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Race to the canopy: the development of tree size hierarchies following a partial disturbance in a boreal old-growth forest

Niko Kulha[a,b,c], **Antti Ahokas**[a], **Sylvie Gauthier**[d], **and Tuomas Aakala**[e]

[a]Department of Forest Sciences, University of Helsinki, P.O. Box 27, 00014 Helsinki, Finland; [b]Natural Resources Institute Finland, Latokartanonkaari 9, 00790 Helsinki, Finland; [c]Biodiversity Unit, Zoological Museum, University of Turku, Henrikinkatu 2, 20014 Turku, Finland; [d]Canadian Forest Service, Laurentian Forestry Centre, P.O. Box 3800, Sainte-Foy, QC GIV 4C7, Canada; [e]School of Forest Sciences, University of Eastern Finland, P.O. Box 111, 80101 Joensuu, Finland

Corresponding author: **Niko Kulha** (email: niko.kulha@luke.fi)

Abstract

In boreal old-growth forests, advance regeneration typically attains canopy dominance through growth release events following partial disturbances. We sampled competing *Picea mariana* (Mill.) and *Abies balsamea* (L.) in disturbed old-growth stands in Quebec, Canada, to understand the intra- and interspecific size hierarchy development. We reconstructed tree size development and examined the role of initial size difference, time between germination and a disturbance, and the strength of response to the disturbance in determining tree size hierarchies. Trees that regenerated first generally dominated their intraspecific competitors also following a disturbance event. However, prolonged time between germination and disturbance resulted in a less deterministic outcome. Tree size difference prior to disturbance also influenced the development of size hierarchies. In interspecific competition between individuals of the same diameter, *A. balsamea* had a 61% probability of gaining dominance over *P. mariana*, the probability being 50% if *P. mariana* was 5 mm larger than *A. balsamea*. Dominant trees generally had the strongest response to the disturbance, reinforcing the existing size hierarchies. The largest trees typically gain dominance after a partial disturbance. However, interspecific competition is less predictable than intraspecific competition, small initial size difference, and prolonged time in suppression potentially changing tree size hierarchies.

Key words: tree size hierarchy, advance regeneration, partial disturbance, competition, *Abies balsamea*, *Picea mariana*, old-growth forest, boreal forest

Résumé

Dans les vieilles forêts boréales, la régénération pré-établies atteint généralement la canopée par le biais d'un ou de plusieurs événements de libération de la croissance à la suite de perturbations partielles. Cependant, on ne sait toujours pas comment les différences dans les stratégies vitales des espèces d'arbres influencent le développement des hiérarchies de taille entre les arbres concurrents. Pour comprendre le développement de ces hiérarchies de taille intra- et interspécifiques des espèces arborescentes, nous avons échantillonné des *Picea mariana* (Mill.) et des *Abies balsamea* (L.) en compétition dans des peuplements anciens perturbés du nord-est du Québec, au Canada. Nous avons reconstitué l'évolution de la taille de paires d'arbres adjacents et examiné le rôle de la différence de taille initiale, du temps écoulé entre la germination et une perturbation, ainsi que la force de la réponse à la perturbation dans la détermination des hiérarchies de taille des arbres. Les arbres qui se sont régénérés en premier ont généralement dominé leurs concurrents intraspécifiques, même après une perturbation. Toutefois, un délai prolongé entre la germination et la perturbation a donné lieu à un résultat moins déterministe. La différence de taille des arbres avant la perturbation a également influencé le développement des hiérarchies de taille. Dans la compétition interspécifique entre individus de même diamètre, *A. balsamea* avait une probabilité de 61% de gagner la dominance sur *P. mariana*, la probabilité étant de 50% si *P. mariana* était 5 mm plus grand que l'A. balsamea en compétition. Les arbres dominants ont généralement réagi à la perturbation par une croissance plus forte que leurs concurrents, renforçant ainsi les hiérarchies de taille existantes. Les différences de taille entre les arbres concurrents influencent fortement l'individu qui devient dominant à la suite d'une perturbation partielle. Cependant, la compétition interspécifique est moins prévisible que la compétition intraspécifique, une faible différence de taille initiale et un temps prolongé de suppression pouvant modifier les hiérarchies de taille des arbres.

Mots-clés : hiérarchie des tailles d'arbres, régénération, perturbation partielle, concurrence, *Abies balsamea*, *Picea mariana*, forêt ancienne, forêt boréale

Introduction

Advance regeneration is crucial in determining how forest ecosystems reorganize after a disturbance (Yamamoto 2000; Seidl and Turner 2022). Hence, if the changes in disturbance regimes change the competitive hierarchies among understory trees, the changing disturbance regimes may alter forest canopy composition also indirectly by changing the competitive interactions (Maleki et al. 2020). Understanding the pathways different tree species take to reach the canopy also enables predicting the indirect consequences that the changing disturbance regimes have on canopy composition (Iljima et al. 2009). This understanding forms the basis for using advance regeneration in forest management (Pothier et al. 1995; Messier et al. 1999; Martin et al. 2020).

Recruitment of advance regeneration into the canopy after a natural or anthropogenic disturbance depends on various factors such as site conditions, disturbance characteristics, and traits of the understory trees (Kuuluvainen 1994; Iljima et al. 2009; Lavoie et al. 2021). When the advance regeneration consists of a single tree species (i.e., intraspecific competition) with identical or near-identical characteristics relative to survival in shade or uptake of other released growth resources, tree size plays a major role in determining the competitive outcomes (Sakai 1995). This is because competition for light—which we consider to mostly limit regeneration in closed-canopy boreal forests (Messier et al. 1999; Pham et al. 2004)—is size-asymmetric, the largest individuals preempting the light resource released in a disturbance. Hence, tree size reflects the resource acquisition capacity of an individual in intraspecific competition (MacFarlane and Kobe 2006). For this reason, in intraspecific competition tree size hierarchies can be expected to stay the same after a partial disturbance, as predicted by the relative dominance hypothesis (Welden and Slauson 1986; D'Amato and Puettmann 2004; Hari et al. 2017).

In contrast to a stand-replacing disturbance, a partial disturbance removes only a fraction of the canopy and typically favors shade-tolerant tree species due to a smaller increase in light influx to the understory (Yamamoto 2000; Girard et al. 2014; Kim et al. 2021). However, different shade-tolerant species have varying growth strategies (or growth schedules) in their sapling stage (Sakai 1995). An important difference in the strategies of shade-tolerant species is in their morphological plasticity and the turnover rates of branches and needles, which are considered an adaptation to certain types of disturbance regimes (Messier et al. 1999). In disturbance regimes where gaps form frequently, an opportunistic strategy with a short lifespan, high turnover rate of branches and needles, and investment in height growth may be beneficial, while a strategy that emphasizes survival, longevity, and reduced height growth may prevail in regimes where gaps form infrequently (Sakai 1995).

Picea and *Abies* are two genera that often co-occur in boreal and temperate forests. While species in both genera are considered shade tolerant, they typically differ in crown architecture and growth patterns (White et al. 1985; Messier et al. 1999). In general, both *Abies* and *Picea* show plastic responses in growth rates of different parts and hence in crown architecture (Takahashi 1996). When in advance regeneration, *Abies* typically aims for growth and a dominant understory position in case of a disturbance (opportunistic growth strategy; Kubota et al. 1994). Compared to *Picea*, *Abies* have higher morphological plasticity in their shoot and crown architecture that is related to a high turnover rate of branches and needles (Takahashi 1996). This allows an *Abies* to maximize height growth in well-illuminated stands, but also to cease height growth and enhance lateral crown development with short-lived branches in shaded stands (Hiura et al. 1996; Duchesneau et al. 2001; Montoro Girona et al. 2018). Consequently, *Abies* can establish and survive in smaller and/or more shaded microsites compared to *Picea* (Kubota et al. 1994; Kneeshaw and Bergeron 1998; Iljima et al. 2009). With its short longevity, strenuous height growth, and potential for high turnover rate of branches and needles, *Abies* displays adaptation to frequent partial disturbances (Lavoie et al. 2019).

Contrary to *Abies*, the strategy of *Picea* is a longer term survival with reduced growth in all directions (conservative growth strategy; Takahashi 1996). In general, *Picea* have lower needle and branch turnover rates and an overall longer lifespan. Consequently, while waiting for a canopy opening, individuals of *Picea* may have longer waiting times (i.e., the time that a tree individual may persist in the shaded understory) and shorter waiting heights in the understory compared to *Abies* (Kubota et al. 1994; Morin and Laprise 1997; Messier et al. 1999). This conservative strategy of *Picea* means a low cost of stem construction and maintenance and is indicative of better adaptation to low frequency of partial disturbances compared to *Abies* (Sakai 1995).

Picea mariana (Mill.) and *Abies balsamea* (L.) exhibit disturbance responses typical to their genera, *A. balsamea* being able to utilize released growth resources more rapidly than *P. mariana* (Morin 1994; Montoro Girona et al. 2018). In favorable conditions, the lifespan of *P. mariana* may vary between 250 and 300 years (Alexander 1980), while *A. balsamea* may reach the age of 200 years (Bakuzis et al. 1965). In late-successional boreal forests of northeastern North America, the two species, together with *Picea glauca* (Moench) Voss, co-occur and dominate on well-drained soils (De Grandpré et al. 2000; Gauthier et al. 2010). While studies at stand and landscape scales have shown that either species may gain dominance after partial disturbances (De Grandpré et al. 2000; Pham et al. 2004; Gauthier et al. 2010), the specific tree-level determinants due to which either species becomes dominant are poorly known.

We studied intra- and interspecific pairs of competing *P. mariana* and *A. balsamea* to examine how differences in the life-history strategies of the two species influence the post-disturbance tree size hierarchy. Specifically, we asked whether and how (1) the initial size difference, (2) the waiting time in suppression, and (3) growth response to a disturbance influence the post-disturbance tree size hierarchy in intra- and interspecific competition between the two species.

Materials and methods

Study area

We sampled eight forest stands in two landscapes, Lac Dionne and Pistuacanis, located in the North Shore region of Quebec, eastern Canada (landscapes described in detail in Kulha et al. 2019). We selected the landscapes based on their accessibility and abundance of old-growth forest, using forestry maps of the Quebec Ministry of Natural Resources (Québec Ministère de l'Énergie et des Ressources naturelles). Of the two landscapes, Lac Dionne (49°36′N, 67°51′W) is mostly dominated by *P. mariana*, with *A. balsamea* dominating restricted parts of the landscape. On the contrary, *A. balsamea* mostly dominates in Pistuacanis (49°31′N, 68°19′W), *P. mariana* occurring only in limited parts of the landscape. Other tree species, such as *P. glauca* and *Betula papyrifera* (Marsh), occur as occasional co-dominant trees in both landscapes.

The climate is humid, with a mean annual temperature of 0 °C (climate data are averages from years 1970 to 2000; Fick and Hijmans 2017). The mean temperatures for January (coldest month) and July (warmest month) are −18 °C and +14 °C, respectively. The average annual precipitation sum is 1100 mm. The landscapes are mosaics of forests on mineral and organic soils and waterbodies. The mineral soils are quaternary glacial deposits and consist mostly of undifferentiated tills. Glaciofluvial sand deposits commonly occur in valley floors, while the summits typically have rocky outcrops. The region has a rugged terrain, the elevation of the landscapes ranging between 300 and 500 m above sea level.

The two landscapes have different disturbance histories. Lac Dionne burned in 1810, while Pistuacanis had not experienced fires at least during the last 200 years (Bouchard et al. 2008). Spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks are a major disturbance factor in the region, the previous severe outbreak occurring from the 1970s to the mid-1980s (Bouchard and Pothier 2010). During the field sampling in 2013, the region was experiencing an outbreak that began in ca. 2006 (Bognounou et al. 2017). Between the outbreaks, partial disturbances driven by, for example, wind drive the development of the old-growth stands (Pham et al. 2004; Martin et al. 2019; Kulha et al. 2020). The studied stands had experienced a single or several partial disturbances that provided new growth resources to the advance regeneration.

Field sampling

We collected data on eight field plots sampled in 2013. The selection of sampling plots and the study landscapes are described in detail in Kulha et al. (2019). Briefly, we overlaid a 2 km × 2 km rectangular grid of 0.1 ha cells over both landscapes and randomly selected nine cells per landscape. Among these cells, in the field we subjectively selected four cells per landscapes as sampling plots for this study. We selected plots that showed evidence of partial disturbance sometime during the last decade and that had pairs of suitable sample trees.

At each plot, we first identified focal trees that (1) were located within a disturbance-induced gap, (2) were the tallest among sapling-sized trees (i.e., height > 1.3 m, diameter < 10 cm at 1.3 m height), and (3) had shorter competitors among neighboring trees, but were visually judged to belong to the same cohort as the competitors. We sampled altogether 49 focal trees (*A. balsamea* $N = 21$, *P. mariana* $N = 28$) and 83 competitors. The intraspecific pairs consisted of 21 focal *A. balsamea* with 21 competing *A. balsamea* and 28 focal *P. mariana* with 24 intraspecific competitors. The 21 focal *A. balsamea* had 16 competing *P. mariana*, and the 28 focal *P. mariana* had 22 *A. balsamea* competitors. The focal trees that did not have interspecific competitors were not consider in the analysis of interspecific competition. For each focal tree and competitor, we measured their heights and extracted two stem disks for further analysis (one from root collar, one from 1.3 m height).

Tree age and growth data

To obtain annual radial increments and tree ages at root collar and at 1.3 m height, we prepared stem disks for measurements by sanding them to progressively finer grit, until the tree ring structure was clearly visible. We scanned the sanded disks and measured their ring-widths along four radii using the WinDendro software (Regent Instruments Inc., Ste-Foy, Canada). Where rings were too narrow to be identified from a scanned image, we used a stereomicroscope to discern individual rings. The measurements resulted in four ring-width increment series per sample. We averaged these into a single average series with the last fully formed ring from the growing season 2012.

Missing and partial rings are common in suppressed saplings of shade-tolerant tree species (Morin and Laprise 1997). While we could not account for missing rings in such slow-growing suppressed trees, we minimized the influence of partial rings by measuring rings along four radii and assigning zero widths to the missing parts of the identified partial rings. Three of the sample disks had decayed inner parts. For a rough approximation of the number of rings lost to decay, we divided the estimated distance to pith by the average growth of the 10 innermost rings that were measurable (Speer 2010).

Relative dominance and waiting times

We inspected the recruitment year of each competitor tree, relative to the year of recruitment of the focal tree at the root collar to test whether tree size hierarchies are maintained through time as predicted by the relative dominance hypothesis. Using the annual measurements of radial increment, we then calculated the size of each focal tree at that year, relative to the size of its competitor at the same time. We used a one-sided Wilcoxon rank sum test to test the hypothesis that the focal trees were significantly larger than their competitors at this initial state.

To assess the role of waiting time as a determinant of the size hierarchies, we used a so-called growth release analysis to determine the timing of overstory disturbance (e.g., Nowacki and Abrams 1997). The analysis is built on the premise that the overstory disturbance prompts a sudden and sustained growth increase in the remaining advance regeneration. Hence, we quantified waiting time as years between tree germination and the start of such growth release. We first analyzed the ring-width series of focal trees to identify growth releases, using the absolute increase method (Fraver and White 2005, as implemented in the R-package TRADER; Altman et al. 2014). We calculated the absolute change in growth rate for a given year as the mean growth rate 10 years after the growth release, relative to growth rate 10 years before the growth release. Following Fraver and White (2005), we used 1.25 × standard deviation as the criterion for the onset of a growth release and visually verified that each identified growth release occurred at the identified year and did not result from spurious growth variations or formation of reaction wood. If an individual series had multiple growth releases, we used the most recent release (i.e., we assumed that the most recent growth release was the most relevant for the current competitive state). In the few cases that the focal tree did not show a growth release (4.8% of the analyzed focal trees), we used the release of the competitor that had an earlier release year. If neither pair showed a release (2.2%), we excluded them from this part of the analysis. Using a one-sided Wilcoxon rank sum test, we tested whether the focal trees had longer waiting times compared to their competitors in both intra- and interspecific pairs, and separately for pairs where the size hierarchies were maintained and for pairs in which the hierarchies changed.

Tree growth responses to disturbances may differ in how rapidly after the disturbance they occur (years) or how strong (the rate of basal area increase) they are. We investigated the speed and rate of response to overstory disturbance by calculating the growth increment for 10 years following the growth release identified in the focal tree. We then subtracted the competitor response from the focal tree response, to calculate the relative response strength.

We used logistic regression models to predict competition outcomes as a function of the three variables: initial size differences, the waiting time, and the response to overstory disturbance. For intraspecific pairs, we formulated the model so that the response variable was the change in size hierarchy from the initial state (hierarchy maintained or hierarchy changed) to year 2013 that was the year of field sampling. For interspecific pairs, we formulated the model so that the response variable was the position of *P. mariana* (*P. mariana* not dominant at the time of field sampling or *P. mariana* dominant at the time of field sampling) after the partial disturbance.

We fitted the models in R (R Core Team 2019) using the package aod (Lesnoff and Lancelot 2012). We first fitted the models with all three predictors and dropped the least significant predictor variable at each iteration until only variables that were significant at the level of 0.05 remained.

Results

The majority (59%) of trees that regenerated first maintained their positions at the height of 1.3 m relative to their intra- and interspecific competitors (Fig. 1A). Similarly, most trees (71%) that reached the height of 1.3 m first retained their dominance after the partial disturbance. The same pattern was evident for intraspecific pairs of both species (Figs. 1B and 1C) and for interspecific pairs of *P. mariana* (Fig. 1D). However, *A. balsamea* that dominated post-disturbance was often able to gain dominance from a worse competitive position despite that competing *P. mariana* reached the height of 1.3 m prior to the *A. balsamea* (Fig. 1E).

In intraspecific pairs of *P. mariana*, the mean root-collar diameter difference at the initial state was 9.6 mm (standard deviation $\sigma = \pm 13.4$ mm), the focal trees being significantly larger than their intraspecific competitor (directional Wilcoxon test, focal tree size > competitor size; $p = 0.001$) (Fig. 2A). For intraspecific pairs of *A. balsamea*, the corresponding difference was 2.9 mm ($\sigma = \pm 4.2$ mm), the focal trees being significantly larger than their intraspecific competitors ($p = 0.002$) (Fig. 2A). The initial size differences were also positive in interspecific pairs. Focal *A. balsamea* had on average 2.4 mm larger diameter ($\sigma = \pm 5.5$ mm, $p = 0.160$), and focal *P. mariana* had 10.8 mm larger diameter ($\sigma = \pm 11.4$ mm, $p < 0.001$) than the competing interspecific trees (Fig. 2B).

In intraspecific pairs of *A. balsamea*, the mean waiting time was 29 years for pairs in which the pre-established size hierarchy remained and 60 years when the hierarchy changed (Wilcoxon test, $p = 0.002$; Fig. 3A). Similar differences were recorded for *P. mariana* (mean waiting time = 36 vs. 55 years when hierarchy remained or changed, respectively), but due to high within-group variation these differences were not statistically significant ($p = 0.133$; Fig. 3A). In interspecific competition, the waiting times did not differ significantly between pairs where hierarchy changed or remained, regardless of focal tree species (Fig. 3B).

For intraspecific pairs, the most parsimonious model for predicting competition outcomes had initial size difference and waiting time as covariates (Table 1). The rate of response to a disturbance and species identity were dropped from the final models as non-significant predictors (Figs. S1–2). The deviance explained by this model was 59.8%. The probability of the size hierarchy remaining increased with increasing focal tree size relative to its competitors (Fig. 4). For example, given a mean waiting time of 41 years among the intraspecific pairs, the size hierarchy was maintained with the probability of 20% in a pair where the currently dominant tree was initially 1 mm smaller than its competitor. This probability increased quickly with increasing size difference, being 92% when the focal tree was initially 5 mm larger than its competitor (Fig. 4).

The pairs showing changes in hierarchy had an initial size difference of −0.4 mm ($\sigma = \pm 0.5$ mm) and −0.6 mm ($\sigma = \pm 0.4$ mm) for *A. balsamea* and *P. mariana*, respectively. Hence, in intraspecific pairs the hierarchy changes were possible only when the initial size differences were small, regardless of species (Fig. 4). However, longer waiting time decreased the

Fig. 1. Development of tree size hierarchies in all intra- and interspecific pairs (A), in intraspecific competition of *P. mariana* (B) or *A. balsamea* (C), and in interspecific competition with *P. mariana* (D) or *A. balsamea* (E) as focal tree. The three rectangles represent size hierarchies at root collar, 1.3 m height, and at the time of field sampling. The sizes of rectangles and pathways between the rectangles indicate number of individuals. Suppr. in rectangles means suppressed.

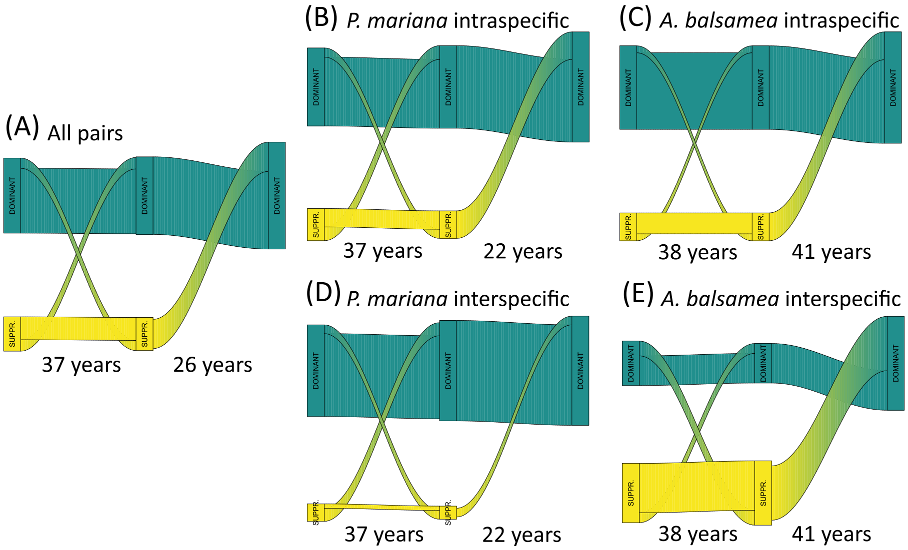


Fig. 2. Initial size differences between the currently dominant focal *A. balsamea* and *P. mariana* and their (A) intra- and (B) interspecific competitors.

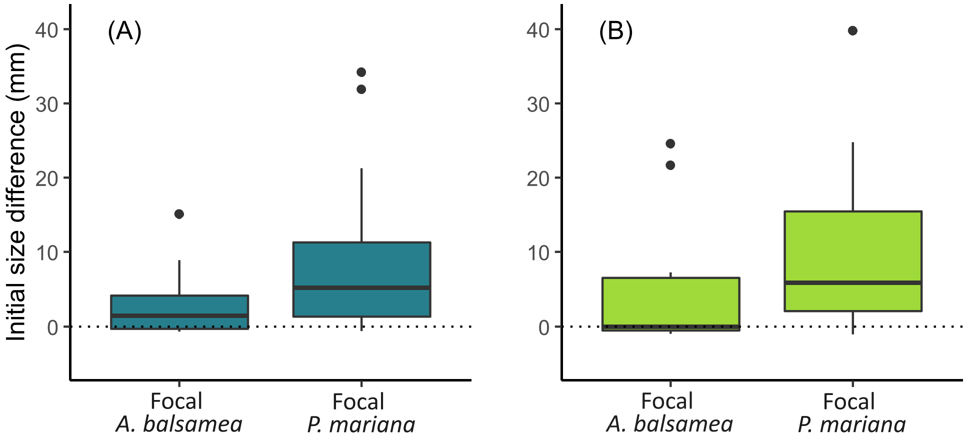


Fig. 3. Waiting times and changes in hierarchy for (A) intra- and (B) interspecific pairs of competing *A. balsamea* and *P. mariana*.

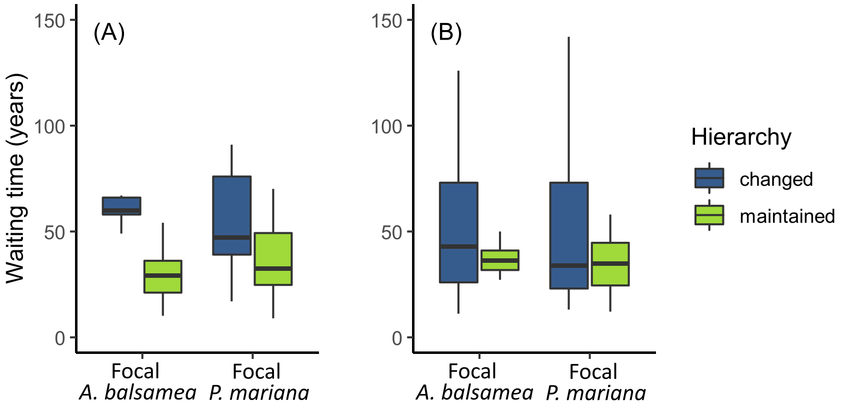


Table 1. Parameter estimates in the logistic regression models predicting the competition outcomes for inter- and intraspecific pairs of *A. balsamea* and *P. mariana*.

Model	Parameter	Estimate	Std. error	*p*
Intraspecific	Intercept	2.57	1.51	0.0887
$N = 37$	Initial size difference	0.78	0.33	0.0165
	Waiting time	−0.08	0.03	0.0172
Interspecific	Intercept	−0.44	0.39	0.2525
$N = 44$	Initial size difference	0.08	0.04	0.0462

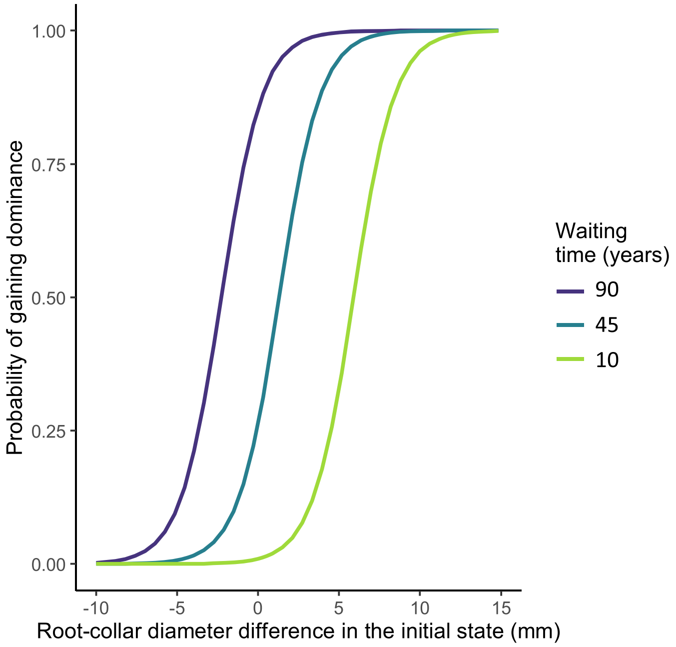


Fig. 4. The probability for a tree to gain dominance against an intraspecific competitor as a function of initial size difference at three waiting times. Negative size difference means that the tree that became dominant tree had a smaller initial size (regenerated later) compared to its competitor. Steep curves indicate that even a small size difference between the competing trees has a large impact on which competitor gains dominance. Prediction intervals are omitted for clarity.

importance of initial size differences, independent of competing species (Fig. 4).

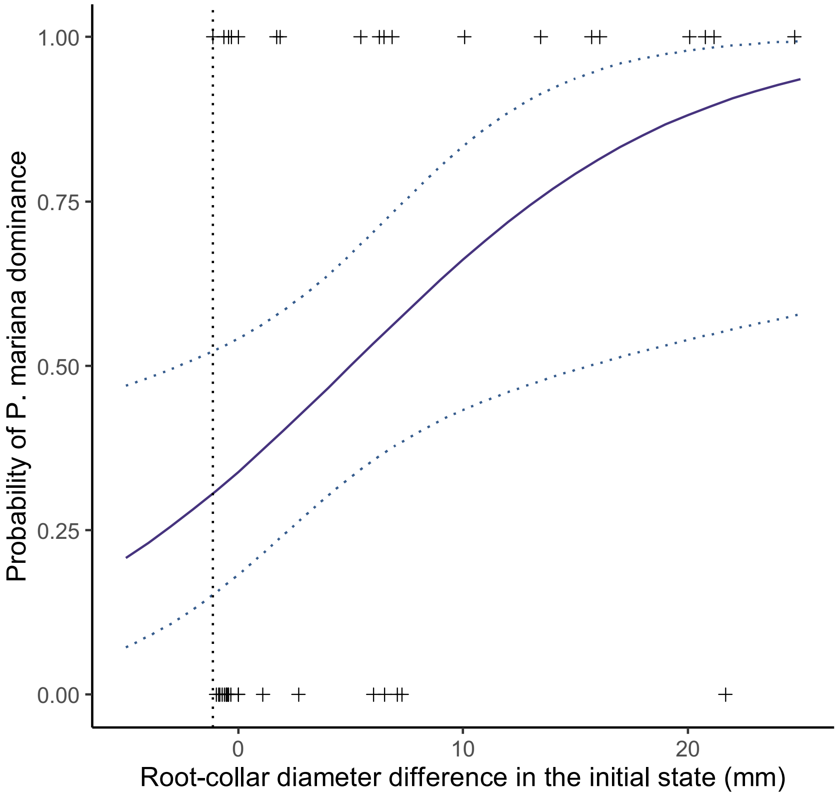
For interspecific pairs, the model showed species-specific differences in how the probability to gain dominance changed with initial differences in tree sizes (Table 1). However, waiting time and strength of response to overstory disturbance were not significant in predicting the change in size hierarchy for either species in interspecific competition (Figs. S1–2). The deviance explained by the model for interspecific pairs was 9%. In general, *P. mariana* needed to be substantially larger than competing *A. balsamea* to gain dominance, small size difference or smaller size of *P. mariana* compared to a competing *A. balsamea* in the initial state resulting in *A. balsamea* dominance (Fig. 5). For trees of the same size, the model predicted a 61% probability for *A. balsamea* dominance, the probability of dominance being equal when *P. mariana* was 5 mm larger than the competing *A. balsamea*. If the initial diameter difference was 20 mm in favor of *P. mariana,* the probability of *A. balsamea* dominance was 23%.

Discussion

Our analysis of canopy accession strategies of *A. balsamea* and *P. mariana* showed that in old-growth boreal forest of northeastern North America, both species typically maintain the initial size hierarchy in understory and after an overstory disturbance when comparing conspecific competitors. This development is consistent with the relative dominance hypothesis that predicts that the size hierarchies of competing trees are maintained through time (Welden and Slauson 1986; D'Amato and Puettmann 2004). Partly, this development can be linked to the size-asymmetric nature of competition for light: the larger an individual is, the larger share of the limited light-resource in the understory it may capture (MacFarlane and Kobe 2006). In addition to light, belowground competition for water and nutrients may also show size-asymmetry, as large saplings typically have larger root systems and thus a better access to soil resources than small saplings (Casper and Jackson 1997). The competition for soil resources may thus also reinforce the existing size hierarchies especially on infertile and/or dry sites (Coomes and Grubb 2000; Pretzsch and Biber 2010). Although small differences in edaphic conditions, microclimate, and competition with other vegetation in the understory may have influenced the observed regeneration patterns and competition outcomes (Montoro Girona et al. 2018; Martin et al. 2020), the size hierarchies established at germination generally prevailed in our study.

While the influence of size differences on tree growth has been shown in a number of both empirical (D'Amato and Puettmann 2004; Aakala et al. 2013; Fraver et al. 2014) and modeling studies (MacFarlane and Kobe 2006; Pukkala et al. 2021), our analyses also showed how waiting time influences the outcome of competition: longer waiting time increased the probability of an initially smaller tree to gain dominance. In other words, increasing waiting time decreases the predictability of the outcome of competition. That increasing waiting time may change the outcome of tree–tree competition could simply be due to longer time interval increasing the probability of encountering a stochastic event that disturbs the deterministic nature of competition (Morin and Laprise 1997). Alternatively, it could also be that with long time intervals, small differences in microclimate, substrate

Fig. 5. Logistic regression model means and 95% prediction intervals on how the size in the initial state determines the outcome of interspecific competition (focal *P. mariana* competes with *A. balsamea*). Negative size differences mean that the currently dominant tree had a smaller initial size (regenerated later) than its competitor. The vertical line shows the largest negative size difference in our data.



conditions, or resource uptake capabilities influence the outcome of competition.

Initial size difference was an important predictor also for the development of interspecific size hierarchies. However, the development was much less predictable compared to intraspecific pairs. We found subtle differences between the examined species, so that a smaller *A. balsamea* may occasionally gain dominance over a competing *P. mariana*. These observations from the interspecific competition may be explained with differences in the strategies of the two genera. Compared to *Picea*, *Abies* has a higher morphological plasticity, partly due to the higher turnover of branches and needles (Takahashi 1996). Consequently, *A. balsamea* may grow a tall vertical stem in shaded conditions (Kubota et al. 1994; Hiura et al. 1996; Duchesneau et al. 2001) and prevail even in small openings (Morin and Laprise 1997; Kneeshaw and Bergeron 1998). Thus, *A. balsamea* may gain relative dominance over *P. mariana* in suppressed conditions. Despite that *A. balsamea* was occasionally able to gain dominance over initially larger *P. mariana*, it is noteworthy that only a minor initial size difference made it possible for a smaller competitor to gain dominance.

Contrary to intraspecific pairs of competing *A. balsamea*, waiting times did not play an important role in defining the outcome of interspecific competition. Owing to the differences in the strategies of the two genera, *Picea* is expected to survive longer in the understory compared to the more opportunistic *Abies* (Kubota et al. 1994; Kneeshaw and Bergeron 1998; Iljima et al. 2009). For this reason, we expected that prolonged waiting times would modify the outcome of interspecific competition in favor of *P. mariana*. However, as species of both genera are considered shade tolerant with capacity of modifying growth rates under suppression (White et al. 1985), also *A. balsamea* may survive long periods under suppression (Messier et al. 1999). Thus, it may be that the waiting times recorded in this study were not long enough for *P. mariana* to gain competitive advantage. The influence of longer waiting times should be considered in future studies on canopy accession.

As an alternative explanation for the observed development of size hierarchies, we explored the strength of the response to overstory disturbance, quantified as the sum of radial increment during the 10 years following a disturbance. On average and irrespective of tree species, focal trees had a stronger response to disturbances than their competitors, despite that *A. balsamea* should be able to utilize released growth resources more rapidly than *P. mariana* (Morin 1994; Montoro Girona et al. 2018). Generally, trees with large stems are better poised to take an advantage of the released growth resources (Sakai 1995). Accordingly, the stronger response primarily strengthened the existing size hierarchies. However, variation in the size, shape, and formation time (i.e., whether they were created by a single or recurring disturbances) may have influenced the response to overstory disturbance. Other confounding factors include fine-scale variability in, for example, topography, soil moisture, and surrounding intact canopy height and cover that may have caused variability in the light environment and thus in regeneration dynamics (Martin et al. 2020), despite that we sampled neighboring trees with apparently similar growth conditions.

A second shortcoming in our analysis was that we measured the strength of the response to overstory disturbance as a sum of radial increments, whereas our response variable (dominant/co-dominant) was based on tree heights. Due to allometric differences, this part of the analysis remains inherently cursory and provides a potential explanation why the release strength was not a significant predictor in the regression models. This also explains why certain trees were initially smaller and showed a weaker radial growth response to disturbance (Q4 in Fig. S2), despite being defined as dominant trees. In future, a more thorough stem analysis based on multiple samples from different heights along the bole (e.g., similar to Sirén 1951) would make it possible to base the analysis on height growth estimates. Nevertheless, for the interspecific pairs (Fig. S2B) it seems that several *A. balsamea* that were initially smaller than their interspecific competitor showed stronger response to overstory disturbance, suggesting that species-specific differences in response strength may also play a role in defining the competitive outcome. A stronger response to overstory disturbance would also be in line with the idea of opportunistic strategy of *A. balsamea*. Shade-tolerant trees, such as those studied here, are typically capable of a growth release (Canham 1988). However, compared to *P. mariana*, *A. balsamea* has been noted to achieve faster growth in the years that follow a disturbance (Doucet and Blais 2000; Lemay et al. 2018). That *A. balsamea* reacts rapidly to disturbances could be due to its high morphological plasticity (Kubota et al. 1994; Takahashi 1996).

The studied stands had opened mostly due to spruce budworm outbreak that occurred in the region between early 1970s and mid-1980s (Bouchard and Pothier 2010). Consequently, the increase in light and soil resource availability was stronger than what would be expected from fine-scale mortality of individual trees that is considered typical in these old-growth forests outside of the outbreaks (Martin et al. 2019; Kulha et al. 2020). Frequent partial disturbances may favor trees with opportunistic life-history traits that allow a tree to grow sufficiently large in suppression, such as *A. balsamea* (Sakai 1995; Messier et al. 1999; Girard et al. 2014).

Looking at the disturbance history of the studied area for the past hundred and forty years, spruce budworm outbreaks have occurred recurrently in the region with an interval of approximately 35 years, the previous outbreak ending in mid-1980s (Bouchard and Pothier 2010). However, the most recent outbreak that began in the region in ca. 2006 started approximately 10 years in advance of a typical outbreak return interval (Bognounou et al. 2017). The current disturbance regime enables the reciprocal replacement and coexistence of the two species with different life-history strategies (De Grandpré et al. 2000; Pham et al. 2004; Gauthier et al. 2010). However, further increase in the frequency of partial disturbances would favor the opportunistic *A. balsamea* over *P. abies* that can wait for a long time in suppression. Increasing dominance of *A. balsamea* would further increase the vulnerability of stands to spruce budworm, as the synchronized budburst and larval emergence makes *A. balsamea* more susceptible to the insect than *P. mariana* (Hennigar et al. 2008; Lavoie et al. 2019).

Implications for forest management

In managed forests, *P. mariana* may reach the upper canopy if it is present as advance regeneration at the time of harvesting, even though the growth rate of *P. mariana* may be less than that of *A. balsamea* immediately after the harvest (Doucet and Blais 2000; Montoro Girona et al. 2018). However, as we showed, *P. mariana* needs to be sufficiently large compared to a competing *A. balsamea* to gain dominance. To manage advance regeneration with different silvicultural approaches, we need to understand the basis for differences in tree growth (Messier et al. 1999; Martin et al. 2020). As the canopy disturbance in our stands resembles variable retention harvesting, understanding the saplings' responses in old-growth forests can be used for planning the use of advance regeneration for forest management practices. In the North Shore region of Quebec, a long-held assumption has been that *A. balsamea* would replace *P. mariana* if advance regeneration were favored (Messier et al. 1999; Doucet and Blais 2000). Our results supported this notion in cases where the advance growth of *P. mariana* was not sufficiently large compared to *A. balsamea*. However, the notion is based on the different abilities of tree species to utilize released growth resources, mainly light. Yet, also other factors, such as availability of viable seeds (Montoro Girona et al. 2018), presence of suitable germination sites (Morin and Laprise 1997), and disturbance frequency (Messier et al. 1999), influence tree species composition of advance regeneration and thus in canopy layer. Hence, favoring advance regeneration may not always favor *A. balsamea* over *P. mariana*.

Conclusions

Better understanding of the mechanisms of how trees with different life-history traits attain canopy position enables predictions of how forests reorganize after a partial disturbance. Our results emphasize that initial size differences between competing saplings play a key role in defining which individual reaches the canopy and gains dominance. Considering *Picea* and *Abies*, the tree that is the largest among advance regeneration at the time of a partial disturbance typically gains dominance, independent of species. However, small initial size difference between the competitors or long disturbance interval may cause the pre-established size hierarchy to change. Consequently, the post-disturbance species compositional development is predictable, suggesting that advance regeneration can be used in planning forest management practices. Further, this type of understanding aids in predicting how forest ecosystems may respond to the changing disturbance regimes.

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Author information

Author ORCIDs

Niko Kulha https://orcid.org/0000-0002-1610-9938

Author notes

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Author contributions

Conceptualization: AA, SG, TA
Data curation: AA, TA
Formal analysis: AA, TA
Funding acquisition: TA
Investigation: NK, AA, SG, TA
Methodology: AA, SG, TA
Project administration: TA
Resources: NK, AA, SG, TA
Software: TA
Supervision: SG, TA
Validation: SG, TA
Visualization: NK, AA, TA
Writing – original draft: NK, TA
Writing – review & editing: NK, AA, SG, TA

Competing interests

The authors declare there are no competing interests.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfr-2022-0224.

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