Agricultural and Forest Meteorology 339 (2023) 109548

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Climatic conditions modulate the effect of spruce budworm outbreaks on black spruce growth

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ARTICLE INFO

Keywords:
Climate change
Defoliation
Disturbances
Dendroecology
Ecological modeling
Forest management

ABSTRACT

Current ecological models predict profound climate change-related effects on the natural disturbance regimes of forests. Spruce budworm (*Choristoneura fumiferana)* (SBW) is the principal insect defoliator in eastern North America, and SBW outbreaks have a major impact on the structure and function of the Canadian boreal forest, as defoliation leads to decreased tree growth, increased mortality, and lower forest productivity. SBW outbreaks have become more severe over the last century with the changing climate; however, little is known about how climate fluctuations affect the growth of SBW host species during the outbreak period. Here we evaluate how climate and outbreak severity combined to affect black spruce (*Picea mariana*) growth during the SBW outbreak that occurred between 1968–1988 and 2006–2017. We compiled dendrochronological series (2271 trees), outbreak severity (estimated by observed aerial defoliation), and climate data for 164 sites in Québec, Canada. We used a linear mixed effect model to determine the impacts of climatic parameters, cumulative defoliation (of the previous five years), and their coupled effect on basal area growth. At maximum outbreak severity, basal area growth of black spruce was reduced by 14%–18% over five years. This outbreak growth response was affected by climate: warmer previous summer minimum temperatures and a higher previous summer climate moisture index further decreased growth by 11% and 4%, respectively. In contrast, a preceding year's warmer spring minimum temperatures (9%) and summer maximum temperatures (7%) attenuated the negative SBW effect. This study adds knowledge to our landscape-level understanding of combined insect–climate effects and helps predictions of future SBW-related damage to forest stands to bolster sustainable forest management. We also recommend that projections of boreal forest ecosystems include several classes of SBW defoliation and multiple climatic scenarios in future simulations.

1. Introduction

Disturbance shapes the structure and functioning of the boreal forest ecosystem (Gauthier et al., 2014; Girona et al., 2019; Labrecque-Foy et al., 2020). Natural disturbances in the boreal biome, such as fire and insect outbreaks, are likely to become more severe and frequent because of climate change (Aakala et al., 2023; Dale et al., 2001; Seidl et al., 2017; Volney and Fleming, 2000). Including disturbances and their relationship to climate variables within ecological models will help managers attain sustainable management goals and adapt these forests to the context of global change (Bergeron and Leduc, 1998; Ciesla, 2011; Girona et al., 2023a; Kwon et al., 2021; Pickett and White, 1985; Reyes et al., 2010). Though forests are directly impacted by climate change, the complexity of interactions in the forest ecosystem indicates that growth can also be affected indirectly as climate influences the disturbances like insect outbreaks (Gauthier et al., 2023; Girona et al., 2023b). Hence, forecasting the impacts of future climate requires understanding how climate change alters forest ecosystem dynamics including disturbance regimes (Achim et al., 2022; Hof et al., 2021; Molina et al., 2022).

In the boreal forest, insect outbreaks are major disturbances

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https://doi.org/10.1016/j.agrformet.2023.109548
Received 11 December 2022; Received in revised form 30 May 2023; Accepted 5 June 2023

(Bergeron et al., 1998, 2002; MacLean, 2016). The eastern spruce budworm (*Choristoneura fumiferana* Clemens, hereafter SBW), a tortricid moth, is recognized as the most important defoliator in the North American boreal forest because of its wide distribution and the marked impact on forest productivity and forest dynamics (Blais, 1983; Cappuccino et al., 1998; Gray and MacKinnon, 2006; MacLean, 2016). The economic and ecological consequences of SBW disturbances have placed these events among the priority topics of Canadian forestry research. Decades of continuous research by various organizations and agencies have improved our understanding of the epidemic cycle (Boulanger and Arseneault, 2004; Girona et al., 2018; Navarro et al., 2018; Ryerson et al., 2003), SBW effects on forest succession (Bergeron et al., 1995; Lavoie et al., 2021; MacLean, 1980, 2016; Martin et al., 2020), the synchrony of outbreaks over large areas (Bouchard et al., 2018; Sturtevant et al., 2015), and SBW population dynamics (Pureswaran et al., 2016; Régnière and Nealis, 2007; Régnière et al., 2019a; Royama, 1984).

The population density of this lepidopteran moth increases periodically to reach an outbreak level (Boulanger and Arseneault, 2004; Régnière and Nealis, 2007; Royama, 1984). In eastern Canada, SBW outbreaks follow a synchronized 30–40 year periodicity (Boulanger and Arseneault, 2004; MacLean, 1996). Over the twentieth century, outbreaks were concentrated into three main periods: 1905–1930 (moderate severity), 1935–1965 (long and less severe), and 1968–1988 (short and severe) (Aakala et al., 2023; Berguet et al., 2021; Navarro et al., 2018). These outbreaks have became more severe (Blais, 1983), synchronized over large forest territories (Jardon et al., 2003), and reached more northern latitudes (Navarro et al., 2018). The final outbreak of the last century (1968–1988) in eastern Canada affected a maximum area of 6 million ha at a moderate defoliation level and 21 million ha at a severe defoliation level. At its peak in 1975, SBW had killed 3 million ha of forest (Lavoie et al., 2019; MNRF, 2021).

The increasing trend of SBW defoliation is interlinked to complex processes occurring within the forest stands. The extent and intensity of defoliation are influenced by factors such as species, tree age, stand composition, the presence or absence of non-host species, the ecoregion (Houndode et al., 2021; Kneeshaw et al., 2015; MacLean, 2016), and climate (Candau and Fleming, 2005, 2011; Debaly et al., 2022). The vulnerability of the host (Nealis and Régnière, 2004), phenological synchrony or resistance (Blais, 1957; Pureswaran et al., 2015), nutritional composition of the needles (Bauce et al., 1994; Fuentealba and Bauce, 2012), and food quality provided by the host (Carisey and Bauce, 2002) also play roles in intensifying or limiting the defoliation impacts on growth. During the defoliation period, SBW generally starts affecting the architecture of the host by causing major damage and/or mortality of the terminal buds and parts of the axes (Hughes et al., 2015; Krause et al., 2012; Simard and Payette, 2003). Eventually, successive defoliation over multiple years leads to growth suppression and heightens the probability of tree mortality (Houndode et al., 2021; MacLean, 1980; Pothier et al., 2012). Balsam fir (*Abies balsamea* [L.] Mill.), white spruce (*Picea glauca* [Moench] Voss), black spruce (*Picea mariana* [Mill.] Britton, Sterns & Poggenburg), and red spruce (*Picea rubens* Sargent) are the main host species of SBW (Hennigar et al., 2008). Black spruce has become increasingly vulnerable to defoliation, leading to marked growth losses (Girona et al., 2023c; Hennigar et al., 2008; Hughes et al., 2015; Lavoie et al., 2019; Simard and Payette, 2003). In sum, defoliation has a multidimensional impact linked to multiple ecological factors interacting within the forest ecosystem (species, stand, climate, and ecoregion), including the active feeding phase of the SBW.

The SBW completes its life cycle within 12 months, which extends over two different years. In late summer, the adult moth mates and lays groups of 10 to 150 eggs on the needles of host trees. The hatched larvae (1st instar) build a silk cocoon to start diapause and be protected during the winter (Ciesla, 2011; Natural Resources Canada, 2018; USDA, 1985). The 2nd instar larvae—inside the hibernaculum—do not feed and their survival depends on the quality of food reserves. Once suitable conditions occur, the larvae emerge (Dickison et al., 1986; Marshall and Roe, 2021). At the beginning of spring, the larvae molt into the 3rd instar phase, and successive larval phases (4–6th instars) feed voraciously on the buds, foliage, and new shoots of host species. The defoliation/infestation peak occurs in summer, mainly in June; such voracious feeding on nutritious foliage strengthens a larva's chances of survival and the following generation's offspring overwintering success (Marshall and Roe, 2021). The 6th instar larvae metamorphose into the pupal phase and then develop into a moth form in July or August (Boulanger et al., 2017). Adult moths lay eggs on the foliage under favorable climate conditions (Régnière and Nealis, 2007).

All the biological events of SBW are linked to climate conditions (Dale et al., 2001; Gray, 2013; Han and Bauce, 1997; Wellington et al., 1950). Temperature and precipitation affect SBW development (Bellemin-Noël et al., 2021; Régnière and Nealis, 2007; Régnière et al., 2012), survivability and mortality (Han and Bauce, 1995, 1997; Régnière et al., 2012), range expansion (Régnière and Nealis, 2007; Régnière et al., 2019b), and SBW behavior in defoliating their hosts (Candau and Fleming, 2011; Gray, 2013). During spring, for example, an increased larval emergence from diapause is observed once the temperature increases above 10 °C (Pureswaran et al., 2018a), and moisture availability in summer alters the SBW diet during its active feeding phase (Carisey and Bauce, 2002). Climate changes in spring and summer (past and current) can affect both the insect and the host species; therefore, climate is a critical element influencing the SBW life cycle activities, e.g., accelerates or delays each stage to affect SBW feeding. This is linked directly to the growth of the host species.

Similarly, tree growth and development are influenced by climate (Girard et al., 2011; Girardin et al., 2012, 2016a; Pappas et al., 2022a). Factors such as temperature, precipitation, and moisture availability influence the phenological cycle and, thus, growth (Guo et al., 2021; Girona et al., 2017; Pureswaran et al., 2018a; Rossi et al., 2011). An example is the earlier budburst because of recent warming (Blais, 1983; Pureswaran et al., 2018a). Several studies have documented that the radial growth of black spruce can be influenced in response to changes in climate—specifically climate of the growing season (Chavardès et al., 2021; Girard et al., 2011; Li et al., 2020; Walker et al., 2015). For example, the onset of growth in black spruce, occurring from late May to mid-June, confirms the importance of favorable temperatures and moisture levels in the summer months (Rossi et al., 2011). Warmer temperatures in the short growing period in cold boreal regions favor black spruce growth (D'Orangeville et al., 2016; Rossi et al., 2011), and increased precipitation also benefits spruce by lowering moisture stress (Fierravanti et al., 2015). As climate also mediates SBW activity, the response of black spruce growth is modified by the SBW–climate links.

Climate fluctuations affect both the insect population and its impact on tree growth (De Grandpré et al., 2018a; Pureswaran et al., 2018b). It is expected that the spring and summer climate of the current and preceding year—closely associated with the active feeding period of SBW larvae and the tree growth—mainly regulate the characteristics of defoliation and the growth of the host species. Moreover, altered temperatures and precipitation during the summer (June–August), the active feeding period of SBW, can influence host–SBW interactions. Recent climate change, for example, has reduced the phenological and climatic mismatch existing between black spruce and SBW (Fuentealba et al., 2017; Pureswaran et al., 2018a). Thus, the recent defoliation trend during SBW outbreaks has raised questions about whether climate change is a major driver of the increased defoliation severity and decreased forest productivity observed during more recent outbreaks. This understanding of climate–defoliation links during insect outbreaks remains incomplete, despite their importance within the context of global change (De Grandpré et al., 2018b; Pureswaran et al., 2018b; Robert et al., 2017). Specifically, no studies have yet to analyze the historical evidence of how climate fluctuations affect SBW defoliation severity, causing growth reductions for vulnerable host species like black spruce.

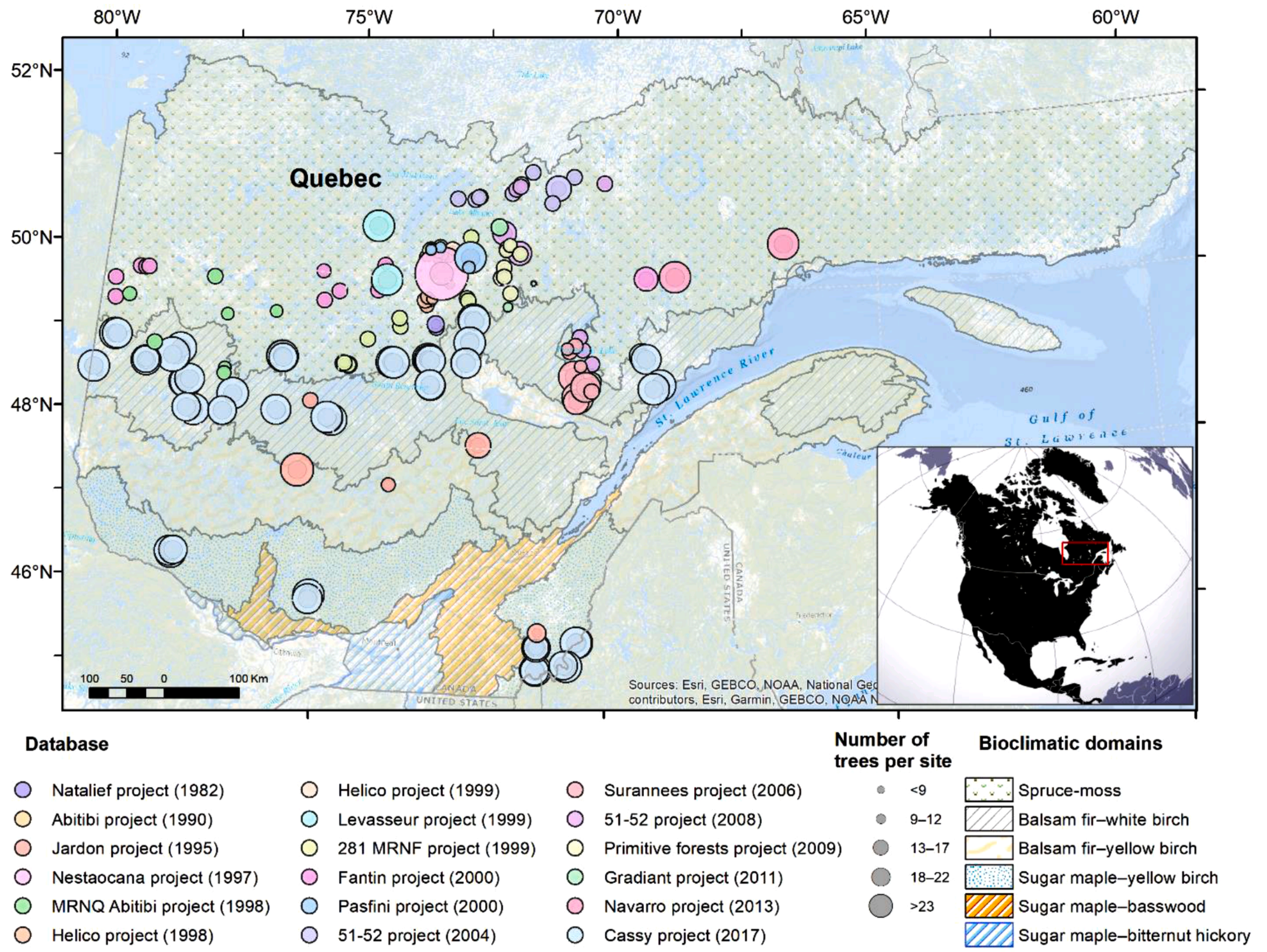

Fig. 1. Location of study sites across the various bioclimatic domains in Québec, Canada. The *colored circles* correspond to those projects included within the dendrochronological database; circle size indicates the number of tree series for each site. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Here, our main goal is to evaluate the influence of climate and outbreak severity on black spruce growth during outbreaks in the latter part of the twentieth century (1968–1988) and a part of the first outbreak of twenty-first century (2006–2017). We rely on a dendroecological database for the province of Québec, Canada, to determine the climatic drivers influencing defoliation severity and leading to growth reductions in black spruce stands during outbreaks. We propose that (1) high temperatures and greater precipitation in the previous spring and summer reduce the current year growth of black spruce because of increased defoliation severity during an outbreak period; and (2) higher June temperatures limit growth by favoring a greater abundance and impact of SBW. Although there are ubiquitous factors influencing growth–defoliation interactions, directly and indirectly, spring and summer climate conditions are expected to have a greater influence. Therefore, this project aims to improve our understanding of how temperature and precipitation modulate growth and SBW severity in the context of climate change.

2. Materials and methods

2.1. Study area

The study area covers nearly 900 000 km^2 of the boreal and northern temperate vegetation zone of Québec (Canada) from 45° to 51°N and 65° to 80°W (Fig. 1). Regional climate is subpolar–subhumid continental, characterized by long, cold winters and short, cool summers (MNRF, 2008). The northern region is characterized by relatively colder/lower precipitation conditions with an annual average temperature of −7.5 °C and annual precipitation of 500 mm, whereas the southern portion is warmer with an annual average temperature of 1 °C and an annual precipitation of 1000 mm (MNRF, 2008). In Québec, the closed boreal forest is dominated by pure black spruce stands in the north and the mixed forests of white spruce, fir, and broadleaf trees in the south (Rossi et al., 2009). The black spruce domain has a relatively short growing period of 93 to 122 days, extending between late May to early October (Rossi et al., 2011).

In the eastern Canadian boreal forest, SBW outbreaks represent one of the major natural disturbances affecting these forests (Cappuccino et al., 1998; MacLean, 2016; Navarro et al., 2018). In the twenty-first century, 170 000 km^2 of forest has already experienced severe defoliation by SBW since the onset of an outbreak in 2006 (Fig. A.1; MNRF, 2021). Fire, with a return interval of 270 to >500 years, is another disturbance influencing insect outbreak dynamics in the boreal forest (Bergeron and Leduc, 1998; Cyr et al., 2007), and consecutive defoliation from insect increases the risk of fire (James et al., 2017). In eastern North America, the frequency of fire and the outbreaks are recorded to have inverse occurrence over the Holocene (Morin et al., 2021).

2.2. Data compilation and experimental design

Our study relied on collected cross-dated dendrochronological series, defoliation surveys, and interpolated weather data sets. We selected to

Table 1
Dendrochronological projects compiled for this study.

ID	Project name	Sampling year	Number of sampled trees	Total number of sites	Trees per site (Min.–Max.)	Max. tree age	References
1	281 MRNF	1999	162	16	9–12	218	–
2	51–52 I	2004	116	11	10–16	247	(Tremblay et al., 2011)
3	51–52 II	2008	90	8	10–15	200	
4	Abitibi	1990	7	1	7	212	–
5	Cassy	2017	1084	57	14–22	227	(Berguet et al., 2021)
6	Fantin	2000	124	12	9–15	179	(Fantin and Morin, 2002)
7	Gradiant	2011	38	5	3–12	171	–
8	Helico I	1998	65	7	7–11	131	–
9	Helico II	1999	49	5	9–11	229	–
10	Jardon	1995	88	6	9–21	352	
11	Levasseur	1999	40	2	20	173	(Levasseur, 2000)
12	MRNQ Abitibi	1998	62	7	8–10	198	–
13	Natalief	1982	31	3	10–11	157	–
14	Navarro	2013	40	2	20	278	(Navarro et al., 2018)
15	Nestaocana	1997	34	1	34	175	–
16	Pasfini	2000	42	4	7–20	191	–
17	Primitive forests	2009	78	8	9–10	276	–
18	Surannees	2006	121	9	8–20	251	–
	Total		2271	164			

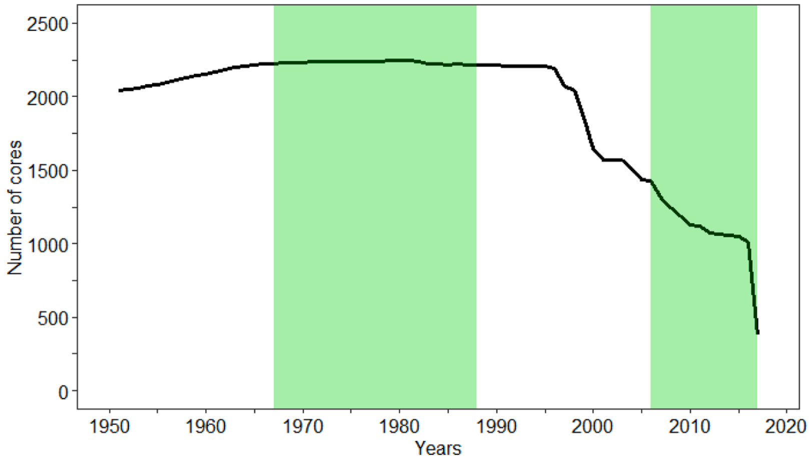

Fig. 2. Number of annual tree cores sampled for each year from 1951 to 2017. The colored area represents the two SBW outbreak periods, 1968–1988 and 2006–2017. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

study the period from 1951 to 2017 (a period for which all data sets overlapped), which covers the third SBW outbreak of the twentieth century (1968–1988) and part of the current outbreak (2006–present; our data set covers 2006–2017). We compiled cross-dated dendrochronological series from 18 existing/previous projects conducted in Québec over the past three decades (1982–2017). The combined database included approximately 4700 trees. From this compilation, we retained only those series corresponding to black spruce, except for a few southern sites that included red and white spruce, which resulted in a total of 2271 tree-ring series (Table 1). These trees were distributed across 164 sites, with an average of 14 trees sampled per site; site size was 400 m^2. In some cases, trees from the same project and ecoregion were merged based on the geographic proximity in ArcGIS; in particular, sites with few black spruce trees were manually merged with a nearby site with more black spruce trees.

2.3. Dendrochronological data sets

Dendrochronology is a powerful tool for studying tree response to anthropogenic and natural disturbances (Gennaretti et al., 2018; Girona et al., 2016; Labrecque-Foy et al., 2020). All selected dendrochronological projects followed standardized protocols for collecting, preparing, measuring, and cross-dating (Krause and Morin, 1995). The ring cores were taken from the field, air-dried, and then sanded after mounting on wooden boards. Ring width was measured either with a WinDendro™ system (Guay et al., 1992; Tremblay et al., 2011) or a manual Henson micrometer having an accuracy of 0.01 mm. The annual growth rings were counted for each sample, and diagnostic rings (light, dark, narrow, or incomplete) were identified to facilitate dating (Girard et al., 2011). These tree rings were cross-dated visually, and cross-checks were made using statistical software such as COFECHA (Holmes, 1983) to identify missing or false rings and verify measurement errors. Accurate cross-dating minimizes errors related to growth anomalies, e.g., missing or false rings (Swetnam et al., 1985). Ring records in our database covered 67 years and varied in yearly abundance from 381 to 2248 tree cores per year (Fig. 2). We converted these ring-width series into basal area increments (BAI, basal area growth is named *growth* hereafter) using the *bai.out* function of the dplR package in R (Eq. (1); Bunn et al., 2021). We used BAI over detrending methods since the latter might eliminate some of the effects of climate on growth: i.e. differences in the mean growth levels between sites and differences due to long-term climate trends (Girardin et al., 2016b).

$$BAI_t = \pi r_t^2 - \pi r_{t-1}^2, \tag{1}$$

where r denotes tree radius, and t is the year of ring formation.

2.4. Defoliation surveys

The defoliation survey data were collected from Québec Ministry of Natural Resources and Forests (MNRF). The collected defoliation data were derived from annual defoliation maps produced by the ministry on a yearly basis since 1967 from aerial surveys of SBW-affected areas (Fig. A.2; Gray et al., 2000). Surveys were conducted from late June in the southwest to early August in the northeastern areas. A topographic map was used to delineate the polygons of insect damage for SBW, and each polygon was assigned a defoliation level for the current year (Gray and MacKinnon, 2006). The defoliation was categorized as light (1%–35%; loss of foliage in the upper third of the crown of some trees), moderate (36%–70%; loss of foliage in the upper half of the crown of most trees), and severe (71%–100%; loss of foliage across the entire length of the crown of most trees) (Gray et al., 2000; MRNF, 2020). Though the variation in the accuracy of the aerial survey across each defoliation class could make the defoliation estimation a bit coarse (MacLean and MacKinnon, 1996), the data was used as it was the only source of annual information about SBW outbreak severity at the provincial scale in Quebec. Because the survey primarily detects defoliation of balsam fir, we created a circular buffer of 20 km around each site and retained only those sites in which balsam fir was present (by relying on the Québec forest inventory data). The buffer of 20 km was selected so as to have an actual idea about the stand composition around the sites, considering the size of the study area (Navarro et al., 2018). Therefore, we used the defoliation class as a proxy of SBW outbreak severity in the landscape surrounding our sampled black spruce stands. For each stand in our dendrochronological data set, we computed for each growth year, the cumulative defoliation of the last five years. For this, the defoliation class for each year was converted to a numerical value: 0 for no active defoliation, 1/3 for light, 2/3 for moderate, and 1 for severe defoliation. We used the five years preceding the sample year, as SBW defoliation generally does not affect radial growth of the same year but rather affects growth with a lag up to five years (Bergeron et al., 1995; Krause et al., 2003, 2012; MacLean, 1980); this means that the defoliation index can reach up to 5 at a maximum. Thus, we obtained a time series of outbreak severity within our study zone from 1968 to 2017.

2.5. Climate series

For each site, we modeled elevation using digital elevation model (DEM) data for Québec. We relied on latitude, longitude, and elevation to interpolate weather variables (at a daily resolution) for each site and year between 1951 and 2017 using the BioSIM software (Régnière et al., 2017). The weather database used were of normal and daily statistics accessed through ftp://ftp.cfl.scf.rncan.gc.ca/regniere/Data11/Weather/ as indicated in the BioSIM User's Manual. The software interpolates the climate parameters utilizing the normal and daily weather records obtained from nearby meteorological stations, acquired from the historical North American (Canada-USA) database accessible by default (Régnière et al., 2017). For selecting the predictors for our model, we calculated climatic summary variables related to important stages in the phenology and biology of SBW (Candau and Fleming, 2005, 2011). These variables included temperature (°C, minimum and maximum) and precipitation (mm) at a seasonal scale—spring (March–May) and summer (June–August)—and at a monthly scale for June, July, and August. We also calculated the climate moisture index (CMI) for the spring, summer, and June-August (for each month) following D'Orangeville et al. (2018); monthly potential evapotranspiration (PET) values were estimated with the Standardized Precipitation Evapotranspiration Index (SPEI) package in R and running the Penman–Monteith algorithm with inputs of monthly average daily minimum and maximum temperature, latitude, incoming solar radiation, temperature at dew point, atmospheric pressure, wind speed at 2 m, and elevation, where all the weather variables were interpolated using BioSIM. The spring and summer CMIs were calculated as the difference between precipitation and potential evapotranspiration over a period I (in mm of water; Eq. (2)).

$$CMI_i = Prec_i - -PET_{i,} \tag{2}$$

In the models presented in the next section, we consider as predictors both the previous year values of the climate variables (calculated at the seasonal scale, i.e., previous spring and previous summer) and current year values (calculated at the monthly scale, from June to August).

2.6. Statistical analysis

Statistical modeling was performed in two steps. In the first step, we modeled the logarithm of the basal area increment (log BAI) for each ring as a function of the log of the current basal area (cumulative BAI of previous rings) and its cambial age (Eq. (3)) using a generalized additive model (GAM) to evaluate tree-specific effects on growth. The basal area (BA; cross-sectional area of the tree at breast height) was calculated for each year for each tree as the cumulative sum of the BAI up to that year. The effect of logarithm of the basal area was expected to be linear, whereas the age effect was modeled as a smoothing spline with $k = 50$ basis functions using the *mgcv* package in R (Wood, 2011).

$$log(BAI) = log(BA) + s(Age, k = 50) + Residuals, \tag{3}$$

The first model, thus, removed the long-term trend specific to each tree (i.e., because of the differences in age, size, genetics, and microsite conditions). The residuals therefore contain the effects of interannual climate variation and SBW outbreaks, which we modeled in the second step. This two-step approach was applied in part because of the excessive computational costs associated with including all effects within the same model, given the size of our database.

In the second step, we used linear mixed effect (LME) models to estimate the effects of climate, outbreak severity, and the links between the two using lme4 package (Bates et al., 2015). At this step, the response variable consisted of the residuals of log(BAI) from the GAM model, averaged by site and year. The predictors were different combinations of cumulative defoliation of the last five years with seasonal (previous spring and summer) and monthly (June, July, and August) climatic variables, along with their relationship to cumulative defoliation. All climatic predictors were standardized before including them in the models to simplify comparing the effect size between the predictors. We also included the random effects of site and year in the models.

Because precipitation and CMI are correlated—via the definition of CMI—we used Akaike's information criterion (AIC) to determine which of these two predictors to use in our models. We also used AIC to determine whether to include a random effect of site, year, or both. (Mazerolle, 2020). For the base model (including all climate variables and their effect on cumulative defoliation), we used diagnostic plots to assess whether the model assumptions were met (normality of residuals and random effects, homoscedasticity, absence of residual trend). We also verified that there was no important collinearity between the variables (VIF <10, Graham (2003); Fig. A.3 & A.4). Then, we determined the statistically significant relationship between predictors and the response on the basis of 95% confidence intervals ($\alpha = 0.05$). Finally, we tested whether we could create a more parsimonious model from our base model by using a backward selection approach to eliminate associations between some of the climate predictors and defoliation; we selected the best model using the model with the lowest AIC. We repeated the same process—analysis of the base model and creation of a parsimonious model—for the monthly climate variables since both seasonal and monthly variables can interchange the interaction effect on the growth of black spruce. All statistical analyses were performed using various packages in R version 4.2.0 (R Core Team, 2022).

Table 2

Summary of the GAM results for the effect of tree size and age.

	Estimate	Std. error	*p*-value	Adj. R^2
Intercept	−3.853	0.023	0.001	0.65
log(BA)	1.001	0.002	0.001	
Significance of the smoothing predictor	edf	*F*	*p*-value	
s (age)	42.11	2504	0.001	

3. Results

3.1. Growth, defoliation, and climate trends

All predictors of the GAM model had a significant effect on tree growth, and the model explained approximately 65% of the variation in basal area increment (Table 2). The model indicated that the average growth–increment process decreased continuously, following a nonlinear trend with tree age.

Mean individual tree growth varied year to year across all sites. Black spruce growth peaked around 1960 and again around 2010 (Fig. 3a). A sharp drop in growth occurred between the early 1960s to around the 1980s, after which there was growth release in the ring widths for approximately five years. The minimum growth was observed between 1995 and 2000. Similarly, the mean cumulative defoliation across all sites reflected peak defoliation between 1970 and 1990; this period overlapped with a period characterized by a steep decline in black spruce growth (Fig. 3b).

Regional climate, averaged across all sites over the 67 years, showed several patterns. Mean spring and summer temperatures were −0.5 °C (min. = −7.0 °C, max. = 5.9 °C) and 14.8 °C (min. = 8.5 °C, max. = 21.1 °C), respectively. Similarly, the average spring and summer CMI were −6.5 mm and −19.1 mm, respectively. Nevertheless, the seasonal climate variables showed a significant ($p < 0.05$) increasing trend for the spring and summer temperatures, whereas the observed decreasing trend for spring and summer CMI was not significant (Fig. 4).

3.2. Growth in response to defoliation and climate

We found that the model with site and year and the model with CMI—rather than precipitation— produced the lowest AIC when choosing between different versions of the random effects and precipitation or CMI as a predictor. Therefore, for all models we used both site and year as random effects and CMI rather than precipitation.

The mixed effect model revealed that the variance of the intercept described by the random effects of the site and year were 0.09 and 0.01, respectively, with a residual variance of 0.04 (Fig. 5a). These model parameters comprising both random and fixed effects explained approximately 70% of the variation in black spruce growth. The main effect of SBW was that for every year with a severe outbreak level within the previous five years (i.e. for an increase of the defoliation index by 1), black spruce growth was reduced by 14%. This effect on growth varied according to its relationship with the climate variables and, here, it is interpreted as a standardized effect, i.e., based on a change of one standard deviation of the climate predictors. In the absence of outbreaks, the previous summer minimum temperature is positively related to growth (11% growth increase), but during the outbreak, this climate effect is null (reduced by 11% from its no-outbreak baseline for a unit increase in the defoliation index). Also, one standard deviation increase in the previous summer CMI further increases the annual growth of black spruce by 8%; this positive response was reduced to 4% due to the SBW effect during the outbreak period. In contrast, the decrease in growth due to an increase in the summer maximum temperature was attenuated by 7% due to the SBW effect. Also, the growth was significantly increased by 9% with increasing spring minimum temperatures during an outbreak. Thus, the SBW effect on black spruce growth varied with the change in temperature and CMI among the levels of defoliation severity.

Our best model improved its predictive performance, as measured by AIC, when we removed the effects of cumulative defoliation coupled with the previous spring CMI and the previous spring maximum temperature (Table 3a & Table A.1). The effect on growth was not significantly lower or higher, i.e., this optimal model preserved almost the same effects of the predictors as they had on our base model, and we identified a linear relationship between growth and the climatic parameters. The prediction graph showed that at the same defoliation

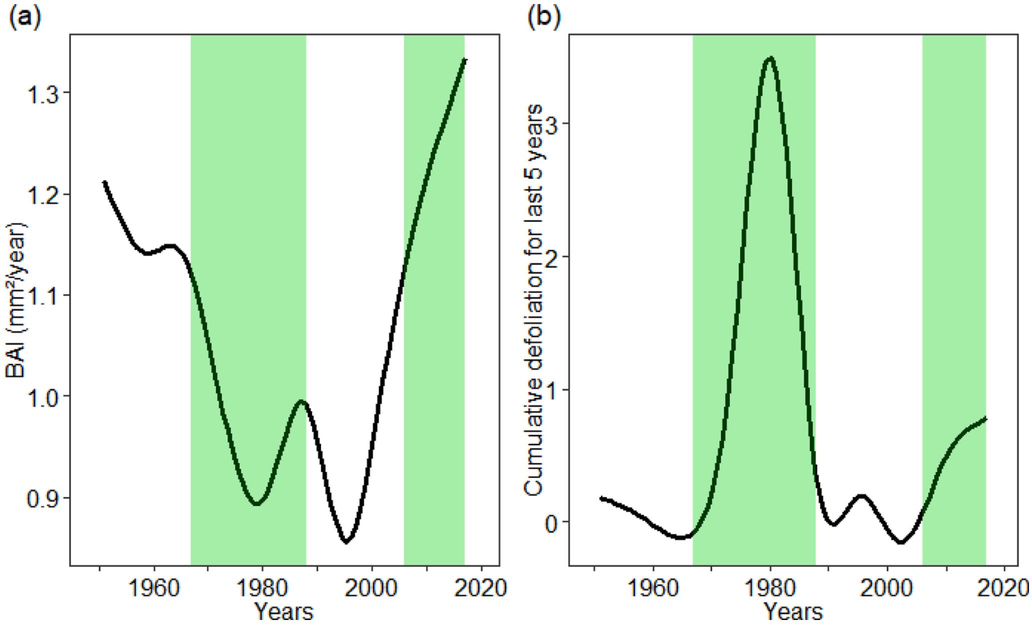

Fig. 3. Trends over study period; **a)** Estimated yearly basal area increment of black spruce after the removal of tree-specific effects; and **b)** the cumulative defoliation by the SBW. The colored regions represent two SBW outbreak duration covered by our study periods. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

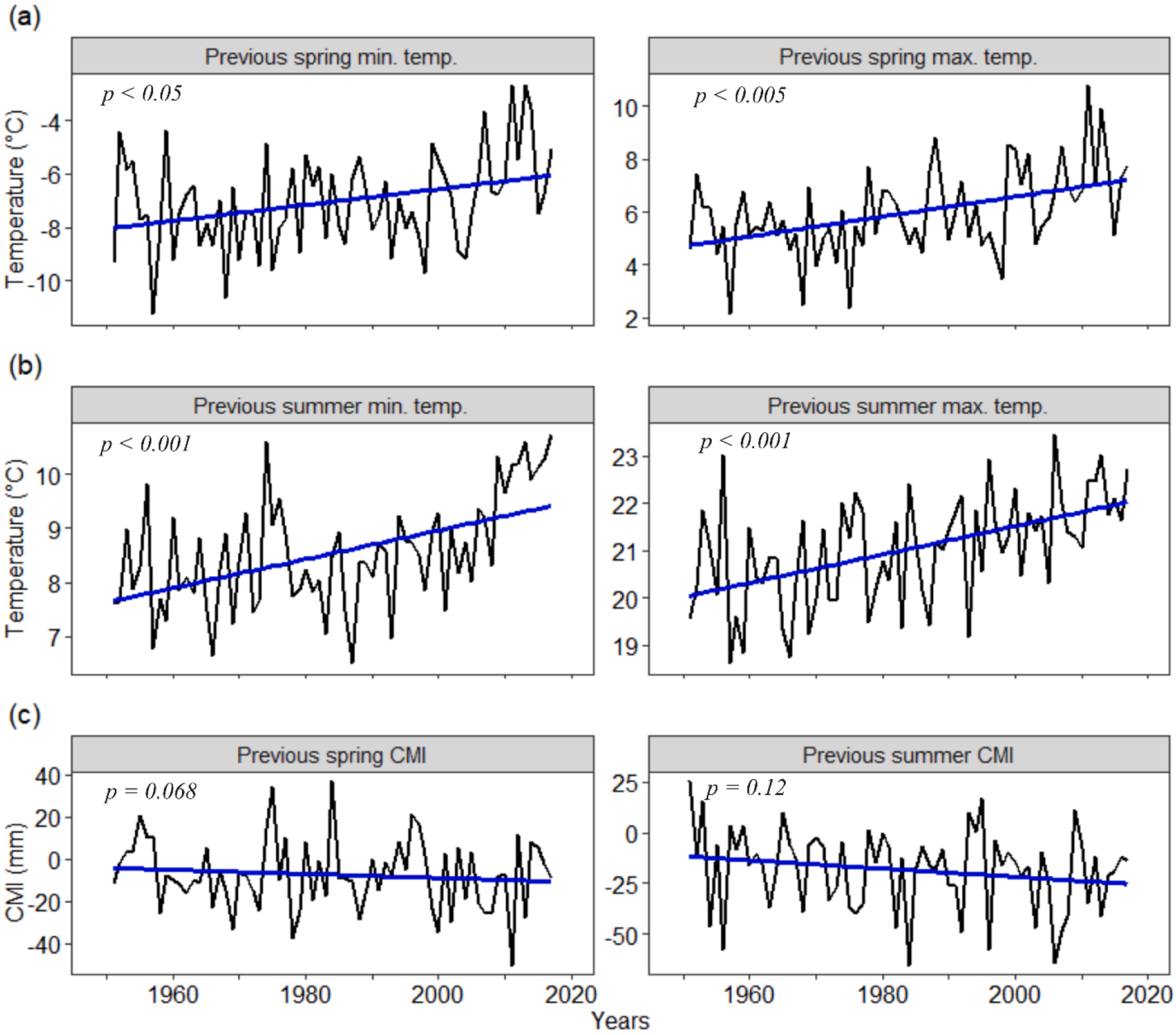

Fig. 4. Trends of the averaged climatic metrics of the previous year for all sites during the study period; **a)** spring minimum and maximum temperatures; **b)** summer minimum and maximum temperatures; and **c)** spring and summer CMI.

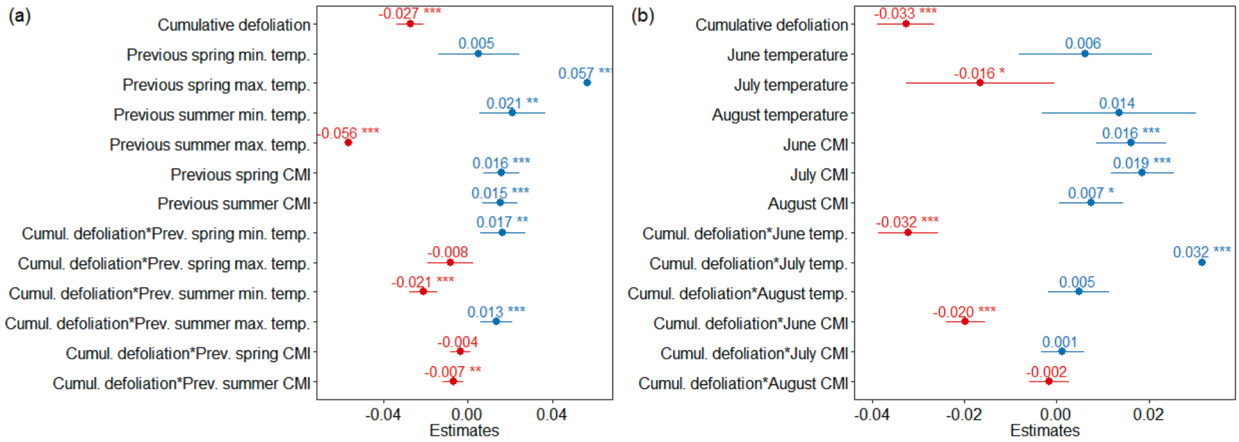

Fig. 5. Effect of seasonal climate variables (a), monthly climate variables (b) and SBW pressure (measured by cumulative defoliation) on the annual growth of black spruce. The climate variables were standardized to represent the number of standard deviations above or below the mean across sites and years, and the cumulative defoliation represents the sum of number of years at maximum outbreak severity across a site over the past five years. Significance: *** $P < 0.0001$; ** $P < 0.001$; * $P < 0.01$.

Table 3
The detailed parameter estimates for the best model identified after comparing the AIC for seasonal predictors (a) and monthly predictors (b). The response represents the residuals of log(BAI) from GAM model that accounts the effects of tree size and age. The climate variables were standardized to represent the number of standard deviations above or below the mean across sites and years, and the cumulative defoliation represents the sum of maximum outbreak severity across a site over the past five years. SD and SE are the standard deviation and the standard error respectively. Note: The width of the confidence interval may be underestimated as the estimates were obtained after the model comparison.

(a) Seasonal predictors **Response:** LogBAI				
Random effects			**Marginal R^2**	**Conditional R^2**
			0.032	0.702
	Variance	**SD**		
Site	0.09123	0.302		
Year	0.01387	0.1178		
Residual	0.04525	0.2127		
Fixed effects				
Predictors	**Coefficients**	**SE**	**Confidence interval**	
			2.5%	97.5%
Cumul. Defoliation (Cum. Def.)	–0.028	0.003	–0.034	–0.022
Prev spring temp. min.	0.009	0.010	–0.010	0.027
Prev spring temp. max	0.051	0.011	0.031	0.072
Prev summer temp. min.	0.019	0.008	0.004	0.035
Prev summer temp. max.	–0.053	0.009	–0.071	–0.036
Prev spring CMI	–0.053	0.009	–0.071	–0.036
Prev summer CMI	0.016	0.004	0.008	0.024
Cum.Def.:Prev spring temp. min.	0.010	0.003	0.004	0.016
Cum.Def.: Prev summer temp. min.	–0.018	0.003	–0.023	–0.013
Cum.Def.:Prev summer temp. max.	0.010	0.003	0.004	0.016
Cum.Def.:Prev summer CMI	–0.008	0.002	–0.013	–0.004

(b) Monthly predictors **Response:** LogBAI				
Random effects:			**Marginal R^2**	**Conditional R^2**
			0.028	0.715
	Variance	**SD**		
Site	0.095	0.308		
Year	0.014	0.119		
Residual	0.045	0.212		
Fixed effects				
Predictors	**Coefficients**	**SE**	**Confidence interval**	
			2.5%	97.5%
Cumul. Defoliation (Cum.Def.)	–0.032	0.003	–0.039	–0.026
June temp.	0.006	0.007	–0.008	0.021
July temp.	–0.016	0.008	–0.032	0.000
August temp.	0.013	0.008	–0.004	0.029
June CMI	0.016	0.004	0.009	0.024
July CMI	0.019	0.003	0.013	0.026
August CMI	0.007	0.003	0.000	0.013
Cum.Def.:June temp.	–0.032	0.003	–0.038	–0.025
Cum.Def.:July temp.	0.030	0.004	0.023	0.038
Cum.Def.:Aug temp.	0.005	0.003	–0.001	0.012
Cum.Def.:June CMI	–0.020	0.002	–0.024	–0.016

Table A.1
Model sets for the seasonal climatic variables reported with their AICc score. Models were produced using different combinations of seasonal climate and defoliation with a backward selection approach, and the best model was identified using AIC. Note: All these models have the random effect of the site and year in addition to the variables presented.

ID	Models	K	AICc	Delta_AICc	AICcWt	Cum. Wt	LL
1	prev_spr_temp_max + cum.def *(prev_spr_temp_min + prev_sum_temp_min + prev_sum_temp_max + prev_sum_CMI)	15	−1345.81	0	0.27	0.27	687.9
2	prev_sum_temp_min + cum.def *(prev_spr_temp_min + prev_spr_temp_max + prev_sum_temp_min + prev_sum_temp_max + prev_spr_CMI + prev_sum_CMI)	17	−1344.6	1.21	0.15	0.42	689.3
3	cum.def *(prev_spr_temp_min + prev_spr_temp_max + prev_sum_temp_min + prev_sum_temp_max + prev_spr_CMI + prev_sum_CMI) (BASE MODEL)	17	−1344.6	1.21	0.15	0.57	689.3
4	prev_sum_temp_max + cum.def *(prev_spr_temp_min + prev_spr_temp_max + prev_sum_temp_min + prev_sum_temp_max + prev_spr_CMI + prev_sum_CMI)	17	−1344.6	1.21	0.15	0.72	689.3
5	prev_spr_temp_max + cum.def *(prev_spr_temp_min + prev_sum_temp_min + prev_sum_temp_max + prev_spr_CMI + prev_sum_CMI)	16	−1344.42	1.4	0.14	0.86	688.2
6	prev_spr_CMI + cum.def *(prev_spr_temp_min + prev_spr_temp_max + prev_sum_temp_min + prev_sum_temp_max + prev_sum_CMI)	16	−1344.27	1.54	0.13	0.99	688.2
7	prev_sum_CMI + cum.def *(prev_spr_temp_min + prev_spr_temp_max + prev_sum_temp_min + prev_sum_temp_max + prev_spr_CMI)	16	−1338.54	7.27	0.01	0.99	685.3
8	prev_spr_temp_min + cum.def *(prev_spr_temp_max + prev_sum_temp_min + prev_sum_temp_max + prev_spr_CMI + prev_sum_CMI)	16	−1337.39	8.42	0	1	684.7
9	prev_spr_temp_max + cum.def *(prev_spr_temp_min + prev_sum_temp_min + prev_sum_temp_max + prev_sum_CMI)	14	−1337.12	8.69	0	1	682.6
10	prev_spr_CMI + cum.def *(prev_spr_temp_min + prev_sum_temp_min + prev_sum_temp_max + prev_sum_CMI)	14	−1324.18	21.63	0	1	676.1
11	cum.def *(prev_spr_temp_min + prev_sum_temp_min + prev_sum_temp_max + prev_sum_CMI)	13	−1323.38	22.43	0	1	674.7

level, the slope linking black spruce growth with climate conditions was either negative or positive depending upon the specific climate variable (Fig. 6a).

The model with monthly climate predictors described approximately 72% of the variation in black spruce growth with the inclusion of the random effects of site and year. During the outbreak period, the growth was reduced by 18% for five years of cumulative severe defoliation (Fig. 5b). Black spruce showed an improved growth with increased June temperature (not significant) and June-August CMI (4–10%), but a significantly negative response with warmer July temperatures (8%). However, all these climate effects were reversed in the presence of a SBW outbreak. With this impact, an increased standard deviation of one for June temperature and June CMI led to a further growth reduction of 17% and 11% respectively (Fig. 6b). Nevertheless, the SBW effect led to increase the growth by 17% with the increase in July temperature—even if it has negative growth relation in the absence of defoliation. Our best-selected monthly model improved its performance when the combined effect of cumulative defoliation and July and August CMI was

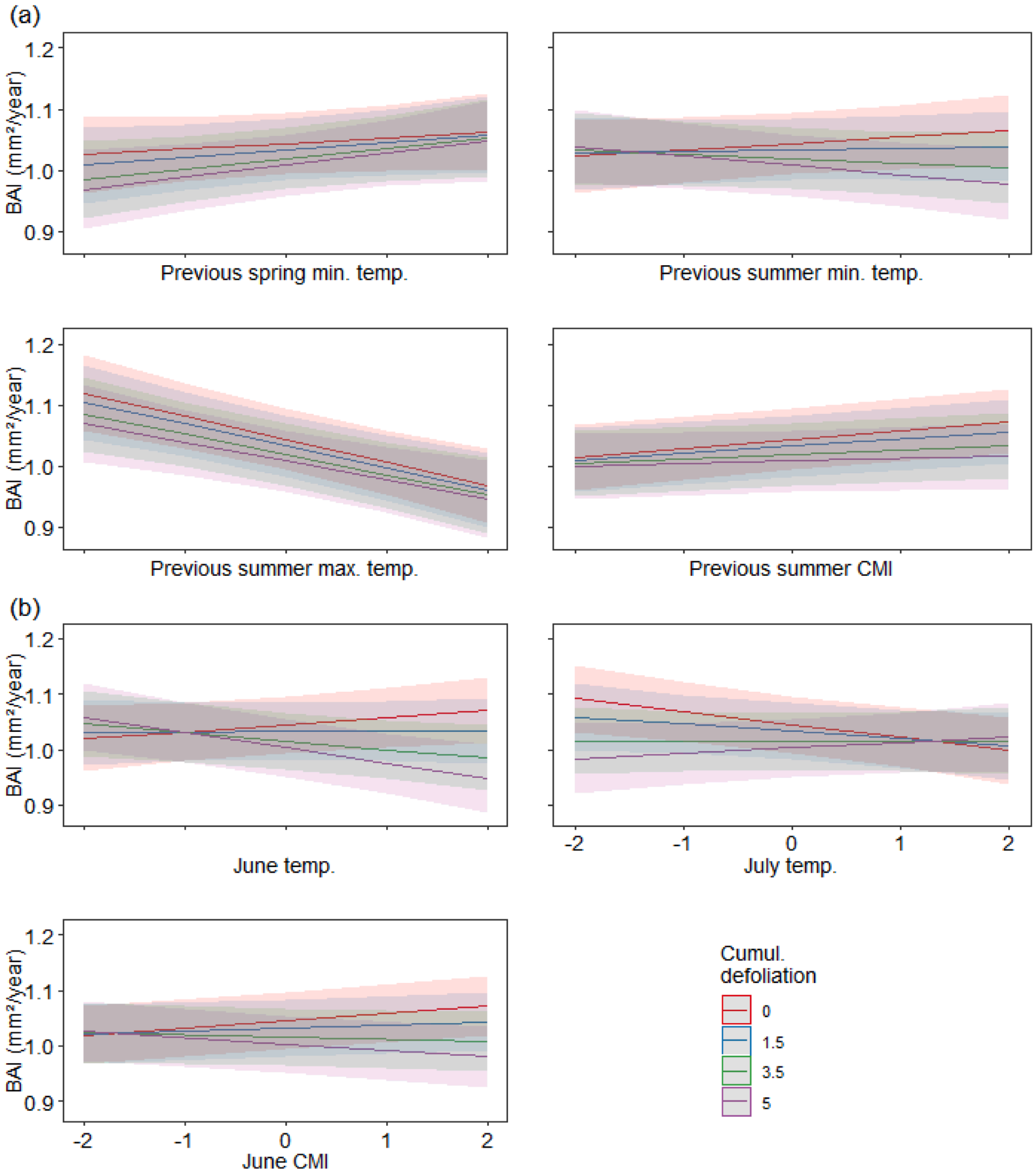

Fig. 6. The effect of the interaction of seasonal climate variables (a) and monthly climate variables (b) with SBW pressure (cumulative defoliation index) on basal area growth among different levels of cumulative defoliation. The climate variables were standardized to represent the number of standard deviations above or below the mean across sites and years, and the cumulative defoliation represents the sum of maximum outbreak severity across a site over the last five years.

removed (Tables 3b & A.2).

4. Discussion

Climate change and disturbance regimes are major drivers in the Canadian boreal forest (Dale et al., 2001; Seidl et al., 2017). We found that 70% of growth variation in black spruce depended on site characteristics, growth-year, and the relationship between insect disturbance and climate. Because climate can alter the life cycle of SBW, which depends on a host tree species for survival, the SBW effect on growth are also driven by climate. Multiple previous studies have found an independent relationship between defoliation and/or climate (Candau and Fleming, 2005, 2011; Debaly et al., 2022) and host species' growth in the boreal forest (D'Orangeville et al., 2018; Marchand et al., 2019; Walker and Johnstone, 2014). In contrast, here we highlight the effect of climate–defoliation on black spruce growth by relying on dendrochronological databases and SBW outbreak records covering the large province of Québec (Canada).

Our models highlighted a reduced black spruce growth in response to defoliation and climate change. This defoliation-related growth reduction (14%–18% per cumulative five-year defoliation when the other climatic variables are at their mean value) is ecologically significant,

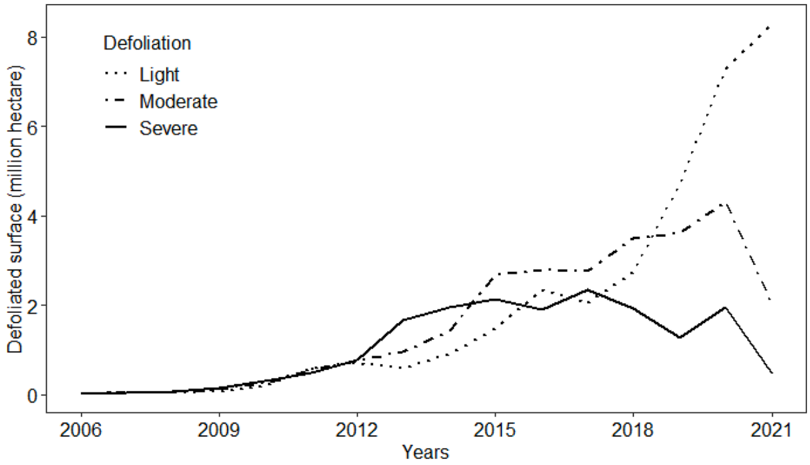

Fig A.1. Area affected by SBW defoliation in Québec from 2006 to 2021, representing the first major SBW outbreak in the twenty-first century (MNRF, 2021).

particularly for a slow-growing species within the boreal zone, which is characterized by a relatively short growing period (93–122 days). The normal growth was hindered (a reduced growth of approximately 3% per year) due to the continuous stress imposed from the SBW defoliation. As a secondary host, black spruce holds the possibility of being less affected by SBW relative to balsam fir and white spruce (Houndode et al., 2021; Nealis and Régnière, 2004). However, some studies previously indicated that the defoliation can cause a growth reduction that could reach up to 50% (Erdle and MacLean, 1999; Krause et al., 2012; Rossi et al., 2018). These studies indicated the direct defoliation impact on growth; whereas, our study highlighted the effect due to the SBW pressure on black spruce during the outbreak period. Nevertheless, the variability in the accuracy of the defoliation survey in categorizing levels of severity can also affect the estimated effect of defoliation on growth (MacLean and MacKinnon, 1996). The disparity of underestimation could be due to the broad spatial scale of the defoliation data that we averaged over the landscape, but it was the only historical information available on yearly basis in the province.

Furthermore, our study demonstrated that the SBW effect on growth is modulated significantly by climate (Fig. 5). Climatic variation influences outbreak severity and the extent of defoliation (Gray, 2013); however, the degree of defoliation also determines the extent to which climate affects host tree growth (Boakye et al., 2022). Both the direct climate effect on growth and the manner by which climate mediates the SBW effect depend on the specific climate variable undergoing change (e.g., spring–summer temperature and precipitation) and time of the year. From an ecological point of view, this complex relationship is modified by other associated factors, e.g., forest composition, site characteristics, and other prevailing disturbances such as fire (Bergeron et al., 2002; Dale et al., 2001); however, we restricted our study specifically to the effect of climate and SBW disturbance. Thus, this macro perspective (large scale in space and time) to detect climate effect determining how much black spruce loses growth during a SBW outbreak is hoped to improve our understanding of the disturbance impact in the boreal region. Nevertheless, we suggest incorporating multi-year tree-level defoliation estimates, in future studies, that could further widen insect-climate effects on growth, in addition to the result obtained here.

4.1. *Effect of climate on growth*

In years outside of SBW outbreaks, we found black spruce growth to be regulated either positively or negatively depending upon whether the models considered seasonal or monthly climate variables. Temperature (minimum and maximum), precipitation, available water, and winter snowfall have been identified as some of the important factors influencing black spruce growth (D'Orangeville et al., 2018; Hoffer and Tardif, 2009; Marchand et al., 2019). During the period when black spruce achieves peak growth, radial growth release occurs in response to increasing temperature (Rossi et al., 2011). In contrast, warmer temperatures in the late summer negatively affect growth (Fierravanti et al., 2015; Huang et al., 2010). The reduced growth with warmer maximum summer temperatures may relate to the heat stress imposed on trees as temperature increases, leading to lower photosynthetic activity and a water deficit (Fierravanti et al., 2015; Girardin et al., 2016b); this reduced growth may also be explained by carbohydrate loss (Amthor, 2000). Such warmer temperatures also increase water stress during photosynthesis for black spruce, thereby suppressing growth (Girardin et al., 2012; Huang et al., 2010). Girard et al. (2011) identified the close association of black spruce growth with precipitation, spring and summer temperature, and snowmelt/snow cover. Our results also support these black spruce growth responses to seasonal temperature and moisture. Moreover, the carbon isotopic analysis of Walker et al. (2015) identified drought stress, i.e., warm spring temperatures and low CMI, as the underlying cause of reduced black spruce growth through desiccation. Walker et al.'s findings are confirmed in part by our study; the growth was limited by lower spring maximum temperature and spring CMI. Moisture availability in spring and summer was also predicted to help trees compensate for the stresses caused by warmer temperatures. Chavardès et al. (2021) identified that higher June and July temperatures limited black spruce growth, and increased precipitation in August favored growth. However, July temperature was nonsignificant in our study. This difference can be explained by the geographic location of the sampled trees and differences in the species composition of the two studies; Chavardès et al. (2021) studied either pure spruce or mixed structure stands with non-host in a region around 49°N, whereas our sites had mixed proportions of balsam fir covering a vast ecoregion from 45° to 51°N. Nevertheless, the observed effects of higher monthly (June, July, and August) CMI indicates the need for sufficiently humid conditions to favor radial growth of black spruce. Overall, we found that black spruce growth was driven more by the effect of temperature than precipitation; nevertheless, various other underlying factors could also affect growth, including the soil organic layer (Drobyshev et al., 2010), soil characteristics (Dufour and Morin, 2013; Girardin et al., 2016a, 2016b), latitudinal constraints (D'Orangeville et al., 2016; Huang et al., 2010), and species composition (Chavardès et al., 2021). We recommend incorporating these factors within future growth–climate models to provide additional insight into the response of boreal tree growth to a changing climate.

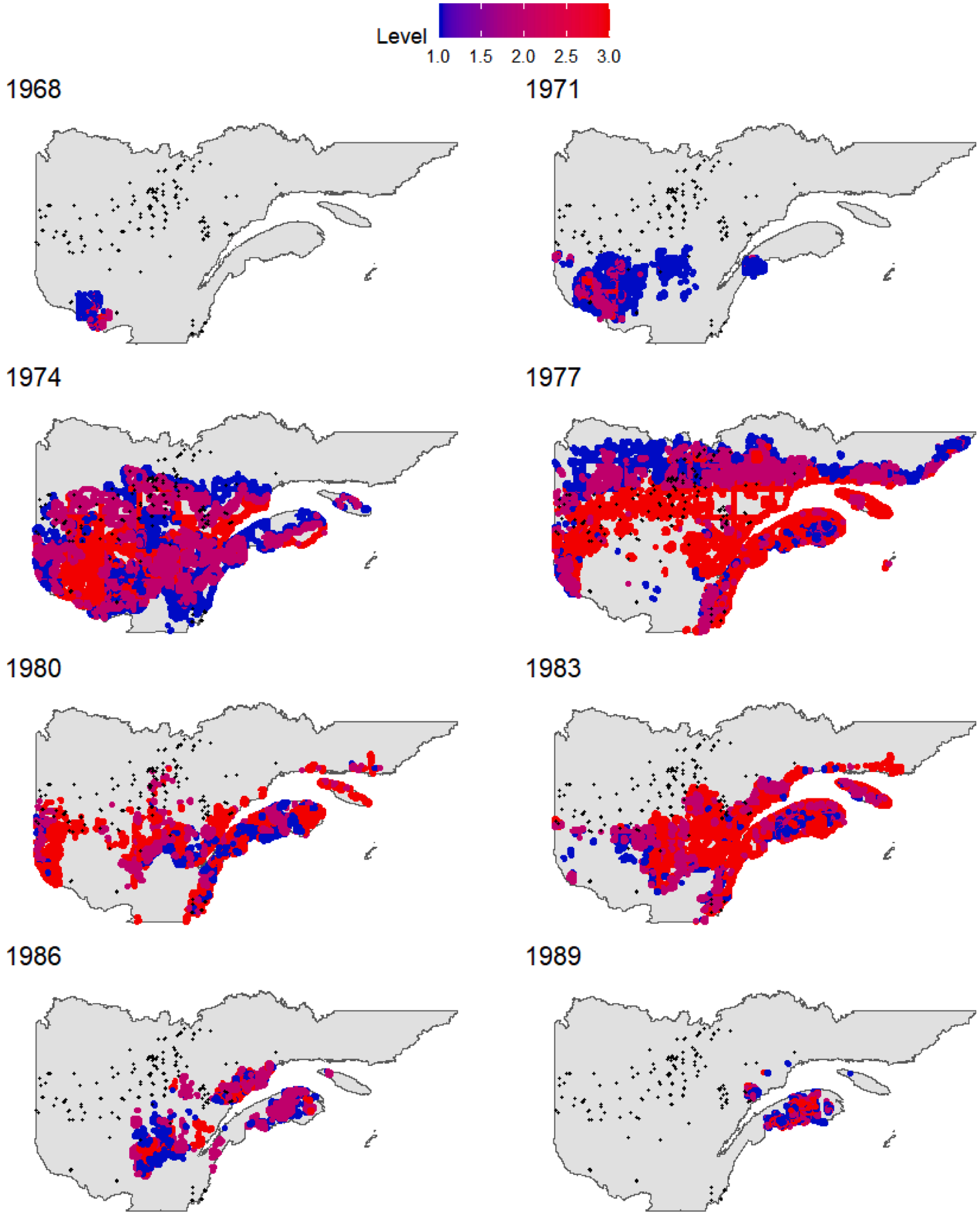

Fig. A.2. Spruce budworm defoliation intensity within the study sites from 1968 to 1989 at three-year intervals; levels 1(*blue*) to 3 (*red*) reflect the increase from light to severe defoliation. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4.2. *Response of black spruce growth to coupled defoliation and climate*

Black spruce growth was influenced by the effect of SBW coupled with climate conditions. Positive climate anomalies of the previous summer can favor SBW activity at all levels of defoliation (Navarro et al., 2018). The warmer summer minimum temperatures create a favorable window for the earlier emergence of SBW larvae from hibernation/winter-sleeping. Pureswaran et al. (2018a), in an experimental setting, observed a similar pattern of earlier larval emergence from diapause with increasing temperatures; therefore, it can be expected that warmer temperatures enhance SBW infestation, which can augment the pressure on black spruce stands leading to the growth reduction. Beyond the active defoliation period, we also observed growth favored by higher summer minimum temperatures. These positive growth response with warmer conditions are reversed during outbreaks period with greater SBW severity. Hence, warmer summer minimum temperatures made black spruce significantly more susceptible to SBW during the active defoliation period.

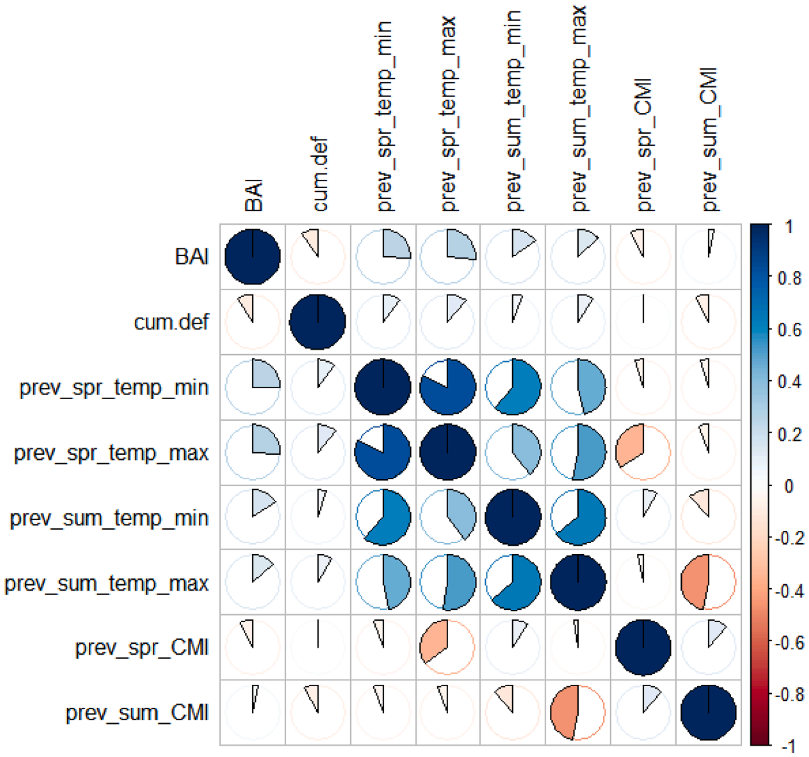

Fig A.3. Correlation matrix for growth, cumulative defoliation, and seasonal climatic variables. The shaded portion within the pie chart denotes the correlation proportion with color indicating the correlation strength and whether the correlation is positive (*blue shades*) or negative (*red shades*). BAI: Basal Area increment; cum. def: cumulative defoliation; prev: previous year; sum: summer; spr: spring; temp: temperature; CMI: Climate Moisture Index; max: maximum; min: minimum. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

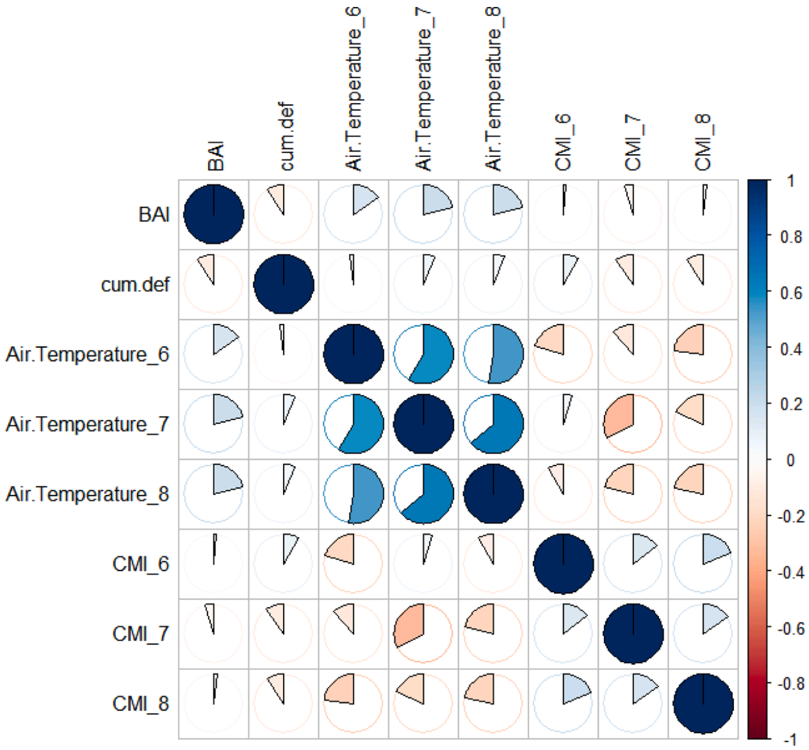

Fig A.4. Correlation matrix between growth, cumulative defoliation, and monthly climatic variables. Suffixes 6, 7, and 8 represent June, July, and August, respectively. The shaded portion within the pie chart denotes the correlation proportion with color indicating the correlation strength and whether the correlation is positive (*blue shades*) or negative (*red shades*). BAI: Basal Area Increment; cum.def: cumulative defoliation; CMI: Climate Moisture Index. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

At a monthly scale, June is a critical month for black spruce growth and the SBW life cycle, as changes in climatic conditions affect bud phenology in black spruce and the defoliation behavior of SBW. Increased temperatures favor an earlier budbreak in black spruce (Bellemin-Noël et al., 2021; Pureswaran et al., 2018a; Rossi and Isabel, 2017), whereas regardless of climate-driven bud bursting, host trees that have undergone previous defoliation tend to advance their budbreak phenology approximately by a week in the year following defoliation (Deslauriers et al., 2019). Thus, we observe the narrowing of the phenological offset with the actively feeding phase of SBW larvae. Moreover, greater budbreak in black spruce increases SBW food availability and enhances feeding opportunities for the SBW larvae. Continuously produced fresh foliage limits any feeding competition among larvae when their populations begin to peak. The increasing damage of

Table A.2
Model sets for the monthly climatic variables reported with their AICc score. Models were produced using different combinations of seasonal climate and defoliation with a backward selection approach, and the best model was identified using AIC. Note: All these models have the random effect of the site and year in addition to the variables presented. The numbers 6, 7, and 8 correspond to June, July, and August, respectively.

ID	Models	K	AICc	Delta_AICc	AICcWt	Cum. Wt	LL
1	CMI_7 + CMI_8 + cum.def *(Air.Temperature_6 + Air.Temperature_7 + Air.Temperature_8 + CMI_6)	15	−1387.6	0	0.33	0.33	708.8
2	CMI_7 + cum.def *(Air.Temperature_6 + Air.Temperature_7 + Air.Temperature_8 + CMI_6 + CMI_8)	16	−1386	1.59	0.15	0.47	709.01
3	CMI_7 + Air.Temperature_8 + cum.def *(Air.Temperature_6 + Air.Temperature_7 + CMI_6 + CMI_8)	15	−1385.9	1.69	0.14	0.62	707.96
4	CMI_8 + cum.def *(Air.Temperature_6 + Air.Temperature_7 + Air.Temperature_8 + CMI_6 + CMI_7)	16	−1385.7	1.82	0.13	0.75	708.9
5	CMI_7 + cum.def *(Air.Temperature_6 + Air.Temperature_7 + Air.Temperature_8 + CMI_6)	14	−1385.6	1.93	0.12	0.87	706.84
6	Air.Temperature_8 + cum.def *(Air.Temperature_6 + Air.Temperature_7 + CMI_6 + CMI_7 + CMI_8)	16	−1384.3	3.26	0.06	0.94	708.18
7	cum.def *(Air.Temperature_6 + Air.Temperature_7 + Air.Temperature_8 + CMI_6 + CMI_7 + CMI_8) (BASE MODEL)	17	−1384.3	3.27	0.06	1	709.18
8	CMI_8 + cum.def *(Air.Temperature_6 + Air.Temperature_7 + Air.Temperature_8 + CMI_6)	14	−1356.5	31.05	0	1	692.28
9	cum.def *(Air.Temperature_6 + Air.Temperature_7 + Air.Temperature_8 + CMI_6)	13	−1351.3	36.25	0	1	688.67
10	Air.Temperature_7 + cum.def *(Air.Temperature_6 + Air.Temperature_8 + CMI_6 + CMI_7 + CMI_8),	16	−1330.8	56.77	0	1	681.42
11	CMI_7 + Air.Temperature_7 + cum.def *(Air.Temperature_6 + Air.Temperature_8 + CMI_6 + CMI_8)	15	−1324.8	62.74	0	1	677.43
12	CMI_7 + CMI_6 + cum.def *(Air.Temperature_6 + Air.Temperature_7 + Air.Temperature_8 + CMI_8)	15	−1302	85.58	0	1	666.01
13	CMI_6 + cum.def *(Air.Temperature_6 + Air.Temperature_7 + Air.Temperature_8 + CMI_7 + CMI_8)	16	−1300	87.57	0	1	666.02
14	CMI_7 + Air.Temperature_6 + cum.def *(Air.Temperature_7 + Air.Temperature_8 + CMI_6 + CMI_8)	15	−1295.3	92.23	0	1	662.69
15	Air.Temperature_6 + cum.def *(Air.Temperature_7 + Air.Temperature_8 + CMI_6 + CMI_7 + CMI_8)	16	−1293.5	94.07	0	1	662.77

the foliage results in a loss of tree vigor that can eventually be lethal to host trees. It also limits the ability of the host trees to expedite photosynthetic processes, specifically for boreal coniferous trees with the short growing period (Liu et al., 2019). Hence, increased synchroneity between budbreak in host species and larval emergence heightens SBW effect on growth in successive years (Bognounou et al., 2017; Candau and Fleming, 2005), and this is enhanced further by the warmer temperatures (Pureswaran et al., 2015).

The growth release due to increase humidity in summer and June was reversed during the active defoliation period, which indicates the higher benefits for the SBW i.e., moisture availability favored SBW more than that for the black spruce, during outbreak. Appropriate moisture availability is recognized to be an important climatic metric contributing to insect activity and outbreaks (Weed et al., 2013). With increased humidity of the summer, the SBW larvae are able to obtain suitable moisture contents from fresh foliage/buds (Carisey and Bauce, 2002). Since SBW do not feed during diapauses, their survivability solely depends on energy reserves transferred to the eggs from parent moth. Nutritious food increases the energy reserve for eggs which favors the survival of the early instar larva and escape potential mortality (Dickison et al., 1986). This means that the larva tends to get higher nutritive advantage from the humid foliage leading to the higher success of the overwintering larva during the hibernation (Carisey and Bauce, 2002). Eventually, this will lead to the high survival rate of SBW larvae in black spruce during the peak defoliation period (Fuentealba et al., 2017). Besides, the moth dispersal is sometime facilitated by suitable humidity and precipitation (Larroque et al., 2022), which suggests the higher possibility of the extension of defoliating larva and immigrating to a new site in successive year. Such circumstances enhanced SBW population level and favored its expansion by elevating defoliation, consequently, leading to the significant growth reduction in black spruce.

However, the interaction effect of spring minimum temperature, summer maximum temperature, and July temperature with SBW favored the growth, i.e., SBW-related growth reductions on black spruce being less at higher values for these listed climate variables. We can explain this pattern through two possibilities: i) such increased temperature values make black spruce less vulnerable to SBW defoliation; or ii) the conditions are less favorable for SBW because of adverse climate conditions for this insect. Fierravanti et al. (2015) identified a reduced vulnerability for black spruce to SBW damage with warmer temperatures. During the spring, when the minimum temperature is almost always below freezing, warmer temperatures can favor greater photosynthesis activity leading to increased growth. Defoliation intensity can be lower with warmer minimum spring temperatures when the temperature increase is insufficient for the larvae to end their diapauses (Han and Bauce, 1997; Pureswaran et al., 2018a). Whereas higher summer maximum temperatures not only stress trees and limit growth (Chavardès et al., 2021; Fierravanti et al., 2015) and productivity of black spruce (Girardin et al., 2016a), but also affect SBW performance because the temperatures may be too warm for SBW survival (Régnière et al., 2012). Although some studies have found that high temperatures can limit black spruce growth (D'Orangeville et al., 2018), we found that the coupling of warmer temperatures and defoliating SBW favored growth. This is potentially because late summer high temperatures can be detrimental to larval survival (Régnière et al., 2012); a heat-related mass mortality of SBW larvae may occur, reducing the SBW effect on growth. Even variable temperatures before the onset or during the diapause phase of larvae profoundly affect the development, survivability, and mortality of the SBW larvae (Han and Bauce, 1997; 1998). Because warmer conditions heighten the metabolic activity in insects, larval forms could develop faster and proceed earlier through their life stages (Bellemin-Noël et al., 2021; Candau and Fleming, 2005; Parmesan, 2007). Given that black and white spruce have similar phenological cycles, SBW larvae can feed on the foliage of white spruce to lower the herbivory pressure on black spruce, thereby increasing black spruce growth (Nealis and Régnière, 2004). Similar circumstances could be expected with increasing July temperatures (negative effect without SBW but positive with SBW presence). In July, the biological stages of SBW have already reached the reproductive period; therefore, limited defoliation can be observed. However, we cannot ignore the influence of natural enemies of the SBW (mainly birds, spiders, bugs, ants, and parasitoids) in the boreal forest that limit SBW populations and favor the growth of SBW host trees (Régnière and Nealis, 2007; USDA, 1985; Venier and Holmes, 2010). Thus, the survivality and mortality of SBW population determines defoliation severity, and ultimately, the extent of SBW pressure on the growth of host species like black spruce in a landscape. All these complex interrelationships raise questions needing to be addressed to broaden our understanding of climate–insect–host dynamics and their interrelationships in the boreal forest.

5. Conclusion

The relationships between defoliation and climate strongly influence black spruce growth. Our seasonal model explained 70% of the growth variation in black spruce modulated by the additive effect of SBW defoliation (14% growth reduction for a cumulative five-year period) and the interactive effect of spring and summer climate (growth reduction 4%–11%). The increased growth response to summer minimum temperature and CMI during the growing season reversed because of how these climate factors influenced the effect of SBW defoliation.

Our monthly model, explaining 72% of the variation, showed a 18% growth reduction because of defoliation, which varied between 11% and 17% because of the interactions of SBW effect and climate. Heightened growth suppression was evident with the warmer June temperatures because of a greater vulnerability of black spruce to SBW-related damage. Hence, seasonal and monthly climate modulates the complex growth–defoliation relationship while also making host trees like black spruce more vulnerable to changing climate.

This observed pronounced effect on growth and productivity is expected to be heightened with future climate change. Our identification of the complex relationships between biotic and abiotic factors within the boreal landscape will help the sustainable management of the boreal forest by identifying stands situated in zones vulnerable to defoliation, given the current trends of climate change across large spatial and temporal scales. We suggest incorporating historical data for landscape-level studies, given their broad applicability within ecological research. This long-term knowledge provides an important direction for future research in building predictive forest growth models with the inclusion of defoliation classes and future climate and forecasting disturbance dynamics in the context of altered climate.

Funding

PM and MMG in collaboration with HM, YB et al. obtained funding from the Natural Sciences and Engineering Research Council of Canada (NSERC) Alliance and the Québec Ministry of Natural Resources and Forests (MRNF) to understand the dynamics of spruce budworm (ALLRP 558267-20). MMG obtained additional funding from an NSERC Discovery grant to reconstruct the regime of natural disturbances in forest ecosystems (RGPIN-2022-05423).

CRediT authorship contribution statement

Anoj Subedi: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. **Philippe Marchand:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Writing – review & editing. **Yves Bergeron:** Validation, Writing – review & editing. **Hubert Morin:** Data curation, Validation, Writing – review & editing. **Miguel Montoro Girona:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Writing – review & editing.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

Acknowledgements

We thank A. Lemay, L. Navarro, and C. Berguet for their assistance during the database compilation and G. Tougas for help with data preparation and curation during the preliminary phase of the project. We recognize the role of F. Gennaretti and K. Waldron in providing constructive suggestions to the manuscript. We acknowledge all the previous projects and researchers from which we compiled the dendrochronological data. We express our sincere gratitude to the Québec Ministry of Natural Resources and Forests (MRNF), from whom we acquired information related to defoliation severity. Additional thanks are given for SmartForest equipment from the Canada Foundation for Innovation (CFI) (Pappas et al., 2022b). We appreciate the time and efforts from the editor and three anonymous reviewers whose suggestions and feedbacks improved the manuscript. This article is a part of the M.Sc. thesis of AS (Subedi, 2023).

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