

Root connections affect radial growth of balsam poplar trees

Kokouvi Emmanuel Adonsou¹ · Igor Drobyshv^{2,3} · Annie DesRochers¹ · Francine Tremblay²

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Abstract

Key message Connected root systems reduced the negative impact of August temperatures and insect outbreak on growth.

Abstract Root connections between trees can be an ecological advantage of clonal plant species in environments with unevenly distributed resources. We investigated the effects of root connectivity in stands of balsam poplar in Quebec (Canada). We evaluated differences in growth response between groups of trees with and without root connections through climate-growth analyses, comparison of the growth dynamics, and analysis of growth response to a severe forest tent caterpillar (FTC) outbreak. Current May temperature had a positive influence on radial growth of both connected and non-connected trees. Growth of non-connected trees was negatively affected by August temperatures ($r = -0.3$) while connected trees did not reveal a significant relationship for that month. A mixed effect ANOVA showed a significant difference ($F_{1, 25} = 5.59$,

$p = 0.02$) in growth responses to FTC outbreak between connected and non-connected trees. Connected trees grew on average 16 % better than unconnected trees during the outbreak, with bootstrapped 95 % confidence range from 2.28 to 31.36 %. The study suggests a sharing of resources through root connections, affecting radial growth of connected balsam poplar trees under both average and extreme environmental conditions.

Keywords *Populus balsamifera* · *Malacosoma disstria* · Root grafting · Insect outbreak · Resource sharing · Tree nutrition · Biotic interactions · Facilitation in plant communities · Forest resilience

Introduction

Balsam poplar (*Populus balsamifera* L.) regenerates vegetatively and extensively at high densities through root suckering in response to anthropic (e.g., harvest) or natural (e.g., fire) disturbances (Peterson and Peterson 1992). This regeneration strategy creates large networks of ramets interconnected through their original parental root or through root grafting (DesRochers and Lieffers 2001; Jelínková et al. 2009), i.e., morphological unions of previously distinct roots from separate trees (Graham and Bormann 1966; Basnet et al. 1993; Mudge et al. 2009). Connected root systems have been found in many tree species (Graham and Bormann 1966) and there is increasing evidence that biological processes in trees may be directly influenced by other trees via root connections, which allow sharing of water, nutrients, and carbohydrate reserves (Fraser et al. 2006; Tarroux et al. 2010; Baret and DesRochers 2011; Adonsou et al. 2016). For example, snags and stumps of *Pinus* spp., which readily form root

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✉ Kokouvi Emmanuel Adonsou
K-Emmanuel.Adonsou@uqat.ca

✉ Annie DesRochers
Annie.Desrochers@uqat.ca

¹ Institut de recherche sur les forêts, Université du Québec en Abitibi-Témiscamingue, 341 rue Principale Nord, Amos, QC J9T 2L8, Canada

² Institut de recherche sur les forêts, Université du Québec en Abitibi-Témiscamingue, 445 boul. Université, Rouyn-Noranda, QC J9X 5E4, Canada

³ Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, PO Box 49, SE-230 53 Alnarp, Sweden

grafts, have been shown to grow 2–18 years following stem removal, using resources transferred across root grafts from neighboring trees (Stone 1974; Tarroux et al. 2010; Tarroux and DesRochers 2011). Root grafting increases the root system absorptive capacity and may result in greater growth rates (Tarroux and DesRochers 2011), greater efficiency of soil resource use, and reduced mortality in trees under unfavorable conditions (Pitelka and Ashmun 1985; Loehle and Jones 1990).

Root connections may affect tree response to environmental stresses, such as unfavourable climatic conditions or insect attacks. Severe tree defoliation by the forest tent caterpillar (FTC) (*Malacosoma disstria* Hubner), and variations in temperature have caused significant reductions in radial growth and hardwood forest decline in boreal ecosystems in Canada (Brandt 1995; Körner 2003; Jones et al. 2004; Sutton and Tardif 2005). It remains unclear whether root connections enable trees to share resources or signals under unfavourable conditions, affecting tree resistance to environmental variability. To the best of our knowledge, no previous studies of growth in adult trees has considered the role of tree connectivity by their root systems.

The main objective of this study was to determine whether root connections among trees affect the growth response of balsam poplar to environmental variability. We hypothesized that interconnected trees would have higher radial growth rate under both average and extreme environmental variability, as compared to non-connected trees. We evaluated differences in growth response between groups of trees with and without root connections through climate-growth analyses, comparison of the growth dynamics, and analysis of growth response to a severe forest tent caterpillar (FTC) outbreak.

Materials and methods

Study area

The study was carried out in three mesic upland sites in Quebec's Abitibi region (Fig. 1): QC1 (48°29'N, 79°24'W, 303 m a.s.l.), QC2 (48°24'N, 79°24'W 298 m a.s.l.) and QC3 (48°32'N, 78°08'W, 315 m a.s.l.). The region is part of the Northern Clay Belt of Quebec and Ontario, which resulted from the maximum extension of the postglacial Lakes Barlow and Ojibway (Vincent and Hardy 1977). The nearest meteorological station to two study sites (QC1, QC2) is at La Sarre, approximately 42 km to the north, while that of the third site (QC3) is at Val-d'Or around 67 km to the south. The average climate for 1971–2000 showed a mean annual temperature of 0.7 °C and mean total annual precipitation of 889 mm, with 643 mm as

rainfall during the growing season (Environment Canada 2012). The mean frost-free period is 64 days but freezing temperature can occur at any time of the year (Environment Canada 2012). The study region is located at the southern limit of the boreal forest, where most stands originate from natural forest fires and are dominated by an association of aspen (*Populus tremuloides* Michx.) and balsam poplar, *Abies balsamea* (L) Mill., *Picea mariana* (Mill.) BSP, *Betula papyrifera* Marsh., and *Picea glauca* (Moench) Voss.

Field sample collection

Pure balsam poplar stands (>75 % of stems), naturally regenerated by root-suckering or seeding after fire, were selected adjacent to a gentle slope with a water supply nearby to facilitate hydraulic excavation (Tarroux and DesRochers 2011). We used a high-pressure water spray from a forest fire pump (Mark III, WAJAX Lachine, Quebec) to uncover the whole root system of three balsam poplar stands. The area of the excavated plots ranged from approximately 50 to 60 m², depending on spatial distribution of the trees, so that at least 10 trees were included at each site. To age trees and to obtain their growth patterns, we felled 43 trees and collected stem cross-sections at the ground level (0 m) and at breast height (1.3 m). To expose all main roots the depth of excavation varied from 30 to 60 cm. Each coarse root was traced until its diameter decreased to less than 2 cm. In each excavated area, all trees, roots, and root connections between trees and the stumps of dead trees were mapped. Parental root connections and root grafts (Fig. 2) between trees were identified, collected and brought to the lab for further analysis. In the field, all suspected root grafts were checked by removing bark and by partial dissection to confirm a common wood layer between the two roots (Tarroux et al. 2010).

Dendrochronological methods

In the laboratory, all stem cross-sectional disks were air-dried and progressively sanded with finer sand paper (80–400 grit) to clearly highlight tree-ring patterns. Images of cross-sectional disks were acquired with an EPSON GT 15,000 scanner at 1200 dpi resolution. Radial growth was measured on cross-sectional disks taken from the stem base (0 m) when possible or at breast height using CDendro and CooRecorder program v. 7.7 (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden). Ring-widths were measured with 0.01 mm precision along two radii per disk. The two curves were averaged into single-tree chronologies which were subsequently cross-dated and verified by using signature years (Stokes and Smiley 1968) and COFECHA program (Grissino-Mayer 2001). The number of sampled

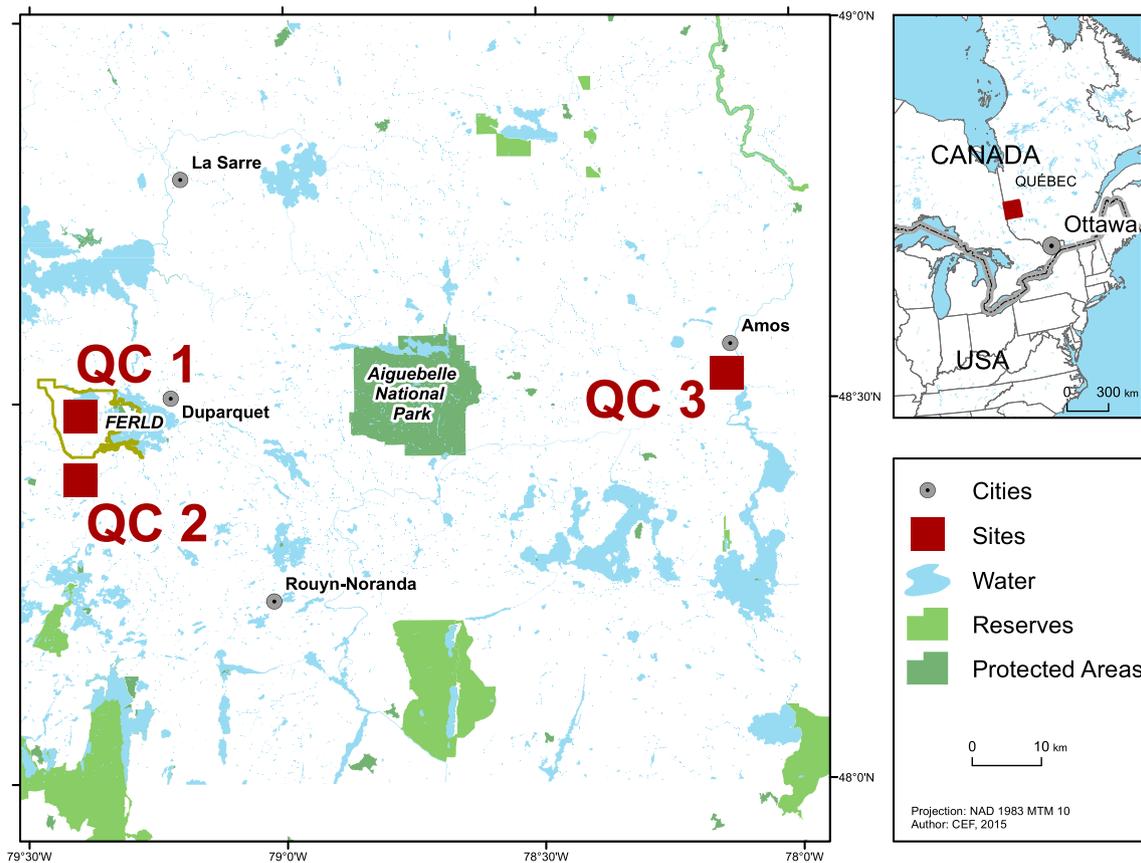
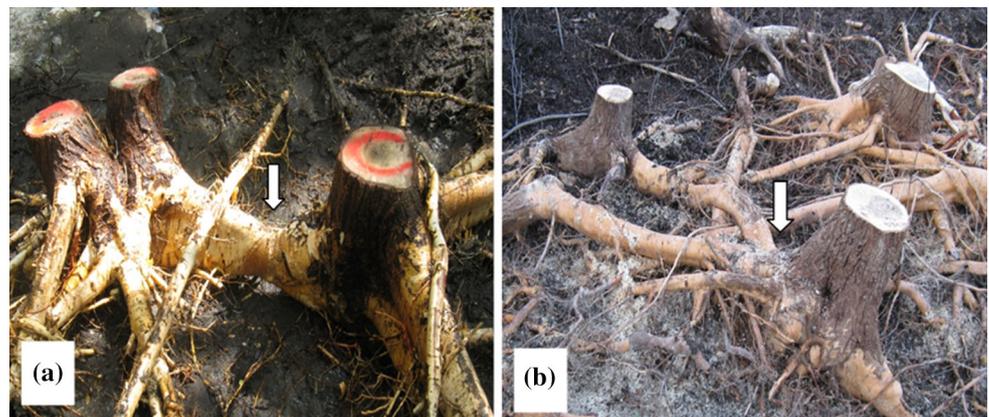


Fig. 1 Location of the sampling sites QC1, QC2, and QC3 in the Abitibi region of northwestern Quebec, Canada

Fig. 2 Photographs of excavated root systems of balsam poplar showing root connections: the *arrows* indicate parental root connection (a) and root graft (b) between trees in Quebec, Canada



trees finally included in the analyses varied between 8 and 12 per site.

Expressed population signal (EPS) and the signal-to-noise-ratio (SNR), both the measures of common signals in chronologies (Wigley et al. 1984), were also calculated. To examine the temporal consistency of climate-growth relationships, we calculated moving correlation between tree-ring growth and mean monthly temperature and precipitation using bootres function (Zang and Biondi 2013).

Residual chronologies resulting from autoregressive modelling of the site chronologies were used to evaluate climate-growth relationships of connected and non-connected trees in response function analysis (RFA) (Cook and Kairiukstis 1990). We limited the analyzed period to 1980–2009. The time frame was a compromise between uncertainty associated with status of the trees (connected vs. non-connected) in the earlier periods of their lifespans and requirements of RFA. Due to a limited length of the

chronology we had to limit the number of predictors in RFA to June through August of the year of growth. Prior to RFA we removed low frequency trends in tree-ring data by detrending single tree chronologies by a cubic spline with a 50 % frequency response at 32 year frequency band. In addition, we used autoregressive modeling [function *detrend* in the R package *dplR* (Bunn 2010)] on the detrended ring-width series to remove temporal autocorrelation in the chronologies. Autoregressive modeling relied on the values of Akaike Information Criterion (AIC) to select optimal order of autoregressive model. We performed RFA in R package *treeclim* (Zang and Biondi 2015).

Mixed effect models were used to evaluate whether root connectivity differentiated the trees in respect to response to the most significant monthly climate variables identified on the previous step of analysis. We used R package *nlme* (Pinheiro and Bates 2006) to run mixed effects models with tree-specific response coefficient as the dependent variable, site identity as the random factor, and tree rooting status as the independent variable.

We bootstrapped results of ANOVA on growth performance during the years with outbreaks with the R package *boot* (Canty 2002), using 1000 iterations and choosing a significance level of $p < 0.05$.

Ordination analyses

We used the ordination package *vegan* in R (Oksanen et al. 2013) to evaluate relationships between climate and growth in trees of different rooting status (connected vs. non-connected). Prior to analysis, climate data were normalized to account for the differences in scales among variables. We used progressive selection of explanatory variables (in the R routine *ordiR2step*) to identify RDA axes which significantly contributed to the overall variability in tree growth. Finally, we tested all canonical axes to evaluate statistical significance of their contribution to growth variability in the R routine ANOVA.CCa, using the step number of 1000.

Impact analysis

We tested whether the root connectivity affected tree response during severe FTC defoliation reported in the study area during 2000–2001 (MFFPQ 2015). To this end we calculated the difference between cumulative increment immediately prior to (1997–1999 inclusive) and following the outbreak (2000–2003 inclusive). The ratio was used as the dependent variable in the mixed model ANOVA with the tree root status (connected vs. non-connected) as the fixed factor and the site identity as the random variable and.

Climate data

Analyses utilized climate data generated in BioSIM 10.0, a set of spatially-explicit bioclimatic models (Régnière 1996). For each sampling site, the model interpolated data from the five closest weather stations and adjusted for differences in latitude, longitude, and elevation between the weather stations and the site location. Due to short distances among sites we aggregated climate data by averaging data from respective sites. Climate variables included monthly mean temperature (°C), monthly total precipitation (mm), monthly total snowfall (mm), total degree-days (>5 °C), and monthly potential evapotranspiration (Thornthwaite method). Preliminary analyses revealed that evapotranspiration was inferior to the other two variables in terms of predictive power, and it was removed from the analyses.

Results

Dendrochronological analysis and clonal integration

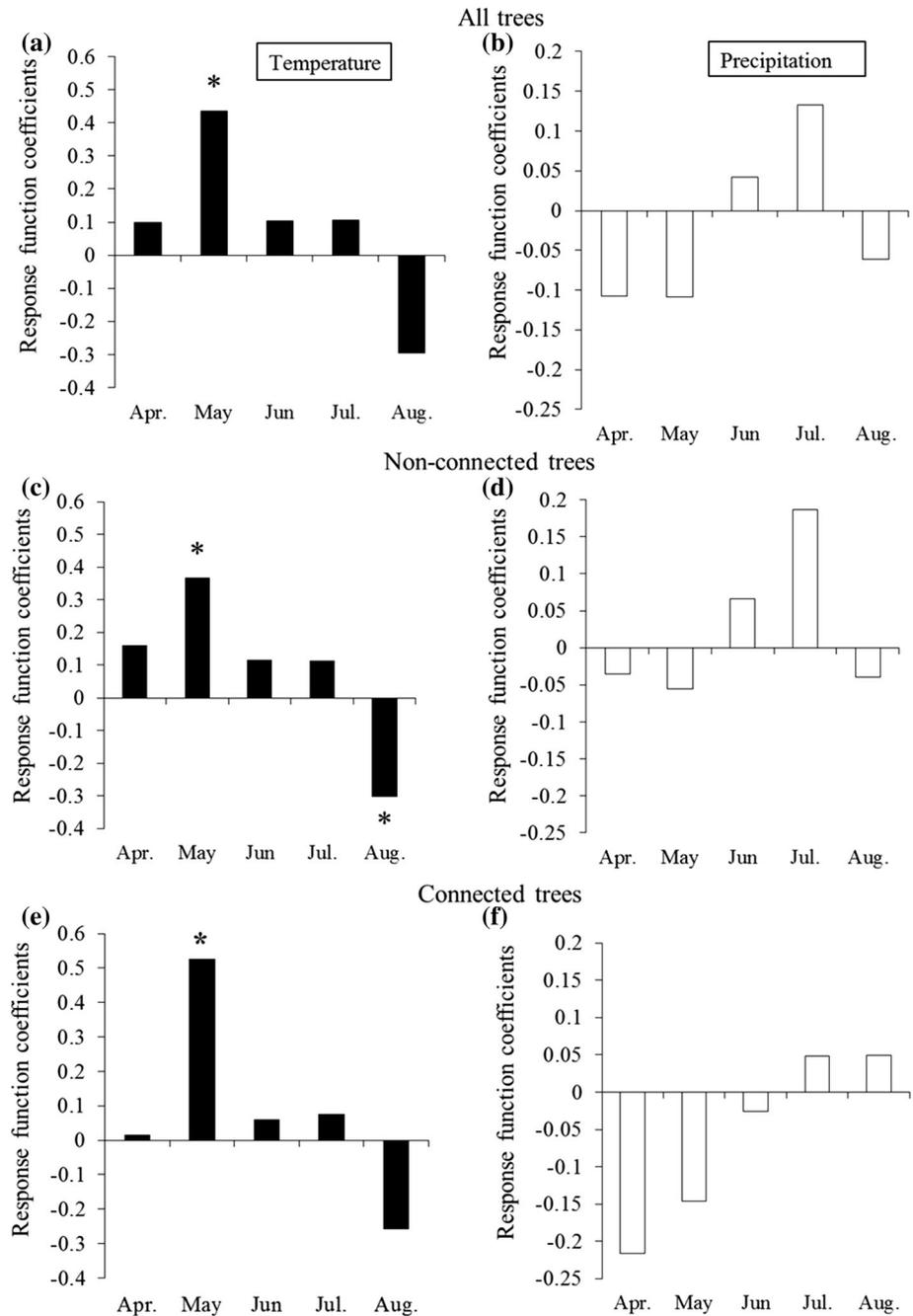
Dendrochronological analysis showed that the ages of sampled sites were 86, 87, and 44 years and were even-aged (age of trees corresponded to age of sites). All excavated trees were of sucker origin, because roots older than the stems were found in the root system of all trees. Parental root connections were found in 25 % of trees linking at least two living trees. Within the excavated sites, 48 % of trees were linked with a root graft to at least one other living tree and lastly, 47 % of excavated trees were not connected to other trees within the excavated area either by parental roots or root grafts.

Pattern of growth response to temperature and precipitations

Over the 1980–2009 period, the single-tree chronologies revealed a strong common signal with the expressed population signal (EPS) and signal-to-noise ratio (SNR) being 0.923 and 12.03, respectively. Current May temperature had positive and significant correlation ($r = 0.43$) with tree-ring chronologies of both connected and non-connected trees over the studied period of time (Fig. 3a). Current growing season precipitation had no significant impact on tree radial growth in either of the groups (Fig. 3b).

Growth of non-connected trees displayed a significant positive response to current May temperature ($r = 0.36$) and significant negative impact of August temperature ($r = -0.3$, Fig. 3c). The connected trees showed a sig-

Fig. 3 Response function coefficients for balsam poplar radial growth and monthly mean temperature (a) and mean precipitation (b) of all trees, monthly mean temperature (c) and mean precipitation (d) of non-connected trees, and monthly mean temperature (e) and mean precipitation (f) of connected trees. Asterisks show significant coefficients at $p = 0.05$ level



nificant positive impact to current May temperature only (Fig. 3e). On the other hand, response function analysis of May ($p = 0.25$) and August ($p = 0.97$) temperatures, which served as our most important monthly climatic predictor variables, did not show any significant difference in radial growth responses between connected and non-connected trees. Moving response function analysis showed generally consistent response of growth to May (positive) and August (negative) temperatures (Fig. 4).

Growth-root connections-climate relationships

Redundancy analysis revealed that non-connected trees exhibited a greater spread of points across the climatic space, indicating a wider variability in the response to climate, as compared to connected trees (Fig. 5 a, b). Indeed, mixed model ANOVA on non-detrended chronologies showed significant difference ($F_{1, 25} = 5.59$, $p = 0.02$) in growth responses to FTC outbreak between

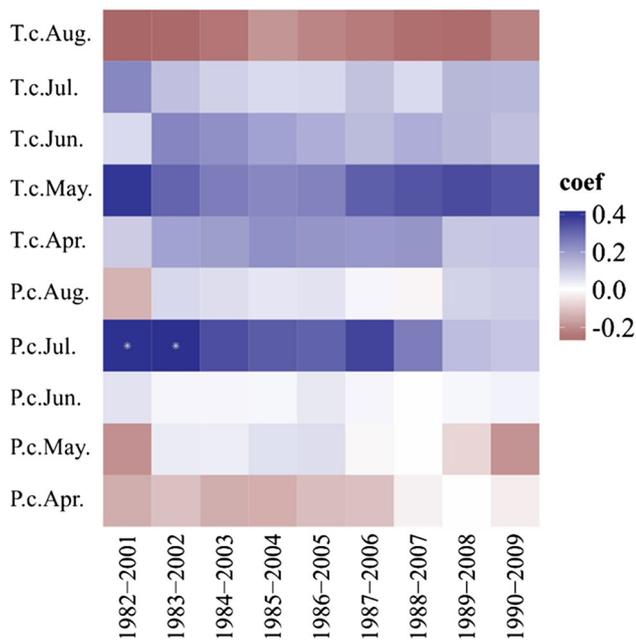


Fig. 4 Moving response function coefficients relating tree-ring growth of connected and non-connected balsam poplar to monthly temperature and precipitation. Asterisk shows significant coefficients at $p = 0.05$ levels. *Note* *Pc* Precipitation current growing season, *Tc* Temperature current growing season, *coef* response function coefficients

connected and non-connected trees (Fig. 6). PCA conducted on the bootstrapped correlation coefficient of the radial growth showed that on average connected trees performed 16 % better than unconnected trees, with a bootstrapped 95 % confidence range being 2.28–31.36 %.

Discussion

Radial growth patterns of studied balsam poplar trees suggested that connected trees were less affected by a severe FTC defoliation as compared to non-connected trees (Fig. 6). Moreover, the range of ring width index was smaller for connected trees; this is evidence that they are sharing resources which would attenuate growth response both to temperature, but also during the FTC outbreak. Severe defoliation reduces levels of non-structural carbohydrates in trees (Hogg et al. 2002; Jones et al. 2004), causing significant reductions in diameter growth during defoliation periods (Blais 1962; Morin et al. 1993). Since non-structural carbohydrates can be shared among connected trees (Fraser et al. 2006), it is likely that transfers occurred between less and more affected trees, resulting in an overall reduced impact of the outbreak for trees sharing communal root systems. Sharing of root systems has been previously observed among trees of the same or different

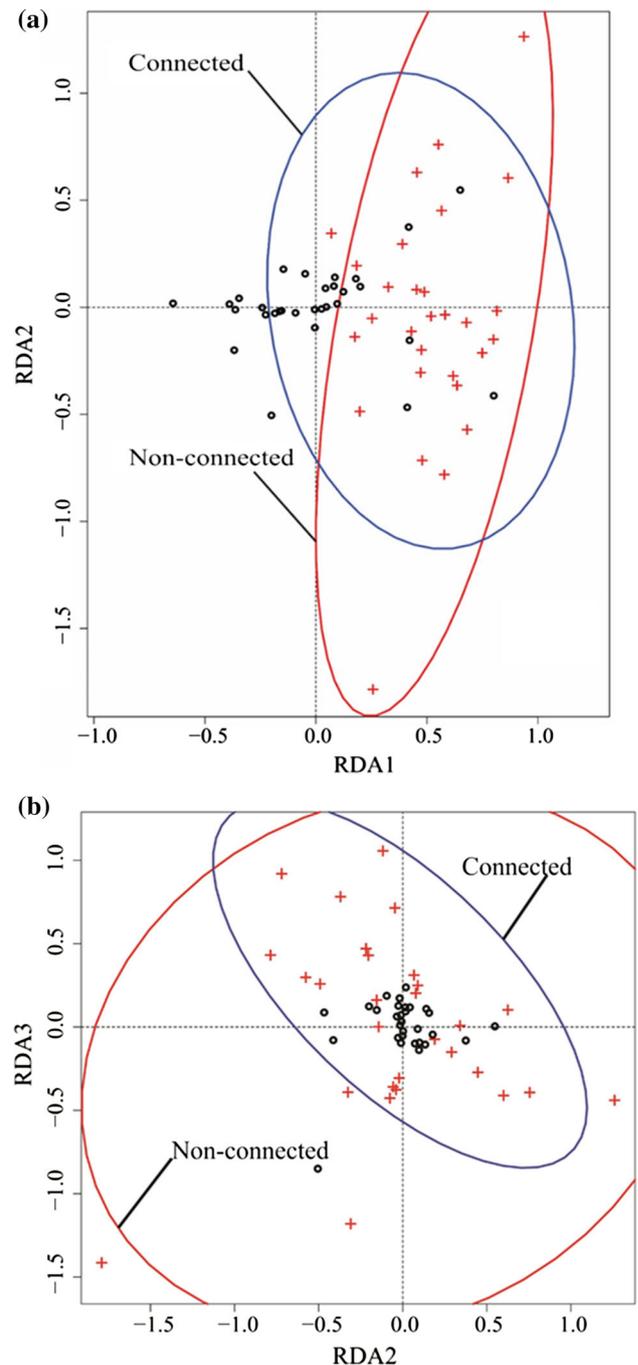


Fig. 5 Biplot scores of environmental variables for the first and second axes of the constrained RDA (a) and for the second and third axes of the constrained RDA (b) of connected trees (black point) and their 95 % confidence area (blue circle) and non-connected trees (red cross) and their 95 % confidence area (red circle)

clones in *Populus* spp. (Jelínková et al. 2009), resulting in physiologically integrated stands.

Root connections may thus help reduce genotype-specific responses in poplar tolerance to FTC outbreaks. *Populus* clones are known to exhibit genotypic variation in

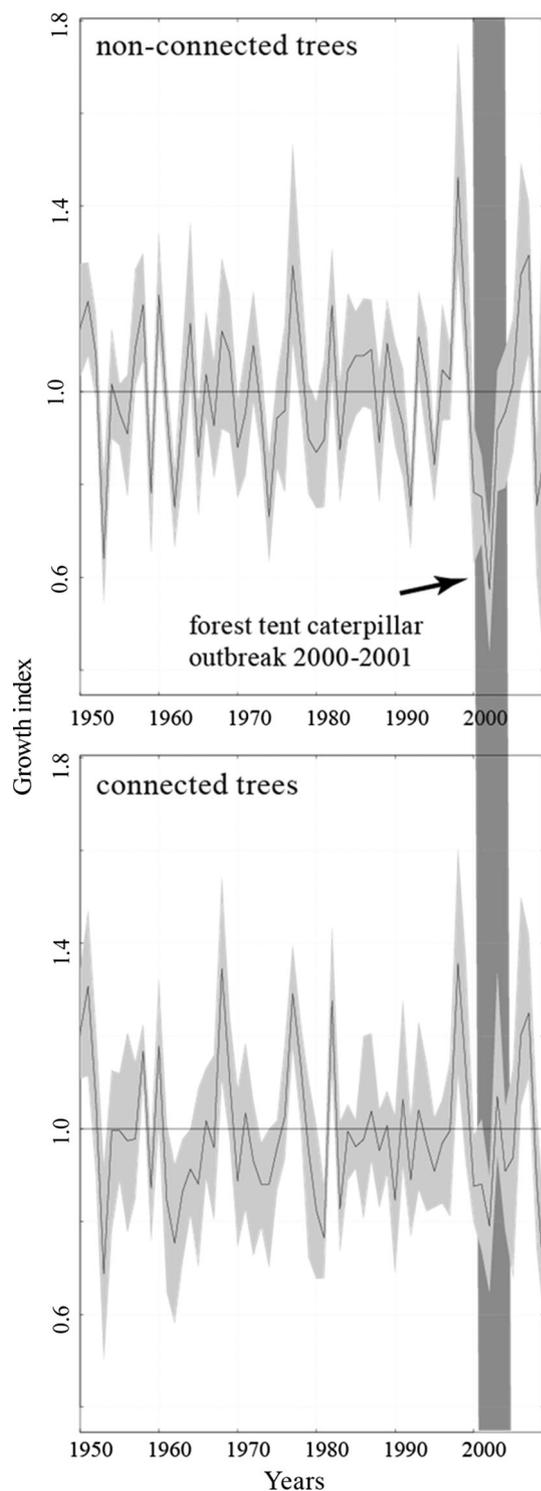


Fig. 6 Master chronologies for non-connected and connected balsam poplar trees for the period 1950–2009, with the period of FTC outbreak indicated by the *dark bar*, and the *gray shaded area* represent the 95 % confidence envelope

tolerance to insect defoliation (Jones and DeByle 1985). Phenolic glycoside concentration in poplar leaves may be an important factor in this context since its variability has

been shown to determine the preference or the performance of defoliating insects (Lindroth et al. 2001; Osier and Lindroth 2001). Recent works have shown the occurrence of root grafting in trees belonging to different clones in trembling aspen (Jelínková et al. 2009) and in balsam poplar (Adonsou et al. 2016). As a result, a clone that is more susceptible to insect defoliation may better mitigate the outbreak effects by being connected to a more resistant clone.

Root connections apparently did not override effects of main climate controls on growth of balsam poplar trees. Irrespective of root connectivity, poplar trees responded positively to May temperatures (Fig. 3a). This result is consistent with previous studies that have emphasized the role of May temperatures as an important factor influencing radial growth, cambial activity and cell differentiation of many tree species in the boreal forest (Körner 2003). Growth of non-connected trees was negatively affected by August temperatures, in contrast to connected trees, although the absolute differences in response appeared low. This negative correlation between August temperatures and balsam poplar radial growth suggested that warm August temperatures might have induced drought stress, which negatively affected tree growth. Similar results have been reported from the same study region in aspen, demonstrating a negative effect of August temperatures or water deficit on tree growth (Drobyshev et al. 2013; Gewehr et al. 2014).

The fact that growth of connected trees was not affected by August temperatures (Fig. 3e) suggests an improved absorptive capacity of the communal root system and transfer of water through root connections among connected trees in the stand (Pitelka and Ashmun 1985; Adonsou et al. 2016). Since water has been shown to be shared among connected trees (Adonsou et al. 2016) we had also expected to find a positive growth response to precipitation, particularly in August, a drought-prone period of the growing season in the study region. Root connections might promote the allocation of resources more efficiently within stands, so that connected trees may stay above a threshold in water availability which would result in a visible growth reduction in the master chronology of non-connected trees.

Our results show that root connections may be an important feature of clonal species or grafted tree response to environmental variability. However, the actual mechanisms of resource partitioning, the associated physiological trade-offs, environmental triggers, and the spatiotemporal pattern of this phenomenon remain largely unknown. For example, one might argue that a smaller individual may benefit from being connected to a larger tree, but perhaps large trees could, with their larger crown and leaf area, preferentially draw soil resources from the network during

times when they are limited. Available studies have indicated that such interactions probably vary among species (Pitelka and Ashmun 1985) and along gradients in environmental conditions (Debyle 1964). The potential role of root connections may depend upon stand age and its history. Young sucker-regenerated stands initiated by rapid and abundant production of ramets, following a stand-replacing disturbance event may display more functional root connections as compared to older stands. It has been suggested that tree mortality and clonal fragmentation disrupt root connections and lower the effects of root connectivity (Barnes 1966; Gatsuk et al. 1980). However, mature and declining aspen stands do not necessarily exhibit clonal fragmentation and decay of root connections between ramets (DesRochers and Lieffers 2001). Therefore, the impacts of root connections on tree growth may last throughout the life of stands. For instance, root connections could play a significant role in forest stand dynamics by delaying self-thinning through higher survival rates of suppressed trees, resulting from carbohydrate and water transfers from vigorous and dominant neighbouring trees (Fraser et al. 2006, this study).

Root connections among trees may represent a physiologically and ecologically important trait in natural tree populations. Forest stands of tree species exhibiting root connections should thus not be considered as groups of individual stems competing with each other for resources, because these connections may allow the sharing of resources such as water or carbohydrates. Likely, the occurrence of root connections between trees should be considered in regards to silvicultural treatments, because treatments applied to stems or stands may also affect neighbouring and intact trees (*see* Tarroux et al. 2010). In the framework of future climate change, where the temperature is expected to increase by an additional 1.5–4.5 °C by 2050 (Boer et al. 2000; Plummer et al. 2006), root connections may also play an increasingly important role.

Author contribution statement K.E. Adonsou contributed to the study design, carried out field and lab work and wrote the first version of the manuscript. I. Drobyshev did the statistical analysis and made some figures, directed the dendrochronology work and contributed in the writing of manuscript. A. DesRochers and F. Tremblay designed the study, co-supervised field and lab work and contributed to the writing of manuscript.

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Compliance with ethical standards

Conflict of interest None.

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