



Effect of tree species and seed origin on climate change trial outcomes in Southern Ontario

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Abstract

Under a changing climate, species will need to rapidly adapt to novel conditions at existing locations, migrate to track suitable climate, or risk widespread declines. For sessile, slow-migrating organisms like trees, adaptive capacity is expected to be particularly important for survival. Alternatively, assisted migration has been proposed as a means to help align tree populations with shifting climate habitats. Here we report on the performance of seed sources and species at broadleaf and conifer climate change trials at 10 and 11 years after planting, respectively. The trials were established in southern Ontario – an important transition zone between boreal and temperate ecosystems – and were designed to assess: (1) the assisted migration potential of six broadleaf species (via northward movements of seed sources), and (2) the adaptive capacity of three conifer species (via southward movements of seed sources). Both broadleaf and coniferous seed sources tolerated significant movements while maintaining reasonable growth and survival rates. In fact, several coniferous seed sources exhibited relatively high growth and survival rates despite southward transfers of more than 1000 km (>5 °C mean annual temperature) – indicating considerable adaptive capacity to climate change in these northern conifer populations. Furthermore, several of the broadleaf species exhibited high levels of growth and survival despite being planted at, or beyond, their current northern range limits – suggesting the potential for modest range expansions via assisted migration. Despite caveats related to the relatively young age of the plantations and deer browsing at the site, these findings help forest managers better understand potential climate change impacts and assisted migration outcomes.

Keywords Climate change · Tree · Growth · Survival · Adaptive capacity · Assisted migration

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Introduction

Climate change impacts have been reported from forested ecosystems around the world (McDowell et al. 2020). Such impacts include both growth declines (Girardin et al. 2016a; Hogg et al. 2017) and increases (Frost and Epstein 2014), drought-driven tree mortality (Senf et al. 2020), increased frequency and severity of forest fires (Hanes et al. 2019), and climate-driven expansions of forest pests (Pureswaran et al. 2018). Given this dire situation, knowledge concerning both the natural adaptive capacity of forests and the efficacy of human-mediated adaptation efforts is critical.

Adaptive capacity refers to the ability of species to cope with and adapt to novel conditions (Glick et al. 2011; Thurman et al. 2020). A key aspect of adaptive capacity, particularly in the near-term, is phenotypic plasticity, whereby individual trees persist by adjusting their morphological and/or physiological traits to novel conditions (Royer-Tardif et al. 2021). For example, plasticity in biomass allocation between roots and leaves has been implicated in the drought response of several Mediterranean oak species (Valladares and Sánchez-Gómez 2006). Understanding the extent to which phenotypic plasticity will allow individuals to persist across a variety of species and regions will allow better projections of climate change impacts on extant populations (Benito-Garzon et al. 2019).

In contrast to natural adaptive capacity, assisted migration – wherein individuals are moved to climatically appropriate locations within and/or beyond existing range limits – has been proposed as a human-mediated climate change adaptation approach (McLachlan et al. 2007). Several types of assisted migration have been distinguished along a gradient of movement distance (Ste Marie et al. 2011), including: (1) assisted population expansion (movement of populations within existing range limits); (2) assisted range expansion (movement of species just beyond existing range limits); and (3) long distance assisted migration (movement of species well outside existing range limits). In the context of commercial forestry, the movement of seed sources within existing range limits – typically poleward or upslope – has become standard practice in some regions (e.g., O’Neill et al. 2017, van Kerkhof et al. 2022). Modest range expansions have also been proposed for a number of tree species in both forestry (O’Neill et al. 2008) and conservation (McLane et al. 2012) settings. Results from assisted migration field trials have been reported for a number of species and locations (Wang et al. 2019; Sáenz-Romero et al. 2020), though few empirical examples exist for broadleaf tree species (but see Etterson et al. 2020).

Southern Ontario represents an important ecological transition zone between the boreal and temperature forest ecosystems. In this region, characteristic boreal species such as black spruce (*Picea mariana*) and Jack pine (*Pinus banksiana*) can be found in remnant populations at their southern range limits. Conversely, Carolinian tree species such as black walnut (*Juglans nigra*), shagbark hickory (*Carya ovata*), and black oak (*Quercus velutina*) reach their northern range limits. As such, this region provides an ideal setting for studying both the northward expansion of southern tree species and the potential response of boreal tree populations to a changing climate.

Here we report on the growth and survival of temperate broadleaf and boreal conifer trees at ages 10 and 11 respectively, from two climate change trials established on former agricultural land in southern Ontario, Canada. The broadleaf trial aims to better understand assisted migration outcomes for six different Carolinian tree species, several of which are at, or beyond, their northern range limits at the study site location. Alternatively, the conifer

trial examines southward movements of northern seed sources for three boreal tree species, with a goal of better understanding the adaptive capacity of these populations to climate change. Overall, this work aims to provide forest managers with information that will help to manage and conserve forests in an era of rapid climate change.

Methods and materials

Study site

The trials were established on former agricultural land near Claremont, Ontario, Canada (Fig. 1). At time of establishment, the site was managed by Transport Canada, but has since been transferred to Parks Canada and is currently part of the Rouge National Urban Park. Climate at the site is characterized by mean annual temperature of 8.2°C, with cool winters (-3.2°C on average) and warm summers (20.6°C on average). Annual precipitation averages 1020 mm, with similar amounts in summer (231 mm) and winter (233 mm). A significant amount of precipitation in winter falls as snow, with accumulations commonly reaching > 10 cm. The site is classified as prime agricultural land, with well-drained soils predominantly comprised of glacial deposits (till) which include clayey silt to silt and a minor component of glacial lake deposits of silt and clay in the southwest corner of the property. Soil textures are predominantly Clay-Loam.

Tree species and seed origins

In establishing these climate change trials, our aim was to incorporate provenances that would be reasonable selections for assisted migration efforts (for the broadleaf trial) or are projected to experience future climate that is similar to that currently found at the study site (for the conifer trial). This very targeted approach means that – unlike a typical provenance study – a significant amount of genetic variation across the range of each species was not incorporated into this study (Fig. S1).

Temperate broadleaf trial

Six species were selected for the temperate broadleaf trial, including black oak (*Quercus velutina*), red oak (*Quercus rubra*), white oak (*Quercus alba*), black walnut (*Juglans nigra*), shagbark hickory (*Carya ovata*), and sugar maple (*Acer saccharum*). These selections included both species with distributions that extend well north of the study site (e.g., sugar maple and red oak) and those distributed primarily to the south of the study site (e.g., black oak, white oak shagbark hickory, and black walnut).

Selection of planting stock origin (seed sources) was based on a climate similarity analysis using Seedwhere (McKenney et al. 1999; <https://cfs.cloud.nrcan.gc.ca/seedwhere/>), which identified candidate seed source locations with recent historical climate that is expected to be similar to future climate at the study site as the current century progresses. We employed 1961–90 as the recent historical climate period because it coincides with peak weather station coverage over much of Canada and precedes recent, rapid changes in climate. Based on this approach, stock was sourced from four locations along a temperature/latitudinal gradi-

ent (Fig. 1), including: (1) Ontario (ON) seed zone 34 – specifically Evrett, ON (for black oak) and Pontypool, ON (for the remaining species), (2) Indiana County, Pennsylvania (PA), (3) Warren County, Tennessee (TN), and (4) Marshall County, Kentucky (KY).

Boreal conifer trial

Three species were selected for the conifer trial, including black spruce (*Picea mariana*), white spruce (*Picea glauca*), and jack pine (*Pinus banksiana*). All of these species are distributed primarily to the north of the study area. Selection of seed sources again involved Seedwhere (McKenney et al. 1999; <https://cfs.cloud.nrcan.gc.ca/seedwhere/>). In this case, conifer seed sources were selected from a range of locations that are currently cooler than the test site. Specifically, we identified locations that were projected to have climate, for a number of future time periods, that was similar to that recently (1961–1990) found at the study site. Based on this approach, stock was sourced from the following six Ontario seed zones (Fig. 1): SZ5, SZ13, SZ18, SZ21, SZ25, SZ28. Note that Ontario has recently updated its seed transfer system and now employs ecodistricts as spatial units (van Kerkhof et al. 2022); however, at time of study establishment, the original seed zones were the basis for seed transfer in the province.

Experimental design

Both trials employed a randomized complete block design. For the broadleaf trial, 5 blocks were established, each containing 24 plots – one for each combination of tree species (6) and seed origin (4). Within each plot, 36 trees were planted in a 6-tree x 6-tree layout, with

Fig. 1 Location of broadleaf (triangles) and coniferous (shaded Ontario seed zones) seed sources planted at two climate change trials near Claremont, Ontario (star)



a spacing of 2.5 m between trees. In total, 4320 trees were used in the broadleaf trial (i.e., 6 tree species x 4 seed origins x 36 seedlings per plot x 5 blocks). For the conifer trial, 5 blocks were established, each containing 18 plots – one for each combination of tree species (3) and seed origin (6). A 6-tree x 6-tree layout was again employed, with a spacing of 2.0 m between trees. In total, 3240 trees were used in this trial (i.e., 3 tree species x 6 seed origins x 36 seedlings per plot x 5 blocks).

Site preparation, planting, maintenance, and measurements

Temperate broadleaf trial

The broadleaf trial site was deep-disc cultivated, rotovated, and cover crop seeded with low-growth white clover prior to planting. Bare root seedlings were hand planted in April 2009. It was challenging to obtain identical planting stock (in terms of age and size) for each species across the various nurseries employed in the experiment; thus, seedlings had typically been in seedbeds for 1–2 years and were typically 15–45 cm in height at time of planting. Survival was assessed in fall 2009 and dead seedlings were replaced in spring 2010, primarily using extra seedlings that had been outplanted on site at time of trial establishment in 2009 to account for attrition.

Tubex™ tree shelters, 75 cm in height, were installed on a stake around each tree shortly after planting. Shelters required some restaking over time due to frost heaving, snow accumulation, and wind damage. Deer browsing was a challenge at the site and efforts were made to extend the height of the tubes where browsing was heavy.

Herbicide was used to reduce vegetation competition at the site. In spring 2009, shortly after planting, the trial was spot sprayed with a tank mix of Princep NineT™ (granular Simazine) at 5% active ingredient and Roundup Weather Max™ at 3% active ingredient. Spraying covered a minimum 50 cm radius around each stem. In 2012, the trial was again sprayed with a tank mix of Simadex Flowable 7.0 kg/ha active ingredient and Roundup WeatherMax at 3% active ingredient. The site was rotary cut 3 times per season in both directions since planting, typically in late spring, mid-summer, and late-summer. Survival and height assessments were carried out in fall 2018, 10 growing seasons after planting.

Boreal conifer trial

The conifer trial site was deep-disc cultivated, rotovated, and cover crop seeded with low-growth white clover prior to planting. Container seedlings were hand-planted in mid-April 2008 following the design described above. Seedlings were inoculated (just prior to planting by dipping the soil plug in a mixture of water and well-ground fungus) with native (northern strain) mycorrhizal fungi to help mitigate the transition to a Southern Ontario agricultural field from a boreal environment. Similar to the broadleaf stock, it was challenging to obtain identical planting stock (in terms of age and size) for each species across the various nurseries employed in the experiment; thus, seedlings had typically been in containers for 1–2 years and were typically 15–45 cm in height at time of planting. Survival was assessed in fall 2009 and dead seedlings were replaced in spring 2010 using extra seedlings that had been outplanted on site at time of trial establishment in 2008. A full complement of seed zone 28 (all 3 species) and seed zone 18 white spruce were in-filled at this time (2010), a

high proportion of seed zone 21 jack pine was also in-filled, as most of this stock did not survive due to initial poor quality stock upon receipt.

Herbicide treatments followed the methodology described above for the broadleaf plantation. Survival and height assessments were carried out in fall 2018, 11 growing seasons after planting.

Climate data

Climate estimates at the planting site and all seed source locations were obtained by interrogating spatial climate models covering North America (McKenney et al. 2011). These thin-plate spline-based models are spatially continuous, allowing them to be queried at any location for which geographic coordinates and elevations are known. Thirty-year average models typically are within measurement errors for temperature (+/- 0.5 °C) and 10–20% for precipitation. Specifically, climate values were generated at seed source origins for each year over the 1961–1990 period – a period prior to rapid climate change that may approximate conditions to which the seed sources are adapted – and at the planting site for each year between establishment and measurement (i.e., 2008–2018).

Statistical approach

We modelled tree height using a mixed effects model:

$$Y_{ijkl} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \gamma_k + \delta_{l(k)} + \epsilon_{ijkl} \quad (1)$$

where, μ is the overall mean, α_i is the (fixed) effect of tree species, β_j is the (fixed) effect of seed origin, $(\alpha\beta)_{ij}$ is the (fixed) interaction effect between species and seed origin, γ_k is the (random) effect of block, $\delta_{l(k)}$ is the (random) effect of plot nested within block, and ϵ_{ijkl} is the model error. The analysis was performed in SAS 9.4 (SAS Institute Inc. 2013.) using PROC GLIMMIX, with a residual pseudo-likelihood estimation method and Kenward-Roger correction to the denominator degrees of freedom. The model specified in Eq. 1 was also used to analyze tree survival, but in this case the logit link and binary distribution were specified in the call to PROC GLIMMIX. The R^2 metric, which is a well-known estimate of the proportion of variance explained by normal linear models, is not typically provided for the generalized linear mixed models used here. Thus, we employed a published SAS Macro routine (Jaeger et al. 2017) to obtain R^2 values for the fixed effects in each of our models.

Results

Broadleaf Trial

The broadleaf seed sources used in this study originated from locations that cover a range of temperature and precipitation conditions (Fig. 2). Temperatures experienced by the growing plantation were generally warmer than historical temperatures at the Ontario seed sources (Pontypool), similar to temperatures associated with the Pennsylvania seed sources (Indiana County), and cooler than those associated with seed sources from Kentucky (Marshall

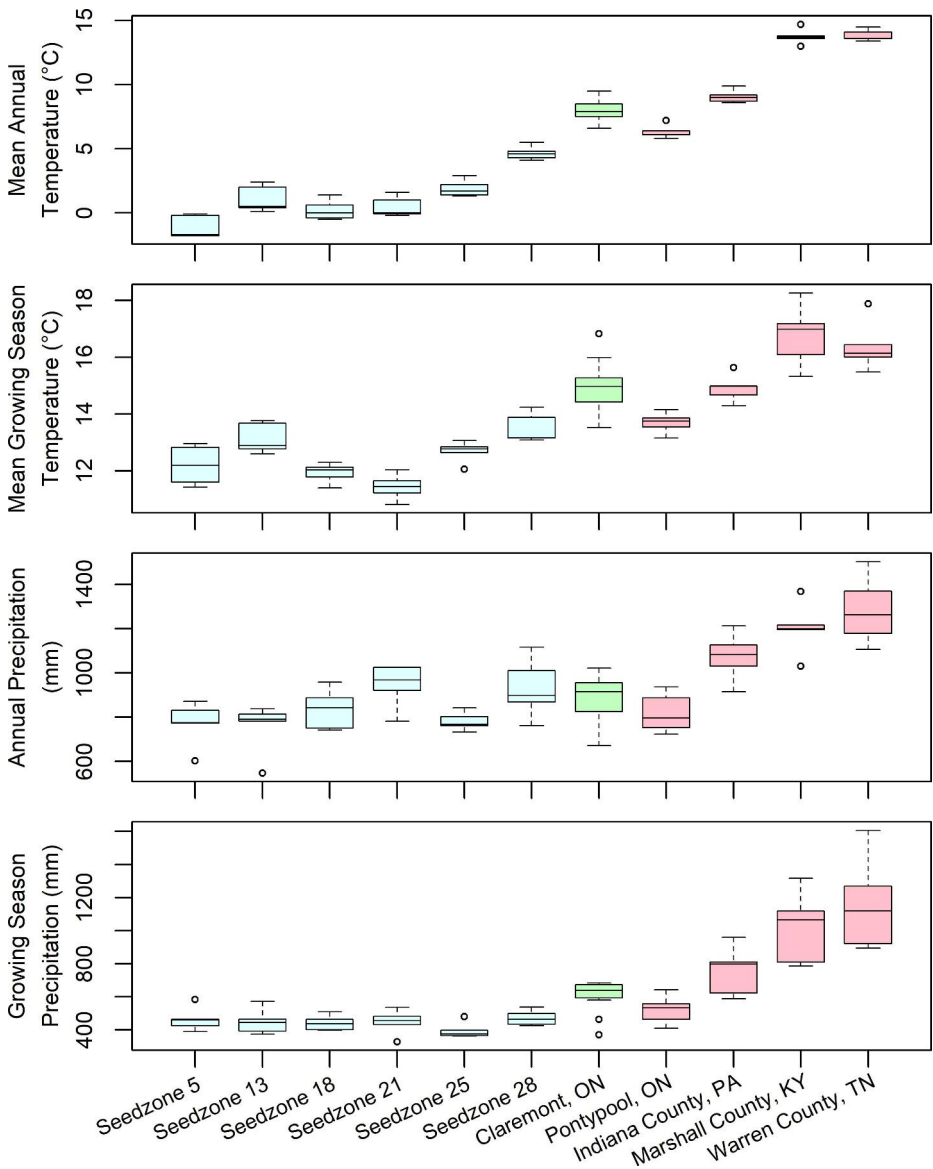


Fig. 2 Annual and growing season temperature and precipitation conditions at coniferous seed sources (blue), deciduous seed sources (red), and plantation site in Claremont, Ontario (green). Seed source climate values are for a historical period (1961–1990) that precedes recent rapid climate change; plantation values are for the period between planting and measurement (i.e., 2008–2018)

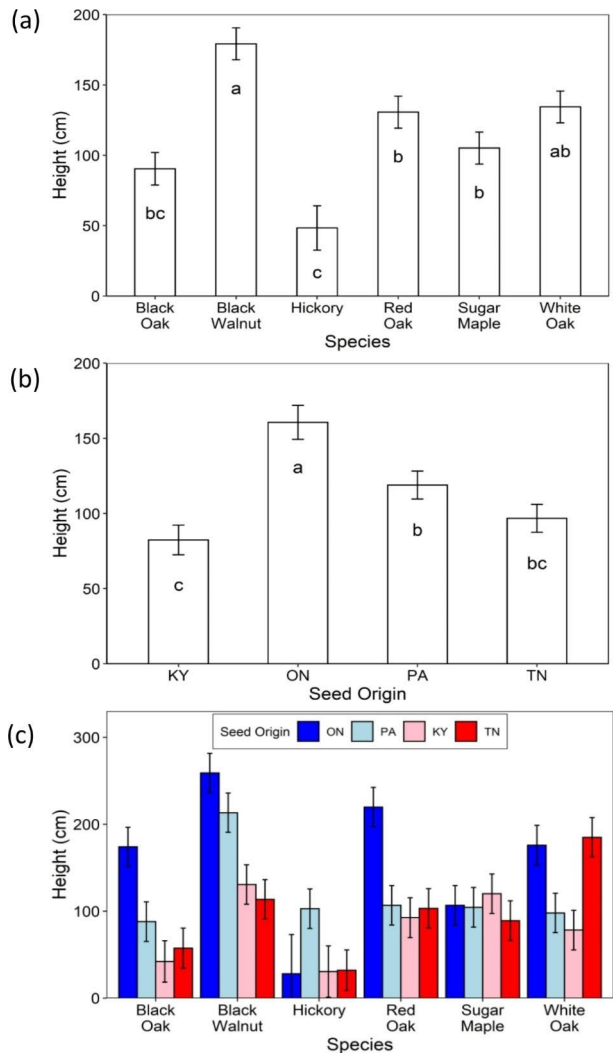
County) and Tennessee (Warren County). Precipitation experienced at the plantation, both annually and during the growing season, was higher than that historically reported at Pontypool, but lower than that historically experienced by the remaining seed sources (Fig. 2).

The mixed model for broadleaf height at age 10 was highly significant ($F_{23,100} = 6.3$, $p < 0.0001$) and explained 59% of variation in seedling height (Table 1). There was a sig-

nificant effect of species, with black walnut growing best, hickory growing worst, and the remaining species exhibiting intermediate growth (Fig. 3a). Height was also significantly affected by seedling origin (Table 1). In this case, stock from Ontario grew significantly better than that from all other locations, while stock from Pennsylvania grew significantly better than that from Kentucky (Fig. 3b). There was a significant interaction between Species and Origin (Table 1), such that the effect of stock origin varied across species (Fig. 3c). For example, stock from Ontario grew best for black walnut, black oak, and red oak, but not for the remaining species. Furthermore, stock from Kentucky grew poorly for most species, but exhibited top growth among sugar maple seed sources.

The mixed model for broadleaf survival was also highly significant ($F_{23,68} = 15.5$, $p < 0.0001$) and explained 84% of variation in seedling survival (Table 1). Survival rates varied significantly across species (Table 1), with black walnut exhibiting a significantly higher survival rate than all other species, hickory exhibiting a significantly lower survival rate

Fig. 3 Least squares mean height at age 10 (\pm S.E.) of broadleaf trees at a trial in Claremont, Ontario in relation to (a) species, (b) seed origin (ON=Ontario, PA=Pennsylvania, KY=Kentucky, and TN=Tennessee), and (c) species by seed origin. Differences between species and/or seed origins not sharing the same letter are statistically significant (i.e., $p < 0.05$)



than all other species, and white oak surviving significantly better than black oak (Fig. 4a). Seedling origin also significantly affected survival (Table 2), with stock from Kentucky exhibiting significantly lower survival than all other locations and stock from Pennsylvania exhibiting significantly higher survival rates than that from Ontario (Fig. 4b). There was a significant interaction between Species and Origin (Table 1); for example, stock from Ontario had the lowest survival rates for hickory and white oak, but the highest survival rates for black walnut, black oak, and red oak (Fig. 4c).

Conifer trial

Coniferous seed sources originated from a range of temperature and precipitation conditions (Fig. 2). Temperatures experienced by the growing plantation were warmer than historical temperatures at all of the seed sources, including those from SZ28, which is located immediately north of the planting site (Fig. 1). Annual precipitation at the plantation was similar to historical precipitation levels at SZ21 and SZ28, but higher than historical levels at the remaining seed zones, while precipitation during the growing season was higher at the plantation than any of the seed zones (Fig. 2).

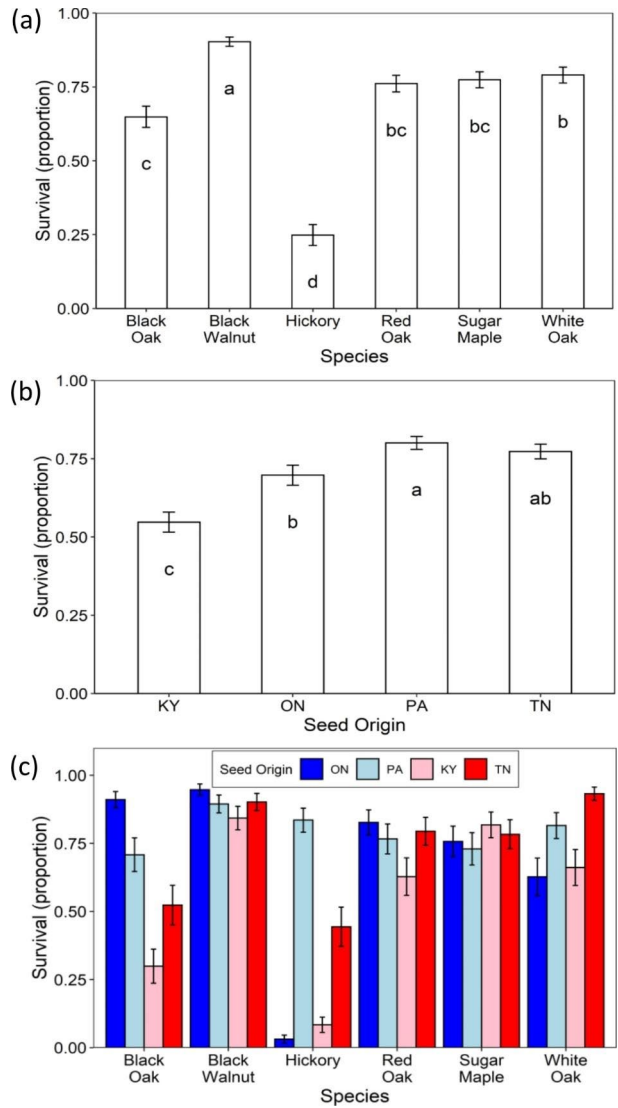
The mixed model for conifer height at age 10 was highly significant ($F_{17,23} = 5.5$, $p < 0.0001$) and explained 80% of the variation in seedling height (Table 2). Height growth differed significantly across species (Table 2), with jack pine exhibiting a higher growth rate than both black and white spruce (Fig. 5a). Height growth also varied in relation to origin (Table 2), with stock originating from SZ13 (northwestern Ontario) exhibiting significantly better growth than that originating from SZ28 (south central Ontario) and SZ18 (northeastern Ontario). Planting stock from SZ25 (central Ontario) and SZ5 (northwestern Ontario) also grew significantly better than that from S28 (Fig. 5b). The interaction between Species and Origin was not significant (Table 2) as evidenced by the relatively consistent growth performance of the various seedling origins across species (Fig. 5c).

The mixed model for conifer survival was also highly significant ($F_{17,62} = 6.5$, $p < 0.0001$) and explained 64% of the variation in tree survival (Table 2). Survival rates varied significantly across species (Table 2), with white spruce exhibiting significantly higher survival rates than black spruce, and jack pine intermediate between the two (Fig. 6a). Survival rate also varied in relation to provenance (Table 2), with stock from SZ28 exhibiting signifi-

Table 1 Significance tests for fixed effects from mixed models relating seedling height and survival to species and seed origin (provenance) for a broadleaf plantation in Clarendon, Ontario

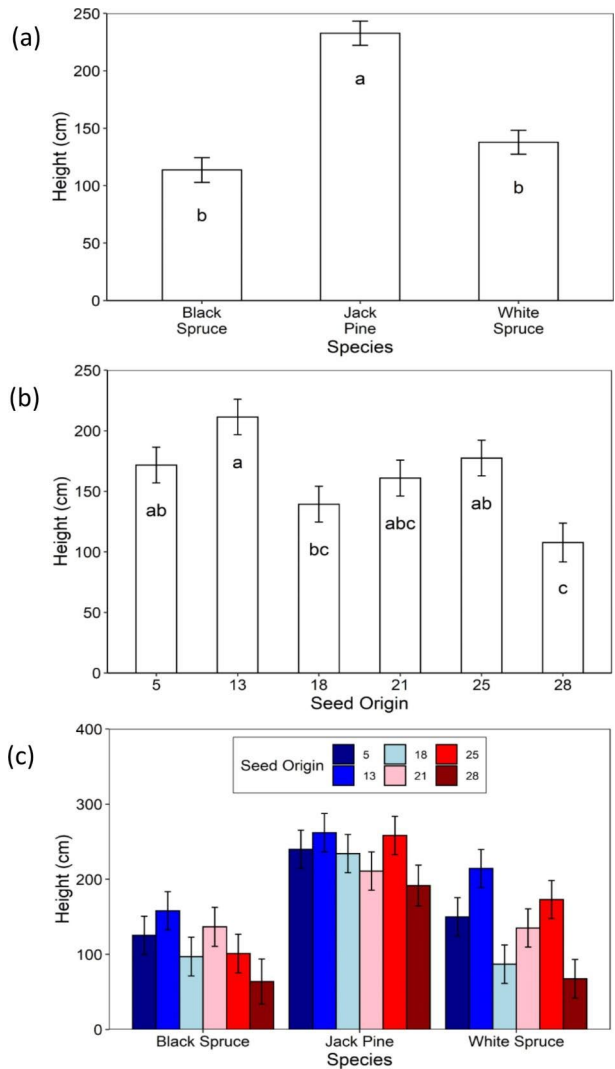
Response	Fixed Effects	DF (numerator)	DF (denominator)	F	Pr>F
Height	Provenance	3	107.6	10.2	<0.0001
	Species	5	103.3	11.8	<0.0001
	Species* Provenance	15	101.2	3.0	0.0006
Survival	Provenance	3	102.2	16.8	<0.0001
	Species	5	100.5	36.9	<0.0001
	Species* Provenance	15	95.01	9.8	<0.0001

Fig. 4 Least squares mean survival at age 10 (\pm S.E.) of broad-leaf trees at a trial in Claremont, Ontario in relation to (a) species, (b) seed origin (ON=Ontario, PA=Pennsylvania, KY=Kentucky, and TN=Tennessee), and (c) species by seed origin. Differences between species and/or seed origins not sharing the same letter are statistically significant (i.e., $p < 0.05$)



cantly lower survival rates than stock originating from the other locations (Fig. 6b). The interaction between Species and Origin was significant, but relatively weak (Table 2). An interaction plot indicated modest changes in performance of the various provenances across species, though stock from SZ13, SZ25 and SZ5 tended to perform well, while stock from SZ28 consistently performed poorly (Fig. 6c).

Fig. 5 Least squares mean height at age 10 (\pm S.E.) of conifer trees at a trial in Claremont, Ontario in relation to (a) species, (b) seed origin (provincial seedzones, see Fig. 1), and (c) species by seed origin. Differences between species and/or seed origins not sharing the same letter are statistically significant (i.e., $p < 0.05$)



Discussion

Results from our broadleaf trial provided a number of insights regarding northward movements of seed sources and species. Local seed sources tended to exhibit the best growth, though this was not the case for all species in the study (e.g., hickory and sugar maple). Furthermore, survival rates were highest for stock from Pennsylvania, followed by Tennessee and Ontario; though again, this order varied by species. Planting stock from Kentucky consistently exhibited the lowest growth and survival rates of the four seed sources in the study. These findings suggest that broadleaf seed sources can be moved considerable distances before exhibiting significant growth and survival losses. For example, stock from Indiana County, PA – approximately 500 km south of the planting site – exhibited above average growth and survival for nearly all species in the study.

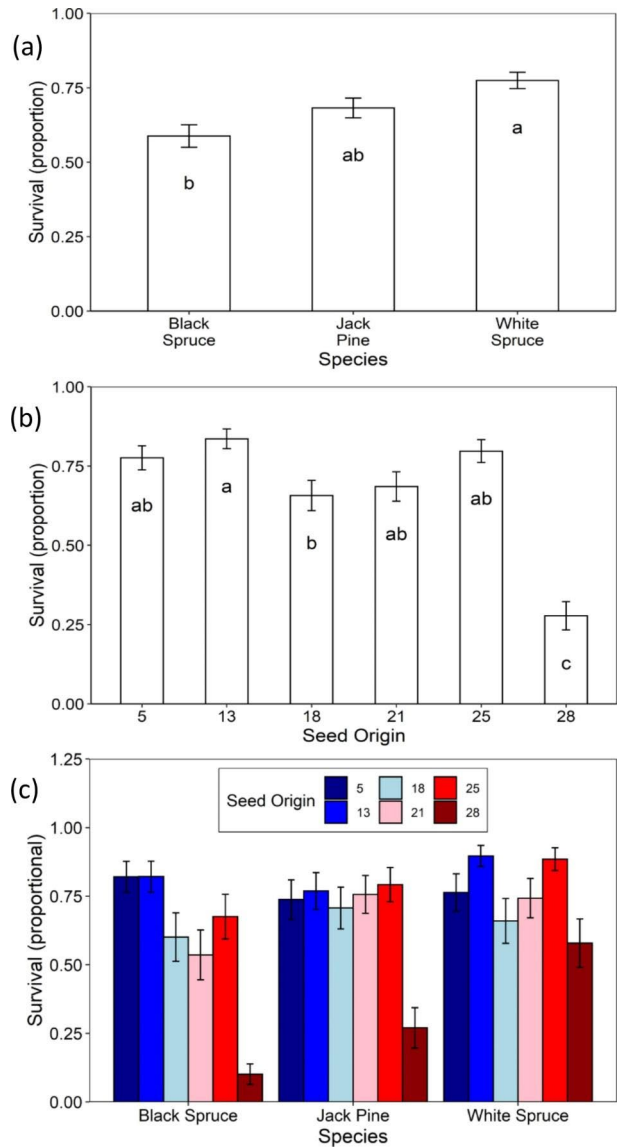
Table 2 Significance tests for fixed effects from mixed models relating seedling height and survival to species and seed origin for a conifer plantation in Claremont, Ontario

Response	Fixed Effects	DF (numerator)	DF (denominator)	F	Pr>F
Height	Provenance	5	74.22	5.35	0.0003
	Species	2	74.64	35.37	<0.0001
	Species* Provenance	10	74.02	0.81	0.6176
Survival	Provenance	5	70.56	17.49	<0.0001
	Species	2	70.76	7.95	0.0008
	Species* Provenance	10	70.27	2.06	0.0393

Three broadleaf species – black oak, black walnut, and shagbark hickory – were planted at, or beyond, their current northern range limits. Growth and survival rates varied widely across these species, with black walnut exhibiting the highest rates in the study, black oak intermediate, and shagbark hickory the lowest. These results suggest that there is potential for species to survive and grow well when moved to locations just north of their current northern range limits (i.e., assisted range expansion), supporting previous studies that have reported successful northward range expansions in forestry (Etterson et al. 2020), restoration (Truax et al. 2018), and horticultural (van der Veken et al. 2008) settings. Note that the poor performance by shagbark hickory reported here is consistent with previous studies that have found this species challenging to establish on former agricultural land (Cogliastro et al. 1997; von Althen 1990). While there has been considerable debate regarding the appropriate use of assisted migration as a climate change adaptation tool (McLachlan et al. 2007; Hewitt et al. 2011), modest movements of tree species, such as those undertaken here, represent a relatively low risk approach that may facilitate northward shifts to track climate change – particularly in landscapes that have been extensively fragmented by human development.

The southward movement of conifer seed sources was designed to examine the extent to which populations can tolerate the climate conditions that they are projected to experience in the coming decades under climate change. Surprisingly, the local seed source (from seed zone 28) exhibited the lowest rates of growth and survival at the planting site. We propose that this poor performance was related to poor quality seedlings at time of planting; in fact, many of the original seedlings from this seed zone died and had to be replanted in subsequent years. Thus, if we assume that the results from seed zone 28 were an anomaly, the remaining seed sources exhibited relatively consistent performance. Of particular note are the seed sources from northwestern Ontario (seed zones 5 and 13), which exhibited some of the highest growth and survival rates in the study, despite originating approximately 1500 km northwest of the planting site – where mean annual temperatures are over 5°C cooler on average. These findings suggest that populations of these conifer species have significant levels of phenotypic plasticity, allowing rapid acclimatization to longer distance seed transfers and potentially novel climate conditions.

Fig. 6 Least squares mean survival at age 10 (\pm S.E.) of conifer trees at a trial in Claremont, Ontario in relation to (a) species, (b) seed origin (provincial seedzones, see Fig. 1), and (c) species by seed origin. Differences between species and/or seed origins not sharing the same letter are statistically significant (i.e., $p < 0.05$)



Previous work, using data from provenance studies, has also reported significant phenotypic plasticity associated with conifer seed sources. Response curves, which plot seed source performance (e.g., height or survival) as a function of climate at a range of planting sites, typically show good performance across a range of conditions (Wang et al. 2006, 2010). For example, Pedlar and McKenney (2017) reported that northern seed sources of five conifer species exhibited growth increases (relative to local) when transferred to planting sites that were up to 8°C of MAT warmer than local conditions. Furthermore, Pedlar et al. (2021) quantified critical seed transfer distances for three boreal conifers and reported that seeds could be moved to planting locations approximately 6°C of MAT cooler or 4°C of

MAT warmer before exhibiting growth forfeitures greater than 10% relative to local. These findings suggest that trees may persist for some time at a given location due to relatively high levels of phenotypic plasticity (see also Benito-Garzon et al. 2019). We note however, that extreme weather events such as droughts, which are expected to increase under climate change (Dai 2013), could overwhelm the temperature-related phenotypic plasticity described here. Indeed, significant drought-related mortality events in northern regions suggest that this may be an important driver of forest change (Senf 2020, Girardin et al. 2016b).

It is important to consider trade-offs between height and survival when assessing seed movements under climate change (Pedlar et al. 2021). Migrated seed sources have been associated with significant mortality events, which can nullify anticipated growth gains (Benito-Garzon 2013). In the broadleaf trial, there was some evidence that long-distance transfers – particularly seed sources from Kentucky – were associated with higher rates of mortality. While these seed sources may grow better than local sources in the long run, these early losses underline the risks involved in long-distance movements. Interestingly, seed sources from slightly further away in Tennessee did not exhibit the same level of mortality.

A growing number of studies are reporting outcomes from climate change and assisted migration trials. Wang et al. (2019) carried out both northward and southward movements of seed sources for two range-restricted perennial forbs in Alberta, Canada. Similar to our results, they found that, for one of the species, northward movements of approximately 500 km were associated with good survival, growth, and flowering relative to local metrics. However, they reported low survival and growth for the other species at all planting sites (similar to hickory in the current study), underlining the high degree of interspecific variation in assisted migration outcomes. Sáenz-Romero et al. (2020) reported on three different assisted migration trials in Canada and Mexico and reported the following general insights: (1) populations of *Picea glauca* × *P. engelmannii* may be safely planted at locations that are 3 °C cooler than local (in terms of mean coldest month temperature); (2) *Pinus albicaulis* can be established outside of its current natural distribution at sites that have climates that are within the species' modelled historic climatic niche, and (3) *Abies religiosa* performs well when moved 400 m upward in elevation. These findings generally support those presented here regarding the suitability of seed sources for northward/upslope movements and the potential for range expansion under climate change. Finally, Etterson et al. (2020) examined the growth of southern and northern seed sources for two oak species in northern Minnesota and found that the southern seed sources generally outperformed the more northern sources – again supporting the notion of northward seed source movements on the scale of several hundred kilometers.

We recognize a number of caveats related to the current work. First, given the relatively young age of the plantations examined here, our findings should be considered preliminary in nature. Provenance studies have reported changes in the ranking of seed source performance over time, which can impact key study outcomes (Rweyongeza 2016). Growth curves could be used to project rank changes among species, though such curves were not available for all species in the current study – and typically do not incorporate climate change. Furthermore, reproductive capacity of trees at the new location may require several decades before being assessed. Nonetheless, the early years of a plantation are recognized as being critical for tree survival (Lutz and Halpern 2006), suggesting that important performance metrics may be measured over this period. Furthermore, results from a 5-year measurement of the current study (not shown) were generally consistent with the findings

reported here. A second caveat relates to deer browsing at the broadleaf site, which has been shown to be a major concern for broadleaf regeneration in the Great Lakes region of North America (Redick and Jacobs 2020). Despite the use of tree shelters, deer caused significant damage by browsing the tops of developing saplings as they emerged from the shelters, which may have impacted both growth and survival measurements. Though we did not carry out extensive browse surveys, casual observations indicated that a range of broadleaf species and seed sources were affected. In fact, the high growth rates exhibited by black walnut may be due, in part, to low levels of browsing on this species – a phenomenon that has been reported in other studies (Schempf and Jacobs 2020).

Conclusion

Our findings support previous work that has shown that broadleaf species can be moved modest distances at, or beyond, their current northern range limits with little impact to growth and survival. One such species, shagbark hickory, did not grow or survive well at our planting site, but this may be due to known challenges with establishing this species in agricultural settings. Both broadleaf and coniferous seed sources were able to tolerate significant movements while maintaining reasonable growth and survival rates. In fact, several coniferous seed sources exhibited relatively high growth and survival rates despite southward transfers of more than 1000 km – indicating significant adaptive capacity to climate change in these northern conifer populations. However, given the potential impacts of extreme weather events such as droughts and late frosts on young plantations, more restrained transfer distances are recommended. Though modest in scope, this work helps to fill a void in the literature concerning climate change impacts on northern conifers and assisted migration outcomes for temperate broadleaf species. Future efforts at this site will help to clarify the longevity of these findings and the response of migrated seed sources to extreme climate events.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11056-023-09965-x>.

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Declarations

Conflict of interest The authors declare no conflict of interest.

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