# UC Davis
## UC Davis Previously Published Works

**Title**

Mixed-provenance plantings and climatic transfer-distance affect the early growth of knobcone-monterey hybrid pine, a fire-resilient alternative for reforestation

**Permalink**

https://escholarship.org/uc/item/49r9v75j

**Authors**

Looney, Christopher E
Stewart, Joseph AE
Wood, Katherine EA

**Publication Date**

2023

**DOI**

10.1007/s11056-023-09991-9

Peer reviewed

**RESEARCH**

# Mixed-provenance plantings and climatic transfer-distance affect the early growth of knobcone-monterey hybrid pine, a fire-resilient alternative for reforestation

Christopher E. Looney[1] · Joseph A.E. Stewart[2] · Katherine E.A. Wood[3]

## Abstract

Given increasing forest disturbances, novel solutions are needed to rapidly recover ecosystem services such as carbon storage, while bolstering climate change adaptation. Reforestation with single-species mixed-provenance plantings is an emerging strategy that may enhance stand productivity and disturbance resistance, while assisted gene flow is a potentially powerful tool for matching seed-source with future planting-site climate. We investigated the potential of mixed-provenance plantings and assisted gene flow for maximizing early growth using a historical dataset for knobcone-Monterey pine (*Pinus x attenuradiata*), a fire-resilient hybrid developed for low-elevation sites in California, USA. We examined (1) 9-year individual-tree relative growth rate (RGR) in response to neighborhood seed-parent provenance diversity at two test sites and (2) 3-year RGR and survival as functions of parent seed-source climate at 4 test sites. We found 9-year RGR varied with seed provenance diversity, with 3 of 5 provenances showing a positive RGR-diversity relationship. Parent seed-source climate affected 3-year RGR but not survival. Closer climate matches in terms of precipitation as snow (PAS) showed fastest growth. Our results suggest careful selection and arrangement of genetically diverse stock may improve carbon sequestration and initial planting success in a hybrid conifer, with implications for reforestation under climate change and reburn risk.

**Keywords** Diversity-ecosystem function · Climatic transfer distance · Assisted gene flow · *Pinus radiata* · *Pinus attenuata* · Climate-change adaptation · Provenance trial

## Introduction

Resilience is the capacity of ecosystems to return to baseline conditions following disturbance or stress (Malmsheimer et al. 2009). In the forests of the western U.S., climate change-related high-severity wildfire and drought are among the most immediate threats to forest ecosystem resilience (Buotte et al. 2019). High-severity fire can challenge forest resilience by eliminating seed sources of most coniferous tree species (Stevens-Rumann et

---

Extended author information available on the last page of the article

al. 2018) and creating high-severity burn areas that exceed typical seed-dispersal distances (Shive et al. 2018). Drought may negatively impact forest resilience by impeding natural regeneration (Davis et al. 2019; Stewart et al. 2021), with replanting commonly required to achieve conifer reforestation goals (Ouzts et al. 2015).

Maximizing young stand growth is a key strategy for rapidly recouping lost forest carbon and promoting stand resilience to wildfire (Zhang et al. 2008). Whereas typical reforestation species such as ponderosa pine (*Pinus ponderosa* ex C. Lawson) have high fire resistance when mature (Johnston et al. 2019), small trees remain vulnerable. Young reforested conifer stands are susceptible to both lethal fire-related girdling and crown scorch, even under low-intensity surface fire (York et al. 2021). Accelerating stand development reduces rotation age, thus lowering risk in the face of increasingly frequent reburns under climate change (Zimová et al. 2020).

In the western U.S., most research has focused on silvicultural practices such as site preparation, competing vegetation control, and fertilization to accelerate young stand development (McDonald and Fiddler 2010; Powers and Reynolds 2011). Promoting genetic diversity during replanting may further enhance young stand resilience via facilitation and, particularly, competition-reduction mechanisms. For example, differences in crown shape or rooting habits may reduce competition by promoting more efficient resource use (Forrester and Bauhus 2016). Intraspecific genetic diversity reduced competition and increased growth in experimental *Eucalyptus* plantations (Boyden et al. 2008). Mixed-family plantings of Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco) outgrew single-family plantings when mixtures were selected either to maximize contrasts in potential genotype growth rates or for highest growth potential (Gould et al. 2011). In a German study of Norway spruce (*Picea abies* L.), mixed-provenance plantings fostered a diversity of crown morphology that enhanced growth by up to 25% relative to single-provenance plantings (Pretzsch 2021).

Mixture effects may also be neutral or negative. An Arizona study of planted cottonwood (*Populus fremontii*) genotypes did not find a positive productivity-diversity relationship (Fischer et al. 2017). A study of loblolly (*Pinus taeda L.*). and slash (*Pinus elliotii* Engelm.) pines found that mixed-family plantings have reduced growth, higher mortality, and greater rust damage compared to single-family deployments (Zhai et al. 2015). Genetic diversity has also been found to increase stand structural complexity, with negative implications for young stand productivity (Aspinwall et al. 2011).

Beyond the potential to enhance overall productivity, mixed-provenance plantings may better insure against poor acclimation, extreme weather events, and insects and pathogens (Yachi and Loreau 1999; Pretzsch 2005; Jucker et al. 2014). A bet-hedging strategy may be particularly important under climate change, given that climate is an uncertain target and seed transfers may lead to unanticipated interactions with forest pests and pathogens (Grady et al. 2015). Whereas provenance test data have been synthesized into climate transfer functions for guiding climate-smart seed selection for reforestation in the western U.S. (Griffin and Conkle 1967; Stewart et al. 2021; St. Clair et al. 2022), research to date has focused on pure conifer species or naturally occurring hybrids (e.g., Rweyongeza et al. 2007; Ukrainetz et al. 2011). Whether similar growth-climate transfer relationships apply to F1 hybrid conifers, where seed and pollen sources can be manipulated independently, is unresolved.

Fire adaptations such as serotiny, in which trees retain a substantial canopy seed bank of fire-opened cones (Rodríguez-Trejo and Fulé 2003), could bolster young-stand resilience from severe wildfire. In interior California, knobcone pine (*Pinus attenuata* Lemmon)

is the only strongly serotinous *Pinus* species. Combining the rapid juvenile growth and straighter stem form of maritime Monterey pine (*Pinus radiata* D. Don) pollen parents with the drought- and frost-tolerance of knobcone pine seed parents yields a drought-resistant, serotinous hybrid (*Pinus x attenuradiata* Stockw. & Right, KMX pine), which Oliver (1979) posited may also help reduce risk from reburns, potentially lending KMX pine renewed relevance today.

This study revisits a historical dataset from a 1963 provenance trial of KMX pine established in Trinity County, CA (Griffin and Conkle 1967). The objective of the original experiment was to evaluate KMX pines derived from knobcone mother trees growing in Oregon's Siskiyou Mountains against stock sourced from knobcone mother trees from California's central Sierra Nevada. Initial results showed high growth and survival that improved upon pure trees of either species (Griffin and Conkle 1967), although the hybrid subsequently proved vulnerable to snow and frost damage (Oliver 1979). The experiment tested ≥ 48 unique genetic combinations across four test sites, with carefully surveyed stem maps and data available through 1973 for two test sites. Overall, it offers a unique spatial dataset for addressing diversity-productivity and climate transfer topics. Using this dataset, we investigated: (1) whether genetically diverse tree neighborhoods altered individual tree growth, and (2) whether climatic transfer distance affected early growth and survival, with implications for productivity in both single- and mixed-provenance stands.

## Methods

### Test sites

The four test sites–Spring Gulch near Douglas City, CA; Tom Lang Gulch near Lewiston, CA; East Fork Burn near French Gulch, CA; and Platina near Platina, CA—were established in 1963–1964 (Fig. 1) on Bureau of Land Management land in the Klamath Mountains of California. Locations were selected to test the potential of KMX pine to convert low-elevation brushfields or low-productivity forestlands into higher productivity timberlands. Soils are generally poorly developed, coarsely textured, and derived from sedimentary or metamorphic parent materials (Table 1). Soils are classified as: fine, oxidic, thermic Haplic Palexeralfs at Spring Gulch; loamy-skeletal, oxidic, mesic Mollic Haploxeralfs at Tom Lang Gulch; loamy-skeletal, mixed, active, mexic Ultic Haploxeralfs at East Fork Burn Site; and loamy-skeletal, mixed, mesic, Dystric Xerochrepts at Platina. The climate is Mediterranean, with hot summers and cool, wet winters with occasional snow and frost. Test sites arranged in order of increasing mean annual precipitation (MAP) are Platina, Tom Lang Gulch, Spring Gulch, and East Fork Burn. Test sites arranged in order of increasing mean annual temperature (MAT) are Spring Gulch, Tom Lang Gulch, East Fork Burn, and Platina. Platina and East Fork Burn have the longest frost-free periods (FFP, Online Table S1).

Test sites were positioned to prioritize uniform site conditions, with terrain characterized by shallow-steep, north-to-east facing slopes. Tom Lang Gulch was historically Oregon white oak (*Quercus garryana* Douglas ex Hook.) and gray pine (*Pinus sabiniana* Douglas ex D. Don) woodland. Spring Gulch and Platina did not historically support forest vegetation and were dominated by chaparral species, principally chamise (*Adenostoma fasciculatum* Hook. & Arn.). East Fork Burn was a ridgetop site burned in 1962 and salvaged. Tom
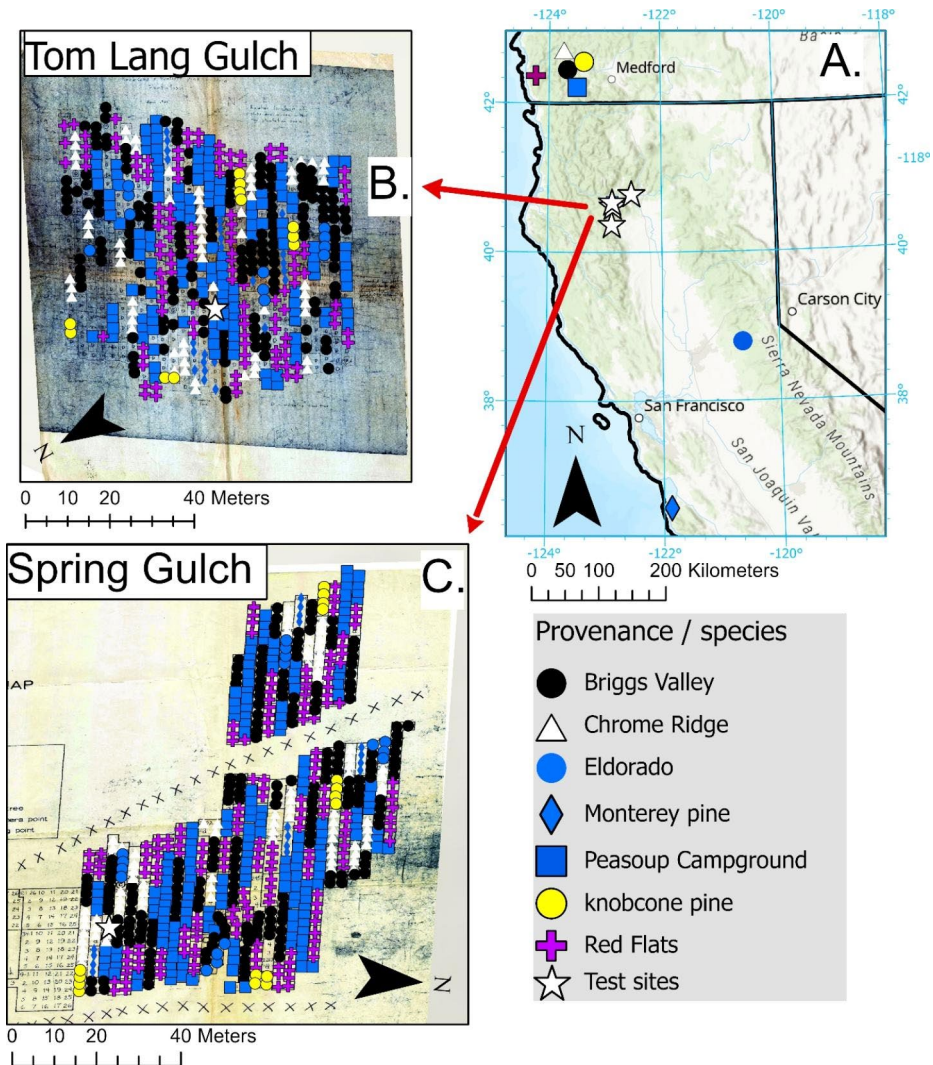
**Fig. 1** Maps showing locations of provenances, test sites, and planting configurations
**(A)** Locations of California and Oregon seedling provenances and California test sites. Knobcone pine parent check, Chrome Ridge and Peasoup Campground provenances were jittered for visibility; actual Briggs Valley location is shown. **(B)** Detail map of georegistered Tom Lang Gulch test site showing survival as of 1966. **(C)** Detail map of georegistered Spring Gulch test site showing survival as of 1966. Single seed-source plots to the left of the digitized mixed-provenance plantings were excluded from the study for lack of post-1966 data

Lang Gulch and East Fork Burn were expected to be the most favorable test sites for survival and growth, with lower performance expected at Spring Gulch and Platina due to steep terrain and lower elevation, respectively (Griffin and Conkle 1967). Platina was established as a smaller, auxiliary test site, whose data were previously unanalyzed. Coordinates were derived from Public Lands Survey System descriptions (PLSS) recorded to the nearest ¼ section (~ 0.65 km$^2$) and precise site locations were collected in 2022.

**Table 1** Location of four knobcone-Monterey pine test sites established by Griffin and Conkle (1967)

| Test Site | Lat | Lon | Elevation (m) | Aspect | Slope | NRCS soil type | Area (ha) |
|---|---|---|---|---|---|---|---|
| Spring Gulch | 40.622 | -122.858 | 976 | 100 | 39% | Spring Gulch/Brock Gulch variant complex, deep gravelly clay loam derived from mica schist and colluvium | 0.46 |
| Tom Lang Gulch | 40.674 | -122.867 | 671 | 315 | 29% | Musherhill-Weaverville complex, gravelly-cobbly clay loam derived from residuum weathered from conglomerate | 0.46 |
| East Fork Burn | 40.787 | -122.529 | 991 | 320 | 17% | Marpa gravelly loam/very gravelly clay loam, derived from shale residuum | 0.46 |
| Platina | 40.374 | -122.875 | 793 | 20 | 16% | Neuns very stony loam, stony-gravelly silty clay loam derived from residuum weathered from greenstone | 0.15 |

**Table 2** Locations and characteristics of provenances of knobcone pine cone parent trees, Monterey pine pollen parents, and pure parent checks of knobcone and Monterey pines

| Seed parent provenance | Code | Seed lots | Seed parent provenance | Lat | Lon | Pollen parent provenance |
|---|---|---|---|---|---|---|
| Red Flats | C | 33–45 | Rocky soil serpentine flat, 823 m elevation | 42.331 | -124.291 | Oregon plantations |
| Peasoup Campground | G2 | 13–25 | Serpentine soil ridge top at 1097 m elevation | 42.396 | -123.631 | Oregon/ mixed |
| Briggs Valley | G4 | 1–12 | Colluvial soil in canyon bottom, 671 m elevation | 42.454 | -123.670 | IFG/Oregon |
| Chrome Ridge | G5 | 26–32 | Rocky serpentine soil ridgetop, 1128 m | 42.528 | -123.691 | IFG |
| Eldorado | E | 46 | Ridgetop near Iowa Hill, CA at 1128 m elevation | 38.786 | -120.617 | IFG: 3-tree mix |
| P. radiata parent check* | R | 47 | Unknown, possibly Del Monte Forest, CA | 36.590 | -121.940 | wind pollinated |
| P. attenuata parent check** | K | 48 | G2 provenance: Serpentine soil ridge top at 1097 m elevation | 42.396 | -123.631 | wind pollinated |

Note: *For *Pinus radiata* and *Pinus attentuata*, provenance reflects the origin of natural wind-pollinated trees, rather than just the seed parent as per these F1 KMX hybrids

## Experimental design and data

### Planting stock

Knobcone pines were sourced from five provenances: four on the Siskiyou National Forest (NF) in Oregon and one from an upslope canyon position on metasedimentary soils on the Eldorado NF in California (Table 2). Of the Oregon provenances, Red Flats was coastal serpentine soil, Peasoup Campground and Chrome Ridge were rocky serpentine ridgetop, and Briggs Valley was colluvial canyon bottom. Seed was collected from 7 to 13 trees for each Oregon provenance, while only a single parent tree was sampled for the Eldorado NF provenance. In addition to the hybrids, a single pure knobcone pine seed lot, corresponding

with one of the serpentine ridgetop provenances, was grown as a pure-species reference. The locations of knobcone parent seed-tree provenances could be identified to the nearest PLSS section ($\sim 2.6$ km$^2$) based on U.S. Public Lands Survey System descriptions. Oregon provenance climates are distinctly cooler than the test sites, with Red Flats also considerably wetter.

Whereas the provenance of the knobcone seed parents was consistently determined, Monterey pollen-tree provenances are unclear based on either study notes or Institute of Forest Genetics (IFG) database records. A single Monterey pine parent grown at the IFG served as the pollen parent for knobcones sourced from the Chrome Ridge provenance. Other Siskiyou NF knobcone seed-tree provenances were crossed with Monterey pine pollen sourced from a combination of IFG and local plantations of Monterey pine planted in Oregon. The Eldorado NF-sourced knobcone seeds were crossed with unspecified Monterey pollen parents from IFG. No other information on the pollen-parent provenances was documented in database records. While IFG collected seed from Monterey pine parents growing in the Del Monte Forest, Monterey, CA, in 1926–1927, tree-breeding efforts involving Monterey pine have also used the geographically close Santa Cruz, CA population (Mead 2013). Consequently, this study can only make inferences based on seed-parent provenance. Knobcone pines were hand-pollinated in 1961, and the resulting seeds were sown at IFG in spring 1963 to produce $1-0$ bare-root stock.

## Test site layout and measurements

All test sites besides Platina followed a randomized complete block experimental design. Each test site was divided into four experimental blocks based on similar within-site growing conditions. Within each block, each of 48 distinct genetic combinations, representing KMX pine families sourced from 5 knobcone pine seed parent provenances and 2 pure-species parent checks of pure knobcone and Monterey pine, were randomly assigned to a 4-tree plot for a total of 192 plots per test site. The spatial arrangement of each seed lot plot was typically linear but varied to square. At Platina, seedlings from seed lots 8, 10, 15, 21, 22, 24, 27, 30, 31, 37, 40, 41, 42, and 43 each were randomly assigned to one of 14 rectangular tree plots ranging in size from 11 to 27 trees. Planted acreage was approximately 0.45 ha at each full site, while Platina measured approximately 0.16 ha. Planting spacing was 2.4 m x 2.4 m (1681 trees ha$^{-1}$) across all test sites in order to match the small available land area.

At Tom Lang Gulch, woodland oak and pine species were harvested, while salvage logging removed snags and a survivor knobcone pine from East Fork Burn. Site preparation at all test sites consisted of bulldozing and windrowing competing chaparral vegetation. Shrub layer recovery was limited through 1966 at all test sites and remained so in 1973 at Spring Gulch and Tom Lang Gulch (Robert F. Powers, *personal observation*). Bare-root seedlings were lifted and planted over a two-week period with the assistance of a "Little Beaver" machine. Crews deployed poisoned grain and installed wicker wire cages over seedlings to reduce animal damage. Cages were removed after 2–3 growing seasons, but not before some physical constriction of seedlings occurred.

Weather was nearly ideal for planting, with cool conditions, minimal wind, and moist subsoils. However, the planting month had abnormally dry conditions, while the subsequent spring was unusually windy. Summer 1964 was hot and dry, with a below-average growing season. Summers 1965 and 1966 were cool and wet by contrast, as were the winters of 1965

and 1966. Heavy snowfall and a hard frost in 1972 led to winter damage and tree mortality on the Spring Gulch and Tom Lang Gulch test sites.

Seedlings were monitored for height and survival in fall 1964, spring 1965, and spring 1966 at all test sites. A final set of height, survival, and damage measurements were taken at Spring Gulch and Tom Lang Gulch in 1973. Tree diameters were not extensively collected at any test site. Dead trees were initially censored from 1964 to 1965 data, but status, height and condition were fully surveyed in 1966 and 1973 (at Spring Gulch and Tom Lang Gulch), allowing for reconstruction of survival trends. Trees were not assigned a unique ID until 1965, preventing us from accounting for initial planting-year size differences. Tree locations were surveyed to make detailed stem maps of survivor trees at Spring Gulch, Tom Lang, and East Fork Burn in 1965–1966.

The primary Spring Gulch test site was established simultaneously with larger, single-seed-lot plantings of up to 26 trees when extra stock was available. Data for these larger, single-seed-lot plots were not available beyond 1966. Because these trees were planted adjacent to the south end of the primary Spring Gulch test site, we excluded two rows (4.8 m) of monitored trees in the primary test site from our response sample but included them for the purposes of characterizing local competition and provenance diversity.

Spacing and planting arrangements were found to be precise at Spring Gulch and Tom Lang Gulch, permitting successful tree identification through 1973 even where tree tags went missing. At East Fork Burn, converging planting rows and columns confounded tree identification (Robert F. Powers, *personal observation*), leading to a number of unidentifiable trees at this site.

## Analytical procedures

### Growth as a function of neighborhood provenance diversity

We limited our analysis of the genetic-diversity effects on tree growth to Spring Gulch and Tom Lang Gulch, the two test sites where measurements continued for 9 growing seasons to April 1973. Rapid juvenile growth rates achieved canopy closure by age 9, based on a combination of field observations and historical photos. Field visits to these two test sites in 2022 revealed that mapped test site boundaries, blocks, windrows, and certain tree locations remained sufficiently distinct to georegister 1966 historical stem maps in ArcGIS Pro (ESRI Inc., 2021; Fig. 1) using a combination of field sub-meter GPS measurements (Juniper systems Geode GNS2 GPS, Logan, UT, USA) and satellite imagery overlays.

Spatial data and randomized assignment of provenances to scattered, typically 4-tree planting plots permitted us to investigate whether local diversity affected growth from an individual-tree perspective. We constructed a set of competing alternative models of tree height increment. Study notes observed variations in initial tree size by seed lot at the time of planting, but because trees were not consistently assigned unique IDs until 1965, initial 1964 tree size could not be used as a predictor. Instead, we used relative growth rate (RGR) as our response variable to help control for size-related variation in growth (Hunt and Cornelissen 1997). We calculated annualized RGR from the difference in log-transformed tree sizes between 1966 and 1973 (Table 3).

Our null model included the random effect of block nested within test site. We did not nest seed lot within block as per the original experimental design, as the small 4-tree size of

**Table 3** Response and predictor variables used in the genetic diversity and climate transfer analyses in this study

| Variable | Category | Description | Unit | Analysis |
|---|---|---|---|---|
| RGR | Response | Relative growth rate based on total height | cm cm$^{-1}$ yr$^{-1}$ | Genetic diversity, climate transfer |
| Status | Response | Tree status code: 0=live tree, 1=mortality tree | binary live/dead | Climate transfer |
| Initial height | Stand structure | Live crown ratio (crown length / total height) | cm | Genetic diversity, climate transfer |
| CI | Stand structure | Size ratio of competitor to focal trees | Summation of ratios | Genetic diversity |
| Block | Sample strata | Random effect of block | factor | Genetic diversity |
| Test site | Sample strata | Fixed effect of test site; used to stratify random position and block effects | factor | Genetic diversity, climate transfer |
| Provenance | Sample strata | Random effect of provenance | factor | Genetic diversity |
| UTM northing | Spatial coordinates | Used in autocorrelation structure | m | Genetic diversity |
| UTM easting | Spatial coordinates | Used in autocorrelation structure | m | Genetic diversity |
| MAP | climate | Mean annual precipitation | mm yr$^{-1}$ | Climate transfer |
| MAT | climate | Mean annual temperature | °C | Climate transfer |
| PAS | climate | Precipitation as snow | mm yr$^{-1}$ | Climate transfer |
| FFP | climate | Frost free period | Days | Climate transfer |
| CMD | climate | Climatic moisture deficit | mm yr$^{-1}$ | Climate transfer |
| MCMT | climate | Mean cold month temperature | °C | Climate transfer |
| RVPPT | climate | Relative volume per planted tree | proportion | Climate transfer |

planted plots of a given seed lot would have masked the genetic diversity effect of primary interest to this study. In addition to the fixed effect of test site (Spring Gulch vs. Tom Lang Gulch), we used an individual-tree point competition index as our null model fixed effect. Because only tree heights were collected, we based our competition index on 1973 tree heights. We assumed tree heights at the end of the measurement interval would be more influential on growth than in 1966, when stands had not achieved crown closure. This index is equivalent to Hegyi's (1974) competition index, but modified to use heights rather than diameters:

$$CI_i = \sum_{j=1}^{n} \left( \frac{Ht_j}{Ht_i} \right)$$

Where CI is the competition index, $Ht_j$ is the height of competitor tree as of 1973, $Ht_i$ is the height of the focal tree $i$ as of 1973, and n is the total number of competitor trees. We built a series of models to determine the maximum search radius for competitor trees, ranging from 3 m to 7m in 1m increments (Aakala et al. 2013). We did not exceed a 7m competitor search radius as greater distances would have extended into unmeasured portions of the Spring Gulch test site and adjacent natural Douglas-fir/mixed-hardwood and ponderosa pine plantation stands. Based on AICc comparisons, we selected 7m as our search radius for

subsequent analyses. We excluded pure Monterey and knobcone parent checks as response subjects from our analysis, as well as KMX hybrids within 7m distance of pure Monterey or knobcone pine neighbors to guard against potential species mixture effects. We also excluded trees with missing 1965 height measurements or negative RGR, as these slow-growing trees were commonly noted as suffering from physical or browse damage. Our final response variable sample size was 842 trees. We quantified local provenance diversity in each 7m tree neighborhood using Shannon's H':

$$H\prime = -\sum_{i=1}^{S} p_i * \ln(p_i)$$

Where $H'$ is the diversity index, $p_i$ is the proportion of provenance $i$, and $s$ is the total number of provenances. Unlike competition, provenance diversity was not weighted by relative tree sizes but was a simpler function of provenance richness and evenness. We investigated whether edge trees might be subject to systematically lower diversity due to fewer competitors but found only a weak relationship between provenance diversity and competition ($R^2 = 6\%$).

Based on the null RGR model, we constructed seven alternative hypothesis models to examine the direct and interactive effects of provenance diversity (Table 4). Our first alternative added the main effect of local provenance diversity (Shannon's H'). Because neighborhood diversity effects on tree increment may be contingent on climate (Gómez-Aparicio

**Table 4** Hypothesis models of longer-term relative growth rate (1966–1973) as a function of genetic diversity and short-term relative growth rate (1965–1966) and survival (1964–1966) as functions of climatic transfer distance

| Analysis | Hypothesis | Response | Response varies as a function of: |
|---|---|---|---|
| Genetic diversity | G0 | RGR | Null model (competition, provenance, and test site; block-in-test site random effect) |
| Genetic diversity | G1 | RGR | Null model, diversity |
| Genetic diversity | G2 | RGR | Null model, diversity, provenance, diversity x provenance |
| Genetic diversity | G3 | RGR | Null model, diversity, competition, diversity x competition |
| Genetic diversity | G4 | RGR | Null model, test site, diversity x test site |
| Climate transfer | C0 | RGR, survival | Null model (competition and test site; block-in-test site random effect) |
| Climate transfer | C1 | RGR, survival | MAT (linear) |
| Climate transfer | C2 | RGR, survival | MAT (quadratic) |
| Climate transfer | C3 | RGR, survival | MAP (linear) |
| Climate transfer | C4 | RGR, survival | MAP (quadratic) |
| Climate transfer | C5 | RGR, survival | PAS (linear) |
| Climate transfer | C6 | RGR, survival | PAS (quadratic) |
| Climate transfer | C7 | RGR, survival | FFP (linear) |
| Climate transfer | C8 | RGR, survival | FFP (quadratic) |
| Climate transfer | C9 | RGR, survival | RVPPT (linear) |
| Climate transfer | C10 | RGR, survival | RVPPT (quadratic) |
| Climate transfer | C11 | RGR, survival | MCMT (linear) |
| Climate transfer | C12 | RGR, survival | MCMT (quadratic) |

Note: See Table 3 for abbreviations

et al. 2011), our second model added both the diversity and diversity x provenance interaction effect. Because diversity effects may range from positive to negative depending on the strength of tree competition (Mina et al. 2018), our third alternative examined whether provenance diversity interacted with competition to influence growth. Our fourth alternative model included diversity as well as the diversity x site interaction to examine whether diversity effects were contingent on site quality, as has been reported for mixed-species stands (Toïgo et al. 2015).

To account for similar growth among adjacent trees in RGR modeling, we modeled spatial autocorrelation in the residuals (Pinheiro and Bates 2000). Variograms of null (initial DBH, provenance, site, and CI-only) models suggested growth was spatially autocorrelated up to a distance of at least 7 m. Based on inspections of variograms and AIC fits with different correlation structures (Zuur et al. 2009), we selected an exponential structure to model autocorrelation. Autocorrelation estimates were based on tree coordinates stratified within a test site. Models for CI distance selection and final analyses were fit with maximum likelihood, while preliminary models to identify the most appropriate autocorrelation structure were fit with restricted maximum likelihood.

## Climate transfer distance

We identified approximate KMX pine seed-parent provenance locations to within ~ 1.6 km based on land survey descriptions, with elevations derived from historical notes. We did not extract climate data for pure Monterey pine given the uncertain origin of Monterey pine pollen parents and parent checks. We extracted climate norms for each location and elevation using the ClimateNA dataset (Wang et al. 2016). For provenance climate, we used long-term norms for the 1961–1990 period. For test site location climates, we took the average of historical climate estimated for each location over the 1964–1966 period, corresponding with the period covered in our climate transfer analysis, to limit the scope of inference to initial establishment success.

We calculated both a univariate and multivariate measure of climate dissimilarity between test sites and KMX pine seed parent provenances (Table 3). Variables included log-transformed total mean annual precipitation (lMAP) and mean annual temperature (MAT). Based on the noted susceptibility of the hybrid to snow and frost damage (Griffin and Conkle 1967; Oliver 1979), we included both the mean length of the frost-free period in days (FFP) and precipitation as snow (PAS). The mean cold month temperature (MCMT) is a commonly used predictor, given the sensitivity of warmer seed sources to cold damage (Bansal et al. 2016). Lastly, we included climatic moisture deficit (CMD), or the difference between potential and actual evapotranspiration, given its demonstrated utility in predicting tree growth and mortality in the region (Lutz et al. 2010; Koontz et al. 2021). Univariate climate transfer distances were calculated as the climate value of the test site minus the climate value of the seed-source provenance. As an alternative to these univariate climate-transfer-distance metrics, we calculated the predicted relative volume per planted tree (RVPPT) based on an ensemble model that incorporated the effects of four climate transfer distance metrics: MAT, MCMT, lMAP, and the differential between mean cold-month temperature and mean warm month temperature (TD). The model was fit to 32-yr provenance test data for *P. contorta*, a species with extensive provenance test data spanning 43 sites and 140 provenances (O'Neill et al. 2014). The ensemble model consisted of the weighted mean pre-

diction (Yao et al. 2018) of three asymmetric, bell-shaped, three-dimensional curves, each fit to climate transfer distances (test site minus provenance) for lMAP and one of the three temperature variables (MAT, MCMT, or TD). Prior to model fitting, RVPPT values for each site-provenance combination were calculated as the mean volume per planted tree divided by the mean value for each site.

We focused our climate transfer analysis on tree measurements from 1966, the last common measurement date across all four test sites. Because initial 1964 tree size could not be used as a predictor, we used RGR based on a single year of tree growth, the difference in log-transformed tree height between 1966 and 1965. We opted to use height RGR rather than total height, as is common in provenance studies (e.g., Rehfeldt et al. 1999), due to study notes indicating there was initial variation in seedling size among seed lots prior to planting. Our null model represented RGR or mortality (cumulative as of 1966) as functions of the random effects of block nested within test site and the fixed effect of test site. For this analysis, we included all trees with positive RGR at Tom Lang Gulch, Spring Gulch, East Fork Burn, and Platina, for a combined sample of 1900 trees. We did not control for neighborhood competition or genetic-diversity, as interactions among 2.4×2.4 m-spaced trees were assumed to remain negligible by age 3 and spatial data was unavailable for East Fork Burn or Platina. We created a series of competing models examining each of the univariate and multivariate RVPPT variables in turn (Table 4). We fit linear and quadratic variants for each predictor variable, as growth is frequently lowest at extremes of climatic transfer distance (Rehfeldt et al. 1999). Models were fit with maximum likelihood estimation. Because stem maps were not available for Platina and converging planting rows prevented locating some trees at East Fork Burn, we could not examine the potential for spatial autocorrelation among adjacent trees with this larger dataset. Small average tree heights as of 1966 (0.57–1.44 m depending on test site, see Results 3.1) would have reduced tree-tree interactions compared to 1973, while the block random effect accounted for areas of broadly similar growing conditions within test sites.

## Statistical inference and model diagnostics

We based statistical inference on comparisons of hypothesis models using Akaike's (1974) adjusted information criterion (AICc). We considered models to have plausible ΔAICc support if within 6 AICc of the best-supported model (Richards 2008). We considered models within ΔAICc of 2 to be equivalent, while nested models that did not reduce AICc by ≥2 were dropped to protect against overfitting (Burnham and Anderson 2002). We calculated marginal (fixed) and conditional (fixed plus random effect) pseudo-$R^2$ statistics (Bartoń 2017) for RGR models, and classification accuracy (area under the receiver-operating characteristic curve or AUC) for mortality models. We report $R^2$ and AUC statistics, F-statistics and p-values for descriptive purposes only and rely on AICc comparisons for inference.

We converted predictor variables to Z-scores to promote model convergence as well as to be able to infer relative effect sizes. We inspected plots of model residuals vs. fits and constructed Q-Q plots to validate model assumptions of normal variances, homoscedasticity, dispersion, and linearity. Plots of predictor variables vs. model residuals supported applying a log-transformation 1965–1966 RGR to assure normality of residuals and to CI to meet assumptions of linearity. We also examined for multicollinearity using variance inflation

factors. Variance inflation factors did not exceed 3 for any model, indicating low-moderate multicollinearity (James et al. 2021).

## Results

### Growth as a function of provenance diversity

By 1973, average tree height was higher at Spring Gulch (5.9±0.06 m S.E. of mean) than Tom Lang Gulch (3.85 m±0.08 m), while Spring Gulch experienced lower mortality (2.4±0.6%) than Tom Lang Gulch (25.7±1.7%). Individual-tree 7 m-radius neighborhoods had a mean of 3.7 distinct provenances at Spring Gulch (S.E. of mean=0.03, range=1–5), and 3.8 provenances at Tom Lang Gulch (S.E. mean=0.03, range=1–5). The best-approximating model (fixed effects $R^2$=27%) included the main effect of provenance diversity, the provenance diversity x focal tree provenance interaction, as well as the null model terms of competition, site, and provenance (Table 5). Under the diversity x provenance interaction in this model (F=5.2, p<0.001), RGR of trees sourced from the Briggs Valley, Chrome Ridge, and Eldorado provenances increased with neighborhood provenance diversity (Fig. 2). In contrast, RGR of trees from the Red Flats and Peasoup Campground provenances was not responsive to neighborhood provenance diversity. Trees from provenances besides Red Flats and Peasoup Campground, when growing in the most diverse neighborhoods (Shannon's H' = 1.59), grew approximately 33% faster than trees growing in the least-diverse neighborhoods (Shannon's H' = 0.0, Fig. 2). Both these models included the null model fixed effects of CI, provenance, and test site, and the random effects of block nested within test site and seed lot nested within test site. Growth declined with neighborhood competition (F=93.1, p<0.001, Fig. 2). There was no discernable variation in mean RGR among provenances (F=1.9, p=0.74), but the RGR of the Red Flats and Peasoup Campground provenances was higher compared to the other three when provenance diversity was low. Relative growth rate varied by site (F=4.1, p=0.04), higher at Tom Lang Gulch (0.23±0.01 cm cm$^{-1}$ yr$^{-1}$) than at Spring Gulch (0.19±0.01 cm cm$^{-1}$ yr$^{-1}$). No other model, including the null model, was plausible (ΔAICc within 6 of the best-approximating model or the addition of a predictor failing to reduce ΔAICc by <2 compared to a simpler, nested alternative model; Burnham and Anderson 2002, Richards 2008).

### Role of climate transfer distance on growth and mortality

Mean tree height in 1966 ranged from 0.57±0.1 m at East Fork Burn to 1.44±0.02 m at Spring Gulch, with intermediate heights at Platina (84.6±0.02 m) and Tom Lang Gulch (73.2±0.01 m). The best-supported RGR model included the linear and quadratic effects of precipitation as snow (PAS, Table 5). The polynomial linear and quadratic effects of PAS-transfer distance was statistically significant (F=5.7, p=0.003), with the model indicating that the most rapid growth occurred when seeds were transferred to test sites with slightly lower (-10%) PAS compared to the provenance (Fig. 3) climate at the time of seedling establishment. Provenances with either low or high PAS relative to planting locations had lower RGR, with source climates having extremes of PAS relative to the test site showing approximately 12% lower RGR compared to the optimum at -10%. Relative growth rate

**Table 5** Model comparison results for the genetic diversity and climate transfer analyses in this study

| Analysis | Test Sites | Response | Hyp. | Model terms | | | | | | | logLik | ΔAICc | R²/AUC |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Test site | PAS | PAS² | CI | Prov. | H' | Prov. x H' | | | |
| Diversity | SG, TLG | RGR: 1966–1973 | G2 | x | NA | NA | x | x | x | x | 30.7 | 0 | 0.26 |
| Diversity | SG, TLG | RGR: 1966–1973 | G0 | x | NA | NA | x | | | | -45.9 | 20 | 0.23 |
| Climate transfer | All | RGR: 1965–1966 | C6 | x | x | x | NA | NA | NA | NA | 1219.1 | 0 | 0.22 |
| Climate transfer | All | RGR: 1965–1966 | C0 | x | | | NA | NA | NA | NA | 1217.2 | 7.4 | 0.22 |
| Climate transfer | All | Survival: 1964–1966 | C0 | x | | | NA | NA | NA | NA | -473.1 | 0 | 0.84 |

Note: Abbreviations are as follows: Hyp.=hypothesis AICc=corrected Akaike's information criterion, PAS=precipitation as snow, CI=competition index, Prov.=seedling provenance, H'=Shannon's diversity index, LogLik=log likelihood, R²=coefficient of determination (fixed-effects only), AUC=area under receiver operating curve (combined fixed and random effects)

was lowest at Tom Lang Gulch (0.44 cm cm$^{-1}$ yr$^{-1}$ ± 0.17 S.E. of mean), highest at Spring Gulch (0.70±0.02 cm cm$^{-1}$ yr$^{-1}$), with intermediate growth at Platina (0.62±0.04 cm cm$^{-1}$ yr$^{-1}$) and East Fork Burn (0.56±0.02 cm cm$^{-1}$ yr$^{-1}$). Together, the fixed effects of this model explained 22% of variance. The null model of RGR as a function of test site (F=34.2, p<0.001) and the block random effect was also plausible based on AIC support (ΔAICc=5.8, R$^2$=22.0%), while there was no AICc support for any alternative climate variable.

Spring Gulch had less than 1% mortality by 1966 (0.07±0.3%), while Tom Lang Gulch had the highest mortality (18.3±4.4%). Mortality was intermediate at Platina (9.7±5.3%) and East Fork Burn (1.2% ± 0.05%). The null model of mortality as a function of test site (F=15.3, p<0.001) and the random effect of block nested in test site was the only plausible model based on AICc. The classification accuracy (AUC) for this model was 83.8%. No alternative model had substantial AIC support.

## Discussion

### Growth as a function of provenance diversity

We found evidence that individual KMX pines grew faster in neighborhoods with a greater diversity of seed-parent provenances, providing the first finding that within-species provenance diversity may promote individual-tree growth in a hybrid conifer. The magnitude of the growth difference between the least and most diverse tree neighborhoods was contingent on provenance. Among the 5 provenances examined, 3 showed a positive response to diversity, with trees in the highest diversity neighborhoods growing approximately 33% faster than trees in the lowest diversity neighborhoods. A study of Norway spruce found that doubling the number of planted provenances from 5 to 10 increased stand-level growth by an average of 28% (Pretzsch 2021). However, this strong response in 3 of 5 provenances was tempered by no diversity response in the remaining 2 provenances. Because the two unresponsive provenances showed faster growth than the three responsive provenances except under high diversity, it is unclear whether the provenance-diversity effect observed in individual trees translates to stand-level gains over single-provenance plantings. Our results suggest that provenance diversity may alter absolute as well as relative growth differences among seed sources. Failure to consider neighborhood provenance diversity may distort the results of provenance trials in which individual seed lots are freely mixed rather than arranged together by provenance.

We found that the diversity effect was dependent on provenance. The two provenances showing no provenance-diversity response were noteworthy for originating on serpentine soils and having the highest PAS values. Gould et al. (2011) found growth increases were strongest in mixtures designed to maximize potential growth differences among provenances, while provenance response was variable in mixtures of families sharing similar growth potentials. Our finding that neighborhood diversity alters growth among provenances highlights that trees are responsive to neighborhood effects rather than stand-level characteristics (Pommerening et al. 2021). Further diversifying by adding more provenances or careful arrangement of provenances to maximize contrasts (e.g., Pretzsch 2021), vs. our random assignment of provenances to planting plots, might have achieved further gains in growth.

**Fig. 2** Relative growth rate (RGR; 1966–1973) as a function of the best-supported model terms of **(A)** neighborhood provenance diversity, and **(B)** neighborhood tree competition. The diversity x provenance interaction effect was approximately 30% the strength of the competition effect
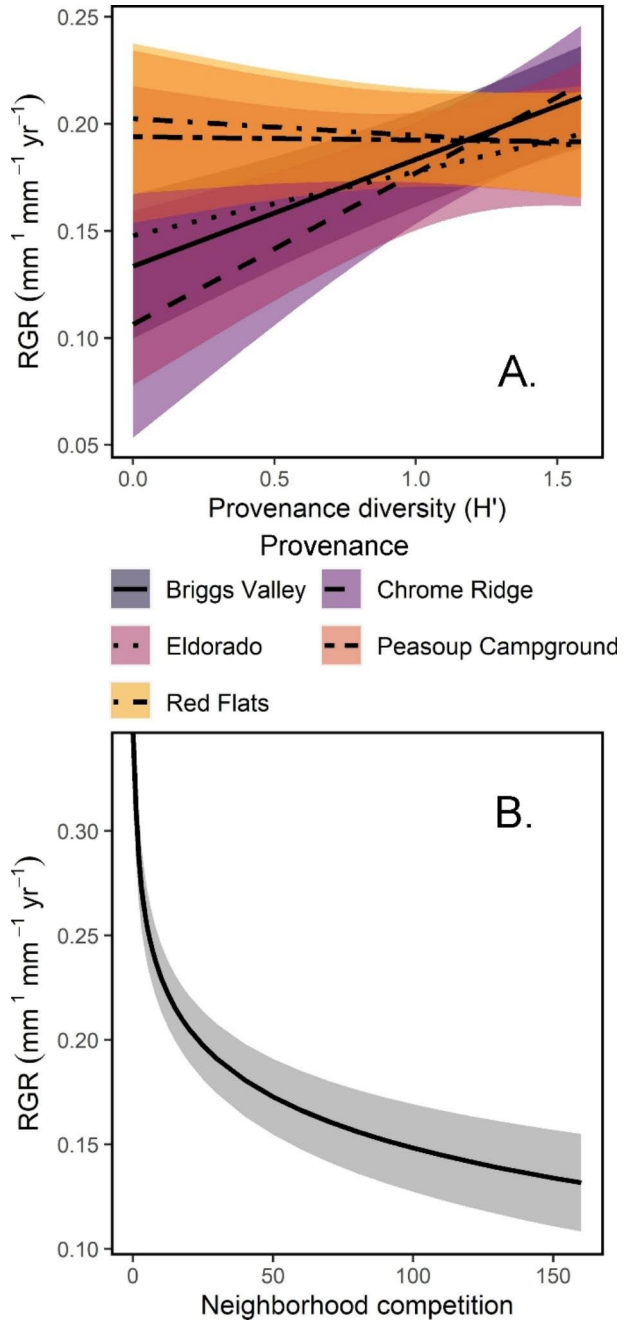


Several non-exclusive mechanisms could be drivers of our finding of a positive growth-diversity effect in KMX hybrid pines. First, provenance diversity may effectively reduce competition by fostering a range of crown characteristics, such as shape, that increase light-use efficiency or reduce crown shyness (Jucker et al. 2015; Williams et al. 2017). Mixed-
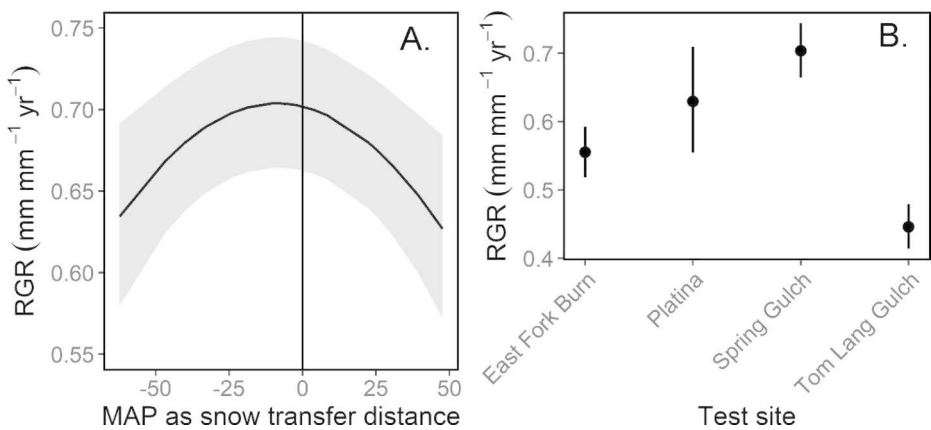
**Fig. 3** Relative growth rate (1965–1966) as a function of the best-supported model terms of mean annual precipitation as snow (PAS, left panel), and test site (right panel)

provenance plantings that improve stand light capture could indirectly translate into faster tree growth through suppression of competing vegetation. Second, in California's Mediterranean climate, particularly on lower-quality test sites like ours where soil moisture is limiting (Zhang et al. 2022), shrub and herbaceous vegetation dramatically limit young stand growth (McDonald and Fiddler 2010). Third, Pretzsch (2021) hypothesized that provenance diversity may reduce competition by promoting complementary phenological differences in bud burst, maximum leaf area, and dormancy. Such phenological differences could alter provenance susceptibility to extreme weather, leading to compensatory growth and helping to stabilize biomass production over time (Jucker et al. 2016).

Variation in belowground functional traits could also foster complementary interactions among provenances. Genetic variation among Monterey pine provenances is linked to differences in ectomycorrhizal symbiont communities (Wright 2007), and provenance diversity could have promoted differentiation in soil microbiota and belowground resource use in this study. Knobcone pine provenances varied in terms of both climate and soil type at the origin of the seed, with seeds sourced from serpentine soils potentially diverging in soil resource use from those on less alkaline soils. We noted that two of the three seed-parent provenances sourced from serpentine soils, Red Flats and Peasoup Campground, lacked a positive RGR-diversity relationship. In common garden trials, ponderosa pines sourced from non-serpentine soils outgrew trees sourced from serpentine soils, a pattern that was reversed when trees were grown on serpentine substrates (Wright 2007). Besides fostering differences in resource use, genetic variation may increase stand resilience to soil-borne pathogens that exhibit genotype-level specialization (Eck et al. 2019). Pathogen abundance and the intensity of negative pathogen effects on temperate tree species are expected to increase with global warming (Liu and He 2021).

Unlike a previous study of positive provenance-diversity effects in Norway spruce (Pretzsch 2021), a pure species with pronounced variation in crown morphology, we investigated a hybrid conifer with a more limited range of crown morphology as well as low shade tolerance and adaptation to moderately frequent high-severity fire. Despite these differences in species traits and ecology, our findings suggest that provenance diversity may promote productivity gains in our knobcone-Monterey pine hybrid that are at least equal to

those reported by Pretzsch ([2021](#)) for Norway spruce. A unique aspect of our study was the use of a hybrid conifer. Considering that the knobcone pine seed-parent provenance was the main factor being manipulated, the strength of the diversity effect is surprising. Study records indicate that a variety of Monterey pine seed lots were used, contributing an additional degree of variation in source climate. Monterey pine displays relatively high genetic diversity for a conifer (Moran et al. [1988](#)). Field notes for this study identified scattered trees intended to be hybrids that had characteristics more consistent with pure knobcone pines, suggesting control over pollination was not always successful. At least some of our observed diversity effect is likely attributable to mixing with accidental pure trees.

Beyond investigating a hybrid conifer, several details of this study may have influenced our results. Given only 9 growing seasons, tree-tree interactions would have been nascent at the time of sampling. In a study of slower-growing boreal forest species, Jucker et al. ([2020](#)) found that positive species-mixture growth effects only developed later in stand history. Whether the positive provenance mixture-effects persist or reverse later in KMX-pine stand development remains unknown. Unfortunately, the rarity of surviving tree monumentation at Spring Gulch, combined with heavy intervening mortality and edge effects from adjacent plantations, pose major challenges to reviving this study today. Structural heterogeneity typically reduces tree growth in young stands (Luu et al. [2013](#); Bourdier et al. [2016](#)), and structural complexity could have increasingly counteracted provenance diversity if interactions among provenances or with the environment diversified tree sizes (Aspinwall et al. [2011](#)). Because this historical dataset did not record stem diameter or volume, we could not investigate whether mixtures altered light competition, as indicated by height: diameter ratio (Forrester et al. [2004](#)). However, tree-height responses are likely conservative, as height is generally less responsive to both competition and compositional diversity than tree diameter (Lanner [1985](#); Pretzsch and Biber [2016](#)). Finally, lack of genotyping does not allow us to infer whether geographic and climatic distances among provenances also translate into genetic differences, although given that climate transfer distances associated with these provenance trials are very short, expectation of finding significant transfer distance effect is low.

## Role of climate transfer distance on growth and mortality

Griffin and Conkle's ([1967](#)) original ANOVA analysis did not find significant growth variation among provenances; instead, within-provenance variation in growth was at least as influential. We found that, when expressed in terms of PAS, climatic transfer distance impacted initial growth by up to 15%. Previous research found that climatic transfer functions apply to naturally occurring Engelmann spruce (*Picea engelmanii* Parry x Engelm.) and white spruce (*Picea glauca* Monech) hybrids (O'Neill et al. [2014](#)), as well as lodgepole-jack pine (*Pinus banksiana* Lamb.) hybrids in Canada (Rweyongeza et al. [2007](#)). Our results suggest that climatic transfer distance may affect artificially produced hybrid-conifer growth similarly to naturally occurring species (Pedlar et al., [2021](#); Rehfeldt et al. [1999](#)).

Our finding of a relationship between initial growth and RGR has two potential implications. Future climate projections indicate shifts from snow- to rain-dominated precipitation in the Klamath Mountains (Klos et al. [2014](#)). Projected rises in climatic moisture deficit will pose challenges to the natural postfire recovery of existing forest types, particularly in the drier eastern part of the Klamath Mountain ecoregion (Tepley et al. [2017](#)). Given the

importance of PAS to initial growth, projected declines in Northern California mountain snowpacks might alter the future suitability of Siskiyou Mountains knobcone pine seed sources to eastern Klamath Mountain sites. Our finding that PAS affects early growth may support a role of source-climate variation in driving the positive RGR-provenance diversity relationship seen in subsequent years. Provenance variation in snow-resistant traits, such as crown width, crown depth, and stem taper (Nykänen et al. 1997) could translate to complementary crown characteristics, improving local light-use efficiency in diverse vs. uniform neighborhoods (Ishii and Asano 2010; Jucker et al. 2015). Phenological differences associated with high provenance PAS, such as delays in bud burst, could also reduce competition for light and soil moisture early in the growing season for low-PAS-provenance neighbors.

A unique aspect of this study was the artificial pollination of F1 KMX hybrids, as opposed to sourcing seeds from natural populations, which allowed us to focus on movement of seed parents in isolation of pollen parents. Differences in source climate were assumed to reflect variation in the seed-parent source climate rather than pollen-parent climates. However, a limitation of this study was the uncertainty introduced by the lack of documentation on Monterey pine pollen-parent sources. Differences in pollen parent provenance could be important considering our finding of a PAS effect on growth, as Santa Cruz populations of Monterey pine are noted for displaying superior cold tolerance relative to other provenances of this species (Mead 2013). The effect of manipulating seed source and pollen source independently in either pure or hybrid conifers would be an interesting topic for future research.

Unlike growth, we did not find evidence that climatic transfer distance played a role in survival. Survival by 1966 was noted as remarkably high (Griffin and Conkle 1967). Field notes documented limited understory recovery, and Oliver (1979) observed that rapid juvenile growth makes KMX pine strongly competitive against the shrub vegetation that commonly limits reforestation success in the region. Survival at Spring Gulch remained greater than 99% by 1966, which likely limited our ability to detect a climatic transfer signal on survival. Mild winters in the first 8 years of stand development may also have obscured critical differences in susceptibility to winter damage.

Despite our finding that growth performance was highest when seeds were transferred to test sites with PAS closely approximating provenance climate, subsequent harsh winters impacted the higher-elevation test sites. A test of unscreened Eldorado NF provenance hybrids adjacent to the Spring Gulch test site proved sensitive to extensive winter damage in 1972–1973 (Oliver 1979), and historical field notes confirm the study was also impacted. By 2022, survivor trees at Spring Gulch and Tom Lang Gulch had extensive sweep and crook, supporting a history of winter damage given a lack of biotic disease issues. Our findings, therefore, should be cautiously interpreted to inform initial planting success rather than the long-term suitability of KMX-hybrid seed sources for future planting sites. Had this study been followed longer, the relationship between performance and PAS or another winter-tolerance indicator may well have shifted to favor trees from harsher winter climates, suggesting that short-term data from contemporary common garden studies must be applied cautiously to guide climate-change adaptation. Evaluating performance over longer-term periods may capture important facets of acclimation such as susceptibility to severe weather or disease that are not apparent in the short-term (St. Clair et al. 2020).

## Conclusions

Our results support the potential of leveraging within-species provenance diversity to enhance early growth. Seed-parent provenance was an important modifier of the growth-diversity relationship, with provenance soil and climate possibly accounting for the variation in response. Our analysis of climate transfer revealed a sensitivity of KMX hybrid pines to seed-parent provenance PAS, with extremes associated with reduced height growth potential during early stand establishment. Survival did not vary with seed source climate. Although both height and survival would need to be tracked for longer periods to develop robust transfer functions for KMX pine, our results highlight possible future directions for assisted gene flow research manipulating seed and pollen parent sources independently.

Our hybrid-pine study species ultimately proved poorly acclimated to the higher-elevation interior California study test sites, where extensive winter damage to the hybrids was observed. Nevertheless, rapid juvenile growth rates and the ability to regenerate from seed after severe wildfire may lend the hybrid renewed interest for reforestation of low-elevation, reburn-prone sites. Projected shifts to rain-dominated precipitation, combined with anticipated declines in natural post-fire conifer regeneration success, could improve both the suitability of the Klamath Mountains for the hybrid as well as a rationale for their deployment. Future work might investigate mixed-provenance plantings of species more commonly used in reforestation. A stand-level experiment, as opposed to our individual-tree analysis, could more clearly demonstrate whether mixed-provenance stands overyield relative to single-provenance plantings.

**Data Availability** The datasets used in this study are available in the USDA Forest Service Research Data Archives, https://www.fs.usda.gov/rds/archive/catalog/RDS-2023-0038.

## Declarations

**Competing interests** The authors declare no conflict of interest.

# References

Aakala T, Fraver S, D'Amato AW, Palik BJ (2013) Influence of competition and age on tree growth in structurally complex old-growth forests in northern Minnesota, USA. For Ecol Manag 308:128–135. https://doi.org/10.1016/j.foreco.2013.07.057

Akaike H (1974) A new look at the statistical model identification. IEEE Trans Autom Control 19:716–723. https://doi.org/10.1109/TAC.1974.1100705

Aspinwall MJ, King JS, McKeand SE, Bullock BP (2011) Genetic effects on stand-level uniformity and above- and belowground dry mass production in juvenile loblolly pine. For Ecol Manag 262:609–619. https://doi.org/10.1016/j.foreco.2011.04.029

Bansal S, Harrington CA, St. Clair JB (2016) Tolerance to multiple climate stressors: a case study of Douglas-fir drought and cold hardiness. Ecol Evol 6:2074–2083. https://doi.org/10.1002/ece3.2007

Bartoń K (2017) MuMIn: Multi-model inference

Bourdier T, Cordonnier T, Kunstler G et al (2016) PLoS ONE 11:e0151852. https://doi.org/10.1371/journal.pone.0151852. Tree Size Inequality Reduces Forest Productivity: An Analysis Combining Inventory Data for Ten European Species and a Light Competition Model

Boyden S, Binkley D, Stape JL (2008) Competition among Eucalyptus Trees depends on genetic variation and resource supply. Ecology 89:2850–2859. https://doi.org/10.1890/07-1733.1

Buotte PC, Levis S, Law BE et al (2019) Near-future forest vulnerability to drought and fire varies across the western United States. Glob Change Biol 25:290–303. https://doi.org/10.1111/gcb.14490

Burnham KP, Anderson DR (2002) Model selection and Multimodel Inference: a practical information-theoretic Approach, 2nd edn. Springer-Verlag, New York

Davis KT, Dobrowski SZ, Higuera PE et al (2019) Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. Proc Natl Acad Sci 116:6193–6198. https://doi.org/10.1073/pnas.1815107116

Eck JL, Stump SM, Delavaux CS et al (2019) Evidence of within-species specialization by soil microbes and the implications for plant community diversity. Proc Natl Acad Sci 116:7371–7376. https://doi.org/10.1073/pnas.1810767116

ESRI inc (2021) ArcGIS Pro [GIS software] Version 2.8. Environmental Systems Research Institute, Redlands, CA.

Fischer DG, Wimp GM, Hersch-Green E et al (2017) Tree genetics strongly affect forest productivity, but intraspecific diversity–productivity relationships do not. Funct Ecol 31:520–529. https://doi.org/10.1111/1365-2435.12733

Forrester DI, Bauhus J (2016) A review of processes behind diversity-productivity relationships in forests. Curr For Rep 2:45–61. https://doi.org/10.1007/s40725-016-0031-2

Forrester DI, Bauhus J, Khanna PK (2004) Growth dynamics in a mixed-species plantation of Eucalyptus globulus and Acacia mearnsii. For Ecol Manag 193:81–95. https://doi.org/10.1016/j.foreco.2004.01.024

Gómez-Aparicio L, García-Valdés R, Ruíz-Benito P, Zavala MA (2011) Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: implications for forest management under global change. Glob Change Biol 17:2400–2414. https://doi.org/10.1111/j.1365-2486.2011.02421.x

Gould PJ, Bradley St, Clair J, Anderson PD (2011) Performance of full-sib families of Douglas-fir in pure-family and mixed-family deployments. For Ecol Manag 262:1417–1425. https://doi.org/10.1016/j.foreco.2011.06.042

Grady KC, Kolb TE, Ikeda DH, Whitham TG (2015) A bridge too far: cold and pathogen constraints to assisted migration of riparian forests. Restor Ecol 23:811–820. https://doi.org/10.1111/rec.12245

Griffin JR, Conkle MT (1967) Early performance of knobcone x monterey pine hybrids… on marginal timber sites. Res note PSW-RN-156 Berkeley CA US Dep Agric for Serv Pac Southwest for Range Exp Stn 10 P

Hegyi F (1974) A simulation model for managing jack-pine stands. Growth Models Tree Stand Simul 74–90

Hunt R, Cornelissen JHC (1997) Components of relative growth rate and their interrelations in 59 temperate plant species. New Phytol 135:395–417. https://doi.org/10.1046/j.1469-8137.1997.00671.x

Ishii H, Asano S (2010) The role of crown architecture, leaf phenology and photosynthetic activity in promoting complementary use of light among coexisting species in temperate forests. Ecol Res 25:715–722. https://doi.org/10.1007/s11284-009-0668-4

James G, Witten D, Hastie T, Tibshirani R (2021) An introduction to statistical learning: with applications in R, 2nd edn. Springer US

Johnston JD, Dunn CJ, Vernon MJ (2019) Tree traits influence response to fire severity in the western Oregon Cascades, USA. For Ecol Manag 433:690–698. https://doi.org/10.1016/j.foreco.2018.11.047

Jucker T, Bouriaud O, Avacaritei D et al (2014) Competition for light and water play contrasting roles in driving diversity–productivity relationships in Iberian forests. J Ecol 102:1202–1213. https://doi.org/10.1111/1365-2745.12276

Jucker T, Bouriaud O, Coomes DA (2015) Crown plasticity enables trees to optimize canopy packing in mixed-species forests. Funct Ecol 29:1078–1086. https://doi.org/10.1111/1365-2435.12428

Jucker T, Avăcăriței D, Bărnoaiea I et al (2016) Climate modulates the effects of tree diversity on forest productivity. J Ecol 104:388–398. https://doi.org/10.1111/1365-2745.12522

Jucker T, Koricheva J, Finér L et al (2020) Good things take time—diversity effects on tree growth shift from negative to positive during stand development in boreal forests. J Ecol 108:2198–2211

Klos PZ, Link TE, Abatzoglou JT (2014) Extent of the rain-snow transition zone in the western U.S. under historic and projected climate. Geophys Res Lett 41:4560–4568. https://doi.org/10.1002/2014GL060500

Koontz MJ, Latimer AM, Mortenson LA et al (2021) Cross-scale interaction of host tree size and climatic water deficit governs bark beetle-induced tree mortality. Nat Commun 12. https://doi.org/10.1038/s41467-020-20455-y

Lanner RM (1985) On the insensitivity of height growth to spacing. For Ecol Manag 13:143–148. https://doi.org/10.1016/0378-1127(85)90030-1

Liu Y, He F (2021) Warming intensifies soil pathogen negative feedback on a temperate tree. New Phytol 231:2297–2307. https://doi.org/10.1111/nph.17409

Lutz JA, van Wagtendonk JW, Franklin JF (2010) Climatic water deficit, tree species ranges, and climate change in Yosemite National Park. J Biogeogr 37:936–950. https://doi.org/10.1111/j.1365-2699.2009.02268.x

Luu TC, Binkley D, Stape JL (2013) Neighborhood uniformity increases growth of individual Eucalyptus trees. For Ecol Manag 289:90–97. https://doi.org/10.1016/j.foreco.2012.09.033

Malmsheimer RW, Heffernan P, Brink S et al (2009) Forest management solutions for mitigating climate change in the United States. Society of American Foresters

McDonald PM, Fiddler GO (2010) Twenty-five years of managing vegetation in conifer plantations in northern and central California: results, application, principles, and challenges. Gen Tech Rep PSW-GTR-231. https://doi.org/10.2737/PSW-GTR-231. Albany CA US Dep Agric For Serv Pac Southwest Res Stn

Mead DJ (2013) Sustainable management of Pinus radiata plantations. Food and Agriculture Organization of the United Nations, Rome, Italy

Mina M, Huber MO, Forrester DI et al (2018) Multiple factors modulate tree growth complementarity in central european mixed forests. J Ecol 106:1106–1119. https://doi.org/10.1111/1365-2745.12846

Moran GF, Bell JC, Eldridge KG (1988) The genetic structure and the conservation of the five natural populations of Pinusradiata. Can J For Res 18:506–514. https://doi.org/10.1139/x88-074

Nykänen M-L, Peltola H, Quine C et al (1997) Factors affecting snow damage of trees with particular reference to european conditions

O'Neill GA, Stoehr M, Jaquish B (2014) Quantifying safe seed transfer distance and impacts of tree breeding on adaptation. For Ecol Manag 328:122–130. https://doi.org/10.1016/j.foreco.2014.05.039

Oliver WW (1979) Growth and mortality of thinned knobcone x Monterey pine saplings affected by engraver beetles and a hard freeze. U.S. Dept. of Agriculture, Forest Service, Pacific Southwest Research Station

Ouzts J, Kolb T, Huffman D, Sánchez Meador A (2015) Post-fire ponderosa pine regeneration with and without planting in Arizona and New Mexico. For Ecol Manag 354:281–290. https://doi.org/10.1016/j.foreco.2015.06.001

Pedlar JH, McKenney DW, Lu P (2021) Critical seed transfer distances for selected tree species in Eastern North America. J Ecol 109:2271–2283. https://doi.org/10.1111/1365-2745.13605

Pinheiro JC, Bates DM (eds) (2000) Mixed-Effects Models in S and S-PLUS. Springer New York, New York, NY, pp 133–199. Fitting Linear Mixed-Effects Models

Pommerening A, Maleki K, Haufe J (2021) Tamm Review: individual-based forest management or seeing the trees for the forest. For Ecol Manag 501:119677. https://doi.org/10.1016/j.foreco.2021.119677

Powers RF, Reynolds PE (2011) Ten-year responses of ponderosa pine plantations to repeated vegetation and nutrient control along an environmental gradient. Can J For Res. https://doi.org/10.1139/x99-104

Pretzsch H (2005) Diversity and productivity in forests: evidence from long-term experimental plots. In: Scherer-Lorenzen M, Körner C, Schulze ED (eds) Forest diversity and function. Springer, Verlag, Berlin-Heidelberg, p 401

Pretzsch H (2021) Genetic diversity reduces competition and increases tree growth on a Norway spruce (Picea abies [L.] Karst.) Provenance mixing experiment. For Ecol Manag 497:119498. https://doi.org/10.1016/j.foreco.2021.119498

Pretzsch H, Biber P (2016) Tree species mixing can increase maximum stand density. Can J For Res 46:1179–1193. https://doi.org/10.1139/cjfr-2015-0413

Rehfeldt GE, Ying CC, Spittlehouse DL, Hamilton Jr DA (1999) Genetic responses to climate in pinus contorta: niche breadth, climate change, and reforestation. Ecol Monogr 69:375–407. https://doi.org/10.1890/0012-9615(1999)069[0375:GRTCIP]2.0.CO;2

Richards SA (2008) Dealing with overdispersed count data in applied ecology. J Appl Ecol 45:218–227. https://doi.org/10.1111/j.1365-2664.2007.01377.x

Rodríguez-Trejo DA, Fulé PZ (2003) Fire ecology of mexican pines and a fire management proposal. Int J Wildland Fire 12:23–37. https://doi.org/10.1071/WF02040

Rweyongeza DM, Dhir NK, Barnhardt LK et al (2007) Population differentiation of the lodgepole pine (Pinus contorta) and jack pine (Pinus banksiana) complex in Alberta: growth, survival, and responses to climate. Can J Bot 85:545–556. https://doi.org/10.1139/B07-053

Shive KL, Preisler HK, Welch KR et al (2018) From the stand scale to the landscape scale: predicting the spatial patterns of forest regeneration after disturbance. Ecol Appl 28:1626–1639. https://doi.org/10.1002/eap.1756

St. Clair JB, Howe GT, Kling JG (2020) The 1912 Douglas-Fir Heredity Study: Long-Term Effects of climatic transfer Distance on Growth and Survival. J For 118:1–13. https://doi.org/10.1093/jofore/fvz064

St. Clair JB, Richardson BA, Stevenson-Molnar N et al (2022) Seedlot Selection Tool and Climate-Smart Restoration Tool: web-based tools for sourcing seed adapted to future climates. Ecosphere 13:e4089. https://doi.org/10.1002/ecs2.4089

Stevens-Rumann CS, Kemp KB, Higuera PE et al (2018) Evidence for declining forest resilience to wildfires under climate change. Ecol Lett 21:243–252. https://doi.org/10.1111/ele.12889

Stewart JAE, van Mantgem PJ, Young DJN et al (2021) Effects of postfire climate and seed availability on postfire conifer regeneration. Ecol Appl 31:e02280. https://doi.org/10.1002/eap.2280

Tepley AJ, Thompson JR, Epstein HE, Anderson-Teixeira KJ (2017) Vulnerability to forest loss through altered postfire recovery dynamics in a warming climate in the Klamath Mountains. Glob Change Biol 23:4117–4132. https://doi.org/10.1111/gcb.13704

Toïgo M, Vallet P, Perot T et al (2015) Overyielding in mixed forests decreases with site productivity. J Ecol 103:502–512. https://doi.org/10.1111/1365-2745.12353

Ukrainetz NK, O'Neill GA, Jaquish B (2011) Comparison of fixed and focal point seed transfer systems for reforestation and assisted migration: a case study for interior spruce in British Columbia. Can J For Res 41:1452–1464. https://doi.org/10.1139/x11-060

Wang T, Hamann A, Spittlehouse D, Carroll C (2016) Locally downscaled and spatially customizable climate data for historical and future periods for North America. PLoS ONE 11:e0156720. https://doi.org/10.1371/journal.pone.0156720

Williams LJ, Paquette A, Cavender-Bares J et al (2017) Spatial complementarity in tree crowns explains overyielding in species mixtures. Nat Ecol Evol 1:1–7. https://doi.org/10.1038/s41559-016-0063

Wright JW (2007) Local adaptation to serpentine soils in Pinus ponderosa. Plant Soil 293:209–217. https://doi.org/10.1007/s11104-006-9181-5

Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proc Natl Acad Sci 96:1463. https://doi.org/10.1073/pnas.96.4.1463

Yao Y, Vehtari A, Simpson D, Gelman A (2018) Using stacking to average bayesian predictive distributions (with discussion). Bayesian Anal 13:917–1007. https://doi.org/10.1214/17-BA1091

York RA, Noble H, Quinn-Davidson LN, Battles JJ (2021) Pyrosilviculture: combining prescribed fire with gap-based silviculture in mixed-conifer forests of the Sierra Nevada. Can J For Res 51:781–791. https://doi.org/10.1139/cjfr-2020-0337

Zhai L, Jokela EJ, Gezan SA, Vogel JG (2015) Family, environment and silviculture effects in pure- and mixed-family stands of loblolly (Pinus taeda L.) and slash (P. elliottii Engelm. Var. Elliotttii) pine. For Ecol Manag 337:28–40. https://doi.org/10.1016/j.foreco.2014.10.030

Zhang J, Webster J, Powers RF, Mills J (2008) Reforestation after the Fountain Fire in Northern California: an untold Success Story. J For 106:425–430. https://doi.org/10.1093/jof/106.8.425

Zhang J, Finley KA, Young DH et al (2022) Growth response of ponderosa pine to intensive cultural treatments varies with site quality and plantation age. For Sci 68

Zimová S, Dobor L, Hlásny T et al (2020) Reducing rotation age to address increasing disturbances in Central Europe: potential and limitations. For Ecol Manag 475:118408. https://doi.org/10.1016/j.foreco.2020.118408

Zuur A, Ieno EN, Walker N et al (2009) Mixed Effects models and extensions in Ecology with R. Springer Science & Business Media

## Authors and Affiliations

**Christopher E. Looney[1] · Joseph A.E. Stewart[2] · Katherine E.A. Wood[3]**

✉  Christopher E. Looney
    christopher.looney@usda.gov

    Joseph A.E. Stewart
    JoeStewart@UcDavis.edu

    Katherine E.A. Wood
    katherine.wood@usda.gov

[1]  USDA, Forest Service Pacific Southwest Research Station, 1731 Research Park Dr, Davis, CA 95618, USA

[2]  Department of Plant Sciences, University of California at Davis, 1 Shields Ave, Davis, CA 95616, USA

[3]  Forest Service Pacific Southwest Research Station, 3644 Avtech Parkway, Redding, CA 96002, USA