How climate change might affect tree regeneration following fire at northern latitudes: a review

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Abstract
Climate change is projected to increase fire severity and frequency in the boreal forest, but it could also directly affect post-fire recruitment processes by impacting seed production, germination, and seedling growth and survival. We reviewed current knowledge regarding the effects of high temperatures and water deficits on post-fire recruitment processes of four major tree species (Picea mariana, Pinus banksiana, Populus tremuloides and Betula papyrifera) in order to anticipate the effects of climate change on forest recovery following fire in the boreal biome. We also produced maps of future vulnerability of post-fire recruitment by combining tree distributions in Canada with projections of temperature, moisture index and fire regime for the 2041–2070 and 2071–2100 periods. Although our review reveals that information is lacking for some regeneration stages, it highlights the response variability to climate conditions between species. The recruitment process of black spruce is likely to be the most affected by rising temperatures and water deficits, but more tolerant species are also at risk of being impacted by projected climate conditions. Our maps suggest that in eastern Canada, tree species will be vulnerable mainly to projected increases in temperature, while forests will be affected mostly by droughts in western Canada. Conifer-dominated forests are at risk of becoming less productive than they currently are, and eventually, timber supplies from deciduous species-dominated forests could also decrease. Our vulnerability maps are useful for prioritizing areas where regeneration monitoring efforts and adaptive measures could be developed.

Keywords Drought · Temperature · Post-fire regeneration · Black spruce · Jack pine · Trembling aspen · Paper birch
Introduction

Wildfires are recurring, stand-replacing disturbances that affect forest dynamics and shape landscape diversity throughout the North American boreal biome (e.g., Van Wagner 1978; DeLong and Tanner 1996). As a consequence, most boreal tree species exhibit strong adaptive traits allowing for their rapid recovery after a fire (Shinneman et al. 2013), such as serotinous cones that occur in pines and spruces (He et al. 2012; Briand et al. 2015), or vegetative reproduction that occurs in aspen (*Populus tremuloides* Michaux). Fire can be beneficial to nutrient availability and site productivity, given that it releases nutrients that would otherwise be tied up in the humus, creates germination seedbeds, and reduces competing vegetation cover (Greene et al. 1999; Prescott et al. 2000; Miyanishi and Johnson 2002). However, fires can lead to a conversion of close stands into open forests (Payette and Delwaide 2018; Girard et al. 2009) or to a shift in forest composition (Johnson et al. 2003; Johnstone and Chapin 2006b; Beck et al. 2011) if they occur before trees have produced sufficient viable seed to ensure regeneration.

Temperature and drought frequency also affect post-fire recruitment processes through their effects on seed production, seed germination, and seedling growth and survival (Boiffin and Munson 2013). The climatic niches of seedlings are narrower than those of conspecific adult trees (Grubb 1977; Hogg and Schwarz 1997; Jackson et al. 2009; Lenoir et al. 2009; Bell et al. 2014; Dobrowski et al. 2015), making seedlings particularly vulnerable to drought (e.g., see Hogg and Schwarz 1997). Therefore, regeneration failures are possible, even under climate conditions that are suitable for mature individuals (Dodson and Root 2013). Furthermore, microclimatic conditions of burned areas are usually more extreme than those of the surrounding forested matrix (Ulery and Graham 1993; Feddema et al. 2013; Savage et al. 2013). They typically exhibit higher local temperatures owing to the increase in solar radiation that reaches the forest floor, the loss of insulating effects provided by the organic layer (Bonan 1989; Feddema et al. 2013; Savage et al. 2013), and the dark colour of burned soils (Ulery and Graham 1993).

Changes in post-fire regeneration have been observed in recent decades in many parts of the world and have been attributed mainly to ongoing climate change (Donato et al. 2016; Rother and Veblen 2016; Stevens-Rumann et al. 2017). For instance, in Alaska and central Canada, more deciduous species are now observed in the regeneration layer after fire rather than conifer species such as black spruce (*Picea mariana* (Mill.) BSP), apparently due to warmer and drier climate conditions (Bond-Lamberty et al. 2007; Kasischke et al. 2007; Johnstone et al. 2010a, b; Beck et al. 2011; Walker et al. 2017). In the Yukon (Canada), warm south-facing slopes support fewer white spruce (*Picea glauca* [Moench] Voss) and more aspen seedlings after fire than have been observed historically (Johnstone et al. 2010b), suggesting an eventual shift in forest composition. In eastern Canada, little evidence of changes in post-fire recruitment has been observed so far, but Van Bogaert et al. (2015) concluded that jack pine (*Pinus banksiana* Lambert) can often be replaced by black spruce following fire on dry sites; these authors also reported greater regeneration failure of jack pine than expected, suggesting that the species is less resilient to fire on dry sites. Such empirical demonstrations of post-fire recovery changes are still scarce, and their underlying processes are not well understood. It is anticipated, however, that fire severity and frequency within the North American boreal biome will increase over the next century under continued warming (Rogers et al. 2011; Flannigan et al. 2013; Barbero et al. 2015; Terrier et al. 2015). Given that regeneration success requires suitable pre-fire seed production and adequate post-fire climatic conditions (Hogg and Wein 2005; Dodson and Root...
The microclimatic conditions of burned areas, in combination with the potential effects of projected climate change, could impair the establishment of some tree species. Such changes need to be anticipated so that adequate adaptive measures can be developed and established in order to attenuate or offset potential negative impacts of climate change, and to support long-term fibre supplies.

In this paper, we first reviewed the literature on the effects of high temperature and water deficits on post-fire recruitment processes, i.e., seed production, seed germination, vegetative reproduction, and seedling growth and survival in North American boreal forests. By focusing on these effects, we wanted to assess whether the expected decrease in the closed-canopy boreal forest that would be due to an increase in fire frequency could be exacerbated in the future (Tepley et al. 2017; Serra-Diaz et al. 2018; Stevens-Rumann et al. 2017). This review also allowed us to highlight research gaps that should be filled to extend our understanding of post-fire recruitment dynamics under a changing climate. We focused on four major boreal tree species found in North American forests, i.e., black spruce, jack pine, trembling aspen, and paper birch (Betula papyrifera Marshall). Together, these species of high commercial value are dominant in some 268 million hectares of forest land in boreal Canada (Brandt 2009). In addition, as a complement to the literature review, we produced maps of the future vulnerability of post-fire recruitment of the four tree species, by combining their distributions in Canada with projected changes in temperature, moisture index and fire regime. These maps will help to spatially anticipate the most probable impacts of climate change on post-fire recruitment for each species.

**Methods**

**Literature review**

We conducted a literature search, initially by focusing on publications reporting the first evidence of climate change impacts on post-fire recruitment. Given the scarcity of these studies, we extended the search to studies on effects of climate conditions on post-fire recruitment. We focused on low water availability and high temperature conditions, based on projected climate conditions. We then extended the search to studies on relationships between recruitment processes and climate variables, specifically water availability and temperature, in contexts other than post-fire conditions. This last category of studies mostly included experiments conducted in controlled environments, with few studies under natural conditions. We limited our search to the main North American boreal species: black spruce, jack pine, paper birch, and trembling aspen. We selected publications that discussed at least one of the recruitment stages: seed production and germination, seedling growth and survival, and vegetative reproduction. In addition, we included studies conducted in natural conditions reporting seedling density after fires. We chose not to address indirect effects of climate change on regeneration, such as the impacts of increased fire severity and frequency on post-fire recruitment. Specifically, the literature search was conducted in the Scopus database (https://www.scopus.com/) for each of the four species, using the following keywords: “climate change” or “climate warming” or “global change” or “global warming” and “boreal forest” and “fire” and “recruitment” or “seed” or “seedling” or “sapling” or “regeneration” or “germination” or “sucker” or “vegetative reproduction” or “recovery”. To search for studies on the effects of climate conditions rather than climate change, we used “drought” or “temperature” or “precipitation” or “water deficit” or
“growth season” instead of the climate change keywords. We removed “fire” as a keyword to search for studies on recruitment processes in contexts other than post-fire conditions. We also included relevant articles found as citations in the searched articles. Overall, we identified 34 relevant publications regarding the effects of temperature and 21 publications regarding the effects of water availability on recruitment processes. For each recruitment stage, tree responses to climate change or climate conditions observed in each study were compiled (Table S1 and S2) and synthesized, allowing for the characterization of potential species sensitivity to temperature increase and drought.

Maps of tree species vulnerability to climate change

To add a spatial dimension to the anticipated impacts of climate change on post-fire recruitment, and to complement the information found in our review, we produced maps of the vulnerability of tree species to changing conditions. In fact, the impacts of climate change on post-fire recruitment will depend not only on species sensitivity, as covered in the literature review, but also on their exposure to change. Specifically, impacts will depend on location within the species’ range (Reich et al. 2015; Chaste et al. 2019) and on the limiting factors of the local conditions (Boisvenue and Running 2006; Terrier et al. 2015; Pedlar and McKenney 2017). Furthermore, temperature, drought frequency and fire frequency projections for the end of the century are spatially heterogeneous throughout Canada, even within a given climatic scenario (Fig. 1). Hence, the vulnerability of post-fire recruitment for a given species should be the highest in locations where the greatest climatic change coincides with the distribution of the species. By overlaying information on climatic envelopes of tree species with climate and fire projections, we can illustrate where the projected climate variables are likely to exceed the climate envelope of a tree species at the pixel level (250 × 250 m).

Species climatic envelopes are useful for illustrating species vulnerability to climatic change (Heikkinen et al. 2006; McKenney et al. 2007; Bell et al. 2014). If the value of a projected climatic variable at a given location exceeds the climatic envelope of a species, it can be assumed that this species will be vulnerable to the new climatic conditions at this location. Climatic envelopes have been calculated for mature trees and are probably larger than those of seedlings or saplings (Grubb 1977; Hogg and Schwarz 1997; Jackson et al. 2009; Bell et al. 2014; Dobrowski et al. 2015), but they constitute the best available information to approximate zones of vulnerability for post-fire tree recruitment. We used mean annual temperature and Climate Moisture Index (CMI) projections that were based on the CanESM2 RCP 8.5 model for 2041–2070 and 2071–2100, provided by the BioSIM v11.5.5.1 software tool for Canada’s entire boreal region (Régnière and St-Amant 2007). The RCP (Representative Concentration Pathway) 8.5 model represents an extreme but realistic situation, characterized by increasing greenhouse gas emissions over time. To produce the maps, we used tree species envelopes produced by McKenney et al. (2007, 2013) for Canada (Table 1), as well as tree species biomass maps created by Beaudoin et al. (2018) with a resolution of 250 m × 250 m. For each pixel, a species was classified as vulnerable when its biomass represented at least 10% of the pixel, and if the projected annual temperature within the pixel was higher than the 95th percentile of its temperature envelope, or if the projected CMI was lower than the 5th percentile of its hydric envelope. Since we aimed to illustrate the vulnerability of species recruitment under post-fire conditions, we also based our maps on fire projections drawn from the same RCP produced by Boulanger
et al. (2014) for 2041–2070 and 2071–2100. We considered that annual burned areas of 0.5–1%, 1–4%, and > 4% represent medium, high and very high risks, respectively. Thus, the post-fire recruitment of a species was considered to be more vulnerable to drought or temperature where the projected annual burned area was high.
**Literature review: effects of climate on tree recruitment**

Temperature and water availability both play important roles in all stages of tree development and reproduction, from seed production to seedling growth and survival, including vegetative reproduction. Depending on the species, certain developmental stages are more vulnerable to variation in these climate variables than are other stages (Ibáñez et al. 2017). In this section, we review the effects of temperature and water availability on sexual and vegetative stages of regeneration: (1) seed production and availability; (2) seed germination; (3) vegetative reproduction; and (4) seedling and sucker growth and survival. The list of relevant articles that discuss how water deficit and temperature affect tree recruitment is presented in Tables S1 and S2, respectively.

**Seed production and availability**

**Temperature**

The role of temperature in the production of viable seeds has been documented for many forest ecosystems (Henttonen et al. 1986; Zasada et al. 1992; Parantainen and Pulkkinen 2002; Roland et al. 2014; Nussbaumer et al. 2018). Low temperatures are usually a factor limiting seed production (including bud differentiation, flowering, pollination, and seed maturation) at the northern limit of a tree’s range (Pigott and Huntley 1981; Morin et al. 2007). Seed production is generally closely related to inter-annual variation in climatic conditions (Henttonen et al. 1986; Woodward et al. 1994; Koenig and Knops 1998; Drobyshhev et al. 2010; Zamorano et al. 2018), warmer and longer growing seasons allowing a greater amount of carbon uptake, and greater carbon allocation to reproduction (Despland and Houle 1997; Lucas-Borja and Vacchiano 2018; Zamorano et al. 2018). However, both cold and hot extremes can be significant causes of early fruit and flower mortality (Krugman et al. 1974; Rodrigo 2000; Vitasse et al. 2018), thereby decreasing the number of viable seeds.

For jack pine trees growing at the northern limit of their distribution range, higher than average temperatures during the three growing seasons required for seed production increase the production of viable seeds (Despland and Houle 1997). Similarly, paper birch produced more seeds on warmer sites in Appalachian forests (Grenier and Sirois 2009). Black spruce cone production does not increase with degree-days or maximum summer temperature in boreal Québec, Canada (Sirois 2000; Messaoud et al. 2007), but the number of filled seeds (with embryo development) per cone is positively correlated with the cumulative number of degree-days (Sirois 2000). At the northern tree line, the seed production of most species, including black spruce, is greatest when high degree-day sums coincide with years in which high precipitation is recorded (Brown et al. 2019).

**Water availability**

Seed production is linked to precipitation and can be reduced by drought (Allen et al. 2014; Roland et al. 2014; O’Brien et al. 2018; Brown et al. 2019). In boreal forests, desiccation has been implicated as one of the key factors involved in seed mortality that occurs during the first summer following fire (Greene et al. 1999), especially in regions where droughts are infrequent (Tweddle et al. 2003). Larger seeds, such as those found in conifers,
generally have higher survival rates than smaller seeds (Greene et al. 1999). However, there have been few studies that examine the impact of water deficit on seed production specifically for black spruce, jack pine, trembling aspen, and paper birch.

Seed germination

Temperature

Temperature is a key factor for seed germination in many boreal tree species (Zasada et al. 1992). Germination generally starts in the spring, when temperatures reach a specific threshold. For example, black spruce seeds germinate at temperatures > 15 °C (Black and Bliss 1980), or when the cumulative heat sum reaches from 800 to 940 degree-days (Munier et al. 2007). Germination success increases with both temperature and degree-days for black spruce (Hobbie and Chapin 1998; Sirotis 2000; Munier et al. 2010), paper birch (Hobbie and Chapin 1998; Grenier and Sirotis 2009), and trembling aspen (Zasada and Viereck 1975; Hobbie and Chapin 1998), up to a maximum threshold. However, Grenier and Sirotis (2009) found higher paper birch germination success on colder sites in Appalachian forests. No black spruce germination was observed beyond 35 °C (Fraser 1970a). Likewise, optimal temperatures for trembling aspen germination in growth chambers range from 20 to 32 °C; while the rate decreases with temperatures above 30 °C, no germination is observed at 40 °C (Faust 1936; McDonough 1979; Fechner et al. 1981). Jack pine seed germination can occur optimally from 15 to 32 °C (Fraser 1970b). Unlike the previous two species, jack pine seeds can germinate at 40 °C, but with limited success (20%; Ackerman and Farrar 1965; Fraser 1970b). Jack pine germination also is faster when exposed to 30 °C/20 °C (day/night) compared to 20 °C/10 °C regimes (Greenwood et al. 2002). Furthermore, seeds from northerly populations of jack pine and paper birch germinated faster than those from southerly populations (Bevington 1986; Benowicz et al. 2001; Greenwood et al. 2002). Indeed, northern provenances of paper birch germinate more rapidly and in higher proportions between 21 and 34 °C, whereas this optimum range is 27–34 °C for southern sources (Bevington 1986). Rapid germination represents an advantageous trait for populations whose growing season duration is limited (Benowicz et al. 2001).

Water availability

Water availability is crucial for boreal species germination. For example, no emergence of jack pine was observed at a moisture level equivalent to 50% of the average daily June rainfall in Ontario, Canada (Herr and Duchesne 1995). The ability of seeds to germinate under moisture deficit conditions differs between species. Sirotis (1993) found a higher germination rate for jack pine, compared to black spruce, on dry substrates following fire in northern Québec, Canada. Thomas and Wein (1985) found similar germination rates between jack pine and black spruce under water-deficit conditions, but observed a higher emergence of jack pine on soils that were watered at different frequencies. They explained these results as greater survival in pre-emergent jack pine seedlings, due to their faster radicle elongation. The germination rate of trembling aspen seeds on a substrate where the water potential was −0.4 MPa was only 50% (McDonough 1979), while no germination was observed at water potential of −0.7 MPa (McDonough 1979; Fechner et al. 1981).

Furthermore, many authors have observed that few seedlings establish on thick residual organic matter after fire (Chrosciewicz 1974; Charron and Greene 2002; Johnstone and...
Chapin 2006a; Hesketh et al. 2009; Boiffin and Munson 2013). The substrate resulting from the incomplete combustion of the organic layer typically exhibits low water retention and high variation in temperature (Duchesne and Sirois 1995; Miyanishi and Johnson 2002; Johnstone and Chapin 2006a), particularly when warm and dry summers follow the fire (Boiffin and Munson 2013). Under these conditions, Boiffin and Munson (2013) observed greater establishment success for jack pine seedlings compared to black spruce in eastern Canada.

**Vegetative reproduction**

Vegetative reproduction circumvents detrimental post-fire conditions, such as extreme temperatures and drought events, by enabling rapid regeneration after fire. While post-fire recruitment through vegetative reproduction is common for trembling aspen, this post-fire regeneration strategy is much less common for paper birch, and is absent in black spruce and jack pine (Foster and King 1986; Perala and Alm 1990; Safford et al. 1990; Zasada et al. 1992).

**Temperature**

Warm soils favour sucker initiation by facilitating auxin degradation, and by promoting root growth and cytokinin synthesis (Schier et al. 1985; Hungerford 1988; Bradley et al. 1992). A soil temperature of 8 °C inhibits the expansion of trembling aspen root suckers (Landhäusser et al. 2006), likely because cold temperatures limit moisture uptake (Wan et al. 1999). Silvicultural practices such as scarification favour aspen suckering because the treatment affects the soil temperature (Lavertu et al. 1994; Paragi and Haggstrom 2007). High temperatures can improve sucker establishment by stimulating early sucker initiation, with positive effects on sucker growth and survival (Fraser et al. 2002; Frey et al. 2003; Landhäusser et al. 2006). Both the number and growth of aspen suckers are optimal between 23 and 30 °C, but they decline at higher temperatures (Maini and Horton 1964, 1966; Zasada and Schier 1973).

**Water availability**

Some studies have suggested that the production of aspen suckers after fire could be affected by drought episodes. In the Yukon, Hogg and Wein (2005) observed that most aspens regenerated after a 1958 fire that originated during a drought-free period, while few aspens were produced during the following severe drought episodes. Very dry soils reduce aspen sucker initiation on root cuttings (Schier et al. 1985), although maximal sucker production was observed at 7% soil moisture content, in an experiment covering a 7–27% gradient (Maini and Horton 1964). Evidence for the detrimental effects of drought on sucker production is not clear. It appears that the sucker initiation process in aspen can occur under moderate water deficits, probably due to the deep root system that draws upon untapped soil moisture reserves, thereby avoiding surficial soil desiccation (Harvey et al. 2016).

We found no studies that investigated the effect of temperature or drought on paper birch resprouting.
Seedling and sucker growth and survival

Temperature

In cold regions, temperature is recognized as the factor that is most limiting to growth (Bonan 1992; Körner 2003; Rossi et al. 2008), and moderate warming generally leads to greater seedling growth and survival, mainly through direct effects on photosynthesis and thus on assimilation rates (Dang and Cheng 2004; Wilmking et al. 2004; Danby and Hik 2007; Pallardy 2008). Temperature also affects indirectly growth through nutrient and water uptake, due to increased metabolism and evapotranspiration under warmer conditions (Bonan 1992). Projected global warming may increase the length of the growing season in cold regions, which in turn may benefit seedling growth (Myneni et al. 1997; Rossi et al. 2011). Furthermore, high soil temperatures following fire result in increased organic matter decomposition and nutrient mineralization, with potential positive effects on post-fire seedling growth (Dyrness and Norum 1983; Viereck 1983). Yet the beneficial effects of such climate warming on boreal tree growth may be short-lived, given concomitant declines in soil moisture storage and availability (D’Orangeville et al. 2018). On one hand, high temperature can induce summer water stress that attenuates or precludes temperature-related growth increases (Briffa et al. 1998; Barber et al. 2000; Lloyd and Fastie 2002; Wilmking et al. 2004; Ols et al. 2016). On the other hand, an increase in winter temperatures could have differing effects from those of summer-time increases (Cannell and Smith 1986; Vitasse et al. 2018). For example, at elevational tree line in Québec, higher winter temperatures and a shortened snow cover duration resulted in decreased seedling survival through early dormancy release, which exposed seedlings to freezing temperatures (Renard et al. 2016).

Black spruce  Growth chamber studies have shown strong interspecific variability in tree seedling responses to temperature variation. Black spruce seedling growth takes advantage of moderate increases in temperature (3–15 °C), but to a lesser extent than do seedlings of deciduous species, (Landhäusser et al. 1996; Peng and Dang 2003; Dang and Cheng 2004). Optimal temperatures for black spruce seedling growth in the laboratory range between 16 and 21 °C (Tjoelker et al. 1998; Peng and Dang 2003; Dang and Cheng 2004; Zhang and Dang 2007; Way and Sage 2008), although good growth has been observed at 27 °C (Zhang and Dang 2007); above these thresholds, decreases in seedling growth are most likely due to the decrease in carbon allocation to the roots at high temperatures (Way and Sage 2008). Only 20% of black spruce seedlings growing at 35 °C over a period of 4 months survived (Peng and Dang 2003; Dang and Cheng 2004). The mortality of black spruce seedlings has been found to be higher on southern rather than northern slope aspects in Alaska, particularly during periods where average daily maximum soil temperatures are above 29 °C (Viereck and Dyrness 1979).

Jack pine  Jack pine seedlings are less responsive to variation in temperature than are black spruce seedlings (Peng and Dang 2003; Dang and Cheng 2004; Zhang and Dang 2007). Moderate temperature increases favour jack pine seedlings, but higher temperatures cause decreased growth (Heninger and White 1974; Peng and Dang 2003; Dang and Cheng 2004; Zhang and Dang 2007; Reich et al. 2015). After 4 months at 35 °C in growth chambers, only 40% of seedlings survived (Peng and Dang 2003; Dang and Cheng 2004). Both a warming of 3.4 °C in Minnesota (Reich et al. 2015) and 4–5 °C above the ambient nighttime tem-
Temperature in a growth chamber (Day et al. 2005) reduced jack pine seedling growth. Thus, an optimal growth temperature for jack pine would be between 22 and 27 °C (Heninger and White 1974; Peng and Dang 2003; Dang and Cheng 2004).

**Trembling aspen** Growth rates of trembling aspen seedlings and suckers are reduced by low soil temperatures (Landhäusser and Lieffers 1998), and are strongly increased with moderate increases in temperature (6–20 °C). Growth chamber studies suggest that the optimal growth temperatures for trembling aspen seedlings and suckers are between 19 and 23 °C (Maini and Horton 1964, 1966; McDonough 1979; Peng and Dang 2003; Dang and Cheng 2004). Seedlings can attain seven times their minimal biomass value at their optimal temperature (Peng and Dang 2003; Dang and Cheng 2004). At a high temperature (35 °C), trembling aspen seedlings showed no mortality after 4 months (Peng and Dang 2003; Dang and Cheng 2004). Warming of 3.4 °C in Minnesota led to a slight increase in trembling aspen seedling growth (Reich et al. 2015), while no significant increase was observed following 3 years of warming of 1 °C in Alaska (Hobbie and Chapin 1998).

**Paper birch** Optimal growth temperatures for paper birch seedlings are estimated to be between 17 and 31 °C (Heninger and White 1974; Zhang and Dang 2007). A warming of 3.4 °C in Minnesota resulted in decreased paper birch seedling growth (Reich et al. 2015), while a warming of 1 °C in Alaska did not affect growth after 3 years (Hobbie and Chapin 1998). High seedling mortality was observed on southern slope aspects in Alaska, where the temperature was often above 29 °C; mortality rates are higher for paper birch than for black spruce (Viereck and Dyrness 1979). Paper birch seedlings from high elevation populations in New Hampshire showed a decrease in growth rate when they were grown at low elevations in warmer temperatures (Ruel and Ayres 1996).

**Water availability**

Moderate water deficiency could affect seedling growth directly through the effects on cambial cells, or indirectly through effects on photosynthesis (Abe and Nakai 1999; Arend and Fromm 2007; Rossi et al. 2009; de Luis et al. 2011), while severe drought can cause tree mortality through hydraulic failure or carbon starvation (Sala et al. 2012; Nardini et al. 2013; Urli et al. 2013; Anderegg et al. 2012, 2016). Tree species possess different strategies to cope with water stress [mainly dehydration avoidance and dehydration tolerance according to Volaire’s definition (2018)] and show different performances under drought stress.

**Black spruce** Black spruce shows anisohydric behaviour by keeping the stomata open and maintains high photosynthetic rates for a long period during water stress (dehydration tolerance), but its risk of hydraulic failure is higher than for isohydric species, especially during intense drought (McDowell et al. 2008; Choat et al. 2012; Sade et al. 2012; Pappas et al. 2018). Black spruce has a higher resistance to embolism than the other boreal species that are covered here, though its low degree of stomatal control increases the probability of embolism (Hacke and Jansen 2009; Choat et al. 2012). Hébert et al. (2006) found lower growth rates for planted black spruce seedlings, compared to jack pine, under dry conditions in boreal lichen woodlands in Québec, although survival was similar between species. Sirois (1993) found greater mortality at 13 months for black
spruce seedlings compared to jack pine on dry substrates following fire in northern Québec. Blake and Li (2003) attributed the lower water stress resistance of black spruce, in comparison with jack pine, to a greater needle area and smaller root system. Black spruce seedlings growing at high temperatures have been found to decrease their biomass allocation to roots, thereby making them more susceptible to episodic soil drying (Way and Sage 2008). Black spruce seedling mortality is generally high during the first year following fire (Black and Bliss 1980), mainly due to seedbed drying (Charron and Greene 2002; Moss and Hermanutz 2009). Mortality also occurs among older seedlings. In a 1-month-long water-stress treatment experiment, Balducci et al. (2013) observed an increase in 4-year-old black spruce seedling mortality, the effect of which was stronger at higher temperatures. Kasischke et al. (2007) found that black spruce recruitment can be dramatically lowered in dry post-fire conditions in Alaska, while Johnstone et al. (2010a) observed black spruce self-replacement primarily on moist sites that burn with low-severity fire.

Jack pine  Jack pine resistance to and survival of water stress is reflected by its occurrence on dry soil deposits (Blake and Li 2003). This species exhibits relatively isohydric behaviour that is characterized by reductions in stomatal conductance to limit transpiration during water deficits (dehydration avoidance) (Ewers et al. 2005; McDowell et al. 2008; Sade et al. 2012; Arango-Velez et al. 2016). Mortality of isohydric species is more likely to occur following prolonged droughts of intermediate intensity, mainly through carbon starvation (McDowell et al. 2008; Choat et al. 2012). Pines have a lower ability to resist embolism than do spruces, but the water potential inducing the embolism threshold is higher (less negative) than that for trembling aspen and paper birch (Sperry and Sullivan 1992; Sperry et al. 1994; Choat et al. 2012). Although jack pine seedlings generally perform better than black spruce under dry conditions (Sirois 1993; Blake and Li 2003; Hébert et al. 2006), they could also be affected by water deficits. Indeed, in an experiment testing different water regimes, no seedlings survived after 3 months in a treatment involving two-fold less frequent watering compared to normal precipitation in eastern Canada (Splawinski et al. 2018). Buxton et al. (1985) observed that only 33% of jack pine seedlings survived after 9 days of drought, compared with 51% survival for black spruce. These results contrast with previously cited studies (Sirois 1993; Blake and Li 2003), probably because of the differences in drought duration and intensity in the experiments, combined with the different hydraulic strategy responses. Jack pine seedlings would be more efficient at avoiding drought stress because of their larger, deeper and more rapidly growing root systems (Grossnickle and Blake 1986; Blake and Li 2003), but are less tolerant than black spruce to actual desiccation of their tissues (Buxton et al. 1985).

Trembling aspen  Trembling aspen exhibits relatively isohydric behaviour (dehydration avoidance) during drought (Ewers et al. 2005). Aspen seedlings are particularly prone to desiccation prior to taproot development (Maini and Cayford 1968; Perala and Alm 1990), since their seeds contain little or no endosperm (Nagaraj 1952; Karrenberg et al. 2002). Germinants must rapidly establish photosynthetic leaf area to support root development and growth (Landhäusser et al. 2010). Post-fire trembling aspen recruitment can be particularly low in dry conditions in Alaska (Kasischke et al. 2007). However, once established, trembling aspen seedlings show greater biomass allocation to roots than do black spruce and jack pine (Peng and Dang 2003), a trait generally correlated with drought survival (Lloret et al. 1999; Paz 2003; Way and Sage 2008; Markesteijn and Poorter 2009).
Paper birch  Paper birch also exhibits relatively isohydric behaviour during drought (dehydration avoidance) (Ewers et al. 2005). This species, which is generally found on mesic sites (Landhäusser et al. 1996; Safford et al. 1990), is not resistant to cavitation (Sperry et al. 1994; Choat et al. 2012). Paper birch seedlings that were exposed to 6 days of water stress showed a decrease in shoot mass, but an increase in root-to-shoot ratio (Landhäusser et al. 1996).

Maps of tree species vulnerability to climate change

Maps showing the spatial distribution of vulnerability associated with post-fire recruitment for the four boreal species are presented in Fig. 2. Black spruce is the most widespread tree species in the Canadian boreal forest and appears to be particularly vulnerable to future climatic conditions. In large areas of northwestern Canada, CMI is projected to fall below the black spruce hydric envelope by 2041–2070, and fires are projected to increase (Fig. 2a, b). In some parts of central and eastern Canada, annual mean temperature is projected to be higher than the black spruce climatic envelope in 2041–2070 (Fig. 2a) and this vulnerability area is expected to strongly increase in 2071–2100 (Fig. 2b); these regions include areas with strong projected increases in fire frequency (in red on Fig. 2b). Black spruce will likely be vulnerable to both temperature and drought in central Canada in 2071–2100 (Fig. 2b). Jack pine post-fire regeneration could be affected by drought in large areas of northwestern Canada in 2041–2070 (Fig. 2c), and by both temperature and drought in central Canada by the end of the century (Fig. 2d). Jack pine post-fire recruitment is projected to be vulnerable to temperature increases over large areas of the eastern boreal forest in 2071–2100, including regions where burned areas are projected to increase (Fig. 2d). Trembling aspen is projected to be vulnerable to temperature for post-fire recruitment in southeastern Canada, and to drought in north-central and western Canada from 2041 (Fig. 2e, f). In the southern part of the boreal forest of central Canada, where fires are projected to be frequent, both temperature and drought are likely to affect aspen post-fire regeneration in 2071–2100 (Fig. 2f). Post-fire recruitment of paper birch is projected to be vulnerable to temperature increases in 2071–2100, mainly at the southernmost limit of the boreal forest in eastern Canada, especially in Québec, where the annual burned area could be > 4% (Fig. 2h). In northwestern Canada, where the burned area also exceeds 4% per year during the two projected periods, paper birch is expected to be vulnerable to drought (Fig. 2g, h).

Discussion

Available knowledge and research gaps

Our review highlights the sensitivity of post-fire recruitment and suggests that substantial increases in temperature and drought frequency could impair one or many of the recruitment stages. This review also highlights the variability in responses to temperature and water deficit between the four main boreal tree species. However, information is lacking for some regeneration stages and species, especially under conditions that are similar to what
Fig. 2  Projected vulnerability associated with drought, temperature (Temp) and annual burned area (%) for 2041–2070 and 2071–2100 for the post-fire recruitment of the four main tree species of the Canadian boreal forest: a black spruce, b jack pine, c trembling aspen, and d paper birch
would be expected in the next few decades, such as very high temperatures, and severe and prolonged water deficits. Nevertheless, our review provides insights regarding future impacts of climate change on post-fire recruitment in the boreal forest (Table 2; Fig. 3).

**Seed production and availability**

Seed production is the least studied stage of recruitment. Many studies report that temperature increases could be beneficial to viable seed production (Despland and Houle 1997; Sirois 2000; Brown et al. 2019), but none have included very high temperature treatments for the four species, nor the potential effects of drought on seed production. Although a decrease in seed production or viability has been reported in response to high temperatures (Redmond et al. 2012; Gruwez et al. 2017) and drought (Mutke et al. 2005; Pérez-Ramos et al. 2010; Roland et al. 2014) for other species, it is not possible to anticipate these effects for the four boreal species that we reviewed.

**Seed germination**

More studies are available regarding the seed germination stage (Tables 1, S1 and S2). For the four boreal tree species, high temperatures increase seed germination rates up to a maximum of 30–33 °C (Faust 1936; Fraser 1970a, b; McDonough 1979; Fechner et al. 1981; Bevington 1986); germination rates decrease beyond this threshold. Germination is also strongly affected by the occurrence of drought, and tolerance to drought differs between species. Among the four species that were reviewed, jack pine is probably the most tolerant of harsh post-fire conditions, as it can germinate both at high temperatures and at low water availability (Fraser 1970b; Sirois 1993; Thomas and Wein 1985; Zasada et al. 1992; Boiffin and Munson 2013). The seeds of deciduous species show less ability to withstand moderate levels of moisture deficit than do those of conifers (Zasada et al. 1992). Still, post-fire jack pine recruitment failures have been reported in recent years (Pinno et al. 2013; Van Bogaert et al. 2015).

Furthermore, since seed viability of the four species is generally less than 1 year on the forest floor (Wilton 1963; Fraser 1976; Zasada et al. 1992), the period of adequate soil moisture for germination after fire is narrowed (Sirois 1995). Dry conditions during this period can thus prevent tree establishment from seeds (Zasada et al. 1992). Yet, species with long-distance seed dispersal, such as trembling aspen, could colonize burned patches over a long period after fire and germinate during drought-free years (Perala and Alm 1990; Harvey et al. 2016).

**Vegetative reproduction**

Vegetative reproduction is also a stage for which limited studies are available. Moderate temperature increases can positively affect sucker initiation (Maini and Horton 1964, 1966; Zasada and Schier 1973; Landhäusser et al. 2006), but sucker production is greatly reduced at 35 °C (Maini and Horton 1964, 1966). Drought appears to reduce trembling aspen sucker initiation (Hogg and Wein 2005), but information is insufficient to anticipate the effects of climate change (Tables 1, S1 and S2). The fact remains that the resprouting strategy allows aspen to better cope with post-fire drought stresses, compared to reproduction by seeds.
Table 2  Potential sensitivity to temperature increase and drought of the four main boreal tree species, according to their post-fire recruitment stages and based on the literature reviewed (see Tables S1 and S2 for complete studies list)

| Tree Species | Temperature Increase | Drought |
|--------------|----------------------|---------|
|              | Response             | Number of studies | Response | Number of studies |
| **Trembling aspen** |                     |                     |          |                   |
| Seed production and availability | ?                     | 0                   | ?                     | 0                   |
| Seed germination | Optimal temperature at 20–32 °C; low germination at 35 °C and no germination at 38–40 °C | 5 (2) | Lower ability to withstand moderate levels of water deficit than pine, spruce and birch; 48% germination at −0.4 MPa, 0% at −0.7 MPa | 4 |
| Vegetative reproduction | Optimal temperature for sucker production at 23–30 °C; production greatly reduced at > 30 °C | 6 (1) | Very dry soil reduces sucker production, but production is higher at 7% moisture compared to a wetter medium | 2 |
| Seedling growth | Optimal temperature at 19–23 °C; strong positive response to moderate increase in temperature; less affected by very high temperatures | 7 (5) | ? | 0 |
| Seedling survival | All seedlings survived at 35 °C | 2 (1) | Very low level of aspen recruitment after fire in soil with 23–37% moisture | 1 |
| **Paper birch** |                     |                     |          |                   |
| Seed production and availability | Moderate increase leads to higher seed production; lack of studies with extreme temperatures | 1 (0) | ? | 0 |
| Seed germination | Optimal temperature probably at 21–34 °C; 80% germination at 35 °C (only one study with high temperatures) | 3 (1) | Lower ability to withstand moderate levels of water deficit than pine and spruce, but higher than aspen | 1 |
| Vegetative reproduction | ?                     | 0                   | ? | 0 |
| Seedling growth | Optimal temperature probably at 27 and 31 °C; no studies with higher temperatures | 7 (3) | Six days without watering induced a decrease in biomass | 1 |
| Seedling survival | Mortality peak was at 29–41 °C; survival was lower than for black spruce | 2 (1) | ? | 0 |
Table 2 (continued)

| Temperature increase | Drought |
|----------------------|---------|
| Response             | Number of studies | Response | Number of studies |

**Black spruce**

Seed production and availability
Moderate increase leads to higher seed production; lack of studies with extreme temperatures
2 (0)

Seed germination
Moderate increase leads to higher germination rate; optimal temperature at 12–32 °C; no germination at > 35 °C
5 (1)

Seedling growth
Optimal probably at 16–22 °C, maybe up to 27 °C; germination decrease above; not much growth difference between temperatures
5 (6)

Seedling survival
Highest mortality at 29–41 °C; 20% of seedlings survived at 35 °C
2 (2)

**Jack pine**

Seed production and availability
Moderate increase leads to higher seed production; lack of studies with extreme temperatures
1 (0)

Seed germination
Optimal temperature at 15–32 °C; germination decrease above; less than 20% germination at 40 °C
3 (1)

Seedling growth
Optimal temperature probably at 22–27 °C; germination decrease at > 27 °C; few growth difference between temperatures; growth decreases with warming of > +3.4 °C
6 (6)
Table 2 (continued)

| Temperature increase | Drought |
|----------------------|---------|
| **Response**         | **Response** | **Number of studies** | **Number of studies** |
| Seedling survival    | 40% of seedlings survived at 35 °C | 1 (1) | Generally better survival than for black spruce; no seedlings survived after 3 months of watering at half the frequency of average rainfall | 4 |

The numbers in parentheses represent the number of studies including high temperatures (i.e. > optimal temperature)
Seedling and sucker growth and survival

The seedling stage has been the most frequently studied in relation to climate variables, although knowledge of this stage is still insufficient, particularly regarding the effects of drought on deciduous species. The four boreal species have different optimum temperatures for seedling growth and they respond differently to temperature increases (Tables 1 and 2).
S1). Paper birch has the highest optimal temperature for seedling growth with 27–31 °C, followed by jack pine, then by aspen and black spruce (Maini and Horton 1964, 1966; Heninger and White 1974; McDonough 1979; Tjoelker et al. 1998; Peng and Dang 2003; Dang and Cheng 2004; Zhang and Dang 2007; Way and Sage 2008). Trembling aspen seedlings survive better than do other boreal species to high temperature, showing no mortality when growing at 35 °C (Viereck and Dyrness 1979; Peng and Dang 2003; Dang and Cheng 2004). Drought also affects the growth and survival of boreal recruits. Black spruce seedlings seem to be less resistant to intense drought than do jack pine seedlings (Sirois 1993; Blake and Li 2003). Trembling aspen recruitment can also be strongly affected by dry conditions after fire (Kasischke et al. 2007).

Spatial distribution of species vulnerability to climate change

Based on climate projections, temperatures above 35 °C and long-lasting droughts are expected to be more frequent in the coming decades. The period during which conditions will be suitable for seed germination following fire will likely be shortened. Seedling growth and survival after fires could also be seriously affected. These factors suggest a future increase in the risk of regeneration failure following fire due to high seedling mortality or insufficient numbers of germinants, especially considering that seed viability of boreal tree species is short (Wilton 1963; Zasada et al. 1992).

Specific effects of climate change on forest stands will also depend on location within the species range (Reich et al. 2015; Ibáñez et al. 2017; Chaste et al. 2019) and on the limiting factors of the local conditions (Boisvenue and Running 2006; Terrier et al. 2015; Nicklen et al. 2016; Pedlar and McKenney 2017). Temperature and drought projections for the current century show a high variability across Canada. Using the climatic envelopes of mature trees, we produced maps showing how post-fire recruitment processes are vulnerable to climate change; these maps allowed us to identify areas where tree species are most likely to be vulnerable to temperature and drought under future climate conditions. Given that climate niches of seedlings are generally narrower than those of mature trees (Hogg and Schwarz 1997; Jackson et al. 2009; Dobrowski et al. 2015), these maps probably underestimate the vulnerability of the species recruitment processes. In eastern Canada, tree species are expected to be more vulnerable to temperature increases, which are predicted to exceed the thresholds of the four species studied by the end of the century, while no significant decrease of the Climate Moisture Index (CMI) is projected (Fig. 2). Black spruce is likely the species with the lowest resistance to high temperatures, not only for the germination and seedling growth stages, but also for seedling survival; the projected temperatures will exceed the current climatic envelope of black spruce over large regions in eastern Canada. Combined with the projected increase in annual burned area, the risk of black spruce regeneration failure following fires in the next decades is high. Large areas of jack pine in eastern Canada are also projected to undergo temperature increases that exceed its climatic envelope. Although jack pine seeds and seedlings would be more heat-tolerant than those of black spruce, jack pine post-fire recruitment is expected to be impacted in large areas of eastern Canada because of the expected amplitude of warming. Post-fire recruitment of trembling aspen and paper birch could also be impacted by the end of the century, even if aspen seedlings generally have better survival rates under high-temperature conditions compared to other species (Peng and Dang 2003; Dang and Cheng 2004).

Forests in western Canada are projected to be affected mostly by drought by 2041–2070, while both temperature and drought increases will affect forests in central Canada by the
end of the century (Fig. 2). Even in the northern territories, CMI is projected to be below the hydric envelope of black spruce. Many areas in western Canada are also projected to undergo an increase in fire frequency. Post-fire conditions will thus occur more frequently where drought will likely affect black spruce and jack pine recruitment. Recruitment processes of jack pine are more resistant to drought than those of other species, but very low CMIs are projected at the end of the century, which could seriously impair recruitment following fire.

Impacts of climate change have already been observed in some areas of the boreal forest, where deciduous species recruitment after fire has been favoured by climate change over the last few decades, at the expense of coniferous species (Bond-Lamberty et al. 2007; Johnstone et al. 2010a, b; Beck et al. 2011; Walker et al. 2017). Even in the absence of fire, a decrease in conifer establishment was observed in the southern Rocky Mountains of Canada between 1975 and 2010, which coincided with a general trend of rising summer temperatures and moisture deficits (Andrus et al. 2018). These observations concur with our vulnerability maps for the end of the century. Knowledge is lacking, however, regarding the effect of drought on specific recruitment stages, but some empirical evidence suggests greater tolerance to drought by aspen recruitment compared to conifers (Johnstone et al. 2010a, b; Harvey et al. 2016). It can be expected that, in the coming decades, this trend will continue and extend to other regions where vulnerability increases have been projected. As the temperatures will be warmer and drought periods more frequent or more severe, deciduous species might also suffer from these changes. Regeneration failures after fire are thus anticipated, leading to a shift from closed-canopy to open forests. The competition with more tolerant shrub species after fire could worsen this trend. Reduction in post-fire regeneration density has been already observed in southern forests, particularly in dry areas (Donato et al. 2016; Rother and Veblen 2016; Stevens-Rumann et al. 2017). A rise in fire frequency increases the probability that fires will occur before trees have reached their optimal seed production (Splawinski et al. 2019). Yet, even when trees are sufficiently mature to produce seeds (or to reproduce vegetatively), future climate conditions are also expected to affect the recruitment process and increase the probability of post-fire regeneration failure. Therefore, we posit that the effects of climate change on regeneration will exacerbate the negative effects of fire frequency increases on post-fire recruitment.

Conclusion

Despite the importance of the regeneration phase for future boreal forest resilience (Kuuluvainen and Gauthier 2018), our literature review revealed significant gaps in understanding the potential regeneration responses to climate change. Globally, further research is needed to better understand the effect of climatic variables on recruitment stages of boreal tree species, including extreme conditions of temperature and moisture deficiencies that have been projected in the coming decades. In addition to growth chamber experiments, there is a need for in situ warming and drought-induced experiments. It would also be relevant to include seedling and sucker measurements within national forest inventory programs to monitor long-term trends in regeneration density, growth and survival.

We have anticipated the effects of climate change on post-fire recruitment to the best of our knowledge, but recognize that our analysis is incomplete. Not only is knowledge lacking for several stages of the recruitment process for certain species, our review did not consider some elements that could modify tree regeneration responses to climate change. For example, negative and positive impacts of climate change on insect pests, tree diseases
and grazing animals (Pureswaran et al. 2015; Chapin et al. 2010; Frelich and Reich 2010) could also affect post-fire tree recruitment. Furthermore, tree species may eventually adapt to drier and warmer conditions. Indeed, trees from northern latitudes exhibit tolerances to temperature that differ from those of conspecific southern genotypes (Aitken et al 2008; Thomson et al. 2009; Pedlar and McKenney 2017). It can thus be asked whether climate change rates will allow trees sufficient time to adapt or acclimate to new conditions.

Despite this uncertainty about the anticipated effects of climate change, post-fire recruitment will likely be affected by warm and dry conditions, at least by the end of this century. In addition to indirect effects of fire frequency increases, the direct effects of a changing climate could have important repercussions on forest timber supply. Conifer-dominated forests may become less productive than they currently are, and timber supplies from deciduous species-dominated forests could also eventually decrease. The vulnerability maps that we produced are useful for identifying areas where species may be the most vulnerable to future climate conditions, where forest stands may be most at risk of regeneration failure, and where regeneration monitoring efforts should be prioritized. If recruitment proves to be deficient in these areas, adaptive silviculture practices such as the use of tree provenances adapted to future conditions (Nagel et al. 2017; Splawinski et al. 2019; Stevens-Rumann and Morgan 2019) could be used to mitigate the negative impacts of climate change on timber supply.

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