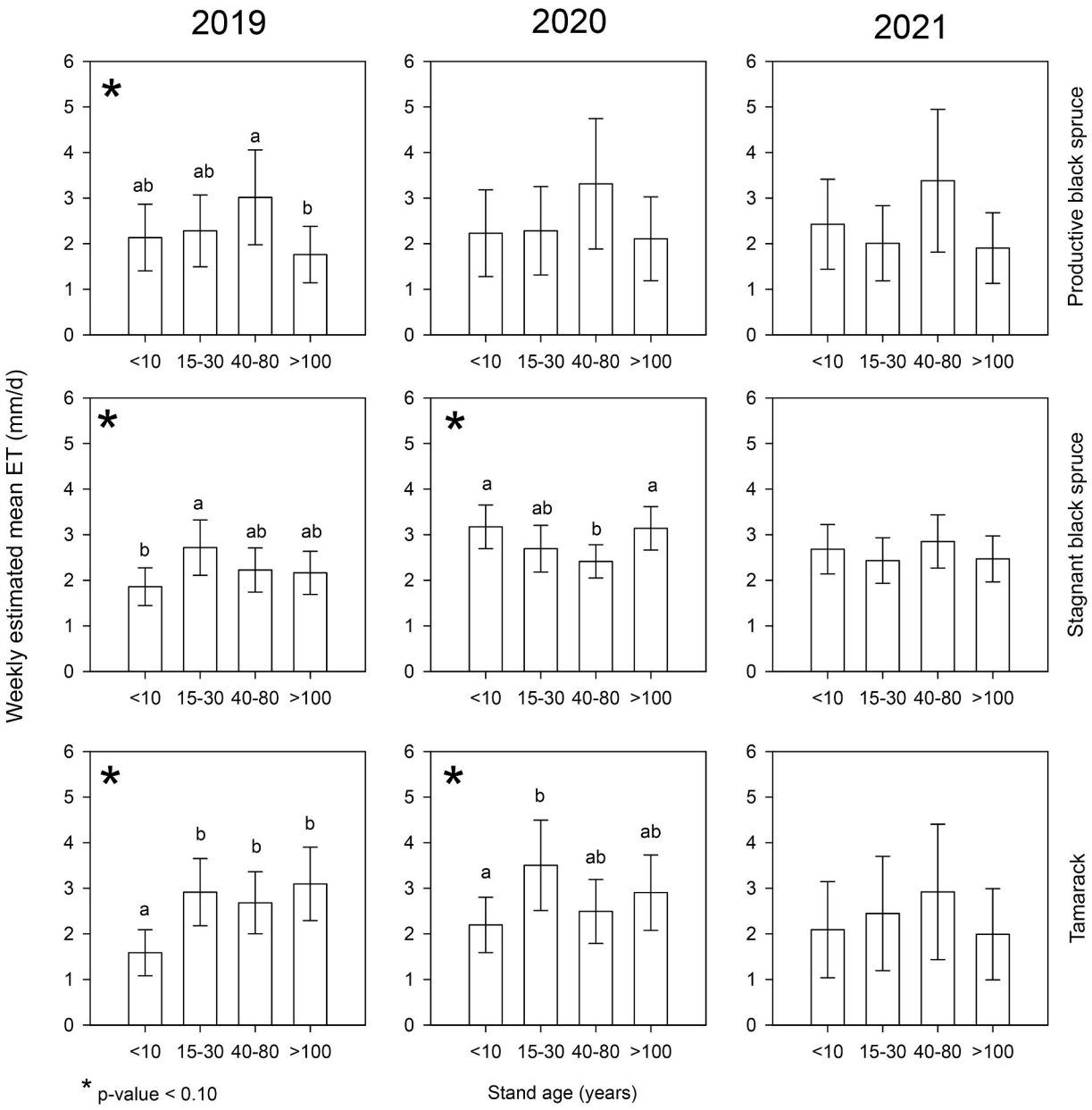

Fig. 6. Estimated weekly mean evapotranspiration (ET) from repeated measures ANOVA by cover type and age class. Asterisks indicate a significant effect of age for a given cover type and year. Means with different letters within a cover type and year are significantly different. Error bars for time series plots are the standard error of the mean.

types, suggesting that any differences in stand-level transpiration among the cover types is offset by corresponding differences in evaporation. More variation was found within cover types by stand age, and these responses are discussed below.

4.2. Peat thickness in relation to cover type and WT dynamics

There was thicker peat at the stagnant black spruce forest sites, which may reflect differences in developmental history and underlying hydrology (Clymo and Fogg, 1984). Additionally, the WT was generally higher in stagnant spruce compared to the other cover types. Such differences in peat depth and WT dynamics may provide indication of sensitivity of response to changing climate. For instance, thicker peat layers can provide buffer against average arid climate, but may be more greatly affected by sudden anomalies, such as drought (Drobyshev et al., 2010). Also, when considering peat thickness as a proxy for site quality in black spruce growth models, it negatively affects tree growth (Hökkä and Groot, 1999; Robichaud and Methven, 1993) which may be reflected in the lack of ET and related effects on the WT in the stagnant spruce cover type. In our study, peat depth was a significant influence on WT at coarse scales (i.e., it was a significant covariate for the yearly growing season mean WT response), but not at finer scales where it was rarely a significant covariate on weekly mean WT depths. This could indicate that peat depth may have different effects depending on the scale of analysis, as in Drobyshev et al. (2010) whereby the ability to buffer at short time periods might be overwhelmed by small high intensity events, such as pluvial or drought.

4.3. Ecohydrological response to stand age in different cover types

Our results indicate a lack of WT response to harvest in the two youngest of our four age classes representing the first 30 years. Previous studies have found water table rise appears to be greatest in the first few years after harvest when changes in the forest canopy are

Table 2
Least-squares regression statistics for response of June–Sept WT elevation (WT) to June–Sept cumulative precipitation.

	y-int	M	p-value	Adj. R^2
Productive black Spruce	**−0.445**	**0.79**	**<0.01**	**0.21**
<10	−0.489	1.11	0.01	0.58
15-30	−0.433	0.79	0.14	0.18
40-80	−0.526	0.66	0.27	0.05
>100	−0.649	1.90	<0.01	0.87
Stagnant Black Spruce	**−0.438**	**0.89**	**<0.01**	**0.31**
<10	−0.592	1.33	0.03	0.44
15-30	−0.681	1.58	<0.01	0.74
40-80	−0.304	0.60	0.20	0.11
>100	−0.178	0.13	0.78	0.13
Tamarack	**−0.590**	**1.43**	**<0.01**	**0.38**
<10	−0.796	2.07	0.01	0.62
15-30	−0.714	1.53	0.01	0.63
40-80	−0.426	1.50	<0.01	0.68
>100	−0.619	1.27	0.06	0.34
All Sites	**−0.497**	**1.06**	**<0.01**	**0.32**

greatest—more pronounced in mineral soils relative to organic soils (Dubé et al., 1995; Leppä et al., 2020; Slesak et al., 2014). Note that our study design is not able to detect short-term differences in water levels immediately after harvest but is robust enough to evaluate if there are long-term effects on WT dynamics. We propose that during the first 10 years after harvest, rapid vegetation growth (Greene et al., 1999; Qi and Scarratt, 1998) coupled with increased near surface evaporation (Nichols and Brown, 1980; Verry, 1986) largely offsets loss of transpiration by black spruce and tamarack, allowing WTs to remain similar to older forests. However, there was an apparent pattern, especially in 2019, of a lower ET in <10-year-old tamarack forests compared to older age classes. This is consistent with what is expected following clearcut regeneration harvest (Proulx et al., 2021), but does not align with the observed WT depths which were similar across age classes. The apparently conflicting response may be due to greater outflow from the peatland associated with disturbance-driven change in hydrologic gradients and an increase importance of macropore water transport (Holden, 2009; Liu et al., 2016; Ours et al., 1997).

When comparing weekly WT across the study, productive black spruce WT were significantly lower in the 40–80-year age class. ET had a complementary response, as it was generally higher in the 40–80-year age class in productive black spruce compared to the other age classes. In general, as forests mature, ET increases in tandem with stand development, eventually declining as age-dependent mortality increases (Barker et al., 2009; Taylor et al., 1988). The patterns in ET we observed in black spruce agree with this general response. The peak ET and lower WTs in the 40–80 years old class occur at a tipping point in forest development, where 40–80 years old black spruce forests reach the stem exclusion stage of stand development with density dependent mortality (Angstmann et al., 2012; Harper et al., 2005; Oliver and Larson, 1996). Black spruce in lowlands mature from full canopy to greater openness via gap dynamics in forests >80 years (St-Denis et al., 2010), and lower ET due to differences in stand volume (Sarkkola et al., 2010), which agrees with our results of the slightly reduced ET and higher WT in the >100 years old age class. The lowland black spruce stem exclusion period can occur past 60–80 years and vary with site index (Gray et al., 2021; Skay et al., 2021).

In contrast, stagnant black spruce did not have any notable response of WTs to stand age during the study period. Stagnant black spruce forests generally have relatively low net productivity throughout stand development compared to other peatland and upland forest types (Grigal et al., 1985) and this may be reflected in the limited differences in

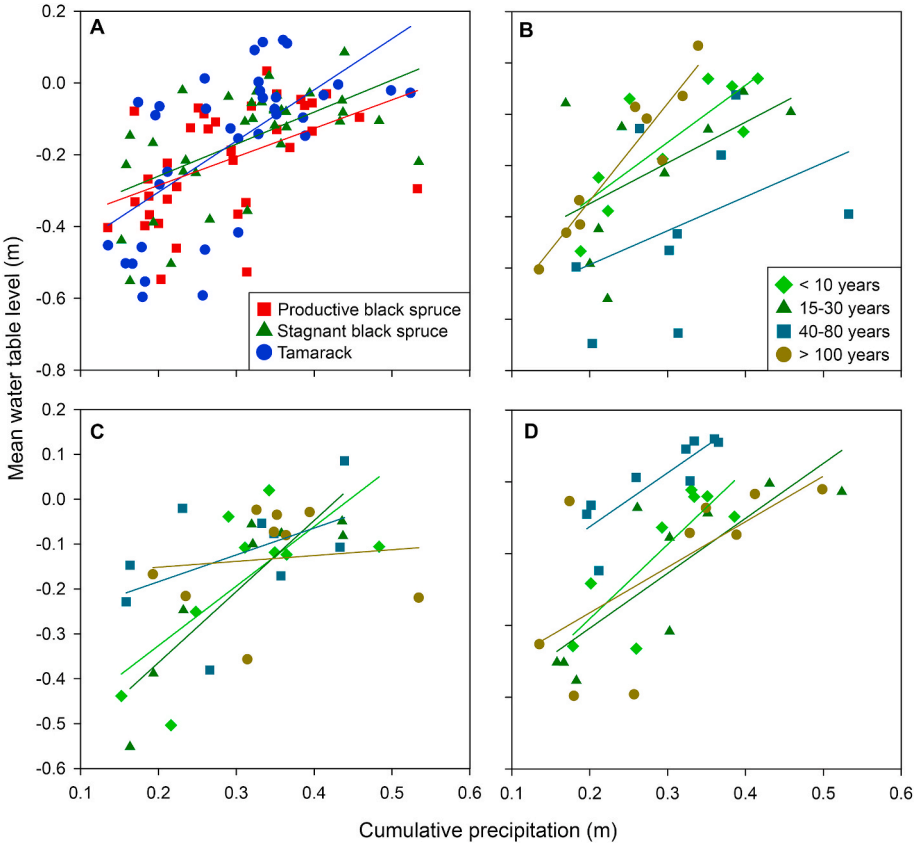

Fig. 7. Ordinary least-squares regressions (see Table 2) of growing season (June–September) mean WT versus cumulative precipitation for the same period. Presented as response of A) each forest cover type, B) productive black spruce stand age classes, C) stagnant black spruce stand age classes, and D) tamarack stand age classes. For regression coefficients and statistics see Table 2. In all sites, WT levels were positively correlated with cumulative precipitation.

WT dynamics across age classes that was observed. Taken together, our findings show that differences in the long-term responses and ecosystem change among the species and age classes is variable, and age of forest sites should be considered in predicting ET and WT sensitivity maximums/minimum over time.

4.4. WT response to precipitation and implications for climate change

Our finding that WT depth is often positively correlated with precipitation was expected given the importance of precipitation to the hydrologic regime of these ecosystems (Belyea and Clymo, 2001; Waddington et al., 2015). However, there are important distinctions among the forest cover types; black spruce cover types were generally less sensitive to changes in precipitation, while tamarack was more sensitive to changes in precipitation as evidenced by the significant regression analyses in all tamarack age classes with WT elevation. Further, the tamarack cover type had the highest overall significant response among the three cover types (Fig. 7A, Table 2).

The greater sensitivity of tamarack peatlands to changes in precipitation may result in reduced ability to buffer changes in the WT such as during drought or flooding conditions. Although mid-latitude and continental precipitation is predicted to increase (Pachauri and Meyer, 2014) increased episodes of precipitation extremes, such as drought or flooding, may become more frequent under climate change (Handler et al., 2014), with tamarack possibly having a more difficult time adapting. Greater changes in WT associated with changing precipitation may have important implications for ecosystem functions such as C storage and aboveground productivity (Blodau and Moore, 2003; Magnan et al., 2020; Waddington et al., 2015).

The differences in of the relationship between WT and precipitation among forest cover types could be due to several ecophysiological and structural factors influencing the ecohydrological feedback. For example, differences due to vegetation cover and related water uses (Waddington et al., 2015), such as differences in interception of rainfall, in rooting depths with respect to cover type-specific WT variability (Lieffers and Rothwell, 1987), and differences of hydraulic conductivity and discharge/recharge regimes within near-surface sphagnum hummock (McCarter and Price, 2014; Price and Whittington, 2010) all have potential to modify the relative influence of precipitation on mean WT depth.

Compared with the long-term climate record, precipitation in 2019 was near mean, 2020 was at or exceeding the 90th percentile, and 2021 year had the lowest precipitation near the 10th percentile (Fig. 2). Thus, we can use these 3 years as proxy for the possible trajectory of response under moderate precipitation (2019), higher than average precipitation (2020), and drought conditions (2021). Indeed, our comparison of mean yearly growing season mean WT depth by cover type illustrates that WTs were significantly lower in all cover types in 2021, with no significant difference between 2019 and 2020 (Fig. 4). We saw little difference however in the drought year with respect to ET, despite a significant drop in WT. This could relate to the limited role that water stress plays in overall water budget in spruce/tamarack peatland (Dunn et al., 2009), or increases in evaporation offsetting loss of transpiration (Verry, 1986).

5. Conclusion

Our study highlights the variability and complexity of WT and ET dynamics across managed lowland conifer forests that grow in high-water table peatland ecosystems of northern Minnesota. We found that tamarack and productive black spruce sites may be more sensitive to future changes in hydroclimate, particularly tamarack as WTs were much more responsive to changes in precipitation across years compared to the other cover types. In contrast, stagnant black spruce sites appear to be less sensitive to changes in precipitation, and generally had lower overall variability in WT levels. Further, there was limited evidence for anomalously high WTs following harvest across all cover types. We conclude that these peatlands return to hydrologic equilibrium relatively quickly post-harvest, likely because of relatively low-intensity management that mitigates long-term effects on site hydrology.

Credit author statement

JM Stelling: Writing-Original Draft, Formal analysis, Methodology, Software, Visualization, Data curation **RA Slesak**: Conceptualization, Methodology, Writing – Review & Editing, **MA Windmuller-Campione**: Conceptualization, Project administration, Writing-Review & Editing, Funding Acquisition, **Alexis Grinde**: Conceptualization, Writing-Review & Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2023.117783.

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