


Review

Analysis of the Effect of Climate Warming on Paludification Processes: Will Soil Conditions Limit the Adaptation of Northern Boreal Forests to Climate Change? A Synthesis

Ahmed Laamrani ^{1,2,*}, Osvaldo Valeria ², Abdelghani Chehbouni ^{1,3} and Yves Bergeron ² 

¹ Center for Remote Sensing Applications, Mohammed VI Polytechnic University, Ben Guerir 43150, Morocco; Abdelghani.Chehbouni@um6p.ma

² Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, QC J9X 5E4, Canada; osvaldo.valeria@uqat.ca (O.V.); Yves.Bergeron@uqat.ca (Y.B.)

³ Centre d'Études Spatiales de la Biosphère/Institut de Recherche pour le Développement (CESBIO/IRD), CNES/CNRS/INRAE/UPS/Université de Toulouse, 31401 Toulouse CEDEX 9, France

* Correspondence: Ahmed.Laamrani@um6p.ma; Tel.: +212-662099650

Received: 29 September 2020; Accepted: 5 November 2020; Published: 7 November 2020



Abstract: Northern boreal forests are characterized by accumulation of accumulation of peat (e.g., known as paludification). The functioning of northern boreal forest species and their capacity to adapt to environmental changes appear to depend on soil conditions. Climate warming is expected to have particularly pronounced effects on paludified boreal ecosystems and can alter current forest species composition and adaptation by changing soil conditions such as moisture, temperature regimes, and soil respiration. In this paper, we review and synthesize results from various reported studies (i.e., 88 research articles cited hereafter) to assess the effects of climatic warming on soil conditions of paludified forests in North America. Predictions that global warming may increase the decomposition rate must be considered in combination with its impact on soil moisture, which appears to be a limiting factor. Local adaptation or acclimation to current climatic conditions is occurring in boreal forests, which is likely to be important for continued ecosystem stability in the context of climate change. The most commonly cited response of boreal forest species to global warming is a northward migration that tracks the climate and soil conditions (e.g., temperature and moisture) to which they are adapted. Yet, some constraints may influence this kind of adaptation, such as water availability, changes in fire regimes, decomposer adaptations, and the dynamic of peat accumulation. In this paper, as a study case, we examined an example of potential effects of climatic warming on future paludification changes in the eastern lowland region of Canada through three different combined hypothetical scenarios based on temperature and precipitation (e.g., unchanged, increase, or decrease). An increase scenario in precipitation will likely favor peat accumulation in boreal forest stands prone to paludification and facilitate forested peatland expansion into upland forest, while decreased or unchanged precipitation combined with an increase in temperature will probably favor succession of forested peatlands to upland boreal forests. Each of the three scenarios were discussed in this study, and consequent silvicultural treatment options were suggested for each scenario to cope with anticipated soil and species changes in the boreal forests. We concluded that, despite the fact boreal soils will not constrain adaptation of boreal forests, some consequences of climatic warming may reduce the ability of certain species to respond to natural disturbances such as pest and disease outbreaks, and extreme weather events.

Keywords: North America; boreal forest; boreal soils; peatlands; adaptation; soil processes; soil warming experiments; climate change precipitation; temperature; paludification; productivity

1. Introduction

The boreal forest biome consists of a broad complex of forested and partially forested ecosystems that form a circumpolar belt through northern Eurasia and North America (Figure 1), and which account for about one-third of the earth's total forested area [1]. Boreal forests cover about 9% (~14 million km²) of the land area between 45° and 75° north latitude [1] and consist of a mosaic of forests and wetlands that reflect the adaptations of different plant species to harsh climatic conditions and a past history of natural disturbances. Boreal forests have been the subject of consequential research in recent years due to their association with increased global greenhouse gas concentrations (GHG; e.g., Carbon dioxide (CO₂), Methane (CH₄) in the atmosphere and for its potential to constitute large carbon reservoirs, which may play an important role in the feedback between the global carbon cycle and climate change [2]). These forests hold about one-third of global forest ecosystem carbon stocks [3] and play a central role in global GHG dynamics [4].

The structure, health, productivity, and distribution of tree species and forest ecosystems across boreal landscapes are mainly controlled by climate, soil conditions, relief, and biota [5]. Current climate models predict that changes in temperature, which is commonly referred to as “global warming”, and changes in precipitation (e.g., regional decreases or increases) are expected to be more pronounced in northern boreal regions [6]. These conditions can cause serious tree-killing in the west of Canada because of drought conditions; however, where precipitation is not a limiting factor, higher forest productivity is expected and would result in a variable response due to rapid ecosystem changes (i.e., changes in soil hydrology, permafrost degradation, more frequent fires, shrub invasions, increases in peak productivity and growing season, enhanced carbon losses, and emissions of greenhouse gases, among many others). For instance, Gauthier et al. [7] reported that by the end of the century (2071–2100), annual mean temperatures in the Canadian boreal region are expected to increase by 3.3 to 5.4 °C, relative to the period 1961–1990. This expected change will, over the long term, result in a spatial redistribution of major forest composition and the potential loss of habitat for some important adapted boreal species [8], which may be further complicated by human interactions or modifications of this ecosystem [9]. In the boreal region, warmer temperatures may expand the growing season and increase productivity [10], but that effect may not be sustained on sites where soil moisture is limiting [11] and low topographic relief may lead to creation of peatlands and favor wetland species over other forest species [12]. For example, under conditions of continued warming, in areas with drier soils and adequate drainage, forests may migrate northward into areas occupied by tundra vegetation (e.g., if soil moisture does not limit tree growth), which may lead to the replacement of certain forest species with steppe communities [13]. Northern boreal forest peatlands are characterized by peat accumulation (known as paludification). Two types of paludification are recognized on the basis of topography and time since the last fire, viz., permanent paludification that dominates in natural depressions within the landscape, and reversible paludification that occurs on flat or sloping terrain over time following fire or mechanical site preparation. Many parts of the circumpolar boreal forest, including interior Alaska, the western Siberian plain, and the Hudson Bay–James Bay Lowlands of Canada, are prone to paludification, more particularly coniferous forests.

Most broadly, the vegetation of the boreal forest can be divided into latitudinal zones through boreal landscapes with significant variation along this gradient due to a multitude of factors (e.g., soils and drainage, nutrient availability, microclimate, fire history). Coniferous boreal forests are widespread in the global boreal forest with black spruce (*Picea mariana* (Mill.) BSP), for instance, as one of the dominant tree species of the boreal forests of North America [14,15]. Black spruce forests occupy both upland and lowland peat bog sites and are well adapted to high soil moisture levels and cold, poorly aerated peat soils with low nutrient availability [16]. These forests generate litter that is relatively resistant to decomposition and, in the absence of severe fire, that promotes the formation of a thick forest floor layer dominated by feather moss and sphagnum that immobilizes nutrients [17]. In the context of global climate change, black spruce forests are important because of the substantial quantity of carbon accumulated in their soils, the occurrence of permafrost, and the close relationship

between black spruce forest type and fire disturbance (e.g., [18,19]). Consequently, expected climatic change in boreal forests [20] may accelerate decomposition rates of organic matter [6], increase soil moisture [21], elevate soil temperatures [22], alter water balance [23], reduce the duration of snow cover [24], degrade permafrost [25–27], and change in the frequency of wildfires [28,29]. Collectively, all of these effects may increase the release of carbon stored in boreal soils and have a significant, positive feedback on global warming through rising atmospheric CO₂ and CH₄ concentrations [30,31]. However, the loss of organic carbon caused by these positive feedbacks may be partially or entirely compensated by the gain in organic carbon stocks resulting from increased productivity or changes in the soil conditions that could include both wetting and drying trends [6].

The response of paludified boreal forests to changes in temperature and precipitation is related to complex interactions between soil, nutrient availability, water table level, soil biota, root respiration, and, where present, permafrost [32]. For instance, peatlands will likely adjust to expected increasing temperature through enhanced soil organic matter decomposition rates, which may make nutrients more readily mineralized and available to plants [33]. A better understanding of the effects of climate change on boreal forested peatlands soils is critical, since the functioning of boreal forest tree species and their capacity to adapt to environmental changes appears to depend mostly on soil conditions. The question that is addressed here is whether or not soil conditions (e.g., temperature, moisture, and soil nutrients) could limit the adaptation of boreal plant species to climate change. Consistent with the definition employed by Trainor et al. [34], “adaptation” is defined here as an adjustment or acclimation in ecological systems in response to actual or expected climatic stimuli and their effects or impacts. Thus, for the purpose of this work, the term adaptation does not refer to any genotypic changes.

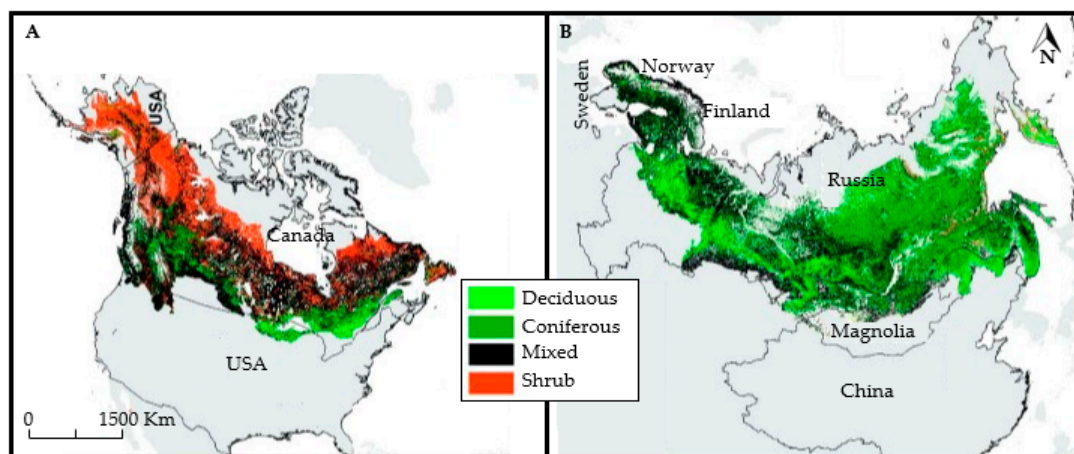


Figure 1. Global extent of the boreal circumpolar forest ((A): North American and (B): Eurasian) and major vegetative cover according to the 2000 Global Landcover dataset (www-tem.jrc.it/glc2000/) and modified after Bradshaw et al. [35].

The main goal of this work is to understand the effects of climate change on North America boreal paludified soils. To this end, we reviewed and synthesize results from reported studies, as well as analyzed studies showing modification of soil conditions as result of global warming and discussed the potential of boreal forest species to adapt to soil conditions under climate warming. We further discuss some processes (e.g., paludification, moisture dynamics) that will likely moderate or constrain the ability of boreal forest species to adapt to changing soil conditions. To this end, this paper will analyze the effects of climate warming on paludification processes in the Clay Belt region using different hypothetical climatic scenarios within northern boreal forested areas of eastern North America.

In this review we focused on studies from North American boreal forested peatlands, but studies from other forest regions or cold biomes were considered when they contributed to the understanding of the process. These studies were performed on a variety of substrates under a variety of conditions,

and have yielded different conclusions regarding the effects of climate warming on boreal soils. We reviewed, analyzed, and synthesized 99 published studies that we extracted from different research databases (i.e., SCOPUS, Web of Science, and Science Direct), and we explain in detail divergences and convergences between reviewed studies. North American boreal forests, Boreal soils; peatlands, adaptation; soil processes; soil warming experiments; climate change; precipitation; temperature; paludification; and productivity were the main keywords used (i.e., single and/or combined) as research criteria

2. Study Area and Boreal Forest Soils

2.1. Study Area

The boreal biome is the second largest biome in the world, and the circumpolar boreal forest stretches across Sweden, Finland, Norway, Russia, Alaska, and northern Canada (Figure 1). Twenty-two percent of the boreal forest is found in Russia (more than three-quarters in Siberia); the remaining majority is split between five other countries: Canada, USA, Sweden, Finland, and Norway (Figure 1). Some large areas of boreal forest are found in northern Mongolia and northeastern China. For the purpose of this synthesis, we defined the study area as the North American boreal forest that stretches across Alaska and Canada (Figure 1A).

2.2. Boreal Forest Soils and Classification

Boreal forests contain substantial amounts of organic carbon (~1700 Pg of C; [36]), which has been accumulating since the last deglaciation (e.g., the retreat of the Laurentide ice sheet in North America, 6000 y BP, [37]). These soils represent one-third of the world's soil organic carbon and are characterized by relatively cool temperatures that limit soil microbial activity and, therefore, decomposition rates [38]. Organic carbon plays a major role in nutrient cycling; as a result, the characteristics and quantity of organic layer input in soils both reflect and control soil development and, ultimately, the productivity of boreal ecosystems. Boreal forests also have an acidic upper soil layer, low evaporation, and frequent wet soil conditions, which tend to limit nutrient cycling [39]. In boreal forests, a variety of soil-forming processes can be found (e.g., organic matter accumulation, leaching, gleying, podzolisation, and clay mineral transformations). Among these, podzolisation is the most common soil-forming process [40], and podzols are therefore the typical soils of boreal forests [41]. Podzolisation is a complex process or number of sub-processes in which organic material and soluble minerals (e.g., commonly Fe and Al) are leached from upper horizons (e.g., A and E) to the lower B horizon [42]. A detailed description of podzolisation processes is provided in [43].

Boreal forest soils are generally young and have developed over time on mineral substrates. The composition of boreal soils commonly ranges from sand, loamy sand, and sandy loam soils (typically moderately acidic to neutral) to silty loam and clay loam heavier soils. Boreal forest soils that occur over bedrock are often of similar bedrock origin (e.g., granitic) and characterized by shallow organic soils or more humus. The influence of topography on boreal soil properties can be more important than other soil-forming factors such as time or parent material [44]. For instance, the flat topography (e.g., low slopes) in the two major peatlands of the world (e.g., the Russian West Siberian Plain and the Canadian Hudson Bay–James Bay Lowlands) illustrates the significance of this factor [45]. These low slopes lead to the important inference that such flat topography promotes the accumulation of organic matter, forming a thick forest floor layer in these regions.

In general, one cannot expect to find a standardized nomenclature of soil horizons because the boreal eco-region biome covers many countries that have their own systems of soil classification. While several studies from North America have used different nomenclatures, soil layer descriptions were occasionally very similar. According to the FAO's international soil classification system (IUSS Working Group WRB, 2015 [46]), the major soil orders in the boreal forest are Podzols, Cryosols, and Retisols, which are mainly conditioned by climate; Gleysols, which are mainly conditioned by

topography and physiography; and Histosols, which are conditioned by both climate, topography, and physiography that promote the accumulation of organic materials. In this paper, we used the Canadian Soil classification [47], which appears to better reflect soil decomposition processes (Table 1) in the North American context.

Table 1. Soil horizon characteristics according to the Canadian Soil classification.

Soil Characteristics/Drainage Conditions	Horizon	Features/Composition
Organic/ Well-drained	L	Fresh organic residues, recognizable plant material, i.e., leaves, on the surface of the forest floor.
	F	Decomposed plant material, i.e., roots, but the origins of plant residues are still distinguishable.
	H	Humified plant material where plant residues are not recognizable, with the exception of some roots or wood.
Organic/ Poorly drained	Of	Fibric horizon where there are more roots and amorphous material than moss detritus
	Om	Mesic horizon where plant residues are partly decomposed/amorphous. Intermediate decomposition between Of and Oh.
	Oh	Humic horizon with highly decomposed organics, amorphous and unrecognizable organics.
Mineral	Ah	Typically a brown silt loam, sometimes grading into sandy loam or loam, occasionally with charcoal and/or rocks

This classification defines organic horizons as layers with more than 17% organic carbon by weight (or more than 30% of organic matter). Organic horizons occur in organic soils or they may be present at the surface of mineral soils. There are two groups of organic horizons: (i) those that are formed in relatively well-drained conditions (LFH) and those that are formed in poorly drained conditions (Of, Om, Oh). A mineral soil horizon (A) is generally formed underneath the organic soil surface and contain less than 17% organic carbon by weight. Horizon A_h is the only mineral horizon included in humus form classification. A_h is at least 0.5% more carbon than the inorganic carbon horizon of the profile.

3. Expected Effect of Climate Warming on Boreal Soil Processes

The Intergovernmental Panel on Climate Change (IPCC; [20]) has arrived at the conclusion that climate change is no longer a subject for debate. Climate change manifests its presence in many ways, including increased temperature, together with changes in precipitation and precipitations trends. Several studies reported that soil temperature is a major factor affecting organic matter decomposition; consequently, global warming may accelerate decomposition processes (e.g., [48]), and the rates of decomposition are linked directly to temperature and moisture or nutrient availability [49], and indirectly to substrate quality [50]. Consequently, soil warming in boreal regions has the potential to create a very large, positive feedback in the global carbon cycle [51] if not compensated by increased forest productivity.

The effects of warmer climate on soil organic processes in cold biomes (e.g., from high latitude or high altitudes) have been the subject of many studies with a variety of substrates and under a variety of conditions (e.g., [52,53]). Yet, these studies have come to different conclusions regarding the effects of warming on important ecological processes (e.g., decomposition and mineralization rates, soil respiration, and soil moisture). Responses to soil warming have varied in the treated ecosystems (e.g., cold biomes or temperate) [54,55]; therefore, soil warming experiments have produced equivocal results. Most of these experiments showed that soil warming could increase litter decomposition, as well as nitrogen and phosphorus mineralization [56]. In contrast, other authors found no significant effects of warming on decomposition [54,57] or soil respiration [58]. Other studies found that litter decomposition could even be reduced by soil warming; this effect was probably caused by increased

drought in the litter [59]. A number of studies have found that respiration rate increases over the first few years (i.e., 2–10 years), with no significant increases in the long-term [56,60].

4. Anticipated Forest Soils and Species Distribution in Response to Global Warming

One of the anticipated responses of boreal forests to global warming is the migration of tree species to higher latitudes as climate and soil conditions to which they are adapted also change. Will such forest movements be realized, as suggested by many Dynamic Global Vegetation Models? Some vegetation models project that forests may eventually replace between 11% and 50% of tundra under doubling atmospheric CO₂ scenarios [61]. However, such migration is likely to be moderated or constrained by many processes, such as soil formation and paludification, moisture dynamics, local genetic adaptations, or topographic gradients, all of which have yet to be considered in most models (e.g., [62]), seed dispersal capacity of some species, and natural disturbances and their increased frequencies (i.e., wildfires and diseases outbreaks). The latter are not dealt with in this synthesis.

In the context of a warming climate, soil temperature and decomposition would likely increase in upland areas of boreal forests where drying occurs as a result of drought and/or well-drainage. For instance, a study [63] demonstrated that under a drier future climate, natural regeneration of conifers could be significantly reduced in the southern boreal forest of western Canada. Therefore, expected increases in boreal soil temperatures may shift boreal vegetation composition from coniferous to deciduous tree species [64]. In addition, greater nitrogen mineralization for deciduous than coniferous stands in both the mineral soil and forest floor of boreal mixedwood forests of northeastern Canada was found [65]. As the rate of decomposition is higher in boreal deciduous forests because of both litter and site conditions, this may further raise nitrogen availability, leading to increase in productivity.

In a two-year in situ soil warming experiment (e.g., 2.3 °C soil heated plots using open-topped chambers) conducted in boreal lowland peat bog forests where the water table is maintained, soil warming was found to have little or no significant impact on soil organic matter decay [57]. Higher water tables would increase soil heat capacity, possibly protecting soil organic against heterotrophic respiration [63]. Thus, climatic warming is expected to have a slight or no effect on decomposition in these lowland areas, which in turn will not affect the adaptation of boreal tree species to the elevated air temperature. Therefore, current soil conditions may persist for many decades in response to increasing temperature and climate change. Similarly, Dabros and Fyles [57] stated it is possible the threshold for changes in soil conditions required to significantly impact decomposition of northern plant species is high enough (e.g., at least within the mixedwood boreal regions) that climatic changes will have a slight or no impact on decomposition in the likely future.

In the context of climate warming, soil responses will likely also vary with site topography. Boreal upland areas with rapid drainage may experience more droughts than lowland peat bog areas, which could limit growth and forest productivity. For instance, a study [64] has found that the effects of a 2001–2003 drought period on net ecosystem productivity at several boreal sites were largely determined by topography. Ultimately, we believe that topography will play a major role in determining microclimate, snow accumulation, growing season length, soil water availability, as well as forest species distribution and adaptation across boreal landscapes. In areas of the northern boreal forest, global warming may lead to higher soil and permafrost temperatures and possibly the development of a deeper active layer [66,67]. As permafrost melts in the northern boreal forest, exposed soil becomes increasingly saturated with water [68]. One particular consequence of increasingly saturated soil, in the absence of high water demand of trees, is forest bogs and the process known as paludification. Paludification is the accumulation of organic layer over time and is generally thought to be caused by increasing soil moisture accumulation [45,69–71]. It reduces soil temperature, decomposition rates, microbial activity, and nutrient availability [45]. This process creates wetter conditions, which promote the growth of Sphagnum mosses [72] and the conversion of potentially forested areas to large bog landscapes that are largely resistant to forest establishment and growth [69].

If paludification occurs as a result of climate warming, boreal plant adaptation (movement toward higher latitudes) will be constrained by predicted changing soil conditions. Indeed, Crawford et al. [69] suggested that paludification may lead to a retreat rather than an advance in the northern limit of the boreal forest, contrary to general expectations. This suggestion was corroborated by another study [73], who reported that climatic warming may result in a retreat southwards of the boreal forest due to increased northerly bog development. However, the progression of forest changes within regions of discontinuous permafrost regions of Canada will be highly variable and potentially linked to local topographic variation induced by permafrost. As characterized by the conceptual models of [74], black spruce forests rise above flooded bogs and fens on peat plateaus underlain by ice-rich permafrost. Melting of permafrost results in subsequent subsidence of the elevated plateau causing inundation of the forest within the permafrost free bog or fen. In the southern regions where permafrost is no longer present, if drainage of the landscape has occurred there is evidence of forest regrowth in former bog locations [27]. These changes suggest various cycles of boreal forest loss and regrowth are highly dependent on the hydrologic functioning within the local environment.

The issue of paludification as a possible consequence of climatic warming and its effects on boreal soils must be further examined (e.g., [69–71]). Therefore, we believe the question of whether or not global warming will cause northern boreal forests to become paludified, together with the projected magnitude of this process, should be a high research priority. To this end, the potential effects of climate warming on paludification processes in the Clay Belt region are discussed hereafter through different hypothetical climatic scenarios.

5. Potential Effects of Climate Warming on Paludification in the Clay Belt Region

The Clay Belt region forms part of the Hudson Bay–James Bay lowlands of boreal eastern Canada. In this region, the mineral substrate is mostly composed of clay deposits resistant to water penetration that were left by pro-glacial Lake Ojibway [75], and which generally has flat topography (e.g., plains broken by gentle undulations or ridges; [76–78]). The location of these deposits promotes the accumulation of organic layer and landscape paludification [45,76,77] as well as an increase in water availability. The latter is related to precipitation (P) exceeding evapotranspiration (ET). In this region, a positive hydrological balance (e.g., P minus ET plus runoff) is critical for the initiation of peat formation and thus, paludification), especially in forested peatlands.

According to Canada's changing climate projections [79], summer temperature and precipitation are expected to increase in the Clay Belt region by 1–5 °C and 20%, respectively. For this region, projected annual mean temperature, precipitation, and maximum annual potential evapotranspiration were projected to increase by 4.7 °C, 15%, and ~12%, respectively, for the period 1951–2099 [80]. Based on many model scenarios we have a rather accurate prediction of future warming trends for the region [81]; however, much uncertainty regarding precipitation and evapotranspiration projections for the Clay Belt have also been identified, which might due to insufficient data to provide reliable and accurate precipitation trends [20].

Within the context of this study, we analyzed the effects of climate warming on paludification processes in the Clay Belt region for one temperature scenario (e.g., increase) and three precipitation scenarios (e.g., increase (S1), decrease (S2), or unchanged (S3)) (Table 2). To do so, we formulated the following questions: (i) how does paludification change across the Clay Belt landscape under climate change? (ii) Given these changes in paludification amplitude, should we also expect to see changes in vegetation composition? (iii) Finally, what would be the relative effects in future silvicultural treatments?

Table 2. Response of paludification to predicted climate change under three different scenarios (S1–S3) in the Clay Belt region, expected vegetation changes, and proposed silvicultural treatments.

Scenarios	Site Response		Vegetation Changes †	Silvicultural Treatments ‡
	Indicators	Paludification		
S1: ↑T & ↑P	↑ ET & WTL = ↑ ET & ↓WTL	= or slightly favored	BS + MW + WS	TC + PB
S2: ↑T & ↓P	↑ decomp. rate ↓ Sphagnum growth	↓ & ↑ soil nutrient availability	AS + JP + WS	TC + PC + Rep.: JP, WS, Po
S3: ↑T & P =	↑ ET & ↓WTL ↑ decomp. rate ↓ Sphagnum growth	↓ stands prone to paludification	AS + MW + BS	TC + PB + Rep.: JP, WS, Po

T = Temperature. P = Precipitation. ET = Evapotranspiration, WTL = Water-table level. Increases are indicated by ↑, decreases by ↓, unchanged by =, and significant increases and decreases by bold ↑ and ↓, respectively. † Expected vegetation changes: BS = black spruce; MW = Mixedwoods, WS = White spruce; AS = Aspen; JP = Jack Pine; Po = Poplar. ‡ Suggested silvicultural treatments for climate change mitigation: TC = Total clear-cutting, PB = Prescribed burn; PC = Partial cutting, Rep. = Replanting.

5.1. The Anticipated Effects on Paludification and Related Changes in Vegetation

The first scenario S1 will show greater precipitation that offsets increased evapotranspiration (ET) in forested peatlands. We believe that this scenario should not lead to significant soil moisture content alterations, an increase in ET and, consequently, water-table level (WTL) would be maintained, and peat accumulation should remain unchanged or be favored. As a result, currently existing paludified sites may persist indefinitely in response to climate warming and in the absence of fire. Under such conditions, mixedwood (MW) and white spruce (*Picea glauca* (Moench) Voss) will eventually replace black spruce (BS) in upland areas, while black spruce stands will likely remain dominant in lowland areas [82] or degrade into forested bogs or open peatlands. Under this scenario there is a possibility that increased precipitation will compensate for increased ET in a warmer climate. However, a recent study by Helbig et al. [83] suggested that there may not be enough precipitation to outpace with the rate at which peatlands are losing water because of increasing temperatures.

In the second scenario S2, soil moisture content in forest peatland is expected to undergo significant alteration, with a much lower WTL and higher ET. Consequently, this would result in an increase in organic matter decomposition, a reduction in sphagnum growth and, therefore, a decrease in the abundance of paludified sites in the Clay Belt. Such conditions may result in excessive soil moisture stress and conversion of peatland forested sites to aspen (*Populus tremuloides* Michx.) (AS) and white spruce (WS) dominated forests. This scenario is expected to lead to an increase in forest productivity.

The third scenario S3 is the reference scenario but with increased temperature combined with unchanged precipitation. This scenario increased ET and decreased WTL, but with lower intensity than S2. As a result, the thick organic layers are expected to dry out and bring about a decline in sphagnum growth within stands that are prone to paludification. Consequently, mixedwood and white spruce will eventually replace black spruce-dominated sites in lowlands and dry, well-drained uplands, respectively.

5.2. Silvicultural Treatment Changes under the Three Scenarios

Given the expected paludification response (i.e., maintaining, adaptation, reversing) to climatic scenarios, we revisited the different silvicultural treatments in regard to the vegetation composition changes following the three scenarios (Table 2). For S1 and S3, summer clear-cut (TC: total clear-cutting) and prescribed burning (PB), when combined with appropriate site preparation that removes the thick organic layers, will have the potential to reduce or reverse paludification and consequently increase site productivity [45,84]). However, we believe that this is a problematic scenario for climate change mitigation that would result in lots of carbon emissions. From an industrial perspective, partial cutting

(PC) is much more expensive than TC. However, TC offers an open sun-exposed habitat that would be favorable to sphagnum growth [85] and increasing the rate of paludification [73].

Under scenario S2, nutrient availability should increase (e.g., nitrogen) because of enhanced decomposition rates and dry conditions in the thick organic layers. In this case, silvicultural treatments such as TC and PC followed by site replanting with non-N-limited boreal species that are adapted to dry soil conditions and shade intolerant (e.g., poplar, birch (*Betula papyrifera* Marshall), jack pine (*Pinus banksiana* Lamb.) (JP), WS) should be more appropriate in the context of reversing paludification.

Under the three scenarios, precipitation is likely to play a major role in the Clay Belt boreal forest. For the 21st century, increased precipitation (e.g., ~15–20%) would likely increase peat accumulation in boreal forest stands that are prone to paludification and facilitate the expansion of forested peatlands into upland forests, while reduced or unchanged precipitation levels combined with increased temperatures (e.g., ~4.7 °C) would most probably favor development of forested peatlands towards upland boreal forests [70].

6. Will Soil Conditions Limit the Adaptation of Boreal Ecosystems to Climate Change? Concluding Synthesis

6.1. Boreal Ecosystem Response to Climate-Induced Changes

Expected climatic warming in boreal forests can clearly alter processes in soils by changing forest composition, vegetation uptake rates, soil conditions, moisture and temperature regimes, and soil microbial activity. Several studies in the literature have shown that these alterations in soil conditions often led to increases in CO₂ emissions [30,31,60,61] and greater nutrient availability (e.g., N and P) [16,45,49]. Warming may affect microbial abundance and biomass as well in different ways and will depend on soil conditions (e.g., drier upland vs. wetland boreal ecosystems). It is also apparent that soil responses to warming can be highly variable and will depend on site conditions. The extent and magnitude of warming on boreal soil conditions will depend on soil types and site (e.g., permafrost sites), with strong regional differences. In addition, some of the variability among results reported in published studies could have arisen from differences in methods used and sampling designs. Indeed, many of the warming soil studies reported in the literature have been short-term, usually less than three years duration with an emphasis on the first year or two [56,60]. Because some impacts on soil could be prolonged or delayed for many years, long-term warming experiments in boreal forests are necessary to evaluate transient responses, to determine longer-term trends, and to give the boreal ecosystem the time necessary to respond to climate-induced changes. Indeed, a number of soil warming studies found that the respiration rate increased over the first few years, but there was no significant increase in the long-term.

6.2. Effects in Future Silvicultural Treatments in the Context of Expected Changes of Paludification under the Three Selected Scenarios

Most of the reviewed studies indicated or inferred that, under soil warming conditions, boreal forests may respond positively to increased CO₂ levels and temperature, provided that water does not act as inhibitor at high and low levels. The most frequently cited response of boreal forest species to global warming is northward migration to track soil conditions (e.g., temperature and moisture) to which they are adapted. Yet, some constraints may influence this kind of adaptation (migration), such as water availability, changes in fire regimes, decomposer adaptations, and paludification. Precipitation played a major role in the potential paludification response. Given the expected climate change in the study region, where precipitation is expected to increase, we believe that S2 appears the least probable outcome. Summer clear-cut harvesting and prescribed burning followed by appropriate site preparation have been suggested for the more probable scenarios S1 and S3. Partial harvesting followed by site replanting with adapted boreal species to dry soil conditions is suggested as well [86].

Because climate change is expected to be more pronounced in boreal regions, efforts to maintain or enhance the ability of boreal forests to adapt to climate alterations are essential. An overview of possible approaches for adapting forests to climate change has been provided in [87,88].

The growing demand for wood products is expected to increase pressure to harvest sites that are undergoing paludification in the Clay Belt region. We believe that forest management practices should be planned in context with forest adaptation to expected climate changes, and eventually under one of the more probable scenarios (S1 or S3). Recent studies by Laamrani et al. [75–77,89] have demonstrated that, in order to maintain or improve forest productivity in the Clay Belt region under current conditions, management strategies should focus on sloping sites rather than on almost flat sites ($\leq 2\%$) that are associated with deep organic layers. The latter are often not suitable for tree plantations [90], provide few ecological or economic motives to manage soils with low slopes [91], and are expected to limit the use of equipment that would be required for mechanical site preparation and harvesting within the highly paludified areas [92–94]. We believe that these studies, for instance, can be used for defining promising areas where efforts and investments should be made to obtain higher soil carbon storing and planting and where structure and biodiversity of paludified forests can be preserved.

Although this analysis was an attempt to predict paludification responses through three hypothetical scenarios for the Clay Belt lowland region, some site-specific features such as topographic depressions with higher peat accumulations [95] should be taken into consideration in the anticipated response. Further research is needed to (i) improve these predictions (e.g., quantitative relationships between precipitation and ET) for a better understanding of the impact of climate change on boreal forest stands prone to paludification. (ii) Incorporate other influential factors in peatland formation such as deposition of dust and pollutants and fire [96,97], and most importantly the roles of human interference as future development that will certainly stress the peatlands including paludified areas. We believe that human impacts on such sensitive areas can even overwhelm the effects of the climate and contribute to drying peatlands, which can lead to releasing stored carbon and contributes to further warming [83,98]. (iii) Explore in detail real climate-induced changes in species diversity, mosses and shrub abundance, and aboveground vascular plant biomass both in Canadian boreal upland and peatland forested regions.

Finally, despite the fact that boreal soils are not expected to constrain adaptation of boreal forests, some consequences of climatic warming may reduce the ability of certain species to respond to natural disturbances (e.g., pest and disease outbreaks, and extreme weather events). Under such conditions, a study [99] predicted a greater extinction risk for a number of species and, given the rapid rate at which climate change is expected to occur, greater pressure for many other species to adapt to their new northern soil conditions.

Author Contributions: All the authors of this manuscript have contributed substantially to the work reported Conceptualization, A.L.; validation, O.V., A.C., Y.B.; formal analysis, A.L.; investigation, A.L.; resources, O.V., A.C., Y.B.; data curation, A.L.; writing—original draft preparation, A.L.; writing—review and editing, O.V., A.C., Y.B.; supervision, O.V., and Y.B.; project administration, O.V.; Y.B.; funding acquisition, Y.B., A.L., O.V. All authors have read and agreed to the published version of the manuscript.

Funding: The lead author was financially supported by the Fonds de Recherche du Québec—Nature et Technologies (FRQNT), Natural Sciences and Engineering Research Council of Canada (NSERC), the Regional conference of elected representatives of James Bay (CRE-James Bay), NSERC-UQAT-UQAM Chair in Sustainable Forest Management, Centre for Forest Research, and Tembec Incorporated. The work reported here was a part of research funded by these funding institutions.

Acknowledgments: The authors would like to acknowledge Pierre Bernier from Natural Resources Canada—Laurentian Forestry Centre, and Francine Tremblay from the IRF-UQAT for reviewing an earlier version of this manuscript and for their helpful comments which greatly improved the manuscript. We also thank the academic editor and three anonymous reviewers for their helpful comments which greatly improved earlier versions of the manuscript.

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

References

1. Thiffault, E. Chapter 5—Boreal forests and soils. *Dev. Soil Sci.* **2019**, *36*, 59–82. [[CrossRef](#)]
2. Mason, K.E.; Oakley, S.; Street, L.E.; Arroñiz-Crespo, M.; Jones, D.L.; DeLuca, T.H.; Ostle, N.J. Boreal Forest Floor Greenhouse Gas Emissions Across a Pleurozium schreberi-Dominated, Wildfire-Disturbed Chronosequence. *Ecosystems* **2019**, *22*, 1381–1392. [[CrossRef](#)]
3. Pan, Y.; Birdsey, R.A.; Fang, J.; Houghton, R.; Kauppi, P.E.; Kurz, W.A.; Phillips, O.L.; Shvidenko, A.; Lewis, S.L.; Canadell, J.G.; et al. A large and persistent carbon sink in the world's forests. *Science* **2011**, *333*, 988–993. [[CrossRef](#)] [[PubMed](#)]
4. McNamara, N.P.; Gregg, R.; Oakley, S.; Stott, A.; Rahman, M.T.; Murrell, J.C.; Wardle, D.A.; Bardgett, R.D.; Ostle, N.J. Soil Methane Sink Capacity Response to a Long-Term Wildfire Chronosequence in Northern Sweden. *PLoS ONE* **2015**, *10*, e0129892. [[CrossRef](#)] [[PubMed](#)]
5. Van Cleve, K.; Powers, R.F. Soil carbon, soil formation, and ecosystem development. In *Carbon Forms and Functions in Forest Soils*. Madison (WI); McFee, W.W., Kelly, J.M., Eds.; Soil Science Society of America: Madison WI, USA, 1995. [[CrossRef](#)]
6. Wickland, K.P.; Neff, J.C. Decomposition of soil organic matter from boreal black spruce forest: Environmental and chemical controls. *Biogeochemistry* **2008**, *87*, 29–47. [[CrossRef](#)]
7. Gauthier, S.; Bernier, P.; Burton, P.J.; Edwards, J.; Isaac, K.; Isabel, N.; Jayen, K.; Le Goff, H.; Nelson, E.A. Climate change vulnerability and adaptation in the managed. *Environ. Rev.* **2014**, *22*, 256–285. [[CrossRef](#)]
8. Hamann, A.; Wang, T. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology* **2006**, *87*, 2773–2786. [[CrossRef](#)]
9. Hannah, L.; Roehrdanz, P.R.; Krishna Bahadur, K.C.; Fraser, E.D.; Donatti, C.I.; Saenz, L.; Wright, T.M.; Hijmans, R.J.; Mulligan, M.; Berg, A.; et al. The environmental consequences of climate-driven agricultural frontiers. *PLoS ONE* **2020**, *15*, e0228305. [[CrossRef](#)] [[PubMed](#)]
10. Zhu, W.H.; Tian, H.; Xu, X.; Pan, Y.; Chen, G.; Lin, W. Extension of the growing season due to delayed autumn over mid and high latitudes in North America during 1982–2006. *Glob. Ecol. Biogeogr.* **2012**, *21*, 260–271. [[CrossRef](#)]
11. D'Orangeville, L.; Houle, D.; Duchesne, L.; Phillips, R.P.; Bergeron, Y.; Kneeshaw, D. Beneficial effects of climate warming on boreal tree growth may be transitory. *Nat. Commun.* **2018**, *9*, 3213. [[CrossRef](#)]
12. Reichsten, M. Impact of climate change on forest soils carbon: Principles, factors, models, uncertainties. *For. Clim. Chang.* **2007**, 125–135. [[CrossRef](#)]
13. Chapin, F.S., III; Callaghan, T.V.; Bergeron, Y.; Fukuda, M.; Johnstone, J.F.; Juday, G.; Zimov, S.A. Global change and the boreal forest: Thresholds, shifting states or gradual change? *Ambio* **2004**, *33*, 361–365. [[CrossRef](#)] [[PubMed](#)]
14. O'Connell, K.E.B.; Gower, S.T.; Norman, J.M. Comparison of net primary production and light-use dynamics of two boreal black spruce forest communities. *Ecosystems* **2003**, *6*, 236–247. [[CrossRef](#)]
15. Bergeron, Y.; Cyr, D.; Girardin, M.P.; Carcaillet, C. Will climate change drive 21st century burn rates in Canadian boreal forests outside of natural variability: Collating global climate model experiments with sedimentary charcoal data. *Int. J. Wildland Fire* **2010**, *19*, 1127–1139. [[CrossRef](#)]
16. Roy, V.; Bernier, P.Y.; Plamondon, A.P.; Ruel, J.C. Effect of drainage and microtopography in forested wetlands on the microenvironment and growth of planted black spruce seedlings. *Can. J. For. Res.* **1999**, *29*, 563–574. [[CrossRef](#)]
17. Oechel, W.C.; Van Cleve, K. The role of bryophytes in nutrient cycling in the taiga. In *Forest Ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function*; van Cleve, K., Chapin, F.S., III, Flanagan, P.W., Viereck, L.A., Dyrness, C.T., Eds.; Springer: New York, NY, USA, 1986; pp. 121–137.
18. Johnstone, J.F.; Kasischke, E.S. Stand-level effects of soil burn severity on postfire regeneration in a recently burned black spruce forest. *Can. J. For. Res.* **2005**, *35*, 2151–2163. [[CrossRef](#)]
19. Vogel, J.G.; Valentine, D.W.; Ruess, R.W. Soil and root respiration in mature Alaskan black spruce forests that vary in soil organic matter decomposition rates. *Can. J. For. Res.* **2005**, *35*, 161–174. [[CrossRef](#)]
20. IPCC. *Climate Change 2014: Mitigation of Climate Change. Contribution of Working Group III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*; Edenhofer, O., Pichs-Madruga, R., Sokona, Y., Farahani, E., Kadner, S., Seyboth, K., Adler, A., Baum, I., Brunner, S., Eickemeier, P., et al., Eds.; Cambridge University Press: Cambridge, UK; New York, NY, USA, 2014.

21. Akinremi, O.O.; McGinn, S.M.; Cutforth, H.W. Precipitation trends on the Canadian prairies. *J. Clim.* **1999**, *12*, 2996–3003. [[CrossRef](#)]
22. Osterkamp, T.E.; Romanovsky, V.E. Evidence for warming and thawing of discontinuous permafrost in Alaska. *Permafrost. Periglac. Process.* **1999**, *10*, 17–37. [[CrossRef](#)]
23. Oechel, W.C.; Vourlitis, G.L.; Hastings, S.J.; Ault, R.P., Jr.; Bryant, P. The effects of water table manipulation and elevated temperature on the net CO₂ flux of wet sedge tundra ecosystems. *Glob. Chang. Biol.* **1998**, *4*, 77–90. [[CrossRef](#)]
24. Beniston, M. Variations of snow depth and duration in the Swiss Alps over the last 50 years: Links to changes in large-scale climatic forcings. *Clim. Chang.* **1997**, *36*, 281–300. [[CrossRef](#)]
25. Sazonova, T.S.; Romanovsky, V.E.; Walsh, J.E.; Sergueev, D.O. Permafrost dynamics in the 20th and 21st centuries along the East Siberian transect. *J. Geophys. Res. Atmos.* **2004**, *109*, 1–20. [[CrossRef](#)]
26. Zhang, T.; Frauenfeld, O.W.; Serreze, M.C.; Etringer, A.; Oelke, C.; McCreight, J.; Barry, R.G.; Gilichinsky, D.; Yang, D.; Ye, H.; et al. Spatial and temporal variability in active layer thickness over the Russian Arctic drainage basin. *J. Geophys. Res. Atmos.* **2005**, *110*, 1–14. [[CrossRef](#)]
27. Carpino, O.A.; Berg, A.A.; Quinton, W.L.; Adams, J.R. Climate change and permafrost thaw-induced boreal forest loss in northwestern Canada. *Environ. Res. Lett.* **2018**, *13*, 084018. [[CrossRef](#)]
28. Gillett, N.P.; Weaver, A.J.; Zwiers, F.W.; Flannigan, M.D. Detecting the effect of climate change on Canadian forest fires. *Geophys. Res. Lett.* **2004**, *31*, 1–4. [[CrossRef](#)]
29. Flannigan, M.D.; Logan, K.A.; Amiro, B.D.; Skinner, W.R.; Stocks, B.J. Future area burned in Canada. *Clim. Chang.* **2005**, *72*, 1–16. [[CrossRef](#)]
30. Keyser, A.R.; Kimball, J.S.; Nemani, R.R.; Running, S.W. Simulating the effects of climate change on the carbon balance of North American high-latitude forests. *Glob. Chang. Biol.* **2000**, *6*, 185–195. [[CrossRef](#)]
31. McGuire, A.D.; Sitch, S.; Clein, J.S.; Dargaville, R.; Esser, G.; Foley, J.; Heimann, M.; Joos, F.; Kaplan, J.; Kicklighter, D.W.; et al. Carbon balance of the terrestrial biosphere in the twentieth century: Analyses of CO₂, climate and land use effects with four process-based ecosystem models. *Glob. Biogeochem. Cycles* **2001**, *15*, 183–206. [[CrossRef](#)]
32. Lafleur, B.; Paré, D.; Fenton, N.J.; Bergeron, Y. Growth and nutrition of black spruce seedlings in response to disruption of Pleurozium and Sphagnum moss carpets in boreal forested peatlands. *Plant. Soil* **2011**, *345*, 141–153. [[CrossRef](#)]
33. Kirschbaum, M.U.F. Forest growth and species distribution in a changing climate. *Tree Physiol.* **2000**, *20*, 309–322. [[CrossRef](#)]
34. Trainor, S.F.; Calef, M.; Natcher, D.; Chapin Iii, F.S.; McGuire, A.D.; Huntington, O.; Duffy, P.; Rupp, T.S.; Dewilde, L.; Kwart, M.; et al. Vulnerability and adaptation to climate-related fire impacts in rural and urban interior Alaska. *Polar Res.* **2009**, *28*, 100–118. [[CrossRef](#)]
35. Bradshaw, C.J.A.; Warkentin, I.G.; Sodhi, N.S. Urgent preservation of boreal carbon stocks and biodiversity. *Trends Ecol. Evol.* **2009**, *24*, 541–548. [[CrossRef](#)]
36. DeLuca, T.H.; Boisvenue, C. Boreal forest soil carbon: Distribution, function, and modelling. *Forestry* **2012**, *85*, 161–184. [[CrossRef](#)]
37. Hawkins, B.A. Summer vegetation, deglaciation and the anomalous bird diversity gradient in eastern North America. *Glob. Ecol. Biogeogr.* **2004**, *13*, 321–325. [[CrossRef](#)]
38. Gorham, E. Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. *Ecol. Appl.* **1991**, *1*, 182–195. [[CrossRef](#)]
39. Bonan, G.B.; Shugart, H.H. Environmental factors and ecological processes in boreal forests. *Annu. Rev. Ecol. Syst.* **1989**, *20*, 1–28. [[CrossRef](#)]
40. Moore, T.R. Soil Formation in Northeastern Canada. *Ann. Assoc. Am. Geogr.* **1978**, *68*, 518–534. [[CrossRef](#)]
41. Stützer, A. Podzolisation as a soil forming process in the alpine belt of Rondane, Norway. *Geoderma* **1999**, *91*, 237–248. [[CrossRef](#)]
42. Lundström, U.S.; Van Breemen, N.; Bain, D. The podzolization process. A review. *Geoderma* **2000**, *94*, 91–107. [[CrossRef](#)]
43. Sauer, D.; Sponagel, H.; Sommer, M.; Giani, L.; Jahn, R.; Stahr, K. Podzol: Soil of the year A review on its genesis, occurrence, and functions. *J. Plant Nutr. Soil Sci.* **2007**, *170*, 581–597. [[CrossRef](#)]
44. Seibert, J.; Stendahl, J.; Sørensen, R. Topographical influences on soil properties in boreal forests. *Geoderma* **2007**, *141*, 139–148. [[CrossRef](#)]

45. Lavoie, M.; Paré, D.; Fenton, N.; Groot, A.; Taylor, K. Paludification and management of forested peatlands in Canada: A literature review. *Environ. Rev.* **2005**, *13*, 21–50. [[CrossRef](#)]
46. IUSS Working Group WRB. *World Reference Base for Soil Resources 2014, Update 2015, International Soil Classification System for Naming Soils*; World Soil Resources Report 106; Food and Agriculture Organization of the United Nations: Rome, Italy, 2015.
47. Soil Classification Working Group. *The Canadian System of Soil Classification*, 3rd ed.; Agriculture and Agri-Food Canada Publication 1646; Agriculture and Agri-Food Canada: Ottawa, ON, Canada, 1998; p. 187.
48. Domisch, T.; Finér, L.; Laine, J.; Laiho, R. Decomposition and nitrogen dynamics of litter in peat soils from two climatic regions under different temperature regimes. *Eur. J. Soil Biol.* **2006**, *42*, 74–81. [[CrossRef](#)]
49. Liski, J.; Nissinen, A.; Erhard, M.; Taskinen, O. Climatic effects on litter decomposition from arctic tundra to tropical rainforest. *Glob. Chang. Biol.* **2003**, *9*, 575–584. [[CrossRef](#)]
50. Shaw, M.R.; Harte, J. Control of litter decomposition in a subalpine meadow–sagebrush steppe ecotone under climate change. *Ecol. Appl.* **2001**, *11*, 1206–1223.
51. Goulden, M.L.; Wofsy, S.C.; Harden, J.W.; Trumbore, S.E.; Crill, P.M.; Gower, S.T.; Fries, T.; Daube, B.C.; Fan, S.M.; Sutton, D.J.; et al. Sensitivity of boreal forest carbon balance to soil thaw. *Science* **1998**, *279*, 214–217. [[CrossRef](#)]
52. Agren, G.I.; Bosatta, E.; Magill, A.H. Combining theory and experiment to understand effects of inorganic nitrogen on litter decomposition. *Oecologia* **2001**, *128*, 94–98. [[CrossRef](#)]
53. Gauthier, S.; Bernier, P.; Kuuluvainen, T.; Shvidenko, A.Z.; Schepaschenko, D.G. Boreal Forest Health and Global Change. *Science* **2015**, *349*, 819–822. [[CrossRef](#)]
54. Aerts, R. The freezer defrosting: Global warming and litter decomposition rates in cold biomes. *J. Ecol.* **2006**, *94*, 713–724. [[CrossRef](#)]
55. Zhang, D.; Hui, D.; Luo, Y.; Zhou, G. Rates of litter decomposition in terrestrial ecosystems: Global patterns and controlling factors. *J. Plant Ecol.* **2008**, *1*, 85–93. [[CrossRef](#)]
56. Rustad, L.E.; Campbell, J.L.; Marion, G.M.; Norby, R.J.; Mitchell, M.J.; Hartley, A.E.; Cornelissen, J.H.C.; Gurevitch, J.; Alward, R.; Beier, C.; et al. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* **2001**, *126*, 543–562. [[CrossRef](#)] [[PubMed](#)]
57. Dabros, A.; Fyles, J.W. Effects of open-top chambers and substrate type on biogeochemical processes at disturbed boreal forest sites in northwestern Quebec. *Plant Soil* **2010**, *327*, 465–469. [[CrossRef](#)]
58. Pajari, B. Soil respiration in a poor upland site of Scots pine stand subjected to elevated temperatures and atmospheric carbon concentration. *Plant Soil* **1995**, *168–169*, 563–570. [[CrossRef](#)]
59. Robinson, C.H.; Wookey, P.A.; Parsons, A.N.; Potter, J.A.; Callaghan, T.V.; Lee, J.A.; Press, M.C.; Welker, J.M. Responses of plant litter decomposition and nitrogen mineralisation to simulated environmental change in a high arctic polar semi-desert and a subarctic dwarf shrub heath. *Oikos* **1995**, *74*, 503–512. [[CrossRef](#)]
60. Eliasson, P.E.; McMurtrie, R.E.; Pepper, D.A.; Strömngren, M.; Linder, S.; Agren, G.I. The response of heterotrophic CO₂ flux to soil warming. *Global. Chang. Biol.* **2005**, *11*, 167–181. [[CrossRef](#)]
61. Kaplan, J.O.; Bigelow, N.H.; Prentice, I.C.; Harrison, S.P.; Bartlein, P.J.; Christensen, T.R.; Cramer, W.; Matveyeva, N.V.; McGuire, A.D.; Murray, D.F.; et al. Climate change and Arctic ecosystems: 2. Modeling, paleodata–model comparisons, and future projections. *J. Geophys. Res. Atmos.* **2003**, *108*, 8171. [[CrossRef](#)]
62. Gamache, I.; Payette, S. Latitudinal response of subarctic tree lines to recent climate change in eastern Canada. *J. Biogeogr.* **2005**, *32*, 849–862. [[CrossRef](#)]
63. Dunn, A.L.; Wofsy, S.C.; Bright, A.V.H. Landscape heterogeneity, soil climate, and carbon exchange in a boreal black spruce forest. *Ecol. Appl.* **2009**, *19*, 495–504. [[CrossRef](#)]
64. Kellomaki, S.; Kolstrom, M. Simulation of tree species composition and organic matter accumulation in Finnish boreal forests under changing climatic conditions. *Vegetation* **1992**, *102*, 47–68. [[CrossRef](#)]
65. Côté, L.; Brown, S.; Paré, D.; Fyles, J.; Bauhus, J. Dynamics of carbon and nitrogen mineralization in relation to stand type, stand age and soil texture in the boreal mixed wood. *Soil Biol. Biochem.* **2000**, *32*, 1079–1090. [[CrossRef](#)]
66. Jin, X.Y.; Jin, H.J.; Iwahana, G.; Marchenko, S.S.; Luo, D.L.; Li, X.Y.; Liang, S.H. Impacts of climate-induced permafrost degradation on vegetation: A review. *Adv. Clim. Chang. Res.* **2020**. [[CrossRef](#)]

67. Serreze, M.C.; Walsh, J.E.; Chapin Iii, F.S.; Osterkamp, T.; Dyurgerov, M.; Romanovsky, V.; Oechel, W.C.; Morison, J.; Zhang, T.; Barry, R.G. Observational evidence of recent change in the northern high-latitude environment. *Clim. Chang.* **2000**, *46*, 159–207. [[CrossRef](#)]
68. Chapin, F.S., III; McGuire, A.D.; Randerson, J.; Pielke, R., Sr.; Baldocchi, D.; Hobbie, S.E.; Roulet, N.; Eugster, W.; Kasischke, E.; Rastetter, E.B.; et al. Arctic and boreal ecosystems of western North America as components of the climate system. *Glob. Chang. Biol.* **2000**, *6*, 211–223. [[CrossRef](#)]
69. Crawford, R.M.M.; Jeffree, C.E.; Rees, W.G. Paludification and forest retreat in northern oceanic environments. *Ann. Bot.* **2003**, *91*, 213–226. [[CrossRef](#)]
70. Lavoie, M.; Paré, D.; Bergeron, Y. Impact of global change and forest management on carbon sequestration in northern forested peatlands. *Environ. Rev.* **2005**, *13*, 199–240. [[CrossRef](#)]
71. Vygodskaya, N.N.; Groisman, P.Y.; Tchekakova, N.M.; Kurbatova, J.A.; Panfyorov, O.; Parfenova, E.I.; Sogachev, A.F. Ecosystems and climate interactions in the boreal zone of northern Eurasia. *Environ. Res. Lett.* **2007**, *2*, 045033. [[CrossRef](#)]
72. Fenton, N.J.; Bergeron, Y. Sphagnum community change after partial harvest in black spruce boreal forests. *For. Ecol. Manag.* **2007**, *242*, 24–33. [[CrossRef](#)]
73. Skre, O.; Baxter, R.; Crawford, R.M.M.; Callaghan, T.V.; Fedorkov, A. How will the tundra-taiga interface respond to climate change? *Ambio* **2002**, *31*, 37–46.
74. Veillette, J.J. Evolution and paleohydrology of glacial Lakes Barlow and Ojibway. *Quat. Sci. Rev.* **1994**, *13*, 945–971. [[CrossRef](#)]
75. Laamrani, A.; Valeria, O.; Fenton, N.; Bergeron, Y. Landscape-scale influence of topography on organic layer accumulation in paludified boreal forests. *For. Sci.* **2014**, *60*, 579–590. [[CrossRef](#)]
76. Laamrani, A.; Valeria, O.; Fenton, N.; Bergeron, Y.; Cheng, L.Z. The role of mineral soil topography on the spatial distribution of organic layer thickness in a paludified boreal landscape. *Geoderma* **2014**, 221–222, 70–78. [[CrossRef](#)]
77. Laamrani, A.; Valeria, O. Ranking Importance of Topographical Surface and Subsurface Parameters on Paludification in Northern Boreal Forests Using Very High Resolution Remotely Sensed Datasets. *Sustainability* **2020**, *12*, 577. [[CrossRef](#)]
78. MacIver, D.C.; Isaac, J.L. *Profils Bioclimatiques Pour le Canada, 1951–1980*; Environnement Canada, Service de L’environnement Atmosphérique: Toronto, ON, Canada, 1989.
79. Bush, E.; Lemmen, D.S. (Eds.) *Canada’s Changing Climate Report*; Government of Canada: Ottawa, ON, Canada, 2019; p. 444. Available online: <https://changingclimate.ca/CCCR2019/> (accessed on 28 September 2020).
80. Houghton, J.T.A. Climate Change 2001: The Scientific Basis. In *Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*; Cambridge University Press: New York, NY, USA, 2001; p. 892.
81. Laamrani, A. Effect of Climate Change on Boreal Forest Soils: Will Soil Conditions Limit the Adaptation of Boreal Ecosystems to Climate Change? Ph.D. Thesis, University of Quebec in Abitibi-Témiscamingue (UQAT), Rouyn-Noranda, QC, Canada, 2010; Environmental Synthesis Report, Environmental Sciences Program. Available online: https://www.researchgate.net/publication/263966215_Effect_of_climate_change_on_boreal_forest_soils_Will_soil_conditions_limit_the_adaptation_of_boreal_ecosystems_to_climate_change (accessed on 29 September 2020).
82. Bonan, G.B.; Shugart, H.H.; Urban, D.L. The sensitivity of some high-latitude boreal forests to climatic parameters. *Clim. Chang.* **1990**, *16*, 9–29. [[CrossRef](#)]
83. Helbig, M.; Waddington, J.M.; Alekseychik, P.; Amiro, B.D.; Aurela, M.; Barr, A.G.; Black, T.A.; Blanken, P.D.; Carey, S.K.; Chen, J.; et al. Increasing contribution of peatlands to boreal evapotranspiration in a warming climate. *Nat. Clim. Chang.* **2020**, *10*, 555–560. [[CrossRef](#)]
84. Spittlehouse, D.L.; Stewart, R.B. Adapting to climate change in forest management. *BC Ecosyst. Manag.* **2003**, *4*, 7–17.
85. Marschall, M.; Proctor, M.C.F. Are Bryophytes Shade Plants? Photosynthetic Light Responses and Proportions of Chlorophyll a, Chlorophyll b and Total Carotenoids. *Ann. Bot.* **2004**, *94*, 593–603. [[CrossRef](#)] [[PubMed](#)]
86. Lafleur, B.; Fenton, N.J.; Bergeron, Y. Forecasting the development of boreal paludified forests in response to climate change: A case study using Ontario ecosite classification. *For. Ecosyst.* **2015**, *2*, 3. [[CrossRef](#)]
87. Spittlehouse, D.L. Integrating climate change adaptation into forest management. *For. Chron.* **2005**, *81*, 691–695. [[CrossRef](#)]

88. Bernier, P.; Schoene, D. Adapting forests and their management to climate change: An overview. *Unasylva* **2009**, *60*, 5–11.
89. Laamrani, A.; Valeria, O.; Fenton, N.; Bergeron, Y.; Cheng, L.Z. Effects of topography and thickness of organic layer on productivity of black spruce boreal forests of the Canadian Clay Belt region. *For. Ecol. Manag.* **2014**, *330*, 144–157. [[CrossRef](#)]
90. Lafleur, B.; Fenton, N.J.; Paré, D.; Simard, M.; Bergeron, Y. Contrasting effects of season and method of harvest on soil properties and the growth of black spruce regeneration in the boreal forested Peatlands of Eastern Canada. *Silva Fenn.* **2010**, *44*, 799–813. [[CrossRef](#)]
91. Simard, M.; Bernier, P.Y.; Bergeron, Y.; Paré, D.; Guérine, L. Paludification dynamics in the boreal forest of the James Bay Lowlands: Effect of time since fire and topography. *Can. J. For. Res.* **2009**, *39*, 546–552. [[CrossRef](#)]
92. Henneb, M.; Valeria, O.; Thiffault, N.; Fenton, N.J.; Bergeron, Y. Effects of Mechanical Site Preparation on Microsite Availability and Growth of Planted Black Spruce in Canadian Paludified Forests. *Forests* **2019**, *10*, 670. [[CrossRef](#)]
93. Lafleur, B.; Fenton, N.J.; Simard, M.; Leduc, A.; Pare, D.; Valeria, O.; Bergeron, Y. Ecosystem management in paludified boreal forests: Enhancing wood production, biodiversity, and carbon sequestration at the landscape level. *For. Ecosyst.* **2018**, *5*, 27. [[CrossRef](#)]
94. Splawinski, T.B.; Schab, A.; Leduc, A.; Valeria, O.; Cyr, D.; Pascual Puigdevall, J.; Gauthier, S.; Bergeron, Y. Ajustement des stratégies de production de bois dans certaines portions sensibles de la forêt boréale. In *Rapport Présenté au Ministère des Forêts, de la Faune et des Parcs Par la Chaire Industrielle CRSNG UQAT-UQAM en Aménagement Forestier Durable*; Ministère des Forêts, de la Faune et des Parcs du Québec: Québec, QC, Canada, 2019; pp. 1–120.
95. Mansuy, N.; Valeria, O.; Laamrani, A.; Fenton, N.; Guindon, L.; Bergeron, Y.; Beaudoin, A.; Légaré, S. Digital mapping of paludification in soils under black spruce forests of eastern Canada. *Geoderma Reg.* **2018**, *15*, e00194. [[CrossRef](#)]
96. Thompson, D.K.; Simpson, B.N.; Whitman, E.; Barber, Q.E.; Parisien, M.-A. Peatland Hydrological Dynamics as A Driver of Landscape Connectivity and Fire Activity in the Boreal Plain of Canada. *Forests* **2019**, *10*, 534. [[CrossRef](#)]
97. Le Stum-Boivin, É.; Magnan, G.; Garneau, M.; Fenton, N.J.; Grondin, P.; Bergeron, Y. Spatiotemporal evolution of paludification associated with autogenic and allogenic factors in the black spruce-moss boreal forest of Québec, Canada. *Quat. Res.* **2019**, *91*, 650–664. [[CrossRef](#)]
98. Kuhry, P. Palsa and peat plateau development in the Hudson Bay Lowlands, Canada: Timing, pathways and causes. *Boreas* **2008**, *37*, 316–327. [[CrossRef](#)]
99. Jump, A.S.; Penuelas, J. Running to stand still: Adaptation and the response of plants to rapid climate change. *Ecol. Lett.* **2005**, *8*, 1010–1020. [[CrossRef](#)]

Publisher’s Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



© 2020 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<http://creativecommons.org/licenses/by/4.0/>).