Assisted migration across fixed seed zones detects adaptation lags in two major North American tree species

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Abstract. Boreal forests are experiencing dramatic climate change, having warmed 1.0°–1.9°C over the last century. Yet forest regeneration practices are often still dictated by a fixed seed zone framework, in which seeds are both harvested from and planted into predefined areas. Our goal was to determine whether seedlings sourced from southern seed zones in Minnesota USA are already better adapted to northerly seed zones because of climate change. Bur oak (Quercus macrocarpa) and northern red oak (Quercus rubra) seedlings from two seed zones (i.e., tree ecotypes) were planted into 16 sites in two northern seed zones and measured for 3 yr. Our hypotheses were threefold: (1) tree species with more southern geographic distributions would thrive in northern forests where climate has already warmed substantially, (2) southern ecotypes of these species would have higher survival and growth than the northern ecotype in northern environments, and (3) natural selection would favor seedlings that expressed phenotypic and phenological traits characteristic of trees sourced from the more southern seed zone. For both species, survival was high (>93%), and southern ecotypes expressed traits consistent with our climate adaptation hypotheses. Ecotypic differences were especially evident for red oak; the southern ecotype had had higher survival, lower specific leaf area (SLA), faster height and diameter growth, and extended leaf phenology relative to the northern ecotype. Bur oak results were weaker, but the southern ecotype also had earlier budburst and lower SLA than the northern ecotype. Models based on the fixed seed zones failed to explain seedling performance as well as those with continuous predictors (e.g., climate and geographical position), suggesting that plant adaptations within current seed zone delineations do align with changing climate conditions. Adding support for this conclusion, natural selection favored traits expressed by the more southern tree ecotypes. Collectively, these results suggest that state seed sourcing guidelines should be reexamined to permit plantings across seed zones, a form of assisted migration. More extensive experiments (i.e., provenance trails) are necessary to make species-specific seed transfer guidelines that account for climate trends while also considering the precise geographic origin of seed sources.

Key words: adaptation lag; assisted migration; boreal forest; climate adaptation; phenology; population differentiation; Quercus macrocarpa; Quercus rubra; seed zone.

INTRODUCTION

Many North American tree species are considered vulnerable to climate change (Landscape Change Research Group 2014, Rogers et al. 2017, Chakraborty et al. 2018) and this is especially true in boreal forests (Gauthier et al. 2015) where climate change is dramatic (Boulanger et al. 2017, Trugman et al. 2018). Tree populations typically exhibit adaptation to local climate (reviewed in Aitken et al. 2008) and other aspects of the environment (Sork et al. 1993) as a consequence of natural selection (Rehfeldt et al. 1999). As the climate changes, one possibility is that tree populations will become increasing maladapted to the prevailing conditions, which would be indicated by increased mortality (Adams et al. 2009, Allen et al. 2010, Williams et al. 2013), reduced growth (Barber et al. 2000), and lack of recruitment (Fischelli et al. 2014a, b). Alternatively, it is also possible that populations at the northern range edge that persist in suboptimal conditions will experience a positive growth response with climate change (Rehfeldt et al. 1999, Pedlar and McKenney 2017) due to an underlying trade-off between cold tolerance and growth rate (Rehfeldt et al. 1999) or due to genetic maladaptation caused by gene flow from the range center into peripheral populations (Lenormand 2002), although northerly gene flow may often be adaptive with climate
change (Kremer et al. 2012). Which outcome is borne out is likely to be species specific (Park et al. 2014) and to depend upon migration rates (McLachlan et al. 2007, Sittaro et al. 2017) and the extent of gene flow among populations (Savolainen et al. 2007). In turn, migration rates and gene flow will influence the scale of adaptation via plasticity (Chevin et al. 2010, Fox et al. 2019) or genetic change (Aihten et al. 2008). Despite these alternative possibilities, the effects of climate change are already manifest in some boreal systems as indicated by climate-related regeneration failures (Walck et al. 2011, Sittaro et al. 2017). Exploration of climate management strategies is especially warranted in regions where the signs of genetic maladaptation due to warming are already apparent (Frank et al. 2017, Otis Prud’homme et al. 2018a, b).

Understanding the potential for tree populations to be mismatched with prevailing conditions under climate change (i.e., adaptation lags) in northern forests can inform the development of silvicultural practices that help forest ecosystems maintain fitness over time (D’Amato et al. 2011, Liu et al. 2012, Lunt et al. 2013, Isaac-Renton et al. 2014, Chakraborty et al. 2018). Three broad climate management strategies for ecosystems have emerged over the last decade: resistance, resilience, and response (sensu Millar et al. 2007, Heller and Zavaleta 2009, also see Stanturf et al. 2014 for a variation). Early management strategies (i.e., prior to 2010) maintained a conservative focus on resistance and resilience (Heller and Zavaleta 2009, Poiani et al. 2011). However, resistance and resilience approaches are often implemented with little regard for maladaptation to current or future climates. “Response” strategies, more commonly termed “transition” strategies in recent years (sensu Nagel et al. 2017 and used hereafter), offer a compelling alternative, one that can complement resilience and resistance measures in areas experiencing dramatic climate change. Land managers are increasingly interested in transition approaches, which specifically address the potential for maladaptation through the introduction of either new species adapted to changed conditions or populations of extant species (“ecotypes” hereafter) that may be better able to cope with changing conditions.

Assisted migration (AM) is a transition strategy that involves selecting source material for restoration or relocation to match or anticipate future climate change (McLachlan et al. 2007). In forestry-AM, populations of common, widespread, tree species are moved within their current native ranges, which may encompass multiple seed zones. Forestry-AM is distinct from species rescue-AM, a practice initiated to avoid extinctions, generally targeted at rare species and often involving movement outside the current native range (Pedlar et al. 2012). Hereafter, when we refer to AM, we specifically refer to forestry-AM (sensu Pedlar et al. 2012). Despite an increasing interest on the part of foresters in implementing AM, the evidence base for the suitability of this practice is currently lacking (Park and Talbot 2018). Criteria for determining if AM is an appropriate climate management approach include (1) observation of biological impacts, (2) demonstration of an adaptation lag, and (3) models that predict climatic changes over the long term (Richardson et al. 2009, Gray et al. 2011). Although there are exceptions (Gray et al. 2011), AM projects commonly meet criteria 1 and 3 but lack a fundamental understanding of the bounds of adaptation, essential to identifying an adaptation lag (criteria (2); Pedlar et al. 2012, Williams and Dumroese 2013; but see Gray et al. 2011). Evidence for adaptation lags has typically been obtained from provenance and genealogical trials (Andalo et al. 2005, St Clair and Howe 2007, Ukrainetz et al. 2011) or common garden studies with temperature and precipitation manipulations (Richter et al. 2012). For most species and regions of the globe, however, such evidence is lacking, and forest managers are therefore reluctant to implement potentially important climate management practices (Benito-Garzón et al. 2013).

In order to avoid maladaptation and select plant material that will thrive in a given site, regulatory entities (e.g., state and federal forestry agencies, nongovernmental restoration organizations) have developed seed sourcing policies that rely on fixed or flexible seed zones. A fixed seed zone is a delineated area within which seeds are both harvested and replanted. The underlying assumption is that species’ populations are locally adapted to this area such that within-zone seed sourcing maximizes forest productivity. Thus, a fixed seed zone approach would not permit among-zone AM. In contrast, a flexible or floating seed zone permits seed movement, including AM, according to seed transfer guidelines that account for plant adaptation across continuous environmental gradients. Rather than define a fixed area that cuts across these clines, a flexible seed zone defines maximum distances or elevational deviations from the source population that will likely avoid maladaptation. These guidelines are typically based on species-specific provenance trial data that are analyzed using continuous climate or geographic variables (Rehfeldt 1988, Lesser and Parker 2006, Hamann et al. 2011). The development of flexible seed zones requires extensive empirical data and often lacks information about the adaptive value of certain traits, such as bud burst phenology (Hamann et al. 2011).

Forests of the northern Great Lakes region may experience some of the most dramatic vegetation changes in response to climate change in the continental United States. In Minnesota, the climate has already warmed substantially, especially in the northeast (+1.0°C to 1.9°C; Fig. 1a). Minnesota’s forests are entering the era of rapid change in a highly degraded state due to historical and modern logging practices (Hale et al. 2006, Schulte et al. 2007, White 2012). Importantly, the species composition of boreal forests has already begun to change as temperate tree species invade (Fischelli et al.
2014a, b) and canopy trees perish due to drought stress and insect damage (Adams et al. 2009, Allen et al. 2010, Muilenburg and Herms 2012). The loss of dominant boreal species and their replacement with deciduous species is projected to continue under all plausible climate change scenarios (Iverson et al. 2008, Ravenscroft et al. 2010), leading to speculation that they may give way to an alternate state, for example savanna (Frelich and Reich 2010). Minnesota may therefore may be an especially good candidate for AM as part of a transition strategy to maintain forest cover and function. We base this assertion on the rapidity of climate change in this region, observations of biological impacts including canopy tree mortality, and predictions for continued forest compositional change. However, current fixed seed zones in Minnesota pose a barrier to AM and other transitional management approaches.

Our study examines whether or not forest regeneration seed sourcing policies and practices as currently implemented by state agencies may contribute to an adaptation lag in the forests of northeastern Minnesota. At issue are the six fixed seed zones established by the Minnesota Department of Natural Resources (MN DNR, hereafter) based on prevailing patterns of temperature and precipitation in 1954 (Rudolph 1956, Rauscher 1984). At present, seeds are bulk collected across these seed zones and mixed-population collections are planted back into sites within the same seed zone, either broadcast planted as seeds or individually planted as seedlings that have been raised at the Minnesota State Nursery. These practices are likely to have a profound impact on the genetic makeup of Minnesota’s forests, given that ~16,000 ha are revegetated each year (D’Amato et al. 2009). Expanding the impact of the fixed seed zone framework, state nursery seedlings are also distributed to federal and county forest managers as well as private landowners for forest regeneration within their respective seed zones. Moreover, the MN DNR excludes seed collections from a unique habitat, the coastal forests adjacent to Lake Superior that experience a moderated climate. Previous MN DNR experience indicates that seeds collected in these forests do not perform well when planted into more interior habitats, however, the converse does not hold. Here we explore whether these state-mandated seed sourcing policies may be contributing to an adaptation lag in a boreal system where climate change impacts are already evident.

This study was conducted within the context of a larger forest restoration project initiated by The Nature Conservancy in northeastern Minnesota (Etterton et al. 2018) where 110,000 tree seedlings were planted into 2,000 acres of mixed boreal forest within two MN DNR seed zones (i.e., N102 and NC104, see Fig. 1a). Here, we report on the survival and growth of two species that are native to the study area but are relatively uncommon and are near their northern range limits, bur oak (Quercus macrocarpa) and northern red oak (Quercus rubra) (Fig. 1b). Both of these species are predicted to thrive under future climate scenarios (Duveneck et al. 2014b). To determine whether the fixed seed zone framework that governs state forest regeneration practices results in the dissemination of plant source material that results in high survival and growth, we planted seedlings obtained from the MN DNR nursery that were sourced from a northern and a more southern seed zone (“tree ecotypes” from seed zones NC104 and C105, Fig. 1a).

Our hypotheses for this AM experiment were three-fold. First, tree species that are relatively rare because they are near their northern range edge will have high survival and growth in northeastern Minnesota, where climate has already warmed substantially. Second, seedlings of these species originating from a more southern seed zone will have higher survival and growth than seedlings from a northern seed zone. Third, southern source populations will thrive in the study area because they express traits that confer tolerance to climate conditions that have already changed. As possible examples of these traits, the southern source material may have higher survival, more rapid height growth that can ultimately confer reproductive advantages (Gamache and Payette 2004), higher radial expansion that has been associated with water balance (Daudet et al. 2005), lower specific leaf area (SLA) that has been shown to promote water conservation in some species (Aranda et al. 2007), and extended leaf phenology that may permit seedlings to photosynthesize throughout longer growing seasons expected with climate change (Gunderson et al. 2012). We anticipated that natural selection would favor traits characteristic of the southern source population (ecotype C105) compared to the northern source population (ecotype NC104). This study demonstrates an approach to providing essential information about adaptation and natural selection that can be used to inform climate-forward seed-sourcing policy in the context of ongoing restoration efforts.

Materials and Methods

Study area

This study was conducted within the northeastern portion of Minnesota’s Laurentian Mixed Forest Province (Cleland et al. 1997). Located within the northern–temperate–southern-boreal forest transition zone, the study area consists of a complex mosaic of forest and wetland communities. At the time of European settlement, conifers, including Pinus banksiana, Pinus strobus, and Pinus resinosa, dominated both upland and lowland forests. Euro-settlement era logging and subsequent catastrophic fires led to a shift in dominance from late-successional and mid-seral conifers to early-successional boreal hardwood species, primarily Populus tremuloides and Betula papyrifera (Schulte et al. 2007).

This region has experienced significant climate warming over the last century (+1.0°C to 1.9°C, Fig. 1a; Melillo et al. 2014), including markedly warmer winters
FIG. 1. (A) Minnesota’s six fixed seed zones for forest regeneration (black lines) shown with mean annual temperature.
and an increased frequency of extreme rainfall and snowfall events. Recent climate trends (1984–2013) indicate regional warming of 0.56°C, with autumn (1.56°C) showing a high rate of temperature increase. Warming trends coupled with deceased summer precipitation (−0.34 cm/yr) likely lead to increased stress on forest ecosystems (Garcia and Townsend 2016). These trends are predicted to continue through 2025, in addition to an increased frequency of heat waves and drought (Minnesota State Climatology Office, April 2018). During the years of data collection reported here, growing degree days calculated from a base of 5°C ranged from 2,469 to 3,168 (Minnesota State Climatology Office, April 2018). The average annual temperature and precipitation in the years of this study were slightly higher than the long-term average in each year (average annual temperature and precipitation 2014–2015 +2.45°C, +83 mm; 2015–2016 +0.43°C, +53 mm).

Study species

Our study focuses on two deciduous species, bur oak (Quercus macrocarpa) and northern red oak (Q. rubra), both of which are at the northern edge of their species’ ranges in the study area (Fig. 1b). In general, bur oak has a more western distribution that extends into the drier Great Plains biome compared to red oak, which occurs at greater abundance in eastern deciduous forests. These distributional differences may be associated with contrasting growth vs. water-use trade-offs. Bur oak has low xylem permeability, high water use efficiency, and slow height growth (Lambers et al. 1998, Guyette and Stambaugh 2004), allocating more resources to below-ground biomass, especially at juvenile stages (Danner and Knapp 2001). Red oak, in contrast, has greater xylem permeability, which allows for increased hydraulic conductivity and growth, but is at higher risk of negative physiological consequences under water stress, such as cavitation (Burns and Honkala 1990, Guyette and Stambaugh 2004). Both species are monecious, deciduous trees that reach reproductive age at 25–35 yr and live 200–400 yr (Iverson et al. 1999). Gene flow in populations of both species is highly variable and includes a mix of local and long-distance migrants (Craft and Ashley 2007, 2010, Moran and Clark 2012).

Experimental design

The planting sites fall within two MN DNR seed zones in north-central and extreme northern Minnesota (Table 1; Fig. 1a, seed zones referred to as NC104 and N102 hereafter; MN DNR 2015). The sites are arrayed across approximately one degree of latitude (47°12′–48°07′ N) and longitude (91°97′–90°70′ W). A north-south temperature gradient (average annual 2.98°–3.92°C) and an east-west precipitation gradient (average annual 722–841 mm) span the study area (Daly 2008) (Table 1). Photoperiod as determined from mean growing season day length in hours (1 May–30 September) varied across the seed zones as follows from south to north: C105, 14.1 h; NC104, 14.2 h; N102, 14.3 h (Thornton et al. 2016; Table 1).

In 2013, seedlings were planted into 16 recently logged sites (2010–2013) each of which had two planting blocks (3,600 m²) except for one site that had eight smaller blocks. For each planting site, the MN DNR seed zone, its geographic position (i.e., latitude and longitude), and climate factors were obtained (Table 1). We also recorded block-specific factors including vegetation composition and structure, slope, aspect, and soil characteristics (i.e., percent sand, silt, and clay; organic layer thickness; A, B, and E horizon thickness; pH). Bur oak and red oak seedlings were acquired from MN DNR State Forest Nursery and originated from two seed zones, a north-central zone and a central zone (referred to as ecotypes NC104 and C105 hereafter, Fig. 1a). The precise location of the source populations(s) could not be ascertained because MN DNR routinely pools seed collections by seed zone prior to planting at the nursery according to standard state seed sourcing practices. This AM experiment violated state seed zone regulation and, therefore, we obtained special permission to do a very limited experiment on federal, state, and county land using two adjacent seed zones as planting locations and two seedling ecotypes. One-year-old red oak and 2-yr-old bur oak bare-root seedlings were planted into 16 sites in a randomized block design from 13 May to 30 May 2013 (2 species × 2 ecotypes × 16 sites × 40 plants per source = 2,560 seedlings). Seedlings were protected from deer herbivory with plastic mesh cages. Brush saw release treatments were implemented annually to reduce competition from understory vegetation.

Measurements

We assessed survival, growth, and phenology for 3 yr (2014–2016). Survival was recorded in both the spring and fall. Height and stem diameter above the root collar were measured annually at the end of the
The growing season. At a single time point, in spring 2014, the uppermost fully expanded leaf was collected from each plant to calculate SLA (m²/kg). Leaves were pressed and dried at 70°C for 5 d and then weighed to the nearest 0.0001 g (Metler Toledo AX504, Mettler Toledo, Columbus, OH, USA). Leaf area was obtained using the following stages: (1) no buds broken, (2) one or more buds broken, (3) one or more immature leaves present, or (4) one or more mature leaves present. We report the day of the year (1 January = 1) that each plant reached stage two and refer to this as the “date of budburst.” In the fall, leaf senescence was tracked using four stages: (1) all leaves green, (2) 33% or more leaves lacking chlorophyll, or (3) 66% of the leaves lacking chlorophyll, and (4) 100% of the leaves lacking chlorophyll or abscised. As with spring phenology, we report the day of the year that each plant reached stage two and refer to this as the “date of leaf senescence.” We also report the number of days between budburst and leaf senescence, which approximates the duration of photosynthetic activity during the growing season. The distance between and remoteness of the sites increased phenological sampling intervals. Although phenological estimates lost some precision with the coarseness of the time intervals, we nonetheless detected a strong signal, both in magnitude and direction, in the response variables.

Three analysis models
We analyzed the measurement data with three different explanatory models were focused on: (1) Seed Zones, (2) Climate factors, or (3) Geographic Position. The seed zone model included following factors: ecotype, seed zone and two random factors site (seed zone), and block (site, seed zone). The climate and geographical models did not include these random effects but, instead, included climate variables or latitude and longitude that uniquely identified each planting block. We evaluated model fit based on $R^2$, RASE (square root of the mean squared prediction error), and AAE (average absolute error). Bur oak and red oak seedlings were analyzed separately because of significant species × ecotype interactions in preliminary analyses. Among the three competing models, if the seed zone model provided the best fit to the data and plant source material from seed zone 104 performed best in sites within seed zone 104, then we would conclude that the MN DNR seed zone policy supports forest productivity because of local adaptation. If, however, the seed zone model provided the best fit to the data but plant material performed best in a more northerly seed zone, we would conclude that short-distance AM across seed zones would relieve the documented adaptation lag between the plants in a given seed zone and the prevailing climate conditions. On the other hand, if one of the other models provided a better fit to the data (i.e., climate or geographic position), this would suggest that the fixed seed zone framework does not provide a good...
description of plant variation across the study area and a flexible seed zone policy with seed transfer guidelines that permit AM should be considered.

To aid understanding of the factors in the models, if the "ecotype" factor is significant; this means that there are genetically based trait differences between plants sampled from different seed zones. If ecotype is the only significant factor in the model, then there is no plasticity in the plant trait. If one of the environmental factors in the model is significant (seed zone, climate factor, latitude/longitude) this would indicate trait plasticity in response to the environment. Finally, if there is a significant interaction between ecotype and any given environmental factor this would suggest that plants sampled from different seed zones respond to the environment in different ways (different patterns of plasticity).

All models shared a fixed effect, plant "ecotype," which accounted for genetic differences between plant source materials sampled from different seed zones (i.e., ecotype NC104 and ecotype C105, Fig 1a). Otherwise, each model had a unique set of factors and interactions. First, the seed zone model included the zone from which seeds were originally sampled (i.e., ecotype seed zone), the zone into which seedlings were planted (i.e., planting seed zone), and the two-way interactions between these factors. Site and planting block nested within site were also included as random factors. The second model, the climate model, included plant ecotype, 2010–2015 July evapotranspiration (Velpuri et al. 2016), and January minimum temperature (PRISM Climate Group 2017). Other climate variables (average annual and growing season temperature and precipitation, and growing degree days) but ultimately eliminated from the final model as they did not significantly affect the response variables. The third model, the Geographic Position model, included the latitude and longitude of each site, and all two-way interactions. It is important to note that the geographic position model implicitly encompasses climate gradients as well other spatial clines such as photoperiod. The latter two models did not include “site” or “planting block” because these factors were fully collinear with site and block-specific geographic coordinates and climate statistics. Preliminary models included site-specific environmental measurements including PCA1 and 2 scores based on the soil measurements. However, none of these were sufficiently important and were eliminated.

Survival data were analyzed with a Generalized Linear Model assuming a binomial distribution and employing a logit transformation (JMP Version Pro 13.1.0; SAS Institute 2016). Initial plant height was included in all three analysis models but was removed because, although it differed significantly between ecotypes, it did not significantly affect mortality. Height and stem diameter growth rates were calculated as the difference in height between 2014 and 2016 divided by 3 yr. These traits were analyzed using mixed model ANOVA. We analyzed phenological trait data using repeated-measures analysis of variance because phenological responses were measured in both 2014 and 2015. Trait data were transformed as necessary to meet the model assumptions, although data figures are shown on the original scale for ease of interpretation (Figs. 2, 3).

To determine whether or not genetically based or plastic responses are likely to be adaptive, we conducted phenotypic selection analyses. Phenotypic selection analyses show the strength and direction of natural selection on measured traits (Lande and Arnold 1983, Lynch and Walsh 1998, Etterson 2004a). Prior to analysis, we divided the data into species subsets and then calculated relative fitness (Lande and Arnold 1983). We used two proxies for seedling fitness: survival from planting in 2013 until fall 2016 and height growth rate (2014–2016). All other traits were standardized (mean = 0, standard deviation = 1) to permit comparison of the strength of selection between species, ecotypes, and traits (Brodie et al. 1995). We estimated the selection intensity, i, which is the covariance between relative fitness and standardized trait values. The sign and magnitude of i is interpreted as the direction and strength of linear selection on the trait, including direct selection and indirect selection due to correlations with other traits. In the first set of analyses, we estimated the covariance between relative fitness based on survival and juvenile traits measured in 2014, including height growth, stem diameter, SLA, the dates of budburst and leaf senescence, and the days of leaf retention. We conducted a second phenotypic selection analysis where height growth rate served as the proxy of fitness. Height growth is a suitable metric of fitness because it is a genetically based trait (Cornelius 1994) that is associated with reproductive advantages (Gamache and Payette 2004).

**RESULTS**

*Model selection*

The two models with continuous explanatory variables (climate and geographic position) provided the best fit for nearly all data (Appendix S1). The seed zone model had the best fit for survival data only (10% of models), and negligibly so. Moreover, in this single instance for which the seed zone model had the best fit, none of the factors that address our central hypotheses was significant (i.e., seed zone, ecotype, or their interaction). For all phenological and growth traits, either the climate model (15%) or the geographic position model (50%) provided the best fit to the data based on $R^2$; the latter two models were tied for best for five traits (25%). There was negligible difference between the fit of the climate and geographic position models, although model fit metrics, namely RASE (square root of the mean squared prediction error) and AAE (average absolute error), generally favored the geographic position model. For simplicity, we describe patterns in the trait data
Survival

Three years after transplantation into the forest regeneration sites, 95.3% of the seedlings were alive experiment-wide. Although the overall survival rate was very high, it was slightly but significantly higher for bur oak than for red oak (96.3% vs. 94.2%; $\chi^2 = 5.77, P = 0.02$, Fig. 2a). None of the main effects in the geographic position model or their interactions significantly explained the negligible mortality recorded for bur oak. Survival of red oak seedlings, in contrast, differed between the ecotypes; C105 had slightly higher survival (+3.6%) than NC104. Red oak survival was also strongly influenced by its planting location as indicated by the effects of latitude, longitude, and the interaction between these two factors (Table 2). Examination of this geographic pattern showed that red oak mortality peaked in northeastern sites (25%) and southwestern sites (15%) but declined in other areas.

Growth rates

On average, experimental seedlings grew 9 cm/yr over each of the three measurement years. Bur oak grew nearly 1 cm/yr more than red oak (8.6 vs. 9.5 cm/yr; $F_{1,2235} = 8.0, P = 0.005$, Fig. 2b). For both species, one of the ecotypes grew significantly faster than the other but the faster-growing ecotype was not the same. For bur oak, NC104 grew 21% faster than C105, but for red oak, NC104 grew 19% slower than C105. Height growth for both species negatively covaried with latitude (slower in the north) and positively with longitude (faster in the east) and was also affected by the interaction between these two factors. In the eastern sites, growth slowed markedly with increasing latitude whereas it was more stable across latitude in the west (Fig. 3a, b). Again, using the change across latitude of bur oak as an example, height growth deviated 20.4 cm/yr in eastern sites but only 0.3 cm/yr in western sites.

Experiment-wide, the diameter of the seedlings’ stems expanded ~1 mm/yr on average, but the rate differed between species (0.87 vs. 0.98 mm/yr for bur oak and red oak, respectively, $F_{1,2195} = 7.17, P = 0.003$, Fig. 2e). In the case of bur oak, radial expansion did not differ by ecotype as a main effect, but did differ as an interaction with longitude. In the western sites, we did not detect ecotypic differences in stem diameter growth rate for bur oak, whereas in eastern sites NC104 stems widened significantly faster than C105. For red oak, ecotypes differed significantly with respect to radial expansion; C105 stems increased in diameter 32% faster than NC104. Red oak stem growth rate negatively covaried with latitude (slower further north) and was affected by the interaction between latitude and longitude. Examination of the interaction plot showed that stem diameter growth peaked in northwestern sites and was slower in all other directions.

Specific leaf area

Specific leaf area was 8.9% lower for red oak than bur oak on average, and this difference was highly significant ($F_{1,2191} = 83.85, P \leq 0.0001$, Fig. 2d). For both species, SLA of C105 leaves was lower than that of NC104 (bur oak −4%; red oak −10%). SLA positively covaried with latitude, increasing from south to north for both species. The interaction between latitude and longitude also strongly affected this trait. Examination of the interaction plots for both species showed that the cline in SLA was steep in eastern sites but not in the western sites (Fig. 3a, b). For example, focusing on the pattern of...
change from south to north for bur oak (Fig. 3a), SLA deviated 12.8 m²/kg in eastern sites, but only 0.8 m²/kg in western sites.

**Phenology**

Seasonal leaf phenology of red and bur oak differed significantly for all measurements, including the date of bud burst ($F_{1,2286} = 98.5, P < 0.0001$), date of leaf senescence ($F_{1,1350} = 69.34, P < 0.0001$) and the number of days between these two events (bur vs. red oak: $+2.2 \text{ d, } F_{1,660} = 20.26, P < 0.0001$). In addition, for both species, the phenology of NC104 and C105 differed either in the spring, fall, or both, such that the ecotypes also differed with respect to the number days that the seedlings retained green leaves during the growing season.

**Fig. 3.** Interaction plots showing the responses of two oak species, bur oak (*Quercus macrocarpa*) and northern red oak (*Q. rubra*), to environmental factors associated with the latitude and longitude of 16 recently harvested sites in northeastern Minnesota: specific leaf area for (A) bur oak and (B) red oak, height growth rate for (C) bur oak and (D) red oak, and day of year of budburst for (E) bur oak and (F) red oak.
TABLE 2. Test statistics from the Geographic Position Model, which was used to analyze survival and early growth traits of two oak species, (A) bur oak (Quercus macrocarpa) and (B) northern red oak (Q. rubra).

| Factor        | 13–16 survival† | 2014 SLA       | 13–16 height growth rate | 13–16 stem diameter growth rate |
|---------------|-----------------|----------------|--------------------------|---------------------------------|
|               | \(\chi^2\)††    | \(P\)          | \(F_1\) \(F_2\) \(P\)  | \(F_1\) \(F_2\) \(P\)         | \(F_1\) \(F_2\) \(P\)         |
| A) Bur oak    |                 |                |                          |                                 |
| Ecotype       | 0.75            | 0.38           | 10.96                    | \(0.001\)                       | 16.30                          | \(<0.0001\)                     | 1.51                            | 0.22                           |
| Latitude      | 2.71            | 0.10           | 62.77                    | \(<0.0001\)                      | 38.33                          | \(<0.0001\)                     | 0.49                            | 0.48                           |
| Longitude     | 0.02            | 0.89           | 0.06                     | 0.80                            | 20.16                          | \(<0.0001\)                     | 0.99                            | 0.32                           |
| Eco × Lat     | 2.02            | 0.15           | 0.07                     | 0.80                            | 1.06                           | 0.30                           | 2.46                            | 0.12                           |
| Eco × Long    | 0.40            | 0.53           | 0.49                     | 0.48                            | 0.89                           | 0.35                           | 8.96                            | \(0.003\)                      |
| Lat × Long    | 0.70            | 0.40           | 36.29                    | \(<0.0001\)                      | 15.44                          | \(<0.0001\)                     | 0.10                            | 0.75                           |
| B) Red oak    |                 |                |                          |                                 |
| Ecotype       | 5.12            | \(0.02\)       | 64.21                    | \(<0.0001\)                      | 10.73                          | \(0.001\)                       | 13.80                           | \(0.0002\)                     |
| Latitude      | 4.51            | \(0.03\)       | 104.48                   | \(<0.0001\)                      | 23.51                          | \(<0.0001\)                     | 12.60                           | \(0.0004\)                     |
| Longitude     | 5.85            | \(0.02\)       | 0.04                     | 0.84                            | 10.57                          | \(0.001\)                       | 0.03                            | 0.86                           |
| Eco × Lat     | 0.004           | 0.94           | 0.39                     | 0.53                            | 0.43                           | 0.51                           | 0.63                            | 0.43                           |
| Eco × Long    | 0.05            | 0.82           | 3.17                     | 0.08                            | 0.40                           | 0.53                           | 0.04                            | 0.84                           |
| Lat × Long    | 6.23            | \(0.01\)       | 75.43                    | \(<0.0001\)                      | 11.61                          | \(0.0007\)                      | 11.42                           | \(0.0008\)                     |

Notes: Bold indicates statistical significance, \(P < 0.05\). Seedlings were sourced from two adjacent seed zones, northcentral (NC104) and central (C105) Minnesota (i.e., Ecotype [Eco] and planted into 16 sites (i.e., Latitude [Lat], Longitude [Lon]). Measured traits included survival from the time of planting in 2013 until 2016 (13–16 survival), specific leaf area measured in 2014 (SLA), and growth rate between 2013 and 2016 in terms of plant height (13–16 height) and stem diameter (13–16 stem diameter).

† df = 1, 1076.
†† df = 1, 1103.
§ df = 1, 1068.
¶ df = 1, 1049.
‖ df = 1, 953.
‖‖ df = 1, 961.

For bur oak, a repeated-measures analysis of variance of the 2014 and 2015 phenology data (Table 3A) showed that the timing of budburst did not differ significantly between the ecotypes (Fig. 2e). However, the interaction between ecotype and latitude was significant. Using 2014 data as an example, NC104 had earlier budburst than C105 in southern sites, but the ecotypes did not differ in northern sites. Bur oak budburst phenology was also strongly influenced by latitude, longitude, and the interaction between these two factors. For example, in 2014, there was a steep cline across latitude in the timing of budburst in eastern sites (Δ40 d), but a shallow cline in western sites (Δ8 d; Fig. 3e). Bur oak budburst phenology did not differ over time either as a main effect or as an interaction with other factors. Budburst of red oak NC104 occurred earlier than C105 (Table 3B, Fig. 2e). Red oak budburst phenology was strongly influenced by environmental factors that covary with latitude, longitude, and interaction between these two factors. Strikingly similar to bur oak (Fig. 3f), the timing of red oak budburst was strongly clinal across latitude in eastern sites (Δ33 d) compared to western sites (Δ3 d). The timing of red oak bud burst differed over time. On average, budburst was 11 d earlier in 2015 compared to 2014. Time interacted with ecotype, ecotype × latitude, and latitude × longitude (Table 3). For each of these interactions, the dominant pattern was that ecotypes differed less in 2015 than in 2014.

In the fall, the timing of bur oak leaf senescence differed between the ecotypes with NC104 leaves turning color earlier than C105 (Table 3A, Fig. 2f). The timing of leaf senescence also varied with longitude and the interaction between latitude and longitude. As with previous traits, we detected a strong cline across latitude for the timing of leaf senescence in eastern sites that was weaker in western sites. However, as with patterns observed for budburst phenology, ecotypic differences diminished between 2014 and 2015, as indicated by significant time × longitude and time × latitude × longitude interactions (Table 3A). The timing of leaf senescence differed only slightly between red oak ecotypes, with NC104 leaves turning less than 1 d earlier than C105 (Table 3B, Fig. 2f). However, the red oak ecotypes also differed across latitude; NC104 leaves changed color earlier at southern sites compared to northern sites, whereas timing of color change for C105 leaves did not vary across latitude. As with previously described traits, these differences were less striking in 2015 relative to 2014, as indicated by significant interactions including time × longitude and time × ecotype × latitude. The different degree to which ecotype differentiation was observed in 2014 vs. 2015 may be due in part to variation in spring temperature between the two years. In 2014, temperatures were cooler than 1981–2010 averages (April, −2.6°C; May, −0.4°C) compared to 2015 (April, 0.2°C; May, −0.4°C). Fall temperatures also varied between 2014 and 2015. In 2014, fall temperatures...
tracked closer to average (September [0.5°C] and October [0.7°C]), whereas while 2015 temperatures were much warmer than average (September [3.3°C] and October [1.6°C]; Midwestern Regional Climate Center 2019).

For both oak species, ecotypic differences were evident for the number of days during the growing season that seedlings bore chlorophyllous leaves. C105 of both bur oak and red oak retained green leaves longer than did NC104 (Table 3A, B, Fig. 2g). Also, for both species, duration of leaf retention was influenced by the environmental gradients associated with latitude and the interaction between latitude and longitude. In parallel with other traits, there was a strong cline across latitude in eastern sites but not in western sites. For bur oak (Table 3A), differences between the ecotypes diminished in 2015 relative to 2014 as reflected in the significant effects of time, time × latitude, time × longitude, and the three-way interaction. For red oak, in contrast (Table 3B, Fig 2g), the number of days of leaf retention was temporally stable even though the onset of budburst and leaf senescence shifted between the years.

### Natural selection

In the first set of analyses, we estimated selection intensities, $i$, based on survival of the seedlings from the date of planting in 2013 until fall 2016 (Table 4A). Overall, the analyses revealed significant selection on slightly more than one-half of the juvenile traits (66%). The direction and magnitude were

| Factor                  | 14–15 date of budburst | 14–15 date of leaf senescence | 14–15 days of leaf retention |
|-------------------------|------------------------|-------------------------------|-----------------------------|
| **A) Bur oak**          |                        |                               |                             |
| Ecotype (Eco)           | 0.08                   | 0.77                          | 68.34                       | <0.0001                    | 6.94             | 0.009       |
| Latitude (Lat)          | 166.07                 | <0.0001                       | 0.28                        | 0.60                       | 58.12            | <0.0001     |
| Longitude (Lon)         | 3.75                   | <0.0001                       | 7.16                        | 0.008                      | 0.69             | 0.41        |
| Eco × Lat               | 4.96                   | 0.03                          | 0.75                        | 0.39                       | 0.02             | 0.90        |
| Eco × Long              | 0.42                   | 0.52                          | 1.92                        | 0.17                       | 0.56             | 0.45        |
| Lat × Long              | **234.29**             | <0.0001                       | **4.33**                    | 0.04                       | 33.12            | <0.0001     |
| Time                    | 2.05                   | 0.15                          | 3.06                        | 0.08                       | 14.27            | 0.0002      |
| Time × Eco              | 0.83                   | 0.36                          | 1.55                        | 0.21                       | 2.23             | 0.14        |
| Time × Lat              | 0.56                   | 0.46                          | 0.18                        | 0.67                       | 7.14             | 0.008       |
| Time × Long             | 2.98                   | 0.08                          | **12.42**                   | 0.0005                     | 20.59            | <0.0001     |
| Time × Eco × Lat        | 0.53                   | 0.47                          | 0.41                        | 0.52                       | 1.10             | 0.30        |
| Time × Eco × Long       | 1.75                   | 0.19                          | 1.29                        | 0.26                       | 1.39             | 0.24        |
| Time × Lat × Long       | 3.24                   | 0.07                          | **6.17**                    | 0.01                       | **8.72**         | 0.003       |

**B) Red oak**

| Factor                  | 14–15 date of budburst | 14–15 date of leaf senescence | 14–15 days of leaf retention |
|-------------------------|------------------------|-------------------------------|-----------------------------|
| Ecotype                 | 5.72                   | 0.02                          | 4.85                        | 0.03                       | 15.64            | <0.0001     |
| Latitude                | 98.15                  | <0.0001                       | 0.06                        | 0.80                       | **49.65**        | <0.0001     |
| Longitude               | 8.84                   | 0.003                         | 8.37                        | 0.004                      | 0.97             | 0.33        |
| Eco × Lat               | 2.6                    | 0.11                          | 7.16                        | 0.008                      | 0.69             | 0.41        |
| Eco × Long              | 1.38                   | 0.24                          | 2.45                        | 0.12                       | 1.31             | 0.25        |
| Lat × Long              | **136.05**             | <0.0001                       | 0.24                        | 0.62                       | **36.40**        | <0.0001     |
| Time                    | 1.71                   | 0.19                          | 0.003                       | 0.95                       | 0.34             | 0.56        |
| Time × Eco              | **4.01**               | 0.05                          | 0.05                        | 0.83                       | 1.23             | 0.27        |
| Time × Lat              | 1.99                   | 0.16                          | 1.95                        | 0.16                       | 1.03             | 0.31        |
| Time × Long             | 0.23                   | 0.63                          | **4.45**                    | 0.04                       | 0.004            | 0.95        |
| Time × Eco × Lat        | **4.68**               | 0.03                          | **11.40**                   | 0.0008                     | 0.18             | 0.67        |
| Time × Eco × Long       | 1.91                   | 0.17                          | 2.77                        | 0.10                       | 0.63             | 0.43        |
| Time × Lat × Long       | **10.58**              | 0.001                         | 0.31                        | 0.58                       | 0.002            | 0.97        |

**Notes:** Bold indicates statistical significance, $P < 0.05$. Seedlings were sourced from two adjacent seed zones, northcentral (NC104) and central (C105) Minnesota (i.e., Ecotype) and planted into 16 sites (i.e., latitude, longitude). Phenological traits measured bimonthly (day of year [time]) in 2014 and 2015 included date of budburst, date of year of leaf senescence, and number of days that leaves were retained on the plant during the growing season.

† df = 1, 1153.
‡ df = 1, 1128.
§ df = 1, 658.
¶ df = 1, 687.
# df = 1, 299.
|| df = 1, 356.
remarkably consistent between species. When survival was used as the metric of fitness, natural selection favored bur oak individuals with faster growth rates, lower SLA (~thicker leaves), and earlier budburst (Table 4A). These results were the same for red oak except that thicker stems and later leaf senescence were also favored. When growth rate was used as a metric of fitness, natural selection favored individuals with thicker stems, lower SLA, earlier budburst and a greater number of days where leaves were retained during the growing season (Table 4B). A later leaf retention date was also favored for bur oak.

**Discussion**

This study was conducted within the southern-boreal–north-temperate forest transition zone with the boreal forest to the north, temperate hardwood dominated forests to the south, and the prairie-forest ecotone to the west. At present, this region is dominated by boreal species at the southern edge of their ranges with relatively low abundance of temperate species close to their northern range limits. However, boreal species are already in decline (Muilenburg and Herms 2012) and forecasts of future species composition predict continued loss of these northern forest constituents and an increase in temperate species, including oaks and northern hardwood species (Duveneck et al. 2014b). Temperate species are also already recruiting into these boreal forests, but this expansion is dominated by few species, especially red oak (*Acer rubrum*) and sugar maple (*Acer saccharum*) (Ravenscroft et al. 2010, Fischelli et al. 2014a, b). We should caution that the differences between species and ecotypes were observed during the first 3 yr following planting. Nonetheless, our early results suggest that forestry-assisted migration (AM) of species with more southern distributions, including source material obtained from one seed zone further south, may be an important strategy to enhance species richness and address adaptation lags in Great Lakes forests as climate changes. Further monitoring of seedlings in the years to come will help determine whether the benefits of an AM approach persist over time.

**Enhancing diversity by planting temperate species into boreal forests as they decline**

In order to transition northern forests into diverse stands that are more likely to persist through climate change, we enhanced forest diversity by planting tree species predicted to thrive in the future. Our results indicate that this climate management strategy may be effective. After four seasons of exposure to natural selection, bur and red oak, each of which is presently at low abundance near the northern periphery of their ranges, had exceptionally high survival and vigorous growth. This result suggests that these species are well adapted to the contemporary climate of this region, which has already warmed substantially. Of course, it is premature to draw firm conclusions based on a short-term study of species that can live for centuries. Nonetheless, vigorous growth at the early stages of seedling establishment is a good indicator of survival and reproductive potential over the longer term (Gamache and Payette 2004), although it is also possible this early growth is not sustainable as climate fluctuates (Jump et al. 2017). We will continue to monitor these trees over time. But, at least at this time point, our transition strategy for forest management appears to be an effective means of transitioning these forests toward a species composition that is more likely to persist into the future.

**Decoupling of plant adaptations within fixed seed zones and current climate**

The failure of the seed zone model to provide the best fit for the data for the majority of traits in this study undermines the assumption of local adaptation upon which the fixed seed zone framework rests. It is possible that this decoupling of plant adaptations within fixed seed zones and current climate is present in any geographic region characterized by local adaptation but also undergoing rapid climate change. The likelihood of adaptation lags underscores the need to experimentally reevaluate fixed seed zones in this era of climate change (Ying and Yanchuk 2006, McKenney et al. 2009, Hamann et al. 2011, Leech et al. 2011, Ukrainetz et al. 2014).

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**Table 4.** The intensity of selection (i) showing the strength and direction of natural selection on a complete set of juvenile morphological and phenological traits measured in 2014.

| Parameter                        | Bur oak          | Red oak        |
|----------------------------------|------------------|----------------|
|                                  | i         | P     | i     | P     |
| A) Survival                      |             |       |       |       |
| Height growth                    | 0.01      | 0.01  | 0.03  | <0.0001 |
| Stem diameter                    | 0.02      | 0.09  | 0.04  | 0.002  |
| Specific leaf area               | -0.04     | <0.0001 | -0.05 | 0.0002 |
| Date of budburst                 | -0.07     | <0.0001 | -0.04 | <0.0001 |
| Date of leaf senescence          | -0.001    | 0.71  | 0.01  | 0.05   |
| Days of leaf retention           | 0.01      | 0.78  | 0.02  | 0.38   |
| B) Height growth rate            |             |       |       |       |
| Stem diameter                    | 0.03      | <0.0001 | 0.04  | <0.0001 |
| Specific leaf area               | -0.05     | <0.0001 | -0.05 | <0.0001 |
| Date of budburst                 | -0.02     | 0.0002 | -0.02 | 0.0008 |
| Date of leaf senescence          | 0.03      | <0.0001 | -0.004 | 0.39  |
| Days of leaf retention           | 0.03      | 0.01  | 0.02  | 0.0006 |

**Notes:** Significant linear selection intensities (*i*, the covariance between relative fitness and standardized trait values) appear in boldface type. Traits were measured on seedlings of two oak species, bur oak (*Quercus macrocarpa*) and northern red oak (*Q. rubra*). Relative fitness was calculated in two ways based on (A) survival from the 2013 planting date until fall 2016 and (B) 2014–2016 average height growth rate.
2011, Loya-Rebollar et al. 2013). Current seed zones in Minnesota are categorical, coarse descriptions of environmental variation over a large geography. The superior performance of the climate and geographic position models, both of which included continuous covariates for the planting sites, suggest that flexible seed zones may be more appropriate.

Our results provide clear evidence that plants sourced by MN DNR from the two seed zones are genetically differentiated. Pronounced differences between ecotypes were found for all red oak traits and 86% of bur oak traits. For all but one trait (survival of bur oak), either the ecotype main effect or its interaction with latitude were significant. Importantly, the southern ecotype of both species expressed traits that are consistent with expectations for climate adaptation. This inference is especially clear for red oak where, relative to the northern ecotype, the southern ecotype had higher survival, lower SLA, faster vertical and radial growth, and an extended leaf phenology that would permit photosynthesis to occur for more days during the growing season. Overall, the results for bur oak were somewhat weaker. Nevertheless, the southern ecotype of bur oak had lower SLA, later leaf senescence, and a longer period of leaf retention. At first glance, the bur oak growth results may seem counterintuitive; C105 had substantially lower growth rates than NC104, the opposite of expectation. However, given bur oak’s tendency to allocate to belowground growth during early Bur stages (Danner and Knapp 2001), this pattern could still be adaptive. To confirm this hypothesis, it will be necessary to sacrifice a subset of trees and measure relative growth allocation to above- and belowground biomass.

Phenotypic selection analyses further supported the hypothesized value of the traits associated with the southern population. For example, selection analyses on red oak showed that faster vertical growth was favored (Table 4A), and it was the southern ecotype, C105, that expressed this trait (Fig. 2b). In other words, across the study area, natural selection appears to be favoring the trait values of the southern ecotype over the northern ecotype. The same logic can be applied to red oak stem growth; C105 had faster radial growth (Fig. 2c) than NC104 and thicker stems were strongly favored in both selection analyses (Table 4A, B). Finally, for both species, C105 had lower SLA than NC104 (Fig. 2d) and lower SLA was consistently favored in the selection analyses. This strongly suggests that populations within seed zones have previously been molded by natural selection, but their adaptations no longer match the conditions that they experienced during the years of this study.

The interpretation of patterns in spring and fall phenology are more complicated. Previous studies have shown that spring phenological events respond to photoperiod, temperature, and chilling in the preceding season (Heide 1974, 1993a, b, 2005, Ghelardini et al. 2010, Polgar and Primack 2011, Basler and Körner 2012, Laube et al. 2014, Polgar et al. 2014, Way and Montgomery 2015). For long-lived species, populations are expected to be differentiated with respect to photoperiodism, which stabilizes the release and onset of dormancy while permitting more minor modulation by temperature (reviewed in Körner and Basler 2010). However, other studies have shown that phenological drivers may be more variable than previously thought (Rohde et al. 2011). And, to the best of our knowledge, the environmental factors that govern phenology in these oak species have not previously been studied. Nevertheless, the present study clearly shows that the ecotypes of these oak species are genetically differentiated with respect to phenology, although we did also observe seasonal differences between the two species. Specifically, bur oak phenology differed between ecotypes in the fall, but not the spring, whereas red oak ecotypes differed in the spring, but not the fall (Fig. 2e, f). It remains to be determined how adaptive these traits are over the longer-term when late spring and early fall frosts may damage plants with extended phenologies (Way 2011, Benito-Garzón et al. 2013, Vitasse et al. 2014).

Given these contrasting phenological difference between the two oak species, we focused on number of days between budburst to chlorophyll degradation, the time when the seedlings could have been actively photosynthesizing. Our hypothesis was that trees that can take advantage of the extended growing season by retaining longer leaf function would be favored by selection (Way 2011). In the years that we collected our data, this hypothesis was supported. Both species were under significant selection for an extended leaf-out period (Table 4), a trait that was exhibited by the southern ecotype of both species (Fig. 2g). Other studies have found similar results where spring and fall phenology and the length of the growth period were related to plant fitness (Menzel and Fabian 1999, Rouss and Pusenius 2005, Menzel et al. 2006, Ibanez et al. 2010). However, some caution is warranted; ecosystem-level observations (models of CO₂ fluxes and remotely sensed vegetation greenness) indicate that northern terrestrial ecosystems are more likely to lose rather than sequester carbon because of differential impacts on photosynthesis and respiration of spring vs. fall warming (Piao et al. 2008). Nevertheless, our study revealed ecotype differences for the vast majority of traits and, in most cases, natural selection across the study area favored the trait values of the southern ecotype of both species. Based on these results, we anticipate that natural selection will continue to hone variation in a way that favors southern ecotypes in these experimental plantings over time. Continued monitoring of these long-lived species is necessary to determine the extent to which this expectation is borne out.

Phenotypic plasticity and its implications for seed transfer guidelines

In this study, we observed striking patterns of phenotypic plasticity in both temporal and spatial dimensions.
Temporal plasticity was evident in spring phenology; ecotype differences were stronger in 2014 than 2015. This apparent plasticity could either mean that the seedlings are sensitive to inter-annual climate variation or that they are acclimating over time. If trees are acclimating, we expect that seedling traits will converge at the planting sites in the future, which will likely enhance their fitness but will reduce our ability to distinguish the ecotypes and erode the advantages of AM that now are apparent. Previous studies have shown that ecotypic differences that were apparent in field populations may not persist when the plants are reared in a common garden (Lee et al. 2005). Such phenotypic plasticity can be adaptive, especially when climate conditions fluctuate (Richter et al. 2012).

Despite the relatively small area encompassed by this study, our analyses also revealed steep phenotypic clines across latitude and longitude, which were remarkably consistent between traits. Within the study area, mesoscale (50–500 km²) differences in temperature and precipitation underlie the position of biome ecotones, leading to variation in growing season evapotranspiration and available soil moisture for plant growth (Velpur et al. 2013). Experiment-wide, 78.6% of the traits studied were strongly influenced by environmental conditions associated with latitude, 64.3% with longitude, and 85.7% with the combination of latitude and longitude. Clines were especially precipitous in eastern sites, whereas they were more gradual, or even nonexistent, in western sites.

Although spatial patterns of plasticity across latitude and longitude were qualitatively similar for bur and red oak, they differed with respect to significance. For bur oak traits, 42% of geographic factors (i.e., latitude, longitude, or latitude × longitude) were statistically significant. In contrast, nearly twice as many of these factors, 83%, were significant for red oak traits. This discrepancy may indicate that red oak is more plastic than bur oak. If phenotypically plastic responses are adaptive, then red oak may have a greater opportunity to acclimate to monotonic changes in climate or respond rapidly to erratic variation over time. Although plasticity in response to a diverse set of environmental treatments has been reported for both bur oak (Tang and Kozlowski 1982, Parker and Pallardy 1988, Woodcock 1989, St-Jaques et al. 1991, Hamerlynck and Knapp 1994, 1996, Danner and Knapp 2001, Drunasky and Struve 2005) and red oak (Kolb and Steiner 1990, Kolb et al. 1990, Abrams 1994, Nagel et al. 1998, Percival 2005, Gunderson et al. 2010, White et al. 2011, Gailing et al. 2012, Bauweraerts et al. 2013), few experiments have included both species simultaneously, making comparison difficult. However, three studies that tested both bur and red oak failed to show species-specific differences in plasticity in response to herbaceous competition or rodent damage (Laliberté et al. 2008), photosynthetic acclimation to warming (Sendall et al. 2015), or to crossed-treatments of temperature, precipitation, and litter depth (Fisichelli et al. 2014a, b). In contrast, the interspecific differences in plasticity observed in our study may have resulted from the source material used for experimentation or the environmental heterogeneity to which seedlings were exposed under natural, rather than experimental, conditions.

Our results suggest two conclusions with respect to phenotypic plasticity. First, the plant ecotypes of both burr and red oak are highly plastic and responded to environmental clines across the study area, which include temperature, precipitation, day length, and distance from Lake Superior. Moreover, it is likely that this plasticity is adaptive because the direction of the plasticity (e.g., earlier budburst and thicker leaves in lower vs. higher latitudes) was also favored by natural selection. Second, the strong pattern of clinal variation across the study area suggests that seed zone boundaries could be more flexible, especially in western sites (longer seed transfer distances), whereas more divisions may be warranted in the east (shorter seed transfer distances). Overall, these results underscore the importance of considering environmental gradients across the landscape, even within existing fixed seed zones, as managers refine seed transfer zone concepts and implementation.

The value of AM in northeastern Minnesota

This study showed that southern source material of bur oak and red oak can thrive in the northerly sites where they were planted. In fact, survival was slightly higher, albeit only significantly so for red oak, for the more southern ecotype of both species. As we continue to monitor survival, growth and phenological traits across the study area, we expect that this pattern will strengthen in the future for several reasons. First, at this point in the experiment, survival is simply high and, as more seedlings die over time, we anticipate having greater statistical power to distinguish the ecotypes and ascertain which traits confer adaptive advantages in the study area. Second, based on ecotypic differences for important functional traits reported herein, such as SLA, stem diameter growth, and leaf phenology, we expect that the southern ecotype for both species will continue to have high performance and eventually attain numerical dominance at the planting sites.

Policy implications

Based on our findings, adjusting the choice of species for forest regeneration in anticipation of future compositional change may be warranted in areas where climate change is occurring rapidly. This approach may be especially valuable as a mechanism to enhance forest diversity within species’ existing ranges. During the transitional period in which plant communities are reorganizing in response to climate change, AM may be especially important to consider in the early phases of assembly (Lockwood et al. 1997). Even before climate
change was driving the conversation, foresters advocated for a “floating principle” of seed transfer, which permits the transfer of a seedlot beyond its seed zone boundaries as long as it remains within its adaptive limits (Rehfeldt 1983). In light of climate change, flexible seed transfer guidelines have already been developed for some North American species based on the best possible information, including provenance trials (Rehfeldt et al. 1999, Rehfeldt 2004, Bower and Aitken 2008, O’Neill et al. 2008, Rehfeldt and Jaquish 2010, Thomson et al. 2010, Chakraborty et al. 2018) and genomic data (Hamann et al. 2011). The vexing issue is that, except for economically important species for forestry, there is little information available on adaptive limits for most species (Shaw and Etterton 2012). The native species of Minnesota forests largely fall into this category. Although we appreciate the value of comprehensive data to inform assisted migration, these pieces of information simply do not exist for the study area.

Recommendations for developing climate-informed seed transfer guidelines

Our recommendations are fourfold. First, provenance trials should be established now that include species predicted to perform well in future environments in this region (Duveneck et al. 2014a). With a more complete data set that includes more species, populations, and environmental variation, species-specific transfer distances can be developed using univariate or multivariate curve-fitting techniques to identify geographic areas where the source material grows fastest and expresses adaptive traits (Raymond and Lindgren 1990, Roberds et al. 1990, Lindgren and Ying 2000, Crowe and Parker 2005). Second, state seed zone guidelines should be made less restrictive such that within-range assisted migration is permitted, at least to the extent that seed sources are rematched with the climates that have already shifted to the north, as was done in this experiment. Such modest adjustments to the current Minnesota seed zone policy could be readily implemented within the existing statewide framework of seed collection and outplanting. Third, the origin of seed sources should be documented, even within the seed zones, so that the Minnesota State Nursery that distributes plant material to federal, state, county, and more entities can proactively recruit these agencies to establish numerous informal experiments over smaller spatial scales that serve the dual function of regenerating forests and providing information to inform development of seed transfer guidelines for our state. Finally, if regional land management agencies are unable to invest in collecting critical information to modify seed zone policy, we suggest turning to national entities for assistance. For example, the USDA Forest Service is currently gathering the basic foundational information needed to develop climate-informed seed transfer guidelines that support a full complement of climate management approaches in forests (Pike et al. 2017).

This study tested forestry-AM practices in the context of the current framework of seed sourcing and seed transfer policies in Minnesota. In Minnesota, population provenance records are not maintained during seed collection. Instead, they are pooled within seed zones, such that some or all of the “local” seed source could have actually originated from outside of the study area. In fact, seedlings obtained from seed zone NC104 could have been sourced from populations living at the prairie–forest border ecotone in central Minnesota, a region >300 km away that is both warmer and drier than the study area. In contrast, it is highly unlikely that the seeds were sourced from further east because the DNR does not harvest from populations adjacent to Lake Superior. This prohibition exists because seeds sampled from the coastal forests frequently fail to establish when planted elsewhere within their seed zones. This, in itself, suggests that an adjustment of seed zone boundaries is warranted or at least should be evaluated more thoroughly in an experiment with greater seed source control. The utility of coarse seed zones for tracking provenance has been greatly diminished as we enter the climate change era. Our study demonstrates the utility of incorporating information about adaptation and natural selection to make climate-informed adjustments to seed sourcing guidelines.

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SUPPORTING INFORMATION
Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2092/full

DATA AVAILABILITY
Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.w3r2280m5