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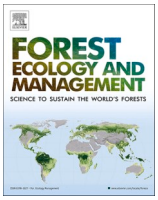

Can the inter-rotational productivity in ponderosa pine plantations be sustained in the face of climatic change?

Jianwei Zhang

USDA Forest Service, Pacific Southwest Research Station, 3644 Avtech Parkway, Redding, CA 96002, USA

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ABSTRACT

Inter-rotational productivity (i.e., productivity of successive rotations) of ponderosa pine plantation was measured on experimentally treated plots with a common design at three diverse sites in northern California. The objectives were to examine the carryover effects of fertilization (F) and understory control by herbicide (H) applied in the first rotation of plantation, on growth in the second rotation and to determine the sustainability of plantation productivity between rotations. Carryover effects varied among the three sites. There was a significant and positive H and F effect ($P < 0.03$) on tree height and aboveground biomass at Whitmore, a site of intermediate quality; only an H effect at Elkhorn ($P < 0.01$), the site of low quality; and an F effect at Feather Falls ($P = 0.05$), the site of high quality. Genetically improved seeds resulted in slightly taller height than the original seed sources, but the difference was not statistically significant. While annual precipitation was similar, growing season precipitation was 6–42 % lesser and air temperature was about 0.9–1.4 °C higher during the second rotation than in the first rotation. Due to the warmer air temperature, the sites likely endured drier air, greater evapotranspiration, and lesser soil water availability. These environmental changes appear to have caused the observed growth reduction in these ponderosa pine plantations. This was despite the management techniques we applied for improved pine growth during the second rotation: genetically improved seeds and control of competing vegetation. It is believed that these are the first reported observations of growth decline in managed ponderosa pine plantations associated with warming climate. If these results are representative of a larger region and a future trend, use of ponderosa pine plantation forestry as a method of increasing forest carbon sequestration, may be overestimated for future rotations.

1. Introduction

Forest plantations have been regarded as an important source to meet an increasing demand for wood and fiber (Powers, 1999) driven by the rapid growth of the world's population along with increases in standard of living (FAO, 2009). Plantations have been also promoted as tools for sequestering more atmospheric CO_2 to offset an exponential increase of CO_2 (Bonan, 2008; Bastin et al., 2019). Concerns have arisen whether productivity of these plantations, often monocultures, can be sustained through the second and future rotations (Keeves, 1966; Whyte, 1973; Powers, 1999; Fox, 2000). The few long-term studies of productivity of continuous rotations of plantations have reported declining, sustaining, and even increasing rates of growth. Results appear to be dependent largely on the silvicultural practices employed during the first rotation harvests or to the specific treatments applied to the second rotations (Powers, 1999; Mead, 2013). For example, significant declines reported for yield of second rotations of *Pinus radiata* (Keeves, 1966; Whyte, 1973) was thought to be due to the method of harvesting and site preparation such as the removal of topsoil and the burning slash in Australia and New Zealand (O'Hehir and Nambiar, 2010; Turner and Lambert, 2013). Another reported decline of second rotation *Picea sitchensis* was thought to be due to whole-tree harvesting (Walmsley et al., 2009). In contrast, increased productivity was reported by Evans (2005) during the second, third, and fourth rotations of *P. patula* in Swaziland, South Africa, when genetically improved seeds were used and where soil organic matter was conserved. Though Evans found that reductions occurred on phosphate-poor soils (Garrett et al., 2015; Mavimbela et al., 2018). Reduced yield of Chinese fir (*Cunninghamia lanceolata*) was observed in the second and third rotations (Ding and Chen, 1995) and reduced yields also were reported for second rotation teak (*Tectona grandis*) in India (Chacko, 1995). Both of these cases of reduced yield also appeared to be related to poor management practices (FAO, 2001) such as removing leaves, twigs, and litter from beneath tree stands or by not using the same sites between rotations.

E-mail address: jianwei.zhang2@usda.gov.

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Even for the earliest report on decline of Norway spruce (*Picea abies* (L.) Karst.), the original thought was that monocultures degraded the soil (Wiedemann, 1923). Later this decline was found to be related to incorrect seed sources (Powers, 1999). Plantations of *P. elliottii* and *P. taeda* sustained productivity in the second rotation plantations (Fox, 2000). A recent experiment of loblolly pine reported that height growth and biomass increment in the second-rotation stands were greater than that in the first rotation when both fertilization and competing vegetation control were applied in both rotations (Subedi et al., 2019). This study also examined carryover effects of treatments and found that application of fertilizer only during the first rotation produced significantly more aboveground biomass in the second rotation when compared to the controls receiving no fertilization in either rotation. Such results suggest that management practice applied at initial rotations can enhance productivity into future rotations. In fact, for the last 60 years, advances in management technologies (nutrition, vegetation control, tree improvement, silviculture, and soil-site classification, etc.) have increased per acre loblolly pine yields by up to six times over those of naturally regenerated second growth stands (Carter and Foster, 2006). These results suggest that inter-rotational productivity can be sustained or even increased with the appropriate management practices that reduce site, stand, and biological limitations (Vance et al., 2010).

Climate is a key factor in determining forest productivity (Powers, 1999; Mead, 2005). Although human activity has significantly increased greenhouse gases that has warmed the atmosphere (IPCC, 2021) climate cannot be readily manipulated by foresters at a site. Climate change, along with rising temperatures, increased CO_2 levels, and nitrogen deposition, has been documented to boost forest growth and increase net carbon uptake (McMahon et al., 2010; Fang et al., 2014; Keenan et al., 2014), although this carbon sink has appeared to reach saturation in European forests (Nabuurs et al., 2013; Williams et al., 2013). Assessments of climate effects on plantation productivity has been limited to comparisons among plantations grown at different climatic sites and modeling exercises (Carrasco et al., 2022). To properly measure climate effects on inter-rotational productivity one would need to control seedling source (e.g., seeds from the same species and genotypes) and plant seedlings at the same site during subsequent rotations (Evans, 1999; 2005). However, such studies have not been tried. Prior studies have used the space-for-time approaches, that is, different sites with varying climate (Pickett, 1989). Space-for-time results can be confounded by the sites introducing additional sources of variation (Powers, 1999).

Process-based approaches that consider nutrient cycling, tree stand physiology, and environmental variables have often suggested a inter-rotational plantations productivity would decline (Liao et al., 2012; Farooq et al., 2021). In a meta-analysis of natural and planted forests, Liao et al. (2012) concluded that consecutive plantation practice had negative impacts on a number of soil properties including bulk density and soil C and N concentrations, suggesting that continuous plantations can potentially lead to the degradation of soil productivity. The dense canopy created by tree plantations can restrict sunlight from reaching the ground, inhibiting the growth of understory vegetation, and reducing biodiversity and subsequently stand productivity (Nakamura et al., 2017; Feng et al., 2022; Hua et al., 2022). An increase in the biodiversity of plants has been shown to increase soil nutrient content and soil health and greater community carbon storage at the Cedar Creek Science Reserve (Furey and Tilman, 2021). Consequently, these indirect effects of rotational tree plantations may contribute to a decline in soil productivity over time.

Ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) is the most widely distributed pine species in North America and has been extensively planted due to its value for timber production (Oliver and Ryker, 1990). Because of its stress resistant capability to various environments, it has been a favorable species used in the postfire reforestation (Stevens-Rumann and Morgan, 2019). Therefore, ponderosa pine has been planted across the west of North America since early of last century and elsewhere in the world such as in the Patagonia region of Argentina. Its growth rate in stem volume can reach as high as 20 m^3 ha^{-1} yr^{-1}, which is comparable to other highly productive conifer species in the world (Zhang et al., 2022). However, to my knowledge, no information is available on the inter-rotational productivity in ponderosa pine, which raises a concern about the biological sustainability if this species is planted in consecutive rotations in the future.

Here, a former study, of ponderosa pine production that received multiple treatments on multiple sites (Powers and Ferrell, 1996; Zhang et al., 2021) was converted to a second rotation experiment after the first rotation trees had been harvested. The goal was to determine the carryover effect of fertilizer and understory vegetation control applied during the first rotation on the stand growth over the second rotation. The specific questions were: (1) Is a carryover effect significant (e.g., are treatments applied only in the first rotation still effective in increasing productivity during the second rotation?). (2) If not, in what ways may productivity be affected? (3) How do genetically improved seeds affect second rotation productivity? (4) What management techniques applied to a ponderosa pine plantation can sustain its productivity in the second rotation when compared to its first rotation?

2. Materials and methods

2.1. Study site

Three sites chosen for this analysis were Elkhorn, a low- productive site, Whitmore, a site of intermediate productivity, and Feather Falls, a high-productive site (Table 1). These sites were part of the previously so-called “Garden of Eden” study of northern California that determined growth potential of ponderosa pine plantation as constrained by nutrient availability and competition by understory vegetation (Powers and Ferrell, 1996). These sites are in the heart of Pacific ponderosa pine ecosystem that has a Mediterranean climate with warm, dry summers and cool, wet winters. Weather data shown in Fig. S1 are from the PRISM climate model at Oregon State University (https://prism.oregonstate.edu/). The three sites had different establishment years for the first rotation (1R), and we calculated means of monthly maximum and minimum temperatures and mean annual precipitation during the period starting from the respective establishment year to the last measurement year in the second rotation (2R).

Trees were measured in the 1R before harvesting, to estimate biomass (Zhang et al., 2021). Whole-tree harvesting was conducted in 2014, the skid trails removed forest floors down to the mineral soils. After harvesting, herbicides (broadcast pre-emergent soil active and/or directed foliar contact/systemic) were applied to the respective treatment plots prior to re-planting.

Table 1
Geographic locations, site characteristics, and information for first rotation (1R) planting year, aboveground tree biomass, and second rotation (2R) planting year of ponderosa pine plantations at three study sites in northern California.

	Elkhorn	Whitmore	Feather Falls
Latitude (N)	40.0824	40.6259	39.6198
Longitude (W)	122.7424	121.8990	121.1966
Elevation (m)	1539	747	1250
Site index (m at age 50)	17	23	30
Parent material	Metasediment	Volcanic	Volcanic
Soil group	Xerochrepts	Haplohumults	Haploxeralfs
Soil type	Sandy loam	Clay	Loam
Vegetation prior to 1R	Plantation	Brushfield	Natural stand
Year planted (1R)	1988	1986	1988
Year planted (2R)	2014	2014	2014
1R AGB at 20 yrs (*Mg/ha*)			
Control	27.2	42.7	155.9
Fertilizer (F)	49.4	85.9	248.8
Herbicide (H)	62.2	118.0	172.5
HF	96.2	145.1	238.5

2.2. Experimental design and treatments

Completely randomized designs were implemented at all sites in both rotations. In the 1R, a treatment was one of eight factorial combinations (2×2×2 factorial treatments) using two levels each of vegetation control, fertilizer, and insect control (i.e., applied or not applied). Each treatment combination was repeated three times and randomly assigned to one of the resultant 24 plots. Treatments were applied several times during the first six years of the 1R plantation growth (Powers and Ferrell, 1996). Vegetation control (H treatment) consisted of herbicides (glyphosate, hexazinone, or triclopyr) following manufacturer's recommendations for the soil type and vegetation present. Fertilizer (F treatment) was applied during four dormant seasons with dry commercial salts of macro and micro elements following a ramp schedule in which nutrient supply increased with demand. The final cumulative amounts applied per hectare were 1074 kg (N), 530 kg (P), 540 kg (K), 416 kg (Ca), 221 kg (Mg), 112 kg (S), 73 kg (Zn), 36 kg (Cu), and 36 kg (B). Due to a lack of measurable insect activity during the 1R, insecticide treatments were dropped. These extra replications were either subsumed into the other two treatments or studied the thinning effect in the 1R. In the 2R, these additional plots were used for studying genetic effect.

In the 2R at each site, 12 plots were planted with original seed source-raised seedlings (G1) and 12 plots were planted with genetically improved seedlings (G2). The 2R seedlings were grown in Styro 6 containers (Beaver Plastic, Alberta, Canada) at the Cal-Forest Nurseries, Etna, California. In 2014, seedlings were planted at the same 2.4 × 2.4 m spacing, as in the 1R. Each treatment plot was ca. 22 × 20 m, the same as in the 1R. A total of 72 trees were planted within each plot and the inner 20 trees composed the measurement plot. Regardless the treatments in the 1R, at just before planting the 2R and for the first three years of growth, competing vegetation was controlled by herbicide across all plots. Herbicides currently registered for forestry use in California were used with the rate based on manufacturer's recommendations for the soil type and vegetation present. No fertilizer was added for the 2R and no additional herbicides were used after the 3rd year. The experiment becomes a complete randomized design with eight treatments replicated three times in the 2R. The treatments are 2 genotypes (G_1 and G_2) in the 2R by 4 silvicultural regimes (F_0, F_1, H_0, and H_1) applied during the 1R. Therefore, eight treatment combinations are $F_0H_0G_1$, $F_0H_0G_2$, $F_0H_1G_1$, $F_0H_1G_2$, $F_1H_0G_1$, $F_1H_0G_2$, $F_1H_1G_1$, and $F_1H_1G_2$. Comparisons among these treatments would test for treatment effects in 2R. Treatment comparisons without genotypes would test carry over effects of the treatments applied during 1R. Comparisons of the 2R treatments to 1R treatments would test for changes in productivity (inter-rotational effect).

2.3. Measurements

Trees – At the three sites, tree heights were measured at ages 3 (2016), 5 (2018), 6 (2019), and 7 (2020). Ground-level diameter (gld, 20 cm above the ground) was measured initially until at ages 3 and 5 at all sites, gld was also measured at ages 3 and 5 at all sites, although we also measured diameter at breast height (dbh) at Feather Falls at age 5 because most trees reached over 1.37 m height.

At age 6, very few trees reached 1.37 m at Elkhorn and therefore, gld was measured. At Whitmore, about 75 % trees reached over 1.37 m and so dbh was measured although we measured both gld and dbh for some trees (25 %). For those trees with <1.37 m in height, only gld was measured. At Feather Falls, all trees except for six had reached 1.37 m and therefore dbh was measured.

During late summer of 2020, at age 7, wildfires burned two sites. The August Complex Fire burned an edge of the Elkhorn site killing some trees. The North Complex Fire killed all trees at Feather Falls. Because terminal buds were formed and height growth ceased before the fires, we measured height during the following winter. Since height was not measured at Whitmore in the 1R at age 7, we also measured age 8 height at Whitmore to match the measurement age of 8 collected in the 1R.

Individual tree biomass was estimated using allometric equations developed with gld or dbh and height for ponderosa pine trees from six different sites in California (Powers et al., 2013). Because tree gld and/or dbh were only measured at certain years and sites during the 1R, only inter-rotation AGB for those years with available 1R data are compared. However, the trends I report here are generally consistent with previous studies of tree ring width, and associated annual basal area calculations, including cellulose biomarkers of a negative relationship between resource-use efficiency and tree growth rates, a relationship that occurs despite expected CO_2 stimulation effects, but one that can be modified by fertilization and competitor removal (Liles et al., 2019).

1R tree data –The measurement procedures for 1R were similar as described above. The details can be found in Powers and Ferrell (1996) and Zhang et al. (2022). Heights were measured more frequently than either gld or dbh in the 1R. Therefore, height was primarily used for the inter-rotational productivity; there was a strong correlation between height and productivity in the early stage of plantation (Powers and Ferrell, 1996). In addition, an age-age correlation was also significant for biomass production (Zhang et al., 2021).

Soil samples - Soil samples were collected in the 2R at age 1 from three depths (0–10, 10–20, and 20–30 cm) using a volumetric core sampler. Soils were collected at three locations evenly distributed in each plot. In the lab, samples were dried at 105 °C to a constant weight, then weighed, then sieved to 2-mm. Rock fragments were weighed. The soil total bulk density and fine bulk density were calculated for these 600 samples, (Han et al., 2016). Total NPK and organic C were analyzed by pooling the three samples from the same depth within each plot. Soil C and N were determined by potassium dichromate oxidation and acid digestion - Auto Analyzer 3 Continuous-Flow Analysis, respectively. Total P and K were analyzed by sodium hydroxide digestion method (Vogt et al., 2015). Water extraction–potentiometric method was used for soil pH and cation exchange capacity (CEC) was determined by the EDTA–ammonium acetate extraction–distillation–hydrochloric acid titration method (Vogt et al., 2015). Concentrations were converted to total content (mass) by multiplying the concentrations by the mean fine fraction bulk density of the three samples that were bulked and corrected for rock volumes.

In addition, we also analyzed some archived soil samples collected at 0–10 and 10–20 cm depths from C, F, H, HF treatment plots at Elkhorn and Feather Falls at year 1 of the 1R in 1988. These samples were collected and processed using the same method described above and analyzed in the same laboratory. Inter-rotational nutrient concentration was compared. Samples were not collected at Whitmore at year 1 of 1R.

2.4. Statistical analysis

All growth variables were analyzed with a repeated-measures analysis of variance for a completely randomized design with all treatments, genotype, and measurement year as the fixed effects and plot as a random effect using SAS PROC MIXED (SAS Institute, 2013). Each site was separately analyzed due to a lack of site and treatment interactions in the first rotation (Zhang et al., 2022). All two-, three-, and four-term interactions were included in the model (Table S1).

Soil chemical variables (organic C, NPK, pH, CEC) measured in 2014 were analyzed with ANOVA model using PROC MIXED. Because the interactions between site and treatments were unknown, we included site into the same model. Both concentrations and contents for C, N, P, and K were analyzed (Tables S2 and S3).

For each analysis, residuals were examined to ensure that statistical assumptions of normality and homoscedasticity were met. If not, a natural log or square-root transformation was applied. Multiple comparisons among treatments (H, F, and G) were conducted for least squares means by the Tukey-Kramer test by controlling for the overall $\alpha = 0.05$. The inter-rotational relationships for all variables were plotted

2R versus 1R and evaluated against a 1:1 line.

3. Results

3.1. Climate data

Air temperatures were higher at all three sites during the 2R versus the 1R (Fig. 1); the mean annual temperature increase was 1.4 °C at the higher elevation sites of Elkhorn and Feather Falls, and 0.9°C at Whitmore. The mean monthly minimum temperatures increased 1.2–2.5°C and the mean monthly maximum temperatures increased 0.5–0.8°C (Fig. S1). Annual precipitation for the first eight years of plantation growth overall was lower in the 2R than in the 1R at Elkhorn (−16 %, −156 mm) and Feather Falls (−5%, −97 mm), but it was 7 % higher (+69 mm) at Whitmore (Fig. 1). Reductions of growing season precipitation (March – July) occurred and ranged from −5.7 % at Whitmore, –23.4 % at Feather Falls, to −41.8 % at Elkhorn during the 2R versus the 1R (Fig. S1).

3.2. Carryover effect from the first rotation treatments

Carryover effects were assessed by comparing growth of aboveground biomass (AGB) and height in 2R for treatments that were applied during 1R to their respective controls. Effects of herbicide and fertilizer were apparent in the 2R growth and became more apparent with increasing age of the plantations (Fig. S2). The effects varied among sites. At the low-quality site, Elkhorn, herbicide applied during 1R showed a significantly and approximately 26 % increase in the final

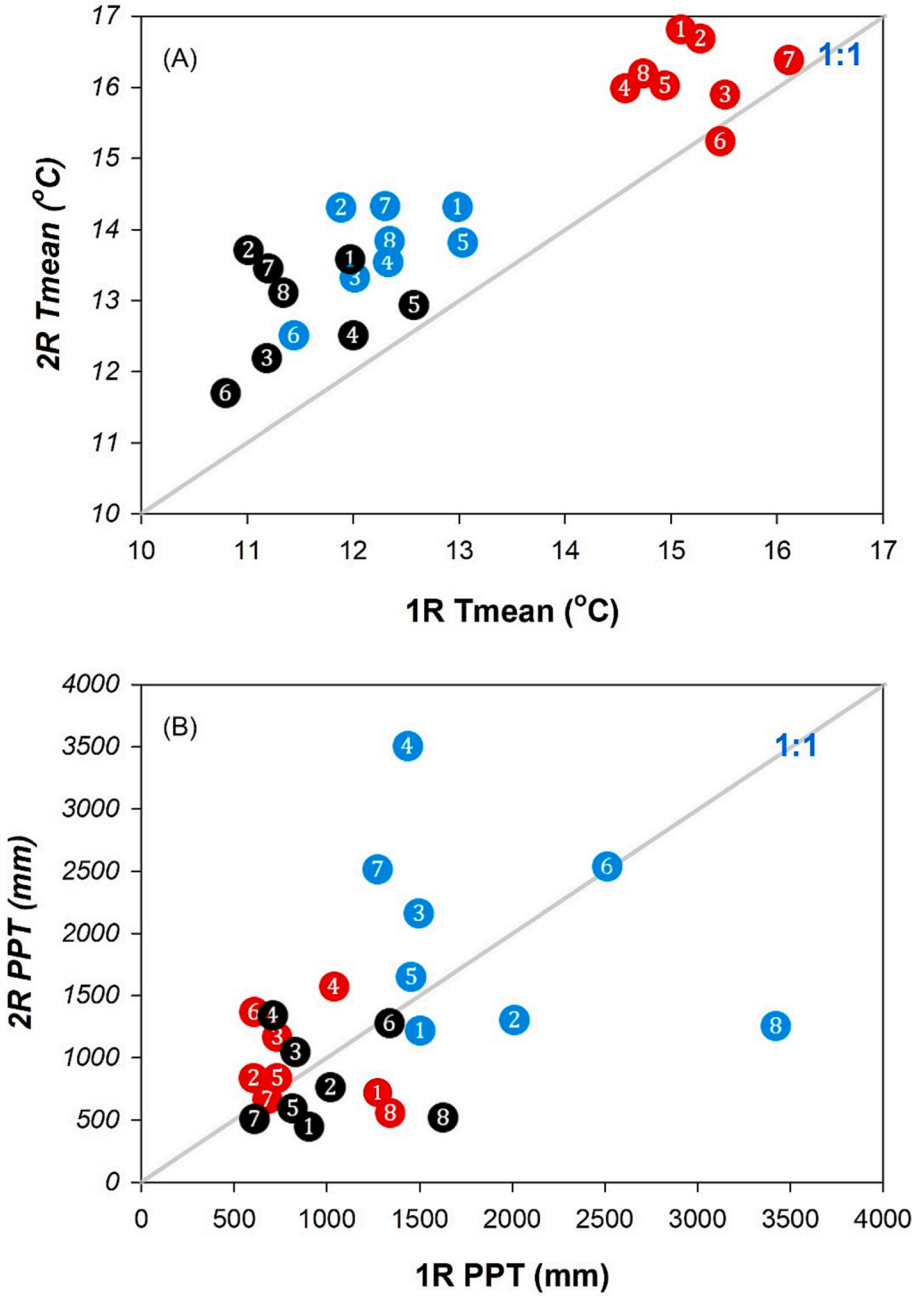

Fig. 1. Mean annual temperature (Tmean) and annual precipitation (PPT) at Elkhorn (black), Whitmore (red), and Feather Falls (blue) during first 8 years (numerals correspond to years 1–8) of plantation growth in the first rotation (1R) and second rotation (2R). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

measure of tree height and 30 % in AGB during 2R, (Table S1, Fig. 2). However, fertilizer application in 1R had essentially no effect or even possibly decreases in 2R growth.

At the intermediate-quality site, Whitmore, both H and F showed the greatest relative growth responses of the three sites. H and F significantly increased AGB and height (Table S1, Fig. 2); F increased growth by 73 % in AGB and 30 % in height and H increased growth by about 22 % in AGB and 10 % in height. The combination of F with H increased AGB by at least 100 % and increase in height by 40 % (Fig. 2).

At the high-quality site, Feather Falls, F carryover effects were also significantly positive but were proportionally smaller than those at Whitmore with 16 % increases in AGB and 5 % in height (Table S1, $P < 0.055$) (Fig. 2). H effects were slightly positive but not significant. Feather Falls AGB growth on controls were already growing well and were at least double controls at of Whitmore and 4-fold greater than Elkhorn (Fig. 2). The carryover effects appeared to have the greatest effect on the lower quality sites, but the treatment effects could not overcome what appeared to be the overall effect of site as even the best growth from treatments at Elkhorn were less than half those of the controls at Feather Falls.

3.3. Genetic effect

Source of the seeds (genetics) positively affected height growth at Elkhorn ($P = 0.032$), and genetic effects were slightly positive but not significant at the other two sites (Table S1). There were no genotype-related interactions. The AGB and heights responses by years 6 and 7 to genetically improved seeds were 12.5 % and 15.7 % at Elkhorn, 7.4 % and 4.7 % at Feather Falls, and 0 % and 1 % at Whitmore, respectively, relative to averages of G1, original seeds used in the 1R (Fig. 2).

3.4. Soil nutrients

More than 20 years after ceasing application of fertilization in the 1R, soil N, P concentrations and CEC were significantly higher in the F and HF than in the C and H in the 2R measured in 2014 (Table S2, Fig. 3). Site effect was always significant as the soil types were substantially different among three sites. All variables (except K) were higher concentrations at the topsoil layer. Interactions between treatment and site or depth were not significant except for P among site*-depth interactions.

Similarly, site effect was highly significant for C, N, P, and stocks (Fig. S3) with notable differences being Feather Falls having higher soil C and Elkhorn having higher K and P. Treatment effect was only found for K and P stocks. Once again, fertilization application in the 1R showed a slightly higher content of C, N, P, and K in 2014.

When R1 was compared to R2, soil nutrients at Elkhorn and Feather Falls were similar between rotations in spite of fertilizer applications (Fig. 4). Slight trends of change at both sites included decreased organic carbon and CEC, and slight increases in total P and.

When compared to their controls in 2014, Fig. 3 showed fertilizer applications were associated with greater concentrations of total P and slightly greater concentrations of total N at both Elkhorn and Whitmore in 2014. There was perhaps a small greater concentration of total P in the topsoil layer at Feather Falls but no difference in total K at any site.

3.5. Inter-rotational productivity

Inter-rotational effects were assessed by comparing growth data from 1R to that of 2R. Height growth was higher in 2R versus 1R for the early years of plantation, but this trend tended to diminish over time. For year 3, tree height was greater in all plots in 2R versus 1R and even

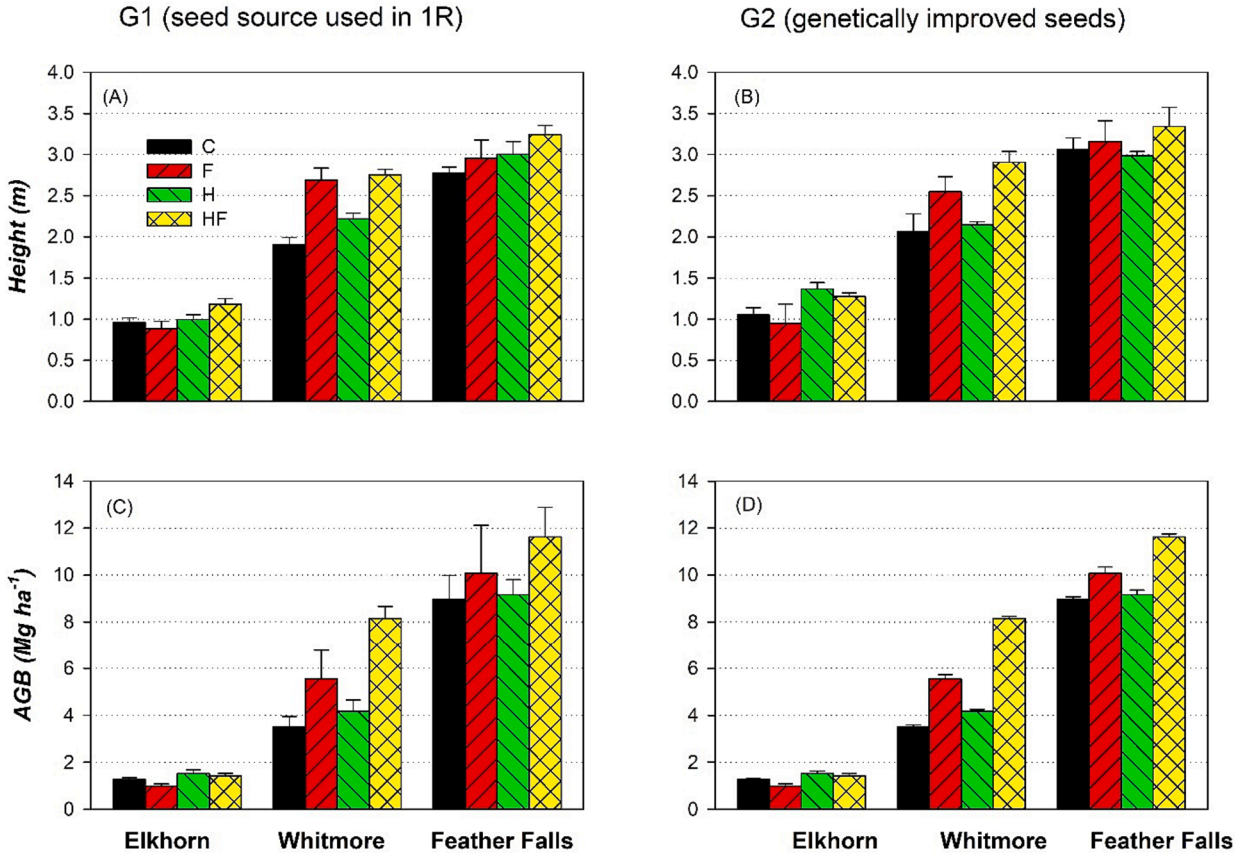

Fig. 2. Height at age 7 and aboveground biomass at age 6 + SE) for ponderosa pine trees grown on Elkhorn, Whitmore, and Feather Falls 2nd-rotation plantations. C: control F0H0, F: F1H0, H: F0H1, HF: F1H1; (A) and (C) are from the seeds that were used in the first rotation; (B) and (D) are from the genetically improved seeds.

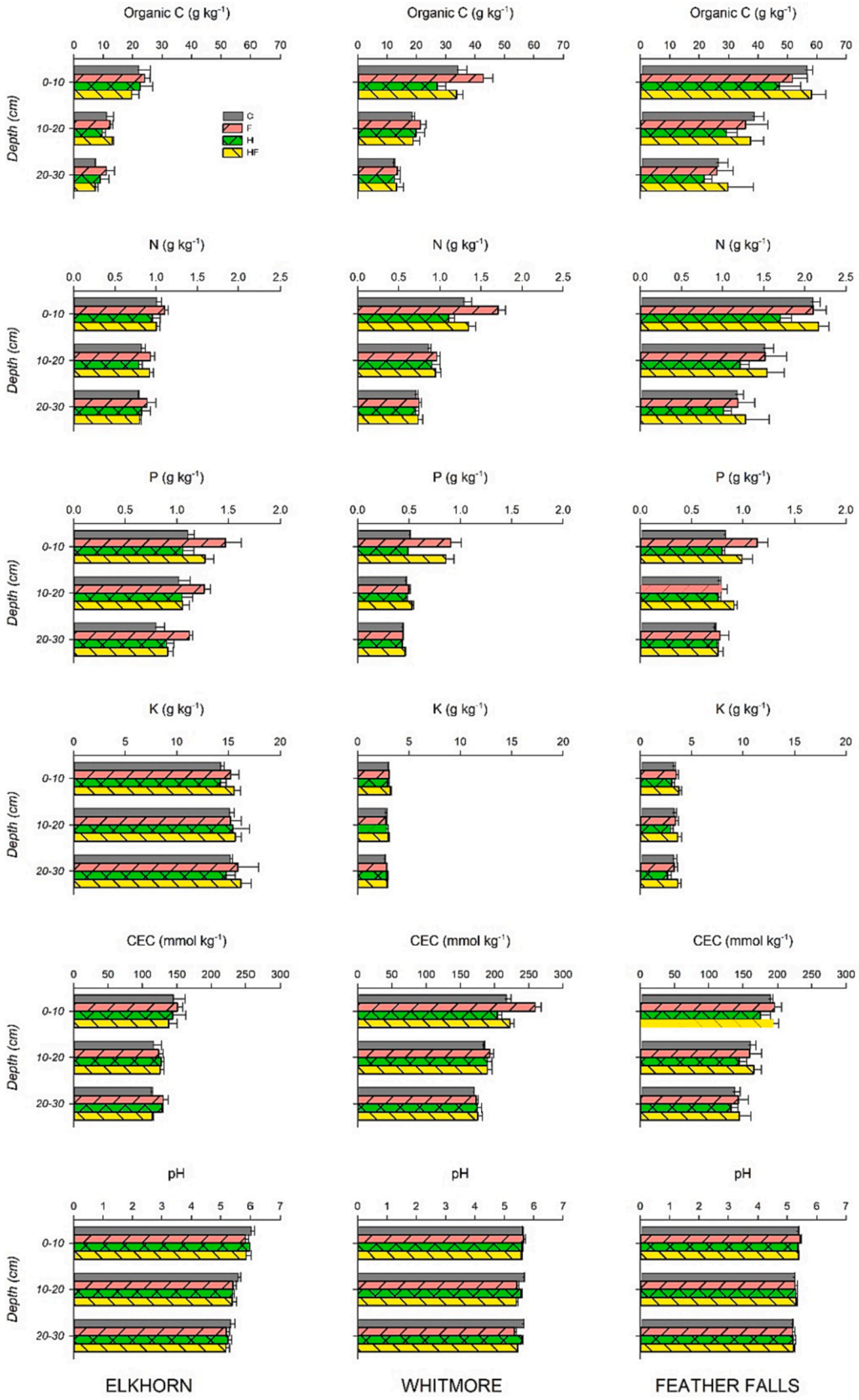

Fig. 3. Concentration means and standard errors for organic C, N, P, K, and cation exchange capacity (CEC) and pH on soils collected from three depths at Elkhorn, Whitmore, and Feather Falls in 2014.

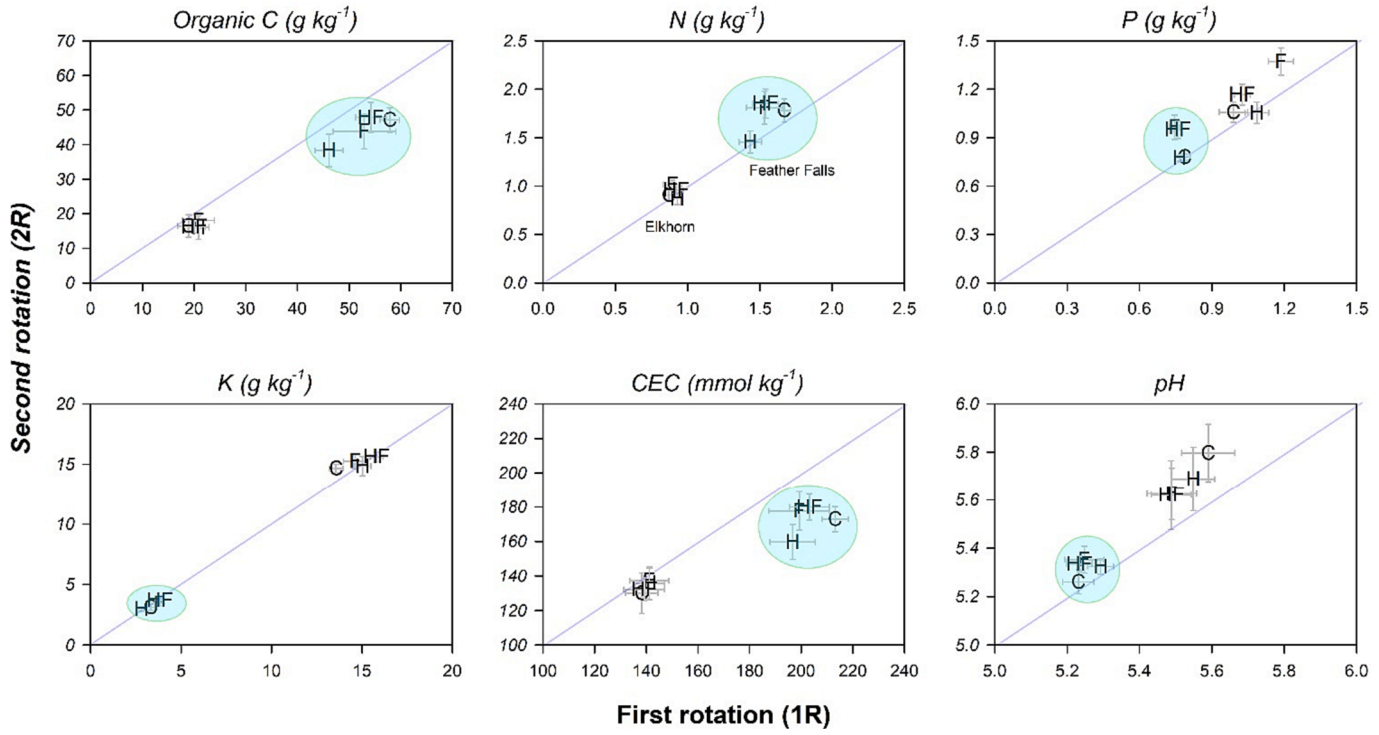

Fig. 4. Inter-rotational soil concentrations of organic carbon, N, P, K, and cation exchange capacity (CEC) and pH in the four treatment plots (C, F, H, HF) at both Feather Falls (shaded) and Elkhorn between rotations. Soil samples were collected in the first year of plantation of both rotations before any other treatments were applied.

in the controls, height was more than twice as great at Elkhorn and Whitmore (Fig. 5A-B and Fig. 6C). But only the H plots at Feather Falls showed greater heights at year 3 (Fig. 6H). By age 6, height growth relative to 1R appeared to be losing these gains particularly in the H treatments to the point where heights in 2R were becoming shorter than 1R. (Fig. 6). By age 7, most H plots at Feather Falls and Elkhorn showed heights of 2R < 1R except perhaps the C treatment. The only plots that still showed greater heights in 2R by year 7 were C and F at Elkhorn and Whitmore and these appeared to be diminishing over time.

Biomass comparisons between 1R and 2R were not as complete among years as heights because biomass was measured less frequently. However, there were similar trends as the heights at each site—generally greater biomass in 2R for Elkhorn and Whitmore, in years 3 and 5 with signs of lower biomass in 2R by year 6 and nearly universally less biomass in 2R at Feather Falls by year 6 (Fig. S4).

4. Discussion

Maintaining plantation productivity across rotations on the same land is a key component of the sustainable forest management, especially for intensively managed plantations (Powers, 1999; Fox, 2000; Vance et al., 2010). While climate, soil, and genetic potential determine site productivity (Powers, 1999), it is the management practices that assure such productivity to be reached and sustained or even improved (Vance et al., 2010; Subedi et al., 2014; 2019). In California, productivity of ponderosa pine plantations is often constrained by lack of soil water, which can be mitigated by controlling competing vegetation (Powers and Ferrell, 1996; Zhang et al., 2006). Control of competing vegetation has proved to be effective in enhancing productivity for ponderosa pine plantation in the first rotation (1R), especially in the lower site quality (Zhang et al., 2013; Zhang et al., 2022). Application of fertilizers also increases plantation productivity with more significant effects in the high-quality sites than in the low-quality sites (Zhang et al., 2022). Results from this study also support these trends, and also show a carryover effect of F and H treatments applied in the 1R plantations on productivity in the second rotation (2R) (Fig. 2, Fig. S2). Similar carryover effects from the application of fertilizer and the control of competing vegetation in the 1R were also found in *P. taeda* plantations in the southeastern United States (Subedi et al., 2014; 2019).

Genetic gains on height and AGB from this this study varied among sites; the greatest effects were observed at Elkhorn, and intermediate effects at Feather Falls, and lack of noticeable gain at Whitmore. Rehfeldt (1980) reported genetic gain in height of 8–14 % for ponderosa selection program in Idaho at age 16. I am not aware any genetic gain for growth that has been reported in California. In *P. taeda*, 7–8 % volume increase has been reported for first generation seed orchard with the open-pollinated families (Li et al., 1999). Our results at Elkorn and Feather Falls are comparable with to these numbers. Yet, lack of effect at Whitmore suggests possible genotype by environment interactions. The best genotypes need to be matched to appropriate management regimes in order for potential genetic gain to be realized (Powers, 1999).

Since these plantations were established in 2014, the trees have grown under the warmest annual global temperatures during the past nine years (2014–2022) based on the modern recordkeeping since 1880 (NOAA, 2023). Comparing the first eight years of the plantation growth (1R late 1980s) and second eight years (2R approximately 20 years later), local average annual temperatures from nearby climate stations show an increase in mean annual temperature between 0.9 and 1.4 °C (Fig. 1A & S1). The magnitudes of increase at these sites were higher than the mean of global temperature increase (0.85 – 0.89°C) for this same period. Global average temperatures during the decade of 2010–2019 have reportedly risen 1.1 °C above mean levels during the years 1850 to 1990 (IPCC, 2021). Temperature at the plantation sites during the 2R, have risen about 1.5 °C above this same pre-industrial global mean, and 1.5 °C has been cited as a tipping point of dangerous climate change by the Paris Agreement in 2015 (Lewis, 2016).

The warming temperatures themselves are not thought to have caused the observed productivity declines in the later years of the 2R plantations. Indeed, studies have shown that boreal and temperate forests have increased their growth and net carbon uptake recently and this

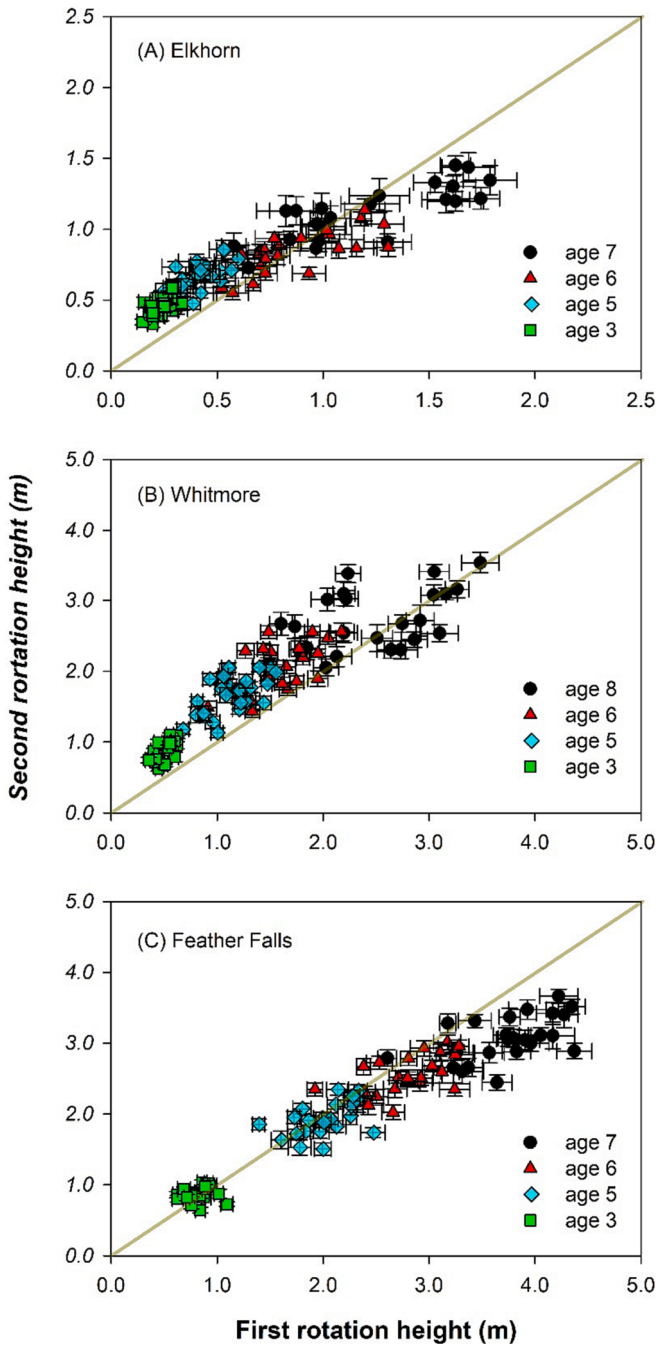

Fig. 5. Inter-rotational relationships for average tree height at Elkhorn, Whitmore, and Feather Falls at plantation ages 3, 5, 6, and 7 or 8. The diagonal lines are 1:1 line.

is presumed to be the results of extended growing seasons, CO_2 increases, increased nitrogen deposition, and increased precipitation (McMahon et al., 2010; Fang et al., 2014; Keenan et al., 2014; Brodribb et al., 2020; Etzold et al., 2020). At these ponderosa study sites, the warmer temperatures during the 2R period themselves had not reached critical levels for physiological effects as no broad mortality was observed and temperatures did not even surpass the optimal temperature ranges reported for ponderosa pine photosynthesis (Helms, 1972) or growth (Larson, 1967). However, warming temperature can drive increased vapor pressure deficits (Williams et al., 2013; Jarecke et al., 2023). In addition, even slightly warmer temperatures will drive a considerable increase of evapotranspiration (Allen et al., 1998). Similar annual or lower growing season precipitation (Fig. S1), combined with high rates of evapotranspiration would have depleted available soil water content at a faster rate. A lack of available soil water would cause trees to close their stomata to maintain plant turgor and to avoid desiccation and subsequently cease carbon fixation (Jarvis and McNaughton, 1986). Ponderosa pine has sensitive stomatal control (Zhang and Marshall, 1995). Conifer growing seasons in these Mediterranean climates are controlled by temperature in that warming temperature initiates the onset of growth (Shestakova et al., 2016) but declining water availability ends the growing season (Zhang et al., 2022). It is more likely that moisture availability was more influential than warming on productivity in these stands. Furthermore, soil water content plays a significant role in nutrient availability and plant nutrient uptake (Nambiar and Sands, 1993; Powers and Ferrell, 1996). Therefore, ponderosa pines at these locations likely face a series of negative effects caused by the warming temperatures, which is supported by abroad trend of decreased productivity (2R < 1R) over stand age beyond age 5 (Figs. 5 and 6).

Inter-rotational productivity response to climate change may also interact with plantation age (Fig. 6). For example, 3-year heights were higher in the 2R than in the 1R for almost all plots at the three sites except for some plots at a high-quality site Feather Falls, where trees grew substantially faster (Fig. 2). After year 3, the 2R growth rates began to fall behind those of 1R except for a few control plots in the 1R (Fig. 5C & 6C). Because a stand with rapid growth and development develops inter-tree competition earlier (Zhang et al., 2013; Zhang et al., 2016), individual trees in rapidly growing stands will be more sensitive to the unfavorable climate conditions (Zhang et al., 2019; Magalhães et al., 2021). At the other two sites with the low (Elkhorn) and intermediate (Whitmore) site quality where tree and stand growth was much slower (Fig. 2), the trend of 2R < 1R did not appear until stand age reached 6 years. This reduction of 2R growth at these sites was most evident on plots that had received herbicides consecutively for first six years in the 1R (Fig. 6 H-HF) as these H plots showed significantly taller trees than F plots and controls in the 1R (Powers and Ferrell, 1996; Zhang et al., 2022).

Why was a declining trend of growth not detected from the beginning in the 2R comparing to 1R since the warmer temperature and lower precipitation was already occurring in 2014? I offer two explanations. First, reforestation techniques have been substantially improved since the late 1980′s, for seeds, seedlings, site preparation, planting, and control of competing vegetation, and these have significantly increased forest productivity (Mead, 2005; Vance et al., 2010). Second, young seedlings planted in the 2.4 by 2.4 m spacing can access sufficient soil water and nutrients where all competing vegetation has been removed or controlled. As discussed in the previous paragraph, this stand 'initiation' stage allows all new seedlings to be freely growing until inter-tree competition begins (Oliver and Larson, 1996). Therefore, the onset of declining rates caused by warming climate is most likely due to the speed of plantation development. This is supported by fact that the significantly faster growth rate in H associated plots (H > C and HF > F) yielded a considerable earlier initiation for 2R < 1R. This is also supported by the observation of the later initiation of the declining trends in the C and F plots compared to the H associated plots. (Fig. 6 C-F).

Higher growth in F and HF for all sites during the 1R than the 2R should have been expected (Fig. 6C & F) because these plots received large doses of nutrients and micronutrients during the first six years of the 1R (Powers and Ferrell, 1996). Since the 1R plots were established from either an unmanaged plantation, brushfield, or natural stand, it is reasonable to expect original nutrients levels would be low across the treatment plots. Because trees on C and H plots had not received any fertilization in the 1R, tree growth on these plots would expected to have been the similar between rotations. However, if data from the 1R F and HF treatments are ignored, the declining trends still exist when plantations reached ages 5 and 6. One might think that this was due to depletion of soil nutrients by the whole tree harvesting in the 1R (Powers, 1999). This hypothesis was not supported by comparing soil

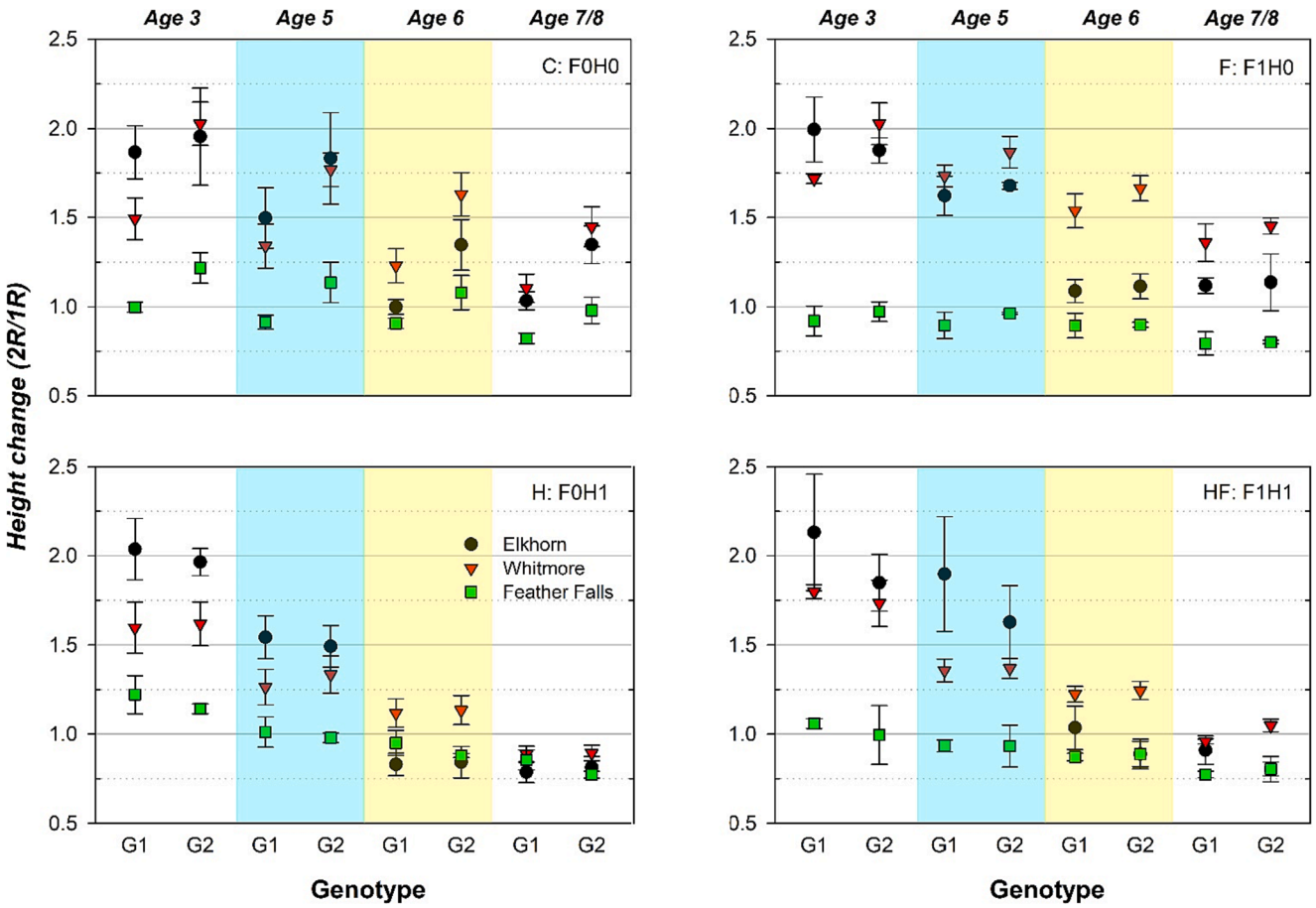

Fig. 6. Relative height change from 1R to 2R for trees at four 1R treatments (C, F, H, and HF) and two 2R genotypes (original seed source used in the and genetically improved seeds collected from see orchard) at age 3 (2016), 5 (2018), 6 (2019), and 7 (2020) (at year 8 instead at Whitmore). Each symbol is a mean of three plots.

data collected when the 1R trees were planted in 1988 with data in the 2R collected in 2014 (Fig. 4). These indirect measures indicated soil degradation did not occur in the 2R comparing to the 1R, which may reflect a lack of multiple rotations (Powers, 1999).

5. Management implications

Climate warming is occurring at an unprecedented rate globally (IPCC, 2021) and perhaps even faster locally (Fig. S1). Global warming is primarily driven by of greenhouse gas emissions, mainly CO_2 (IPCC, 2021). Forests play a significant role in sequestering C from atmosphere (Bonan, 2008; Bastin et al., 2019; Domke et al., 2020). Therefore, the Trillion Trees Initiative calls for additional forest trees planted with a hope for mitigating climate change by sequestrating additional carbon from atmosphere (https://www.1t.org/). In addition, climate change is thought to be related to or induces additional disturbances such as mega fires and insect outbreaks (Millar and Stephenson, 2015; Seidl et al., 2017), which not only releases significant amount of greenhouse gas to the atmosphere, but also cuts back forest capability of removing them. As a result, reforestation is an important response and therefore more plantations will likely be established in the future (Hansen et al., 2013). Therefore, any available management tools and genetically improved seeds must be ready for implementation to ensure a rapid plantation establishment and growth. If warming climate is already affecting stand productivity, any growth models developed in the past may overestimate growth potentials for the new plantation forests. Forest researchers and practitioners need to continue gaining knowledge of effects of climate on plantation growth and development and improving genetic stocks and management techniques that offset the decline of plantation productivity caused by climate change.

6. Conclusions

Fertilizer and herbicide applied in the first-rotation plantation can still affect the growth of second-rotation plantation during the early years although the degree and type of carryover effects were site specific. Herbicide and fertilizer combinations had the greatest relative growth response at the intermediate site. Herbicide had the greatest growth enhancement at the lowest site quality and fertilizer effect was greatest is at the highest site quality, though response was relatively low. Genetically improved seeds resulted a slightly taller growth than the bulk seed sources, but difference was not statistically significant. Due to the warming temperature and lesser growing season precipitation, productivity increases in the second rotation versus the first that were observed in the early years diminished or reversed in the later years where growth rates were less in the second rotation than the first. This suggests the currently management techniques and genotypes were not sufficient to maintain the early period of increased growth to the later years of the plantations. If these observations are universal and widespread, efforts will be needed to find new tools and techniques maintain productivity of future plantations.

Author contribution

Author designed the second rotation study, supervised data collection, performed analyses and wrote the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121499.

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