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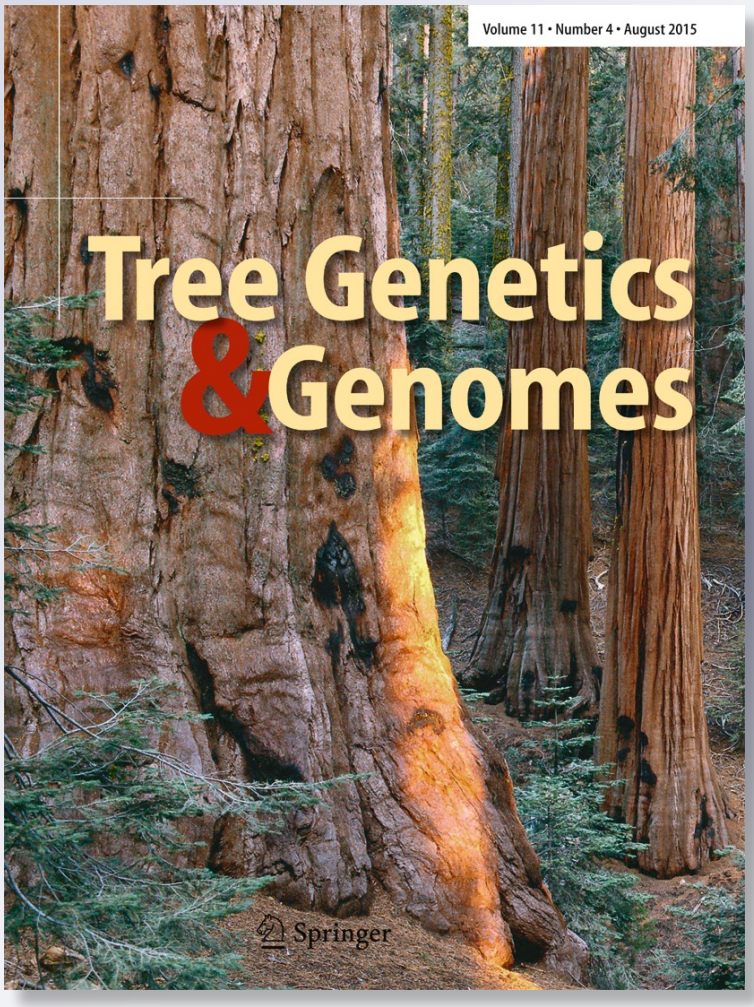

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ORIGINAL ARTICLE

The effects of genetic diversity, climate and defoliation events on trembling aspen growth performance across Canada

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Abstract Tree genetic makeup may provide an important control of growth dynamics; however, no studies have previously attempted to evaluate its effects in natural trembling aspen stands. In this study, we examined the relative contribution of genetics (i.e. clonal diversity, observed heterozygosity) and environmental conditions (i.e. insects, climate) on aspen growth as represented by mean inter-tree correlation (RBAR), tree basal area increment (TBAI) and inter-annual growth variability (MS). We sampled 440 trees in 22 even-aged natural stands dominated by aspen along an east-west continental gradient of decreasing annual precipitation in the Canadian boreal forest. Linear and mixed-effect models tested the relationships between tree growth, genetics and environmental factors. We showed that clonal diversity and number of years with forest tent caterpillar (FTC) defoliation (N_{FTC}) reduced and increased the level of growth synchronicity (RBAR), respectively. Clonal diversity explained 30 % of variation in RBAR among sites. TBAI was positively influenced by high moisture conditions while N_{FTC} and climate explained the variation in MS among trees for each site. No genetic effect could explain either TBAI or the MS variation. Climate and N_{FTC} drive annual growth variability in trembling aspen at stand and subcontinental scales. Tree genetic makeup contributed to these dynamics, the annual growth dynamics of multiclonal stands being less homogeneous than those of monoclonal stands. Maintaining diverse aspen stands may ensure a wider range of growth responses to environmental variability, which in turn may help maintain resilience of aspen stands under future climate.

Keywords Climate moisture index · Forest tent caterpillar · Genetic diversity · Heterozygosity · Radial growth · Trembling aspen

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Introduction

Trembling aspen (*Populus tremuloides* Michaux) is the most widely distributed and abundant deciduous tree species in North America (Little 1971), particularly in Canadian boreal forests, where it covers 11.6 % of the national forested land base (Peterson and Peterson 1992). Over the last two decades, widespread aspen decline and mortality has been observed mainly in western North America and, to a lesser extent, in eastern Canada. These observations have led to a growing interest in understanding the causes and underlying mechanisms of aspen growth variation (e.g. Frey et al. 2004; Hogg et al. 2008; Michaelian et al. 2011).

Species-specific responses to short-term environmental variation suggest that tree growth responses to climatic fluctuations would not likely be synchronised among species in a mixedwood boreal forest that was composed of aspen and spruce (Drobyshev et al. 2013). This could thus lead to

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changes in the structure and composition of future forest communities (Drobyshev et al. 2013). Tree-ring width analysis is a powerful proxy for estimating tree growth (Fritts 1976) and has been successfully used in trembling aspen to evaluate stand productivity (Hogg et al. 2008) and climate-growth relationships (Hogg 2001; Hogg and Bernier 2005; Leonelli et al. 2008). Variation in inter-annual aspen growth is especially sensitive to the effects of defoliation by the forest tent caterpillar (FTC; *Malacosoma disstria* Hübner), soil moisture availability (as measured using a climatic moisture index, CMI), accumulated growing degree days and snow depth (Hogg et al. 2002a). However, the genetic composition of populations under investigation is not explicitly considered in most studies, and the observed changes are assumed to be driven primarily by physiological responses to climatic change, without a significant genetic contribution (King et al. 2013).

In a clonal species such as trembling aspen, one single genotype (also referred to as "clone") can cover vast areas (e.g. the 43 ha Pando clone in south-central Utah; Grant et al. 1992; DeWoody et al. 2008) that could be affected by sudden declines following severe environmental variations, such as drought (e.g. Worrall et al. 2013), due to maladaptation of certain genotypes to the new conditions. It is equally possible that either no response or a positive response would be observed for some genotypes that are better adapted to the changing conditions. The growth performance of a population could thus be, on average, similar over time if populations consist of multiple clones with different climatic tolerances. Most of the variation would then be observed between genotypes within populations.

Mitton and Grant (1996) hypothesised that regional differences in terms of genetic and clonal structures in aspen populations reflect the aridity of the climate, the propensity for clonal reproduction or the predominant mode of reproduction (sexual or asexual). Within its range, clonal diversity is generally assumed to decrease from west to east, while population heterozygosity would tend to increase. However, few studies have examined this source of variation at a continental scale (Callahan et al. 2013). Recent work has shown that regional differences in genetic variation among populations across aspen's distributional range are less important than was previously thought due to recent sexual reproduction events (Mock et al. 2008; Long and Mock 2012). However, at regional and local scales, Mitton and Grant (1984) made the hypothesis that higher individual heterozygosity could provide greater flexibility in their growth responses to environmental variation, resulting in higher average aspen radial growth (Jelinski and Cheliak 1992; Cole et al. 2010). An average 20 % of tree growth variation (a value between 10 and 40 %, depending upon the species) is under genetic control (Cornelius 1994; Beaulieu and Bousquet 2010). Geographic variation between aspen provenances that were tested in common garden experiments has been reported (Gray et al. 2010; Li et al. 2010; Schreiber et al. 2013), showing that growth is partly under genetic control. Broad-sense heritability (h_2: proportion of phenotypic variance that is subject to genetic control) for height and diameter at breast height (DBH at 1.3 m) respectively averaged 0.45 and 0.43 for aspen clones in common garden trials (Gylander et al. 2012).

In most studies, intra-population genetic structure has not been considered and was not expected to affect stand growth responses. In this study, our specific objective was to investigate whether the level of genetic variation in natural aspen stands is associated with differential growth responses to environmental conditions, viz severe FTC defoliation and water stress (estimated by the average CMI). Tree growth was analysed using a dendrochronological approach (Fritts 1976) to quantify the tree basal area increment (TBAI), the mean sensitivity (MS) of growth, and the mean inter-tree correlation (RBAR). TBAI is the mean annual basal area increment calculated for each tree sampled and measures wood production in volume. MS quantifies the inter-annual variation in tree-ring widths (Fritts 1976), while RBAR is a measure of the strength of the common variation in radial growth between all possible pairs in tree-ring width chronologies (Cook and Pederson 2010). Higher values of MS are associated with high tree growth sensitivity to inter-annual climatic variations, whereas variation in RBAR illustrates changes in the strength of common patterns of tree growth over time. More specifically, we hypothesised that (i) higher aspen TBAI is correlated with higher genetic diversity of aspen stands and (ii) both growth synchronicity (RBAR) among trees within a site and year-to-year growth variability (MS) are negatively correlated with genetic diversity of aspen stands.

Materials and methods

Study area and sampling

The study sites consisted of 22 plots, each measuring 400 m^2 (11.28 m radius), which had been established in dominant (>75 % basal area), even-aged and mature (50 years old) trembling aspen stands across Canada (48° 33′ 36″ N to 58° 20′ 01″ N; 67° 59′ 07″ W to 117° 14′ 13″ W; Fig. 1). The 22 plot locations coincided with the 0±1 °C isothermal envelope over the period 1971–2000 (Environment Canada 2014), except for two sites that were 2 °C above this value (ON95 and ON94) and two sites that were 2 °C below this value (MB97 and MB99). This pan-Canadian transect represents an east-west gradient of decreasing annual precipitation (from 1000 to 400 mm/year; Fig. 1), which allowed a wide range of environmental conditions and genetic variability to be covered. The general topography was gently rolling, with elevations ranging from 195 to 675 m asl (Table 1). Soil conditions were

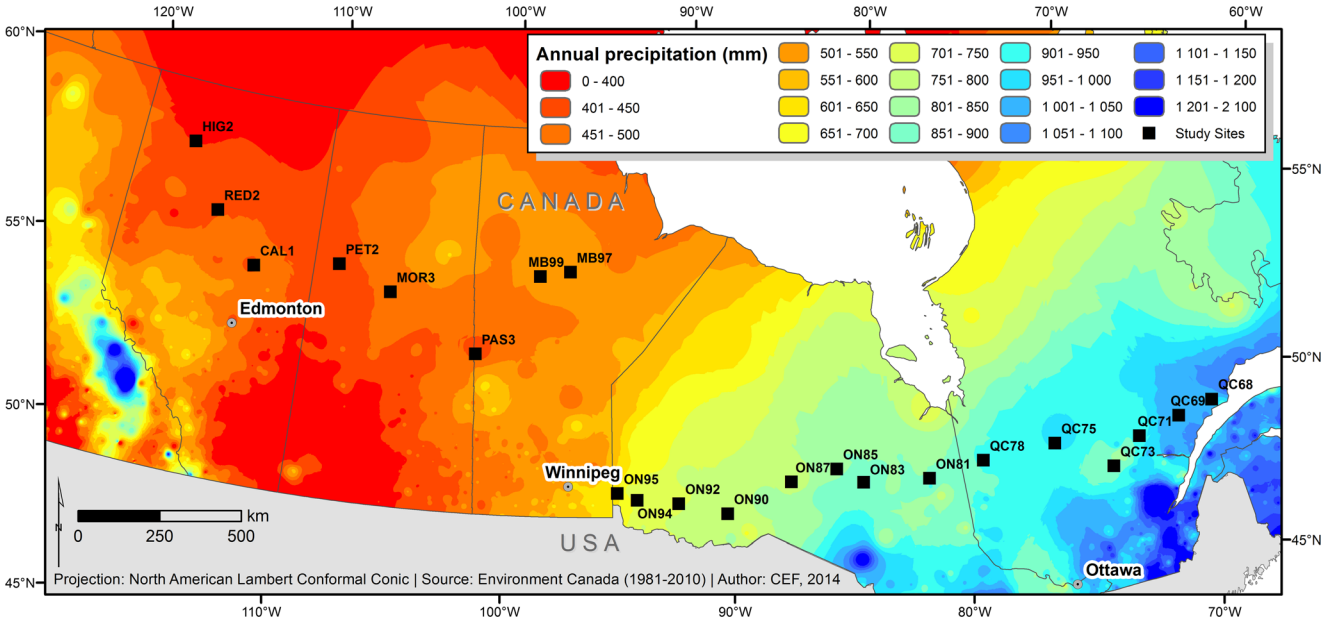

Fig. 1 Study sites along the east-west gradient of decreasing annual precipitation (Environment Canada 2014) where 22 *Populus tremuloides* populations were sampled

selected to be as similar as possible (mesic clayey soils) to reduce variation between sites. Site index was obtained from stem analysis of three dominant trees (suppression-free trees with a normally formed canopy) per plot that were sampled in 2010 and 2011, as explained in Hanson et al. (2003). Cookies were taken every metre from the base to the top of each tree, and ring widths were measured. We obtained age-height curves for these trees and computed a site index (SI) based on the average of the mean height at age 50 years in a given plot. Within each plot, the DBH and the height of every mature tree (DBH≥10 cm) were measured. Among these individuals, 20 trees were selected per plot. Each tree was tagged, mapped and sampled (DNA from root cambium tissue and increment cores) for analysis. All analyses were performed based on ring widths over the period between 1959 and 2009 (50 years).

Tree-ring width measurement and cross-dating

Tree increment cores were mounted on wood and progressively polished with up to 600-grit sandpaper to permit clear recognition and differentiation of annual rings under the microscope (magnification ×20). Annual ring widths were measured with +0.01 mm accuracy using a LINTAB measuring stage (RINNTECH Inc., St. Charles, IL, USA) and TSAP 3.0 software (Rinn 1996). For each plot, the individual ring width series were visually compared during ongoing measurements to avoid any evident shifts between chronologies. The chronologies were then carefully cross-dated by progressively detecting regional pointer years using the method developed by Becker (1989). Methods and thresholds that were used to define pointer years were performed according to Lebourgeois et al. (2013). Pointer years were calculated in the R statistical environment (version 2.15.0, R Development Core Team 2013) using the function *pointer* in the package *dplR* (Bunn 2008). Absolute dating was checked with the application INTERDAT (Bunn 2008), which identifies locations within each ring series that may be subject to erroneous cross-dating (Becker 1989; Mérian and Lebourgeois 2011).

Tree basal area increment calculation TBAI (mm^2) was preferred to ring width because the former provides a better estimate of annual growth (Valentine 1985; LeBlanc 1990; Briffa et al. 1998; Yang et al. 2009). We calculated the TBAI at breast height, following the equation $TBAI=\pi\ (R_t^2-R_{t-1}^2)$, where R_t is the stem radius at the end of the annual increment, and R_{t-1} is the stem radius at the beginning of the annual increment. For cores with missing pith, the first radius R corresponding to the distance between the pith and the first recorded ring was estimated with the pith locator method (Applequist 1958). In some cases (107 cores, i.e. 12 % of total cores), this method could not be used accurately due to a broken core or branch in the pith, and thus, the TBAIs were calculated backwards with the radius of the last year of growth (2010; see Online Resource 1). Eventually, the TBAI series were averaged to create a single basal area increment series for each site (40 cores for 20 trees), and the mean TBAI for the 1959–2009 period was calculated for each tree and then used in the later analysis. Due to incomplete core series, we were not able to calculate the TBAI for 23 trees over all sites. A final data set of 417 trees with complete TBAI values was then used to analyse relationships with selected variables.

Table 1 Tree-ring analysis statistics based on raw ring widths per population

Site	Longitude	Latitude	Elevation (m)	Slope (%)	Site index	Age	Density (trees/ha)	*P* (cm)	CMI (cm)	*P* summer (cm)	Severe defoliation (years)[a]	Mean DBH (cm)	Mean height (m)	Basal area (m^2/ha)	MRW (mm)[a,b]	TBAI (mm^2)[a,b]	MS[a,c]	RBAR[a,c]
HIG2	−117.24	58.34	343	8.7	19.9	67	1225	40.89	−1.74	13.34	5	19.79	21.585	37.649	1.051	3.995	0.373	0.722
RED2	−115.31	56.61	521	12.1	24.6	57	1350	43.46	0.53	15.8	1	22.5	22.195	38.197	1.918	7.4	0.194	0.481
CAL1	−112.97	55.29	675	0.6	19.7	64	1925	47.74	6.68	17.14	6	18.135	19.645	36.343	1.363	3.861	0.332	0.676
PET2	−108.78	55.74	490	1.1	20.8	61	1100	45.52	8.06	14.54	13	20.79	23.11	36.972	1.462	5.45	0.476	0.646
MOR3	−106.07	55.14	444	10.8	13.4	72	950	47.22	7.39	15.75	10	21.75	21.485	29.725	1.078	4.775	0.375	0.666
PAS3	−101.68	53.6	279	1.6	17.9	65	1125	43.68	0.72	14.52	7	19.69	19.675	34.021	1.208	4.29	0.309	0.608
MB99	−98.68	55.89	279	3.8	14.8	78	1200	50.62	16.12	15.76	9	19.09	19.16	31.807	0.976	3.968	0.406	0.677
MB97	−97.16	56.03	233	2.5	12.9	80	1450	50.24	15.51	15.45	6	18.97	17.525	32.632	0.975	3.711	0.313	0.638
ON95	−94.94	49.7	358	7	20.8	56	900	63.40	17.47	22.91	6	23.64	21.035	36.596	1.798	6.609	0.286	0.654
ON94	−94.06	49.49	385	8.5	17.3	79	1200	68.89	24.28	24.87	9	25.96	22.215	40.786	1.151	6.243	0.405	0.735
ON92	−92.22	49.36	434	10	14.8	84	525	72.33	27.79	25.46	10	27.075	24.16	30.139	1.284	7.188	0.364	0.622
ON90	−90.08	48.99	496	5	18.1	83	925	76.18	28.79	25.89	5	23.54	23.44	32.029	1.126	5.461	0.196	0.442
ON87	−87.14	49.75	364	2.8	21.1	75	900	75.40	33.26	23.73	3	27.885	25.62	36.571	1.352	8.013	0.251	0.493
ON85	−85.06	49.97	195	7.8	15.8	93	1250	78.48	39.81	24.48	6	27.49	25.36	54.511	1.036	6.455	0.288	0.629
ON83	−83.94	49.49	238	3	19.2	69	875	84.80	41.84	25.34	9	31.185	23.795	44.701	1.734	10.035	0.341	0.701
ON81	−81.03	49.31	248	1.1	21	75	450	85.13	42.81	25.66	7	30.64	26.4	33.488	1.612	9.709	0.235	0.422
QC78	−78.52	49.53	306	1.1	13	88	825	87.40	47.30	26.28	4	24.995	23.521	39.298	1.054	5.928	0.198	0.341
QC75	−75.25	49.57	376	5	20.4	86	1050	97.95	60.50	28.27	5	30.645	24.56	55.929	1.009	6.712	0.21	0.453
QC73	−72.97	48.5	526	11.2	21.6	69	1550	87.38	49.08	26.35	5	21.2	21.585	45.542	1.233	5.055	0.253	0.468
QC71	−71.54	49.15	304	30.5	21.3	61	1525	94.97	52.23	27.14	4	21.11	22.585	41.281	1.465	5.993	0.232	0.652
QC69	−69.6	49.39	286	19.5	21.1	61	775	93.86	48.65	28.64	6	28.84	25.18	47.653	2.053	10.622	0.234	0.662
QC68	−67.99	49.54	337	31	20.4	53	1425	99.95	62.99	30.68	4	19.225	18.925	33.137	1.649	5.064	0.236	0.482

P precipitation, *CMI* climate moisture index, *DBH* diameter at breast height, *MRW* mean ring width, *TBAI* tree basal areal increment, *RBAR* mean inter-tree correlation

[a] Calculated for the past 50 years (1959–2009)

[b] Calculated from raw data

[c] Calculated from detrended data

Inter-annual growth variability and growth synchronicity calculations The raw tree-ring chronologies were computed and detrended to remove medium- and low-frequency signals, thereby emphasising inter-annual variation. The maximum period that was common to all chronologies within a data set was used (1959–2009). Each series was detrended by fitting a cubic smoothing spline with 50 % frequency response cut-off and a rigidity of 33 % of series length (Cook and Peters 1981; Bunn 2008; Mérian 2012). For each tree (two series per tree) and then each plot (20 trees per plot), the growth indices were averaged by year using a bi-weighted robust mean to develop a mean growth chronology, which represented the common high-frequency variation of the individual series (Cook 1985). To evaluate the effect of climate, insects and genetic diversity on inter-annual growth variability and inter-tree growth synchronicity across sites, the MS (Briffa and Jones 1990; Cook and Pederson 2010) and the RBAR (Cook and Pederson 2010) were respectively calculated on the growth indices. MS is a measure of the relative change in ring width index from one year to the next and reflects the proportion of high-frequency variance (short period) in the chronology (Cook and Kariukstis 1990). MS was calculated for each tree to measure year-to-year variability (Fritts 1976) as follows:

$$\mathrm{MS} = \frac{1}{n-1}\sum_{i=2}^{n}\left|\frac{2(x_i - x_{i-1})}{(x_i + x_{i-1})}\right|$$

where x_i is the arithmetic mean for tree-ring series of length n. Bunn et al. (2013) showed that MS is nearly proportional to the standard deviation of a time series when using random data sets and we used this definition of MS in our study (standard deviation of detrended ring widths). The RBAR is the arithmetic mean of the correlation coefficient $r_{jj'}$ between each possible pair of chronologies j and j' over the t trees calculated within each plot as follows:

$$\mathrm{RBAR} = \frac{1}{2t(t-1)}\left(\sum_{j=1}^{t=1}\sum_{\substack{j'=1\\ j'>j}}^{t} r_{jj'}\right)$$

This metric varies from 0 when series are strictly independent of one another to 1 where the trees show identical growth patterns (Briffa and Jones 1990; Cook and Pederson 2010). RBAR also measures the proximity between the theoretical population chronology and the observed mean growth chronology (Wigley et al. 1984).

Environmental data

Climatic data The CMI was selected as the climatic variable to estimate water stress (Hogg 1997; Hogg and Bernier 2005; Hogg et al. 2005; Lemprière et al. 2008; Michaelian et al. 2011). CMI was previously calculated from mean monthly precipitation (mm) and potential evapotranspiration (PET; mm) that were simulated for all sites using BioSIM 10 (Régnière et al. 2013), based on the daily database for Canada covering the years 1901 to 2011. The CMI is the difference between precipitation and PET and is calculated for the period between August and the following July to take into account possible winter water deficits that could affect the next year's growth (Hogg 1997; Hogg et al. 2005; Hogg et al. 2008).

Forest tent caterpillar defoliation Forest tent caterpillar defoliation causes the non-systematic presence of "white tree ring" or "missing ring" values, which are indicative of a severe FTC defoliation causing a reduction in growth and an increase in tree mortality (Hogg et al. 2002b; Moulinier et al. 2014). White tree rings are anomalously pale-coloured, low-density tree rings that are formed during severe early season defoliation in both young and mature aspen (Hogg et al. 2002b; Hogg et al. 2005). Years in which white tree rings occurred were recorded for each core and on three stems per site during stem analysis. For each plot and year during the 1959–2009 period, years with severe defoliation were calculated as described in the Online Resource 2. The cumulative number of years with severe FTC defoliations (N_{FTC}) over the past 50 years (1959–2009) was then used as an explanatory variable in model building.

Clonal structure and genetic diversity

Root cambium tissue was collected, dried in silica gel and conserved at room temperature. DNA was extracted using Extract-N-Amp™ Plant kit (Sigma-Aldrich, St. Louis, MO, USA). Individuals were genotyped at seven microsatellite loci (Table 2). Each PCR was performed upon a 10-μL total volume: 2 μL DNA extract, which was diluted to one tenth; 5 μL QIAGEN® Multiplex PCR Kit (Qiagen, Venlo, Limburg, The Netherlands); and 1 μL H_2O and 2 μL primer mix solution at 2 μM, for a final concentration of 0.4 μM. PCR was carried out separately for each primer. Reactions were performed in a Mastercycler® Pro Thermal Cycler (Eppendorf, Hamburg, Germany) with the following protocol: an initial denaturation step at 95 °C for 15 min, followed by 36 cycles of 94 °C for 30 s, primer-specific annealing temperature for 90 s, 72 °C for 60 s, and a final extension at 60 °C for 30 min. PCR products were analysed on an ABI 3730 Automated Capillary DNA Sequencer (Applied Biosystems, Foster City, CA, USA). Allele sizes were scored using GeneMapper version 5.0 (Applied Biosystems) and only nine samples were not genotyped at all seven loci. We used GenoDive (Meirmans and Van Tienderen 2004) to assign clone identities based on the stepwise mutation model. The ramet data set included all of the trees (440 sampled trees), while the genet set included the unique multi-locus genotype (118 unique genets). Ramet

Table 2 Primer sequences, size range (in base pairs, bp) and number of alleles observed for seven microsatellite loci of *Populus tremuloides*

Locus	Repeat	Primer sequence (5′→3′)	Dye colour	Size range (bp)	Number of alleles	Source
PTR1	(GGT)n (AGG)n	AGCGCGTGCGGATTGCCATT (F) TTAGTTTCCCGTCACCTCCTGTTAT (R)	FAM (blue)	239–278	12	Dayanandan et al. (1998)
PTR2	(TGG)n	AAGAAGAACTCGAAGATGAAGAACT (F) ACTGACAAAACCCCTAATCTAACAA (R)	VIC (green)	202–229	10	Dayanandan et al. (1998)
PTR3	(TC)n	CACTCGTGTTGTCCTTTTCTTTTCT (F) AGGATCCCTTCCCTTTAGTAT (R)	NED (black)	186–260	19	Dayanandan et al. (1998)
PTR4	(TC)n	AATGTCGAGGCCTTTCTAAATGTCT (F) GCTTGAGCAACAAACACACCAGATG (R)	PET (red)	200–234	11	Dayanandan et al. (1998)
PTR6	(AT)n	AGAAAAGCAGATTGAGAAAAGAC (F) CTAGTATAGAGAAAGAAGAAGCAGAAA (R)	VIC (green)	184–211	9	Rahman et al. (2000)
PTR14	(TGG)n	TCCGTTTTTGCATCTCAAGAATCAC (F) ATACTCGCTTTATAACACCATTGTC (R)	NED (black)	140–200	14	Rahman et al. (2000)
WPMS16	(GTC)n (ATCCTC)n	CTCGTACTATTTCCGATGATGACC (F) AGATTATTAGGTGGGCCAAGGACT (R)	FAM (blue)	148–196	9	Smulders et al. (2001)

data were used to estimate clonal heterogeneity (Dorken and Eckert 2001), which was calculated as the Simpson diversity index (D) and evenness (E). Clonal diversity (R) was also estimated, which is the proportion of different genotypes in a population (Arnaud-Haond et al. 2007). Genet data were used to evaluate genetic diversity: observed heterozygosity (H_o), observed heterozygosity per individual (individual H_o), expected heterozygosity (H_e), average allelic richness (average number of alleles observed per loci: A) and the inbreeding coefficient G_{is} (an analogue of F_{is}). All of these measures were estimated with the software GenoDive (Meirmans and Van Tienderen 2004), except individual H_o, which was calculated as the sum of loci with more than one allele divided by the total number of loci that were used.

Statistical analysis

Annual growth and inter-tree growth variability Mixed effects modelling was used to analyse the fixed effects of the genetics (H_o or individual H_o, A and D), the environment (moisture index CMI and N_{FTC}) and tree ages on TBAI and MS, while including random effects that were due to the experimental design (CloneID nested in SiteID). The random effects only consisted of the (random) intercepts. Nesting of CloneID within SiteID allowed us to take into account that each clone within a population responds differently to the explanatory variables for a given response variable. We considered a set of 10 candidate models to explain the variation in TBAI and MS (see results tables for the models list). The same set of models was tested with either H_o or individual H_o. Clonal diversity (R) was not included since R and D are highly correlated measures of clonal richness (Pearson product-moment correlation: r=0.86, P<0.01). Assumptions of homogeneity of variance and normality were verified graphically. TBAI and MS were transformed with a log and a square root function, respectively, to meet normality and constant variance assumptions. Parameters in the candidate models were estimated by maximum likelihood with the *lme* function from the *nmle* package in R (Pinheiro et al. 2013; R Development Core Team 2013). We compared the models using the Akaike information criterion corrected for small sample sizes (AICc; Burnham and Anderson 2004) with the *aictab.lme* function from the AICcmodavg package (Mazerolle 2013). When the top-ranked model had an Akaike weight (ωi) <0.9, we computed the model-averaged estimates of the explanatory variables and their 95 % confidence intervals (Burnham and Anderson 2004) with the *modavg.lme* and *modavgpred* function of the AICcmodavg library (Mazerolle 2013). A confidence interval excluding 0 indicated that the response variable varied with the explanatory variable of interest. Multi-model predictions and figures were obtained with the *modavg* function of the AICcmodavg library (Mazerolle 2013).

Mean inter-tree correlation Lastly, we carried out multiple linear regressions with the function *lm* to evaluate the relationship between RBAR and a set of 5 explanatory variables (CMI, FTC defoliation, R, A and H_o), which were combined in a set of 10 different models (see results table for the models list). A maximum of three different explanatory variables were included in each model to maintain high statistical power (a large number of parameters decrease precision of estimates; Kullback and Leibler 1951; Verbeke and Molenberghs 2009; Zuur et al. 2009). The variable D was not included because it was strongly correlated with R. We tested the set of 10 models with different combinations of the explanatory variables. We then compared the models using the Akaike information criterion with the functions described above. The model assumptions (homogeneity of variance and normality) were verified and partial regression plots were computed with the function *avPlots* of the *car* package (Fox and Weisberg 2011).

Results

Descriptive tree-ring analysis

The variables of interest per site are presented in Table 1. The average TBAI was 6.206 mm^2/year. The minimum TBAI per site was 3.711 mm^2/year, while the maximum was 10.622 mm^2/year. With respect to MS, its average value for all sites was 0.296; MS ranged from 0.21 to 0.658 for trees. We found higher values of MS (ANOVA, $F_{1,438}=130.8$, $P<0.001$) and lower values of TBAI (ANOVA, $F_{1,415}=64.72$, $P<0.01$) in western Canada (ON94 to HIG2) than in eastern Canada (QC68 to ON92). RBAR averaged 0.585 and ranged from 0.341 to 0.735. The average total number of years with severe FTC defoliation (N_{FTC}) between 1959 and 2009 was 6.4 defoliations, with extreme values of 13 and 1, meaning that a severe defoliation occurred every 8 years on average. The climate moisture index (CMI) and N_{FTC} were not significantly correlated (Pearson product-moment correlation: $r=-0.26$, $P=0.2415$).

Descriptive genetic statistics

All 7 loci were highly polymorphic and the number of alleles per locus ranged from 9 (PTR6 and WPMS16) to 19 (PTR3; Table 2). All descriptive genetic data are presented in Table 3.

Ramet data set Clonal (genotypic) diversity and the Simpson diversity index (D) ranged between 0 (monoclonal sites) and 1, but did not vary significantly along the longitudinal gradient (Pearson product-moment correlation: $r=0.0064$, $P=0.7223$). The highest value for evenness (E) was $E=1$ and the lowest value was $E=0.308$, where the differences in the size of each clone within the stand were large.

Genet data set Averaged allelic richness (A) ranged from 1.3 to 6.1, with an average value of 3.5 across populations. Observed heterozygosity (H_o) had a mean value of 0.622 and varied from 0.286 to 0.857. The mean H_e was 0.603, with values ranging from 0.429 to 0.724. Values of H_o were slightly higher than H_e, but these differences were not significant (paired t test: $t=1.37$, $df=21$, $P=0.19$). H_o did not vary significantly along the

Table 3 Genetic variability of 22 aspen populations sampled across Canada

Population	N	G[a]	R[a]	A[b]	H_o[b]	H_e[b]	G_{is}[b]	D[a]	E[a]
HIG2	20	2	0.053	1.714	0.286	0.429	0.333	0.1	0.552
RED2	20	4	0.158	3.286	0.679	0.658	−0.031	0.432	0.424
CAL1	20	4	0.158	3.429	0.75	0.674	−0.113	0.553	0.526
PET2	20	11	0.526	4.429	0.656	0.642	−0.022	0.9	0.627
MOR3	20	3	0.105	2.143	0.571	0.438	−0.304	0.279	0.454
PAS3	20	4	0.158	3.429	0.607	0.594	−0.022	0.432	0.424
MB99	20	5	0.211	3.857	0.564	0.585	0.036	0.558	0.426
MB97	20	3	0.105	3	0.714	0.694	−0.029	0.279	0.454
ON95	20	5	0.211	4.143	0.857	0.686	−0.25	0.511	0.388
ON94	20	1	0.000	1.286	0.286	0.286	0	0	1
ON92	20	6	0.263	4.143	0.643	0.621	−0.035	0.674	0.463
ON90	20	8	0.368	4.429	0.633	0.62	−0.021	0.868	0.714
ON87	20	7	0.316	4.286	0.694	0.61	−0.137	0.679	0.402
ON85	20	5	0.211	3.429	0.543	0.566	0.04	0.368	0.308
ON83	20	8	0.368	5.714	0.768	0.677	−0.135	0.7	0.373
ON81	20	9	0.421	5.714	0.667	0.694	0.04	0.853	0.585
QC78	20	20	1	6.143	0.677	0.636	−0.065	1	1
QC75	20	4	0.158	3.143	0.607	0.6	−0.012	0.363	0.382
QC73	20	2	0.053	2.714	0.714	0.724	0.013	0.189	0.61
QC71	20	1	0	1.714	0.714	0.714	0	0	1
QC69	20	1	0	1.429	0.429	0.429	0	0	1
QC68	20	5	0.211	4.286	0.629	0.692	0.092	0.505	0.385

N number of individuals genotyped, G number of unique genets, R clonal diversity, A average allelic richness, H_o observed heterozygosity, H_e expected heterozygosity, G_{is} interbreeding coefficient, D Simpson diversity index, E evenness

[a] Calculated from the ramet data set

[b] Calculated from the genet data set

Table 4 AICc candidate models for the log-transformed average tree basal area increment (TBAI) of *Populus tremuloides* in Canada, derived from raw ring widths

Candidate models	K^a	AICc[b]	ΔAICc[c]	AICcWt[d]	Cumwt
TBAI~CMI+FTC+age	7	487.23	0	0.52	0.52
TBAI~CMI	5	489.8	2.58	0.14	0.66
TBAI~age	5	490.1	2.87	0.12	0.78
TBAI~H_o+A+D+age	8	491.07	3.84	0.08	0.86
TBAI~CMI+FTC+H_o+A+D+age (global model)	10	491.55	4.32	0.06	0.92
TBAI~CMI+FTC	6	491.75	4.52	0.05	0.97
TBAI~H_o+A+D	7	495.68	8.45	0.01	0.98
TBAI~D	5	496.56	9.33	0	0.99
TBAI~FTC	5	496.63	9.4	0	0.99
TBAI~H_o	5	496.8	9.57	0	1
TBAI~H_o	6	496.95	9.72	0	1

TBAI (ΔAICc<3) and therefore multi-model inference was performed

[a] Number of parameters

[b] AICc coefficient

[c] AIC relative to the best model

[d] AIC model weight (for more details see Burnham and Anderson 2004)

longitudinal gradient (Pearson product-moment correlation: r= 0.01896, P=0.5412). Individual H_o varied from 0.143 to 1. For each locus, G_{is} varied from −0.092 (PTR14) to 0.038 (PTR3), with a global G_{is} value of −0.015.

Modelling growth responses to genetics and environmental data

Annual growth and inter-tree growth variability Many candidate models (ΔAICc<3) could explain the differences in TBAI. Therefore, multi-model inference was used to calculate the averaged predictors for the different variables in these models (tree age, N_{FTC}, CMI, D, A and H_o or individual H_o; Tables 4 and 6). TBAI was best explained in the mixed-effects models by CMI, N_{FTC} and tree age (estimated R^2=0.45, P<0.001). On average, TBAI was significantly higher on sites with lower CMI (Fig. 2a), while the other variables were not significant (Table 4 and Fig. 2b–f). This analysis revealed no significant effects of the tested genetic parameters. Annual growth was only influenced by climatic conditions (Table 6).

Concerning the inter-tree growth variability that was estimated by the MS, only one model had a ΔAICc<3 and, therefore, multi-model inference was not used (Table 5). N_{FTC} and

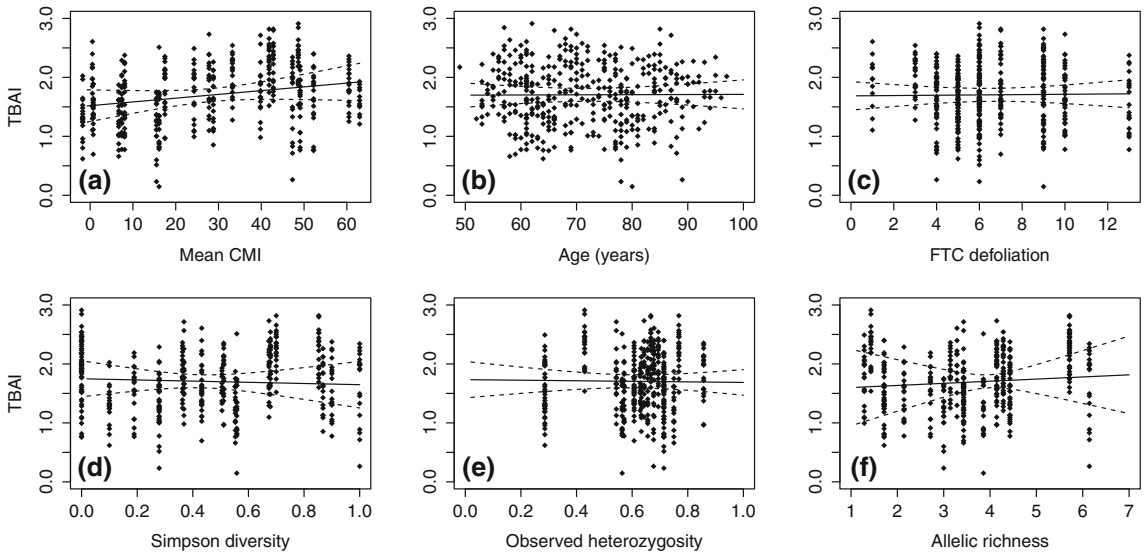

Fig. 2 **a**–**f** Observed (*filled diamonds*) and predicted logarithm of mean basal area increment (TBAI; *solid line*) in response to all explanatory variables that were used for multi-model averaging of the best candidate models (n=417) in Canada. *Dashed lines* show 95 % confidence bands

Table 5 AICc candidate models for the MS (square root-transformed mean sensitivity) of *Populus tremuloides* growth in Canada, determined from detrended ring widths

Candidate models	K^a	AICc[b]	ΔAICc[c]	AICcWt[d]	Cumwt
MS~CMI+FTC	6	−1617.48	0	0.99	0.99
MS~FTC	5	−1607.82	9.66	0.01	1
MS~CMI	5	−1585.58	31.9	0	1
MS~H_o	5	−1578.07	39.41	0	1
MS~D	5	−1577.32	40.16	0	1
MS~CMI+FTC+age	7	−1576.64	40.84	0	1
MS~H_o+A	6	−1576.1	41.38	0	1
MS~H_o+A+D	7	−1575.75	41.73	0	1
MS~CMI+FTC+H_o+A+D+age (global model)	10	−1573.89	43.59	0	1
MS~age	5	−1539.31	78.17	0	1
MS~H_o+A+D+age	8	−1535.58	81.9	0	1

Only one model explained √MS (ΔAICc<3) and no multi-model inference was performed

[a] Number of parameters

[b] AICc coefficient

[c] AIC relative to the best model

[d] AIC model weight (for more details see Burnham and Anderson 2004)

CMI were the most significant predictors explaining variation in MS (estimated R^2=0.87, P<0.001). Our results showed that MS was not influenced by genetic diversity (neither H_o nor individual H_o, D and A) or tree ages. These variables were not included in the best-fitting models (Table 6). Model predictions suggested that an increasing N_{FTC} increased MS (Fig. 3a), while a higher CMI (wetter conditions) tended to decrease MS (Fig. 3b).

Mean inter-tree correlation Only one model (R^2=0.683, P<0.001; ΔAICc<3), which included clonal diversity (R), N_{FTC} and CMI, explained the variability in RBAR across Canada. CMI was not a significant predictor (P=0.083; Table 6) in the model. Therefore, multi-model inference was not used (Table 7). When taken separately, a total of 30 % of variation in RBAR was explained by clonal diversity (R^2=0.304, P=0.007), while 28 % was explained by N_{FTC} (R^2=0.279, P=0.012). Clonal diversity was negatively associated with RBAR (Fig. 4a) and positively associated with N_{FTC} (Fig. 4b). CMI had no significant effect (Table 6, Fig. 4c) on the RBAR even when this predictor was included in the best-fitting model.

Table 6 Results of the best-fitting models (linear mixed-effect (LME) and multiple linear regression) explaining the relationship between TBAI (a), MS (b) and RBAR (c), and the explanatory variables (H_o, R, A, D, age, FTC and CMI)

Response	Predictor	Estimate	Lower 95 % CI	Upper 95 % CI
(a) TBAI	CMI	0.0081	0.0023	0.014
	FTC	0.0042	−0.0362	0.0447
	Age	0.0003	−0.0085	0.0091
	D	−0.7249	−1.8957	0.4458
	H_o	−0.3288	−1.4236	0.766
	A	0.2234	−0.0491	0.4958
(b) MS	FTC	17.452e−03	13.641e−03	21.263e−03
	CMI	−1.064e−03	−1.625e−03	−0.503e−03
(c) RBAR	R	−0.2804	−0.4154	−0.1453
	FTC	0.02065	0.00939	0.03192
	CMI	−1.422e−03	−2.942e−03	0.097e−03

In the LME, each unique genotype within sites was treated as a random effect, nested within each of the 22 sites. The best model was selected according to AICc (Tables 4 and 5 for LME and Table 7 for multiple linear regression).

Discussion

Variability in growth responses to climate for trembling aspen have been acknowledged in the literature (Hogg et al. 2005; Drobyshev et al. 2013; Huang et al. 2013), although few studies have attempted to quantify this variation in terms of genetic diversity. This study on aspen populations along an east-west Canadian transect demonstrated that higher levels of clonal diversity were associated with lower growth response synchronicity (low RBAR values). In contrast, environmental factors such as N_{FTC} and soil moisture conditions (CMI) were the major factors explaining variation in mean sensitivity (MS) between populations, while average tree basal area increment (TBAI) varied only with CMI.

Descriptive genetic statistics

The level of genetic polymorphism that was observed with the set of seven loci was similar to what has been found in previous studies and reflected the highly diverse genetic pool of aspen in Canada's boreal forest (Dayanandan et al. 1998;

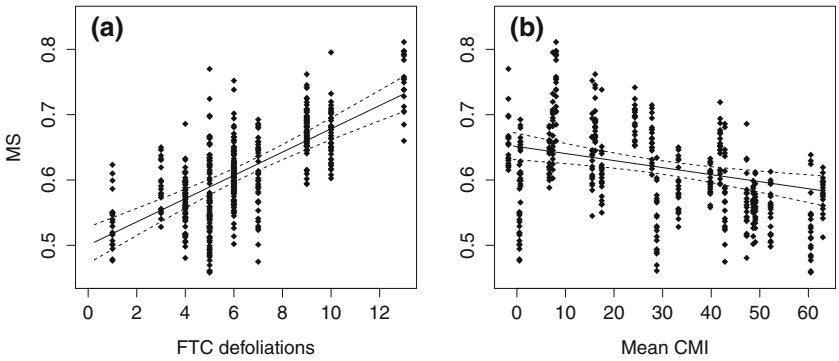

Fig. 3 **a**–**b** Observed (*filled diamonds*) and predicted square root-transformed mean sensitivity (MS; *solid line*) in response to the explanatory variables present in the best candidate model (n=440) in Canada. *Dashed lines* show 95 % confidence bands

Rahman et al. 2000; Smulders et al. 2001; Namroud et al. 2005). Mean H_o and H_e were very high for most sites, reflecting substantial genetic diversity (Wyman et al. 2003; Namroud et al. 2005). For all loci that were considered, we observed slightly higher values of H_o compared to H_e, with a slight excess of heterozygotes. This trend was confirmed by negative G_{is} values for each locus. Generally, if heterozygotes have a fitness advantage, this tends to generate negative G values, although a negative G does not necessarily mean that there was heterozygote advantage (Jelinski and Cheliak 1992). Further, negative G_{is} are observed when a relatively small number of samples (unique genotype) are analysed per site (Meirmans and Van Tienderen 2004), which was the case with the genet data set. No relationship between the level of genetic diversity and environmental conditions could be established. Clonal diversity (R) similarly varied along the climatic gradient, but no significant differences in this value were found between eastern and western Canada. Indeed, monoclonal and highly diverse polyclonal aspen stands were encountered throughout Canada.

Modelling growth responses to genetics and environmental data

Annual growth and inter-tree growth variability TBAI was best explained by regional differences in CMI. Genetic diversity (H_o, A and D) could not explain the differences in TBAI that have been observed in the Canadian boreal forest. Mitton and Grant (1980) and Jelinski and Cheliak (1992) have suggested that heterozygotes may have greater physiological versatility than homozygotes, which would permit more flexible responses to environmental variation. In general, heterozygotes had no better growth than homozygotes in terms of TBAI (Fig. 2) and mean H_o was not significant. Clonal richness had no effect on the standard deviation of TBAI (data not shown), meaning that the mean growth of all genotypes varied with similar amplitude in response to external environmental conditions. Our results supported a relationship between CMI and TBAI, as has been previously reported by Hogg et al. (2005) in the western boreal forest. In a recent study, Anyomi et al. (2014) also showed a decline in aspen productivity with

Table 7 AICc candidate models for the RBAR (mean inter-tree correlation) of *Populus tremuloides* in Canada, determined from detrended ring widths

Candidate models	K[a]	AICc[b]	ΔAICc[c]	AICcWt[d]	Cumwt
RBAR ~ CMI+FTC+R	5	−49.53	0	0.8	0.8
RBAR ~ CMI+FTC+R+H_o+A (global model)	7	−46.03	3.5	0.14	0.94
RBAR ~ FTC+H_o+A	5	−44.2	5.33	0.06	0.99
RBAR ~ CMI+FTC	4	−37.18	12.35	0	1
RBAR ~ R	3	−36.25	13.28	0	1
RBAR ~ CMI+H_o+A	5	−36.14	13.39	0	1
RBAR ~ FTC	3	−35.46	14.06	0	1
RBAR ~ CMI	3	−33.53	15.99	0	1
RBAR ~ R+H_o+A	4	−33.49	16.04	0	1
RBAR ~ CMI+H_o+A	5	−33.08	16.44	0	1
RBAR ~ H_o+A	3	−30.84	18.69	0	1

Only one model explained √MS (ΔAICc<3) and no multi-model inference was performed

[a] Number of parameters

[b] AICc coefficient

[c] AIC relative to the best model

[d] AIC model weight (for more details see Burnham and Anderson 2004)

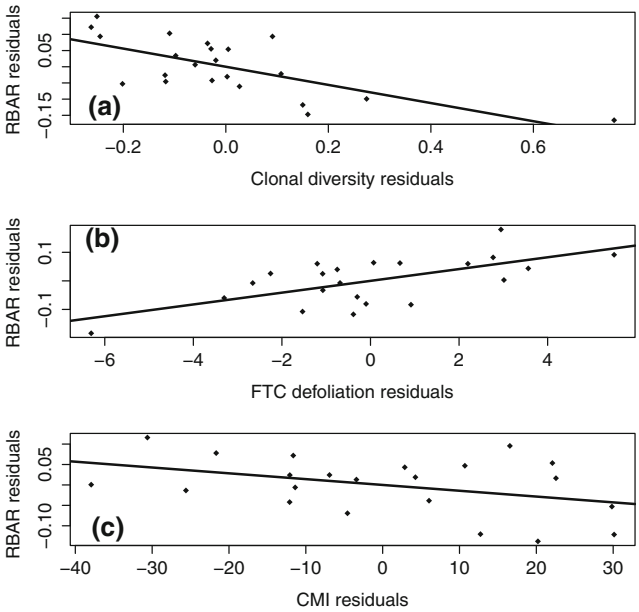

Fig. 4 Partial regression plots showing the relationship between **a** RBAR residuals vs clonal diversity residuals, **b** RBAR residuals vs forest tent caterpillar extreme defoliation residuals and **c** RBAR residuals vs CMI residuals for 22 populations of *Populus tremuloides* that were located across boreal Canada

high moisture deficits at a continental scale. In their study, King et al. (2013) reported that tree-ring width variation in European larch (*Larix decidua*) and Norway spruce (*Picea abies*) that were growing in the Alps were more strongly driven by climate than by genetics at regional and larger scales.

A high MS value is characteristic of high inter-annual variation in growth (Cook and Kariukstis 1990; Biondi and Qeadan 2008; Schreiber et al. 2013) and is an approximation of the time series standard deviation (Bunn et al. 2013). Hogg et al. (2002a) demonstrated that defoliation by FTC was the most important factor causing inter-annual variation in annual growth before pointing out the combined influence of inter-annual variation in the CMI and FTC defoliation on those variations in growth. During years of severe early season defoliation by insects, anomalously pale-coloured, low-density tree rings are formed (Hogg et al. 2005), and reduced growth or no growth is observed. Our results (Fig. 3) supported the idea that the frequency of these outbreaks (N_{FTC}) increased inter-annual variation, given that year-to-year growth variability was observed. Climatic conditions are the other important component that would explain this variation. A more favourable climate (high CMI) reduced inter-annual differences in growth, thereby lowering MS. Regions with moister climate are less subject to extreme drought events, and thus, variation in inter-annual growth responses are expected to be more homogeneous in eastern than in western Canada. The fact that genetic variables (H_o, D and A) did not significantly influence variation in MS demonstrated that even in extreme climatic conditions, there were no differences in growth response among genotypes within sites. It is possible that higher levels of diversity could allow the trees to have a more flexible response in the case of poorer than normal environmental conditions (Nicotra et al. 2010). Contrary to our hypothesis, clonal (R or D) and genetic diversity (H_o, A) of the population did not explain variation in MS and higher levels of diversity could not buffer growth reductions and variation during extreme events.

Mean inter-tree correlation Our results partly validated our hypothesis for a relationship between genetic characteristics and growth responses in aspen. RBAR was mainly influenced by clonal diversity and N_{FTC}. Clonal diversity was the most important factor. It increased the differences between individual chronologies and the average growth response per site. In contrast, N_{FTC} had a homogenising effect on RBAR, suggesting that insects similarly and severely affect all of the trees and genotypes. Osier and Lindroth (2001) showed that the primary source of variation in gypsy moth (*Lymantria dispar*) performance was aspen genotype (different ranges of resistance against this insect), which we did not observe here, most probably because we focused only on severe defoliation. Severe defoliation is known to reduce tree growth (Moulinier et al. 2014), which could affect all genotypes. Consequently, the growth response was more homogeneous within ramets (high RBAR, with low R) of the same genotype than between ramets of different genotypes. In general, a complex assemblage of different genotypes (high R) would likely increase differences in genotype growth patterns (phenotypic responses for this trait) to the same environmental factors of low intensity, whereas severe events would affect them strongly and similarly. The effect of other environmental factors, such as moisture, could not be isolated because of the predominant effects of N_{FTC} and clonal diversity, together with the noise that was introduced by these factors. Differences in genetic diversity could not explain variation in RBAR and no signal was detected. This response can probably be explained by the high level of genetic diversity that was measured by H_o and by the fact that H_o is quite homogenous, even when RBAR varies among sites. Phenotypic differences that were observed among clones (genotypes), rather than overall genetic diversity, likely created most of the variability and are the source of the differences among chronologies.

Conclusions and perspectives

The current study is the first continental-scale study to examine trembling aspen radial growth in relation to population genetic data in the Canadian boreal forest. In general, the assumption that has been made regarding growth studies is that inter-annual variation in growth is driven

primarily by physiological responses to climatic variables (Parmesan 2006; King et al. 2013). This work confirmed previous findings (Hogg et al. 2005), showing that environmental disturbances are the main drivers of average and inter-annual growth variation and that annual growth variation is more strongly driven by climate than by genetics at regional and broader scales.

Higher aspen TBAI was not correlated with higher genetic diversity. We cannot exclude the possibility that the absence of correlation between "multi-locus heterozygosity" and the fitness of our trees (evaluated by different radial growth measures) could be due to an insufficient number of markers considered to represent the genome-wide diversity (Hansson and Westerberg 2002). However, the correlation between genome-wide heterozygosity and multi-locus estimates is relatively high with a median value across studies of 0.83 for microsatellites (Mittell et al. 2015). Mittell et al. (2015) argued that a relatively small number of microsatellite loci and number of individuals genotyped are sufficient to give an accurate estimate of genome-wide diversity. However, they also shown that the ability of current molecular genetic diversity estimates to predict average heritability has an upper bound of 0.26 and that additional genotyping will probably not improve the ability of these markers to predict adaptive potential.

Genetic factors should subsequently be taken into account in future studies, since our results have shown their importance in growth synchronicity. Multi-clonal aspen stands would likely be, on average, more resilient to year-to-year events of small intensity (e.g. climate or insect outbreaks) and less sensitive to rapid declines because their growth responses were less homogeneous due to the complex assemblage of many different genotypes. Our results emphasise the importance of trying to maintain highly diverse (genetic and clonal diversity) aspen stands. It is especially crucial in the context of global change where an alteration in the genetic composition could lead to a reduction in the ability of a stand to resist and recover from environmental disturbances (Jump and Peñuelas 2005), thereby causing extensive stand decline, especially in the western part of the species' range (e.g. Hogg et al. 2008; Worrall et al. 2008; Worrall et al. 2013).

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References

Anyomi KA, Lorenzetti F, Bergeron Y, Leduc A (2014) Stand dynamics, humus type and water balance explain aspen long term productivity across Canada. Forests 62:416–432

Applequist MB (1958) A simple pith locator for use with off-center increment cores. J For 562:141

Arnaud-Haond S, Duarte CM, Alberto F, Serrão EA (2007) Standardizing methods to address clonality in population studies. Mol Ecol 1624: 5115–5139

Beaulieu J, Bousquet J (2010) Facteurs génétiques affectant la variabilité des cernes annuels chez les espéces arborescentes nordiques. In: Payette S, Filion L (eds) La dendroécologie: principes, méthodes et applications. Presses de l'Université Laval, Québec City (QC), Canada, pp 137–163

Becker M (1989) The role of climate on present and past vitality of silver fir forests in the Vosges mountains of northeastern France. Can J For Res 199:1110–1117

Biondi F, Qeadan F (2008) Inequality in paleorecords. Ecology 894: 1056–1067

Briffa KR, Jones PD (1990) Basic chronology statistics and assessment. In: Cook ER, Kairiukstis LAE (eds) Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, pp 137–152

Briffa KR, Schweingruber FH, Jones PD, Osborn TJ, Harris IC, Shiyatov SG, Vaganov EA, Grudd H (1998) Trees tell of past climates: but are they speaking less clearly today? Philos Trans R Soc Lond B Biol Sci 353:65–73

Bunn AG (2008) A dendrochronology program library in R (dplR). Dendrochronologia 262:115–124

Bunn AG, Jansma E, Korpela M, Westfall RD, Baldwin J (2013) Using simulations and data to evaluate mean sensitivity (zeta) as a useful statistic in dendrochronology. Dendrochronologia 313:250–254

Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. Sociol Methods Res 332:261–304

Callahan CM, Rowe CA, Ryel RJ, Shaw JD, Madritch MD, Mock KE (2013) Continental-scale assessment of genetic diversity and population structure in quaking aspen (*Populus tremuloides*). J Biogeogr 409:1780–1791

Cole CT, Anderson JE, Lindroth RL, Waller DM (2010) Rising concentrations of atmospheric CO2 have increased growth in natural stands of quaking aspen (*Populus tremuloides*). Glob Chang Biol 16:2186–2197

Cook ER (1985) A time series analysis approach to tree ring standardization. PhD thesis, University of Arizona, Tucson, AZ.

Cook EK, Kariukstis AL (1990) Methods of dendrochronology—applications in the environmental sciences. Kluwer Academic Publishers and International Institute for Applied Systems Analysis, Dordrecht

Cook ER, Pederson N (2010) Uncertainty, emergence, and statistics in dendrochronology. In: Hughes MK, Swetnam TW, Diaz HF (eds) Dendroclimatology: progress and prospects. Springer Science and Business Media, New York, pp 77–112

Cook ER, Peters K (1981) The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. Tree-Ring Bull 41:45–53

Cornelius J (1994) Heritabilities and additive genetic coefficients of variation in forest trees. Can J For Res 242:372–379

Dayanandan S, Rajora OP, Bawa KS (1998) Isolation and characterization of microsatellites in trembling aspen (*Populus tremuloides*). Theor Appl Genet 966–7:950–956

DeWoody J, Rowe CA, Hipkins VD, Mock KE (2008) "Pando" lives: molecular genetic evidence of a giant aspen clone in central Utah. Am Nat 684:493–497

Dorken ME, Eckert CG (2001) Severely reduced sexual reproduction in northern populations of a clonal plant, *Decodon verticillatus* (Lythraceae). J Ecol 893:339–350

Drobyshev I, Gewehr S, Berninger F, Bergeron Y (2013) Species-specific growth responses of black spruce and trembling aspen may enhance resilience of boreal forest to climate change. J Ecol 1011:231–242

Environment Canada (2014) Calculation of the 1971 to 2000 climate normals for Canada. http://climate.weather.gc.ca/climate_normals/normals_documentation_e.html?docID=1971 (Accessed May 3 2014)

Fox J, Weisberg S (2011) An *R* companion to applied regression, second edition. Thousand Oaks, California. Available at: http://socserv.socsci.mcmaster.ca/jfox/Books/Companion. (Accessed: February 20 2015)

Frey BR, Lieffers VJ, Hogg EH, Landhäusser SM (2004) Predicting landscape patterns of aspen dieback: mechanisms and knowledge gaps. Can J For Res 347:1379–1390

Fritts HC (1976) Tree rings and climate. Academic, New York

Grant MC, Mitton JB, Linhart YB (1992) Even larger organisms. Nature 3606401:216–216

Gray LK, Gylander T, Mbogga MS, Chen P-Y, Hamann A (2010) Assisted migration to address climate change: recommendations for aspen reforestation in western Canada. Ecol Appl 215:1591–1603

Gylander T, Hamann A, Brouard JS, Thomas BR (2012) The potential of aspen clonal forestry in Alberta: breeding regions and estimates of genetic gain from selection. PLoS ONE 78, e44303. doi:10.1371/journal.pone.0044303

Hanson EJ, Azuma DL, Hiserote BA (2003) Site index equations and mean annual increment equations for Pacific Northwest Research Station forest inventory and analysis inventories, 1985–2001. US Department of Agriculture, Forest Service Pacific Northwest Research Station, Portland, **Research Note PNW-RN-533 26p**

Hansson B, Westerberg L (2002) On the correlation between heterozygosity and fitness in natural populations. Mol Ecol 11:2467–2474

Hogg EH (1997) Temporal scaling of moisture and the forest-grassland boundary in western Canada. Agric For Meteorol 841–2:115–122

Hogg EH (2001) Modeling aspen responses to climatic warming and insect defoliation in western Canada. In: Proceedings of the Sustaining Aspen in Western Landscapes Symposium, Grand Junction, CO (ed). USDA Forest Service Proceedings RMRS-P-18. Rocky Mountain Research Station, Ft. Collins, CO, pp. 325–337

Hogg EHT, Bernier PY (2005) Climate change impacts on drought-prone forests in western Canada. For Chron 815:675–682

Hogg EH, Brandt JP, Kochtubajda B (2002a) Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. Can J For Res 325:823–832

Hogg EH, Hart M, Lieffers VJ (2002b) White tree rings formed in trembling aspen saplings following experimental defoliation. Can J For Res 3211:1929–1934

Hogg EH, Brandt JP, Kochtubajda B (2005) Factors affecting interannual variation in growth of western Canadian aspen forests during 1951–2000. Can J For Res 353:610–622

Hogg EH, Brandt JP, Michaelian M (2008) Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. Can J For Res 386:1373–1384

Huang J-G, Stadt KJ, Dawson A, Comeau PG (2013) Modelling growth-competition relationships in trembling aspen and white spruce mixed boreal forests of western Canada. PLoS ONE 810, e77607. doi:10.1371/journal.pone.0077607

Jelinski DE, Cheliak WM (1992) Genetic diversity and spatial subdivision of *Populus tremuloides* (Salicaceae) in a heterogeneous landscape. Am J Bot 797:728–736

Jump AS, Peñuelas J (2005) Running to stand still: adaptation and the response of plants to rapid climate change. Ecol Lett 89:1010–1020

King GM, Gugerli F, Fonti P, Frank DC (2013) Tree growth response along an elevational gradient: climate or genetics? Oecologia 1734:1587–1600

Kullback S, Leibler RA (1951) On information and sufficiency. Ann Math Stat 22:79–86

LeBlanc DC (1990) Relationships between breast-height and whole-stem growth indices for red spruce on Whiteface Mountain, New York. Can J For Res 209:1399–1407

Lebourgeois F, Gomez N, Pinto P, Mérian P (2013) Mixed stands reduce Abies alba tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. For Ecol Manag 303:61–71

Lemprière T, Bernier PY, Carroll AL, Flannigan MD, Gilsenan RP, McKenney DW, Hogg EH, Pedlar JH, Blain D (2008) The importance of forest sector adaptation to climate change. Information Report NOR-X-416E. Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Edmonton, **78p**

Leonelli G, Denneler B, Bergeron Y (2008) Climate sensitivity of trembling aspen radial growth along a productivity gradient in northeastern British Columbia, Canada. Can J For Res 385:1211–1222

Li H, Wang X, Hamann A (2010) Genetic adaptation of aspen (Populus tremuloides) populations to spring risk environments: a novel remote sensing approach. Can J For Res 4011:2082–2090

Little EL (1971) Atlas of United States trees, vol 1, Conifers and important hardwoods. U.S. Department of Agriculture, Forest Service, Washington, DC, **Miscellaneous Publication 1146, 200 maps**

Long JN, Mock K (2012) Changing perspectives on regeneration ecology and genetic diversity in western quaking aspen: implications for silviculture. Can J For Res 4212:2011–2021

Mazerolle MJ (2013) AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 1.35. http://cran.rproject.org/web/packages/AICcmodavg/index.html. (Accessed February 20 2015)

Meirmans PG, Van Tienderen PH (2004) Genotype and genodive: two programs for the analysis of genetic diversity of asexual organisms. Mol Ecol Notes 44:792–794

Mérian P (2012) POINTER and DENDRO—two applications under R software for analyzing tree response to climate using dendroecological approach. Revue Forestière Française 646:789–798

Mérian P, Lebourgeois F (2011) Size-mediated climate–growth relationships in temperate forests: a multi-species analysis. For Ecol Manag 2618:1382–1391

Michaelian M, Hogg EH, Hall RJ, Arsenault E (2011) Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. Glob Chang Biol 176:2084–2094

Mittell EA, Nakagawa S, Hadfield JD (2015) Are molecular markers useful predictors of adaptive potential? Ecol Lett 18:772–778

Mitton JB, Grant MC (1980) Observations on the ecology and evolution of quaking aspen, *Populus tremuloides*, in the Colorado Front Range. Am J Bot 202–209

Mitton JB, Grant MC (1984) Associations among protein heterozygosity, growth rate, and developmental homeostasis. Annu Rev Ecol Syst 15:479–499

Mitton JB, Grant MC (1996) Genetic variation and the natural history of quaking aspen. Bioscience 461:25–31

Mock KE, Rowe CA, Hooten MB, Dewoody J, Hipkins VD (2008) Clonal dynamics in western North American aspen (*Populus tremuloides*). Mol Ecol 1722:4827–4844

Moulinier J, Lorenzetti F, Bergeron Y (2014) Growth and mortality of trembling aspen (*Populus tremuloides*) in response to artificial defoliation. Acta Oecol 550:104–112

Namroud MC, Tremblay F, Bergeron Y (2005) Temporal variation in quaking aspen (*Populus tremuloides*) genetic and clonal structures in the mixedwood boreal forest of eastern Canada. Ecoscience 121:82–91

Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD, Richards CL, Valladares F,

van Kleunen M (2010) Plant phenotypic plasticity in a changing climate. Trends Plant Sci 1512:684–692

Osier TL, Lindroth RL (2001) Effects of genotype, nutrient availability, and defoliation on aspen phytochemistry and insect performance. J Chem Ecol 277:1289–1313

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol Syst 371:637–669

Peterson EB, Peterson NM (1992) Ecology, management, and use of aspen and balsam poplar in the prairie provinces. Forestry Canada Northwest Region, Northern Forestry Center, Canada, Edmonton, **Special Report 1. 252p**

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2013) nlme: linear and nonlinear mixed effects models, R package version 3.1-113. http://cran.rproject.org/web/packages/nlme/index.html. (Accessed: February 20 2015)

R Development Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing. http://www.R-project.org/. (Accessed: February 20 2015)

Rahman MH, Dayanandan S, Rajora OP (2000) Microsatellite DNA markers in *Populus tremuloides*. Genome 432:293–297

Régnière J, St-Amant R, Béchard A (2013) BioSIM 10 User's manual, Information Report LAU-X-137E. Natural Resources Canada, Laurentian Forest Centre, Québec City, QC, Canada. ftp://ftp.cfl.scf.rncan.gc.ca/regniere/software/BioSIM/Doc/LAU-X-137E.zip (Accessed September 10 2013)

Rinn F (1996) TSAP—time series analysis and precipitation. Version 3 Reference Manual. Heidelberg,

Schreiber SG, Ding C, Hamann A, Hacke UG, Thomas BR, Brouard JS (2013) Frost hardiness vs. growth performance in trembling aspen: an experimental test of assisted migration. J Appl Ecol 504:939–949

Smulders MJM, Van Der Schoot J, Arens P, Vosman B (2001) Trinucleotide repeat microsatellite markers for black poplar (*Populus nigra* L.). Mol Ecol Notes 13:188–190

Valentine HT (1985) Tree-growth models: derivations employing the pipe-model theory. J Theor Biol 1174:579–585

Verbeke G, Molenberghs G (2009) Linear mixed models for longitudinal data. Springer Science and Business Media, New York

Wigley TML, Briffa KR, Jones PD (1984) On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. J Clim Appl Meteorol 232:201–213

Worrall JJ, Egeland L, Eager T, Mask RA, Johnson EW, Kemp PA, Shepperd WD (2008) Rapid mortality of *Populus tremuloides* in southwestern Colorado, USA. For Ecol Manag 2553:686–696

Worrall JJ, Rehfeldt GE, Hamann A, Hogg EH, Marchetti SB, Michaelian M, Gray LK (2013) Recent declines of *Populus tremuloides* in North America linked to climate. For Ecol Manag 299:35–51

Wyman J, Bruneau A, Tremblay MF (2003) Microsatellite analysis of genetic diversity in four populations of *Populus tremuloides* in Quebec. Can J Bot 814:360–367

Yang Y, Huang S, Meng SX, Trincado G, VanderSchaaf CL (2009) A multilevel individual tree basal area increment model for aspen in boreal mixedwood stands. Can J For Res 3911:2203–2214

Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer Science and Business Media, New York