

Site quality and intensive early stand management practices affect growth dominance, structural complexity, and tree growth in ponderosa pine plantations

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ABSTRACT

During stand initiation, the influences of silvicultural practices such as competing vegetation control and fertilization have been primarily examined in terms of stand-level growth rather than structural complexity. Understanding how intensive silvicultural treatments alter the long-term trajectory of stand development may be critical to meeting management objectives, such as habitat restoration, minimizing ladder fuels, or carbon sequestration. Previous studies have found mixed evidence for an effect of vegetation control and fertilization on structural complexity. Investigating how early pulse treatments drive tree size differentiation in young stands, as indicated by growth dominance (GD), could potentially allow managers to anticipate or design treatments to alter the development of structural complexity later in stand development. We reanalyzed data from the Garden of Eden experiment, a full-factorial study investigating how competing vegetation and nutrients impact ponderosa pine growth and yield over a gradient of site quality in northern California, USA. Our goals were to determine whether these silvicultural practices alter GD and structural complexity, and whether GD and structural complexity created potential feedbacks to alter stand productivity. We examined data for the first 20 years of stand development across 6 study sites. For each site and observation period, we calculated the growth dominance coefficient of total cubic volume to represent GD and the Gini coefficient of inequality in basal area distribution (GC) to represent structural complexity. We created a series of competing generalized additive mixed models (GAMMs) to disentangle the roles of site, stand age, and treatment on GD and GC. We created a set of competing individual-tree GAMMs at age 20 to isolate the influences of GC and GD on volume increment, controlling for the effects of competition, tree size, site, and treatment influences. In agreement with previous research, we found that GD deviated little from size-symmetry (tree growth being roughly proportional to tree size) and did not vary consistently with treatment. Competing vegetation control and higher site quality promoted lower GC, indicative of lower structural complexity. Fertilization increased structural complexity relative to other treatments on two sites in particular, which may reflect unintentional increases in drought stress from fertilization on sites with metasedimentary soils. While GD had limited influence on individual-tree growth, GC interacted with tree size such that small-medium sized trees grew more rapidly on structurally simple plots. Our results have implications for balancing objectives such as fire risk, carbon sequestration, and habitat during reforestation projects.

1. Introduction

During stand initiation, applying silvicultural practices such as competing vegetation control and fertilization can dramatically increase tree-layer productivity (Ferreira et al., 2020). Competing vegetation control is among the most effective approaches for enhancing young stand growth and yield in a wide range of forest ecosystems (Fox et al.,

2007; Nambiar and Sands, 1993; Ponder et al., 2012). Reducing competing vegetation can enhance availability of soil water and nutrients to planted seedlings while improving light condition for crop trees in the later stand developmental stages. Early stand fertilization can also increase stand growth in short-rotation plantations (Ferreira et al., 2020; Nambiar and Sands, 1993), particularly in conjunction with vegetation control (Powers and Reynolds, 1999). When used together, fertilization

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Table 1

Site information of six Garden of Eden installations in northern California. Weather data are summarized for their respective durations. Annual precipitation is calculated from October of the previous year to September of the current year. Information is .

	Chester	Elkhorn	Feather Falls	Jaws	Pondosa	Whitmore
Latitude (N)	40° 18' 28"	40° 4' 57"	39° 37' 11"	41° 53' 12"	41° 12' 30"	40° 37' 33"
Longitude (W)	121° 5' 59"	122° 44' 33"	121° 11' 48"	123° 3' 19"	121° 37' 31"	121° 53' 56"
Elevation (m)	1533	1539	1250	1018	1181	747
Site index (m at age 50)	20	17	30	23	18	23
Annual mean Temp (°C)	8.3	11.8	12.6	11.3	9.8	15.4
Annual precipitation (mm)	859	1010	2035	736	755	1030
Parent material	Volcanic	Metasediment	Volcanic	Metasediment	Volcanic	Volcanic
Previous vegetation	Brushfield	Plantation	Natural stand	Natural stand	Brushfield	Brushfield
Year planted	1987	1988	1988	1988	1988	1986

adapted from Zhang et al. (2022)

Table 2

Hypothesis models with constituent variables.

Response	Hypothesis	Response varies as a function of:
GD	GD0	Null model (Site, s(age), s(age * site))
GD	GD1	Null model, treatment
OGD	GD2	Null model, treatment, treatment × site
GD	GD3	Null model, treatment, s(age * treatment)
GC	GC0	Null model (Site, s(age), s(age * site))
GC	GC1	Null model, treatment
GC	GC2	Null model, treatment, treatment * site
GC	GC3	Null model, treatment, s(age * treatment)
PAI	PAI0	Null model (site, treatment, site * treatment, s(DBH), s(BAL))
PAI	PAI1	Null model, s(GC)
PAI	PAI2	Null model, s(GD)
PAI	PAI3	Null model, s(GC), s(GC) * s(DBH)
PAI	PAI4	Null model, s(GD), s(GD) * s(DBH)
PAI	PAI5	Null model, s(GC), s(GD)
PAI	PAI6	Null model, s(GC), s(GD), s(GD) * s(DBH)
PAI	PAI7	Null model, s(GC), s(GD), s(GC) * s(DBH)
PAI	PAI8	Null model, s(GC), s(GC * treatment)
PAI	PAI9	Null model, s(GC), GD, s(GC * treatment)

Notes: s() signifies a smoothing function was applied to a given predictor via generalized additive mixed modeling. Other abbreviations are as follows: GC = Gini coefficient of basal area, GD = growth dominance coefficient, PAI = periodic annual volume increment, BAL = basal area level.

and competing vegetation control can increase recovery of stand resistance to disturbances such as fire by accelerating tree growth and stand maturation. The effects of vegetation control may be most pronounced on high quality sites where other vegetation would otherwise continue to compete with desired conifer species throughout the rotation (Richardson, 1993). In regions such as California where shade-intolerant, small-statured shrubs comprise the competing vegetation, vegetation control is commonly most effective on low-quality sites (Zhang et al., 2022,2013).

The influence of these silvicultural practices during stand initiation has primarily been evaluated in terms of stand-level growth, which does not fully illuminate the processes mediating resource availability and

the development of stand structural complexity (Forrester, 2019). Stand structural complexity, or the vertical and horizontal arrangement of biomass in a stand, influences forest productivity. Lower stand complexity is often linked to more rapid growth (Luu et al., 2013; Yáñez et al., 2017; Zhang et al., 2008), although studies have occasionally found positive growth-complexity relationships, particularly in older stands (Forrester, 2019; Zeller and Pretzsch, 2019). Structural complexity governs other ecosystem properties such as wildlife habitat, aesthetics, as well as susceptibility to disturbance (McElhinny et al., 2005). Manipulating structural complexity may also hold benefits for increasing resistance to disturbances such as bark beetle outbreaks and wind damage (Knapp et al., 2017; Pukkala et al., 2016).

Previous studies have not found a consistent response of structural complexity to competing vegetation control and fertilization. In western redcedar (*Thuja plicata* Donn ex D.Don) forests, Harrington and Devine (2011) found that fertilization increases variation in tree diameters, reflecting a combination of faster large-tree growth and lower small-tree mortality. Harrington and Devine's (2011) finding is consistent with lowered stress allowing for greater concentration of stand growth in large trees (Pretzsch and Dieler, 2010). In contrast, Harrington et al. (1991) attributed a decrease in Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) size variation under vegetation control to more trees reaching the overstory. The structural complexity of intensive short-rotation loblolly pine (*Pinus taeda* L.) plantations declines in response to combined fertilization and vegetation control (Ferreira et al., 2020; Nilsson and Allen, 2003). In ponderosa pine (*Pinus ponderosa* Laws.) plantations in California, Oregon, and Washington, competing vegetation control and fertilization reduce tree size variation (McGown et al., 2015; Zhang et al. 2022). A broader understanding of how early pulse treatments drive tree size differentiation in young stands could potentially allow foresters to better predict the development of structural complexity later in stand development.

Binkley (2004), Binkley et al. (2006) proposed growth dominance (GD) as a means of establishing a linkage between tree and stand level growth, thus providing a measure of how trees of different sizes contribute to production. Positive values of GD correspond with disproportionately rapid large-tree growth, while negative values

Table 3

Plausible stand-level models of the Gini coefficient of basal area and growth dominance, based on corrected Akaike's Information Criterion (AICc).

Response	Hypos	Model terms						logLik	ΔAICc	R ²
		Site	s(age)	s(age × site)	s(age × trt)	trt	site × trt			
GD	GD3	x	x	x	x	x	x	1483.1	0.0	0.08
	GD0	x	x	x	x			1454.5	18.4	0.01
GC	GC3	x	x	x	x	x	x	797.1	0.0	0.70
	GC0	x	x	x	x			605.4	266.9	0.40

Note: abbreviations are as follows: Loglik = log likelihood, ΔAICc = difference in corrected Akaike's information criterion compared to best-approximating model, R² = coefficient of determination, trt = treatment, s() = smoother applied to term in GAMM. Models with ΔAICc < 6 of the best-approximating model and which do not contain simpler nested models with greater AICc support are considered plausible.

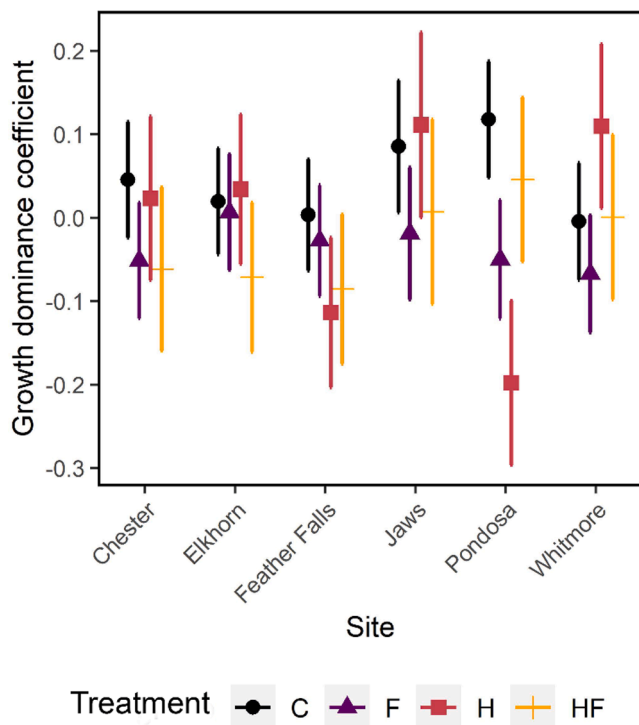


Fig. 1. Predicted values of the growth dominance coefficient (mean $\pm$ S.E.) by treatment, for six Garden of Eden sites, adjusting for age effects.

correspond with disproportionately rapid small-tree growth, reflecting size-related variation in tree resource-use efficiency (Binkley et al., 2006). Size-related variations in resource-use efficiency may fluctuate over time in response to autogenic factors, giving rise to shifts in GD between large and small trees during stand development (Binkley et al., 2006). Research suggests GD and the related concept of tree size-growth relationships (Forrester, 2019) respond to indicators of site quality such as abiotic stress from drought and air pollution (Dye et al., 2019; Looney et al., 2021; Pretzsch and Dieler, 2010). Elevated abiotic stress disproportionately reduces large tree growth (Castagneri et al., 2012; Looney et al., 2021; Pretzsch and Dieler, 2010), which in the absence of tree mortality would be expected to simplify stand structure over time (Forrester, 2019).

Whereas competing vegetation control and fertilization might logically be expected to improve site quality, whether they predictably alter GD or structural complexity and whether such change influences forest productivity has not been resolved. Martin and Jokela (2004) found stronger size-asymmetric growth dominance in both loblolly pine and slash pine (*Pinus eliottii* Engelm.) under combined fertilization and vegetation control relative to untreated plots. Growth dominance and light-use efficiency increased in loblolly pine in response to fertilization (Campoe et al., 2013), yet a second study of this species found no treatment effect on GD (Ferreira et al., 2020). In a study of even-aged ponderosa pine, McGown et al. (2015) did not report substantial variation in GD or structural complexity between plots with and without vegetation control over a range of stand densities, although only a single site encompassing a limited range of site quality was examined and differences among treatments were not formally tested. In a fertilization trial in Pacific northwest stands aged 15–74 years, Chen et al. (2022) found GD increased under fertilization in western redcedar-dominated stands, but not in more inland Douglas-fir and grand fir (*Abies grandis* (Douglas ex D. Don) Lindley) stands. A study of conifer-dominated California and Pacific Northwest forest inventory plots found that large tree growth efficiency improved under nitrogen deposition from air pollution (Looney et al., 2021), which at low-moderate intensities can have a fertilization effect (Fenn et al., 2020).

When large trees dominate stand growth, greater shading of subordinate crown classes may accelerate self-thinning mortality, offsetting size differentiation driven by large tree growth (Looney et al., 2021; Pretzsch and Dieler, 2010). While low structural complexity is associated with higher productivity in observational studies of young stands (Pothier, 2017; Zeller and Pretzsch, 2019), silvicultural treatment legacies may be partly responsible for driving this relationship (Luu et al., 2013). If early stand management practices alter the development of structural complexity, understanding the factors responsible could aid in developing practices to foster structural complexity where desirable to meet management objectives (DeBell et al., 1997).

To investigate how GD varies in response to competing vegetation control and fertilization, we revisited a long-term study of experimental ponderosa pine plantations in northern California, USA (Powers and Ferrell, 1996). This full factorial study replicates competing vegetation control and early stand fertilization across six sites spanning a gradient of site quality, offering a powerful platform for disentangling controls on stand development. We examined how GD, structural complexity, and individual-tree growth varied over 20 years in response to the legacy of pulse treatments during stand establishment. Our goals were to determine (1) whether competing vegetation control and fertilization in plantations spanning a wide range of site quality alter the development over time of (a) GD and (b) structural complexity measured as the GINI coefficient of tree sizes, and (2) how growth dominance and structural complexity influence individual-tree growth, once accounting for treatment and site effects. Our overarching goal was to inform western U.S. reforestation efforts, where the careful design of early stand management practices may be critical to meeting long-term objectives, such as creating structural complexity, minimizing ladder fuels, or maximizing carbon sequestration, given frequent lack of resources for subsequent intermediate treatments (North et al., 2019).

2. Materials and methods

2.1. Experimental design

This research leverages data from the Garden of Eden study established in 1986–1988 by late Robert F. Powers to investigate factors limiting ponderosa pine plantation productivity over a gradient of site quality in Northern California, USA (Powers and Ferrell, 1996). The current study follows the development of 6 installations (Zhang et al., 2022). All sites are characterized by a Mediterranean climate with hot summers and mild, moist winters, although precipitation and temperature among sites vary considerably (Table 1). Sites span a range of site quality from a ponderosa pine site index of 17–30 m (base age 50 years; Table 1). Initial within-site variation in productivity, soils, and landform was no more than 20% (Powers and Ferrell, 1996). Prior to study establishment, vegetation represented a mixture of brushfields and cleared forestland (Table 1).

A rectangular matrix of 24 planted plots was established at each site. Plots consisted of ponderosa pine seedlings planted at 2.4×2.4 m square spacing ($1681 \text{ trees ha}^{-1}$). Each plot measured approximately 21.9×19.5 m (0.0427 ha). Plots included two unmeasured buffer rows of plantings to guard against forest edge and adjacent treatment influences surrounding an interior 12×9.6 m (0.0115 ha) measurement plot of 20 trees (Curtis and Marshall, 2005). Bareroot 1–0 seedlings of ponderosa pine were grown from the best-suited seed stock for a given location and were out-planted in spring into augured holes.

A full factorial combination of three treatments was randomly assigned to plots, for a control plus three treatment replicates per installation: insecticide (I), herbicide (H), and fertilization (F). (Please see Powers and Ferrell (1996) for detailed descriptions of treatments summarized here.) Insecticide treatments involved the application of acephate and dimephorate in spring to new shoots. Competing vegetation control involved repeated annual spring applications of herbicides (glyphosate, triclopyr, or hexazinone as indicated by local conditions

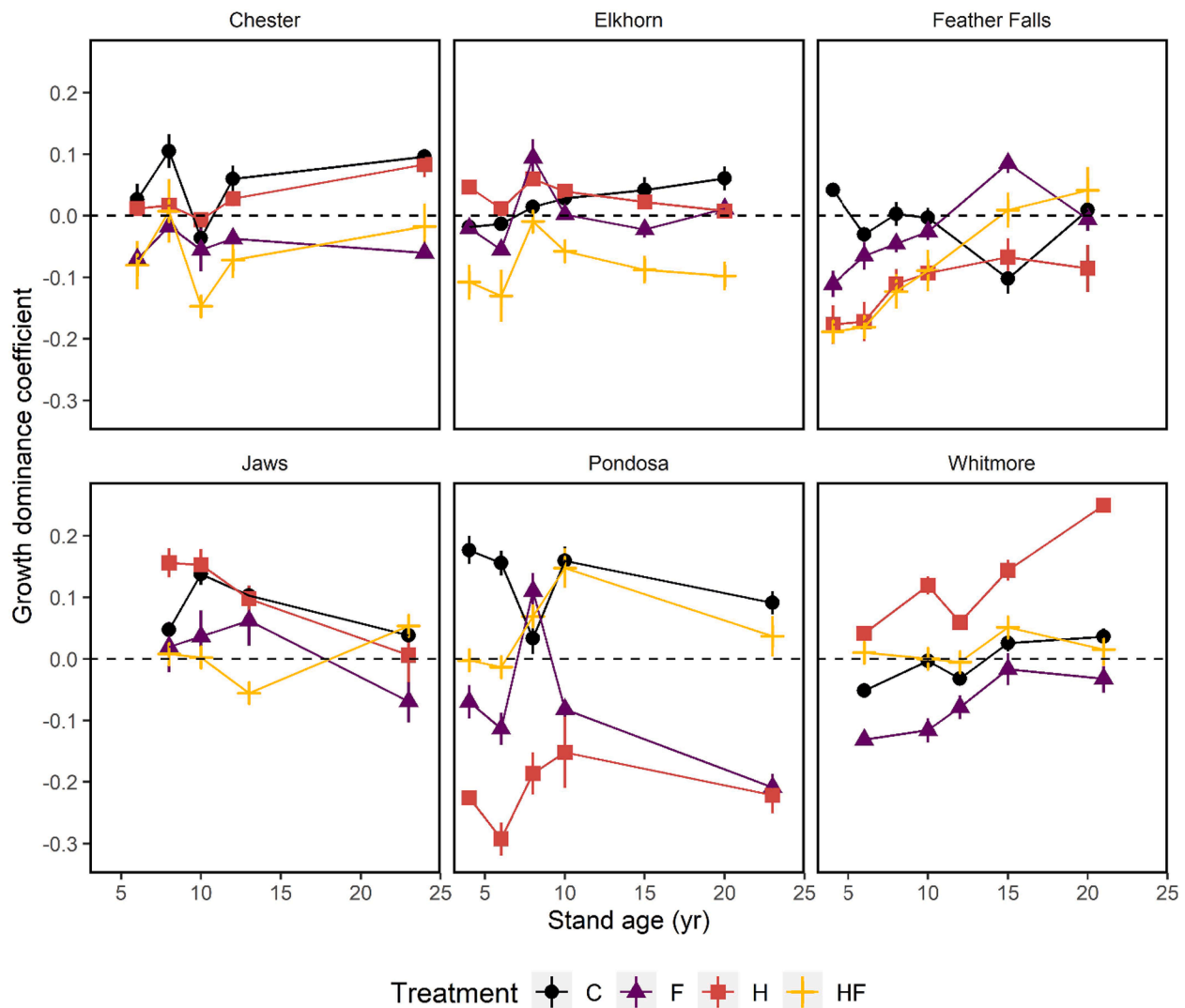


Fig. 2. Mean values of the growth dominance coefficient ($\pm$ S.E.) for each treatment and time period at six Garden of Eden study sites. The dashed line represents size-symmetric growth.

and manufacturers' recommendations) for the first six years. Herbicides were applied with backpack sprayers and seedlings were shielded during application. Fertilization followed a ramped design, applying progressively greater quantities at ages 1, 3, 5 and 7 in salt form. Fertilization delivered totals of 1074 kg ha⁻¹N, 530 kg ha⁻¹P, 540 kg ha⁻¹P, 416 kg ha⁻¹Ca, 221 kg ha⁻¹S, 73 kg ha⁻¹Zn, 36 kg ha⁻¹Cu, and 36 kg ha⁻¹B.

Measurement plot trees were consistently surveyed for height and stem diameter at 20 cm above ground level for tree heights <1.37 m, and DBH for heights $\geq$ 1.37 m. Every site was measured at ages 6 and 10, with the schedule of subsequent measurements varying by site due to limited resources. Whitmore received more frequent surveys due to close proximity to field staff. A lack of insect issues across the experiment has consistently rendered no insecticide treatment effect (Zhang et al., 2022), and for the purposes of this study, we pooled I plots and FI plots into C and F groups, respectively. To avoid the confounding influences of thinning on growth dominance and structural complexity, we excluded HI and HFI plots on all sites but Elkhorn, the least productive site, because these plots received a 50% precommercial thinning at age 8–12. At Chester and Pondosa, where measurements continued beyond 25 years, we limited our analysis to the first 25 years to provide a comparable range of stand age across all sites.

2.2. Growth dominance and structural complexity indicators

We calculated GD using Binkley's (2004) method, as mathematically defined by West (2014) and based on total cubic volume:

$$GDI = \sum_{i=1}^{nl} (vol_{il} - vol_{il-1}) (\Delta vol_{il} + \Delta vol_{il-1})$$

where n is the number of trees in the measurement plot, vol_i the cumulative proportional volume of tree i , and Δvol_i is the cumulative proportional volume increment of tree i (see Table A.1 in the Appendix for the full list of variables used in modeling). We used stem volume, as opposed to biomass given that biomass equations specific to this study did not encompass the smallest tree sizes in the data (Zhang et al., 2021). Although similar metrics are available based on the relationships between tree size and growth (Forrester, 2019), we selected Binkley's method due to its use of standardization facilitating interpretation, as well as its greater integration with literature on stand development and intensive plantation management (Baret et al., 2017; Binkley et al., 2006; Doi et al., 2010). This index is bounded between -1 and 1; positive values indicate that stand growth is disproportionately concentrated in large trees, while negative values indicate stand growth is disproportionately concentrated in small trees. For saplings smaller than DBH, we used conic formula to calculate volume based on diameter at

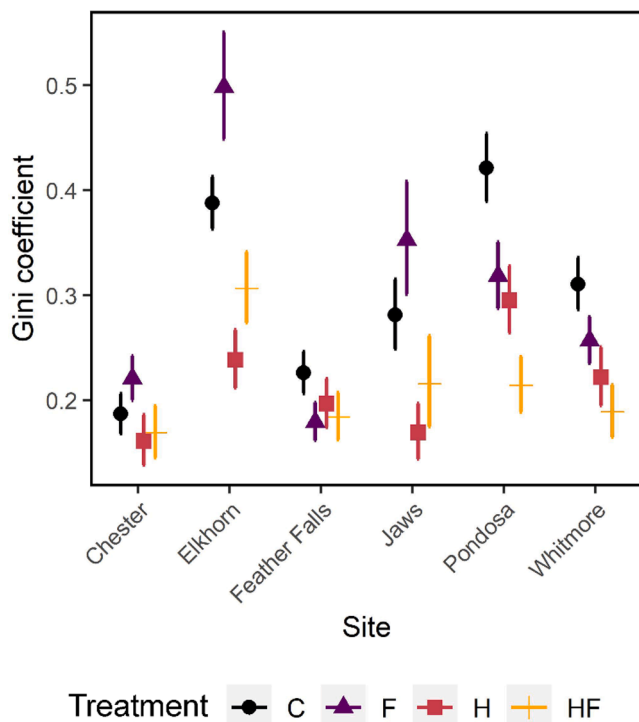


Fig. 3. Predicted values of the Gini coefficient of basal area (mean $\pm$ S.E.) by treatment, for six Garden of Eden sites, adjusting for age effects.

20 cm height. For larger trees, we calculated GD based on diameter-only tree volume equations developed through destructive sampling at the high-quality Feather Falls, low-quality Elkhorn, and intermediate-quality Whitmore sites (Zhang et al., 2021). Due to a lack of significant treatment effects on stem form (Zhang et al., 2021), we applied generic volume equations developed for trees at each site rather than treatment-specific equations. We applied equations from Whitmore to the other three intermediate-quality sites: Chester, Jaws, and Ponderosa (Zhang et al., 2021).

We expressed structural complexity in terms of the Gini coefficient (GC), which has a long history of application to plant ecology studies (Weiner and Solbrig, 1984). The GC is relatively insensitive to variations in sample size compared to alternatives (such as applying Shannon's H' to diameter classes) and has a strong ability to discriminate among diameter distributions varying in shape, including the normal-to-uniform distributions characteristic of this study (Lexnerød and Eid, 2006). The GC also forms a conceptual basis for Binkley's GD coefficient, which reflects the degree to which individual trees monopolize stand growth and biomass (Binkley et al., 2006). Values of GC range between 0 and 1; values of 0 would indicate that trees share stand basal area equally, while a value approaching 1 would indicate a single tree monopolizes nearly all stand basal area. We calculated GC based on basal area (Lexnerød and Eid, 2006), using an adjustment for small sample sizes (Weiner and Solbrig, 1984):

$$GCI = \left(\frac{n}{nl - 1} \right) \left(\frac{\sum_{i=1}^n \sum_{j=1}^{nl} |ba_{iil} - ba_{jj}|}{2n^2 ba_{\bar{x}}} \right)$$

where n is the total number of trees per measurement plot, ba_{iil} is the basal area of tree of rank size i , ba_{jj} is the basal area of tree of rank size j , and $ba_{\bar{x}}$ is the mean tree basal area.

2.3. Stand-level growth dominance and structural complexity models

We built a set of competing generalized additive mixed models (GAMM) of GD, GC, and periodic annual increment (PAI). General

additive mixed models are a semi-parametric technique which flexibly accommodates nonlinear trends in ecological data (Zuur et al., 2009), including long-term forest growth and yield studies (e.g., Zeller and Pretzsch, 2019). Nonlinear relationships between predictors and response variables were fitted with smoothed functions based on penalized regression splines, using generalized cross-validation to protect against over-fitting (Wood, 2017; Zuur et al., 2009). We used GAMM to flexibly accommodate age-related fluctuations in GD and GC (Wood, 2017). Given visible differences in trends of these variables among sites over time, as well as varying times and frequencies of measurements at each site, we included both a main effect of age as well as an age $\times$ site interaction term in all of the stand-level response models.

To investigate whether treatment effects altered GD and GC over time in plantations spanning a range of site quality, we built a series of progressively more complex GD and GC models for later use in model comparisons. In our null model, GD and GC varied with site, stand age, and the site $\times$ stand age interaction (Table 2). Site quality may accelerate the development of structural complexity (Larson et al., 2008), prompting us to also include site and the site $\times$ age interaction as fixed factors in GC models. Because GD and the similar size-growth relationship are responsive to site quality (Pothier, 2017; Pretzsch and Dieler, 2010), we included site and the site $\times$ age interaction as fixed factors in accordance with the original study design as well as consistent with findings of strong site effects on stand growth across the study (Powers and Ferrell, 1996; Powers and Reynolds, 1999; Zhang et al., 2022). Growth dominance typically declines following stand establishment (Binkley et al., 2006; Pothier, 2017), but may.

show nonlinear patterns with age in young, intensively managed plantations (Binkley, 2004), and graphical examination of the data suggested that age-related trends for GD and GC were non-linear over time and warranted treating age as a smoothed term. Our first alternative model added the main effect of treatment to the null model terms of site, age, and age by site. The second alternative included the treatment $\times$ site interaction in addition to the main effect of treatment, given the strong dependence of fertilization and herbicide effects on site quality (Powers and Reynolds, 2011; Zhang et al., 2022). A third alternative included the main effect of treatment as well as an age $\times$ treatment term to account for a potential convergence of treated and untreated stand structures following the initial pulse effects of H, F, and HF treatments early in stand development, a pattern reported for ponderosa pine under competing vegetation control (Zhang et al., 2006). Random effects common to all GD and GC models included site and treatment plot nested within site to account for non-independence arising from repeated measures of the same experimental units.

2.4. Tree-level volume increment models

To examine how GD and GC influenced stand productivity after controlling for treatment and site effects, we built a series of individual-tree periodic annual increment models. Compared to stand-level models of volume increment, individual-tree modeling commonly allows for more accurate prediction by incorporating dynamic information on individual tree size, competitive neighborhoods, and stand conditions (Pretzsch, 2009). In particular, we sought to investigate whether GD or GC might interact with tree size to alter the efficiency of tree growth across the range of diameters in this study. We used periodic annual volume increment as our response variable. We focused on trees with positive increment and height exceeding 1.37 m, using measurements from the latest common measurement period across sites (ages 20–23, depending on site). Our basic null model included initial DBH, site, treatment, the treatment $\times$ site interaction, and basal area level (BAL). Site was included as a fixed effect in accordance with the original study design, while we included the treatment $\times$ site interaction to account for strong treatment $\times$ site effects on plot-level volume increment (Powers and Reynolds, 2011). We did not include site quality indicators due to

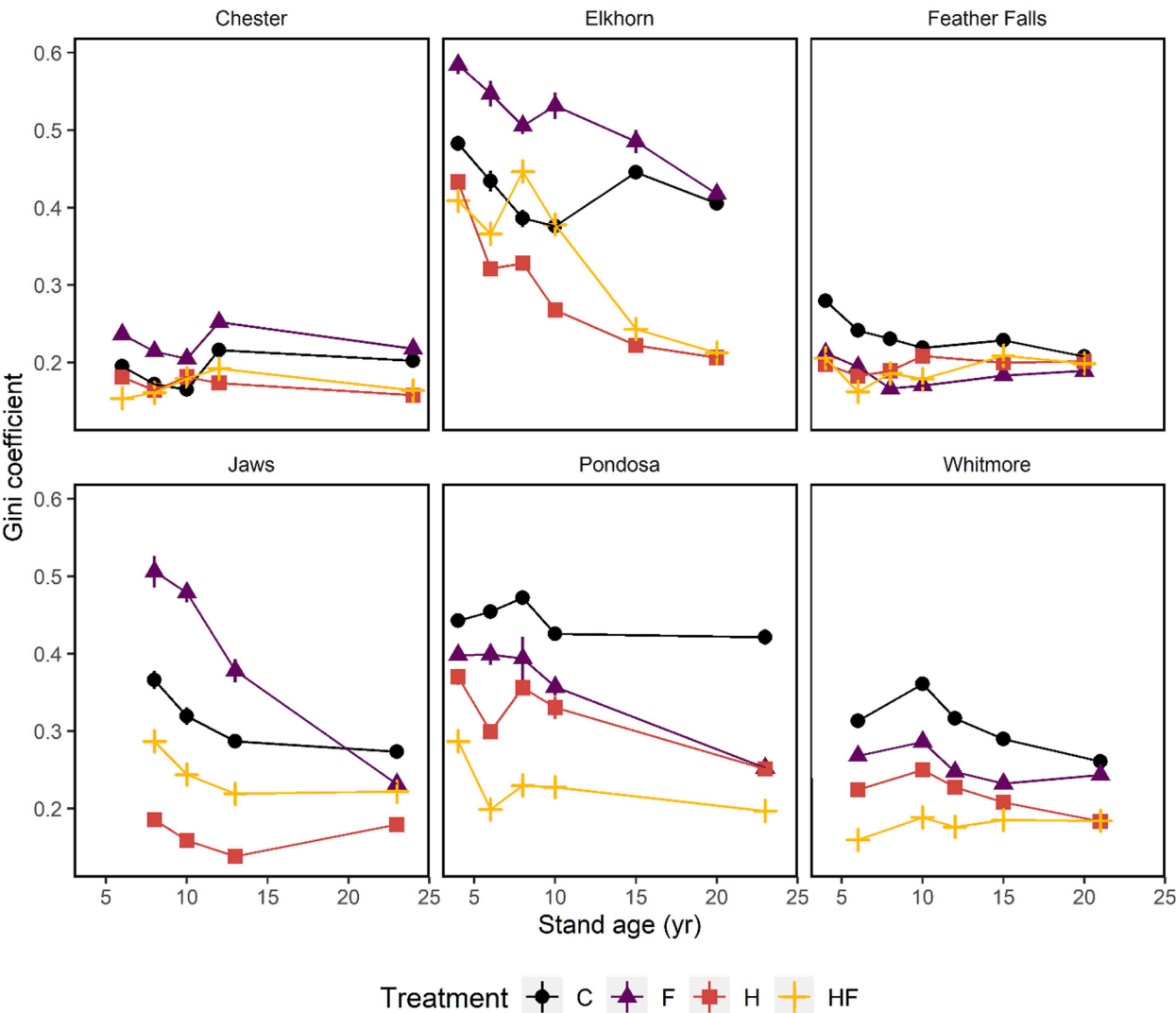


Fig. 4. Mean values of the Gini coefficient of basal area ($\pm$ S.E.) for each treatment and time period at six Garden of Eden study sites.

Table 4
Plausible individual tree periodic annual volume increment models at age 20 based on corrected Akaike’s Information Criterion (AICc).

Hypos	Model terms								logLik	Δ AICc	R^2
	Site	s(DBH)	Trt	BAL	Site $\times$ Trt	s(GC)	s(GD)	s(GC $\times$ DBH)			
PAI7	x	x	x	x	X	x	x	x	3315.5	0	0.89
PAI0	x	x	x	x	X				3029.57	274.6	0.87

Notes: abbreviations are as follows: PAI = periodic annual volume increment, trt = treatment, s() = smooth applied to term via generalized additive mixed modeling, BAL = basal area level, GC = Gini coefficient of basal area, GD = growth dominance coefficient, Loglik = log likelihood, Δ AICc = difference in corrected Akaike’s information criterion compared to best-approximating model, R^2 = coefficient of determination.

minimal within-site variation in topography and fertility (Powers and Ferrell, 1996). Basal area level served as an individual-tree, distance-independent competition index (Wykoff, 1990). Basal area level is an integral part of the large-tree growth equations in the Forest Vegetation Simulator (Wykoff, 1990), previously found to perform well for experimental ponderosa pine plantations subject to density management (Uzoh and Oliver, 2008):

$$BAL_{ii} = \sum_{j=1}^n DBH_{ji}^2 * 0.0007854$$

$D_j > D_{ii}$

where BAL is the basal area level index calculated for subject tree i , DBH_j

is the diameter at breast height of a given competitor tree, D_i is the diameter of subject tree i , and n is the total number of competitor trees sharing a given treatment plot with the subject tree. We smoothed DBH, BAL, GD and GC terms using GAMM to account for nonlinear relationships with volume increment across the broad range of stand development in this study.

To examine whether structural complexity altered individual tree volume increment and growth dominance, we used this null model to build a set of 9 alternative models. We included a tree size $\times$ GC interaction to evaluate whether the effects of structural diversity on growth are contingent on tree size (Luu et al., 2013). Changes in growth dominance, and size-growth relationships more generally, are thought to primarily reflect differences in large-tree growth (Binkley, 2004;

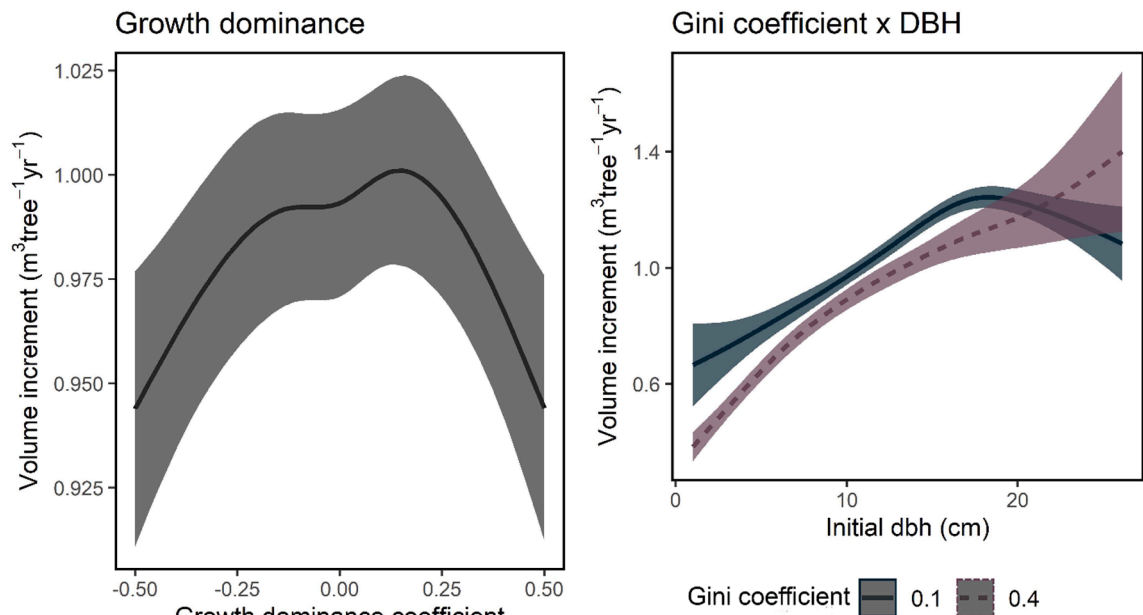


Fig. 5. Predicted values of individual-tree volume increment as functions of the growth dominance coefficient (left panel) and the DBH × Gini coefficient interaction (right panel).

Table A.1
Variables used in growth dominance, Gini coefficient and individual-tree volume increment modeling.

Analysis	Abbreviation	Description	Level
GC, GD, PAI, PAI	Site	Study site	Site
GC, GD, PAI, PAI	Plot	random effect of treatment plot	Plot
PAI	Tree	random effect of tree-in-plot	Tree
GC, GD, PAI	Stand age	Stand age from time of planting (yr)	Site
	age	stand age (yr)	Site
GD, GC	GD	Growth dominance coefficient of cubic volume, as formulated by West (2014)	Plot
GC, PAI	GC	Gini coefficient of basal area	Plot
PAI	PAI	Periodic annual tree volume increment	Plot
PAI	BAL	Basal area of plot trees larger than the subject tree, divided by subject tree DBH	Tree
PAI	DBH	Diameter at breast height (cm, @1.37 m)**	Tree

Note: Abbreviations are as follows: GC = Gini coefficient; GD = growth dominance; PAI = periodic annual volume increment; BAL = basal area level; DBH = diameter at breast height (1.37 m).

Forrester, 2019), a possibility we examined by including the GD × DBH interaction. We also built models with the GC × treatment interaction in order to examine the potential role of uneven treatment effectiveness in creating spurious complexity-growth relationships. Our first 4 alternatives included either GD or GC main effects, with or without their interactions with DBH. Alternatives 5–7 included both GD and GC main effects, with or without either the GD × DBH or GC × DBH interaction. The 8th alternative included GC and the GC × treatment interaction. The 9th alternative was identical to the 8th, but added the main effect of GD. All volume increment models included the random effects of plot nested within site and site to account for spatially autocorrelated growth, as well as to properly stratify site, plot, and tree-level terms.

2.5. Statistical procedures and model selection

All analyses were conducted in R (R Core Team, 2018). We use the *trapz* function in the *caTools* package (Tuszynski and Tuszynski, 2007) for R (R Core Team, 2018) to perform the trapezoidal integration

involved in calculating GD. We used the *Gini* function in the *DescTools* package to calculate GC (Signorell et al., 2019). We used the *gam* function in the *mgcv* package (Wood, 2012) for GAMMs. Models were fit with maximum likelihood estimation. We fit smoothed terms using thin-plate regressions (Wood, 2017). For the GD × DBH and GC × DBH interactions between continuous covariates in individual-tree models, we used tensor interactions to provide results more analogous to traditional ANOVA (Wood, 2017). To protect against overfitting, we set the gamma parameter in all models to 1.4 (Wood, 2017). We used the *sjPlot* package (Lüdtke and Schwemmer, 2017) to summarize main effects, explore interactions, and interpret smoothed terms.

We graphically examined all GAMMs for normality of residuals and homogeneous variances (Wood, 2017), as well as plotted model residuals against predictors to identify potential nonlinearity or missing terms (Zuur et al., 2009). To meet model assumptions, we applied a log transformation to GC and a cube-root transformation to individual-tree PAI. We corrected for heteroskedasticity in GC models by using weighted least-squares based on the inverse of trees ha⁻¹ (Zuur et al., 2009). We inspected the data for potential collinearity by constructing correlation matrices of predictors. Bivariate correlations between predictors did not exceed *r* = 0.7.

We compared evidence for alternative hypothesis models following the information-theoretic approach (Burnham and Anderson, 2002) with corrected Akaike’s information criterion (Sugiura, 1978). We considered models to be plausible when ΔAICc values were within 6 units’ distance of the best-approximating model that did not contain better-supported nested models (Richards, 2008). We also excluded models with stronger AICc support if they were within 2 ΔAICc of simpler nested alternatives (Burnham and Anderson, 2002). We performed AICc model comparisons using the *MuMin* package (Barton, 2017). We present *R*² results, calculated via the *mgcv* package (Wood, 2012), for descriptive purposes only and relied on AICc for model selection and inference.

3. Results

3.1. Growth dominance

Growth dominance on measurement plots ranged from a reverse size-

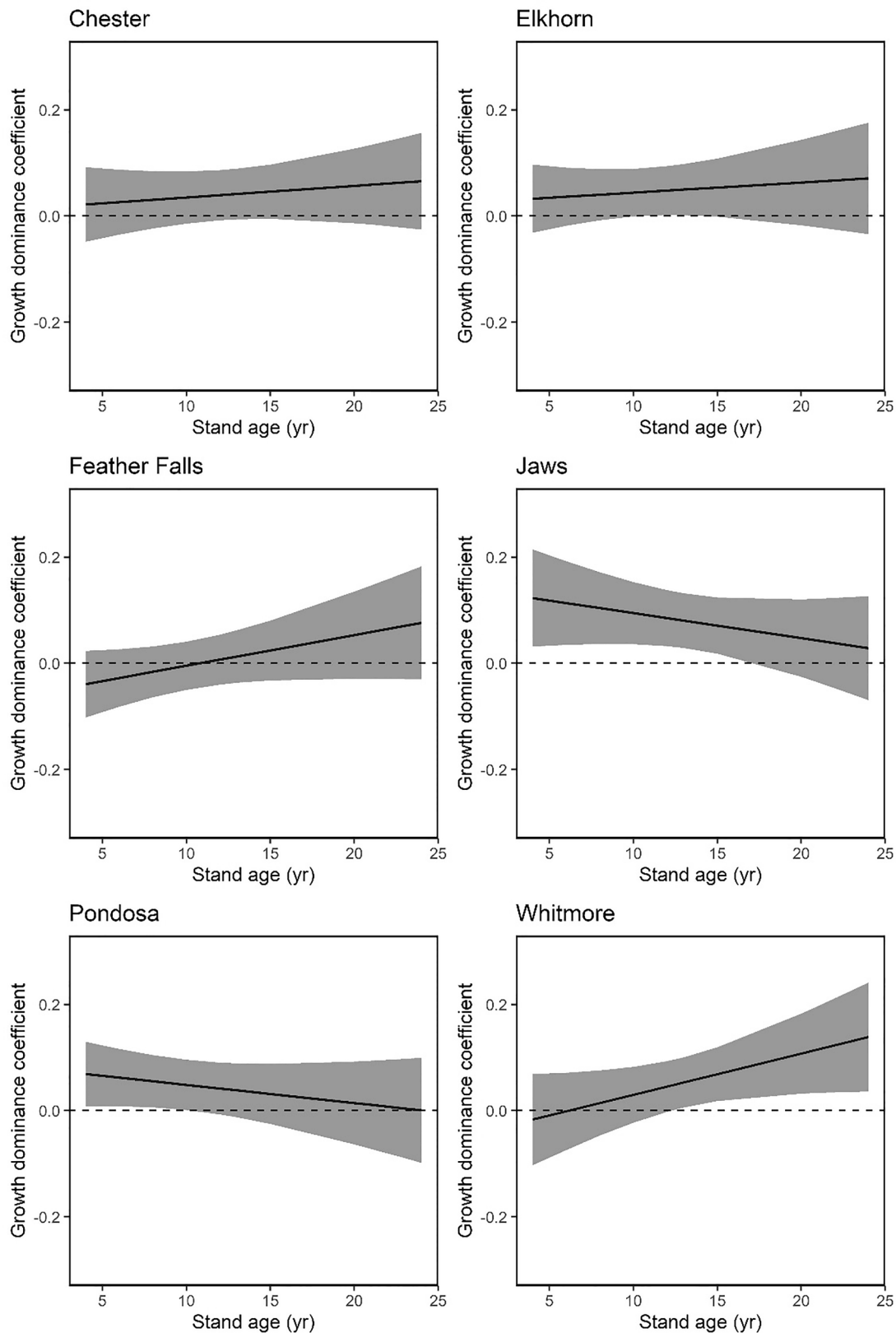


Fig. A.1. . Predicted values of the growth dominance coefficient over time for six Garden of Eden study sites, based on generalized additive mixed model results.

asymmetric (small trees contributing disproportionately more to stand volume) value of 0.51, to a size-asymmetric (large trees contributing disproportionately more to stand volume) value of 0.52. The average study-wide value was 0.0 (SD = 0.07), or nearly size-symmetric (all trees

contributing proportionately to stand volume). The best-approximating model (GD3 in Table 2) described GD as a function of treatment, site, the treatment $\times$ site interaction, smoothed age, and the smoothed age $\times$ site interaction (Table 3).

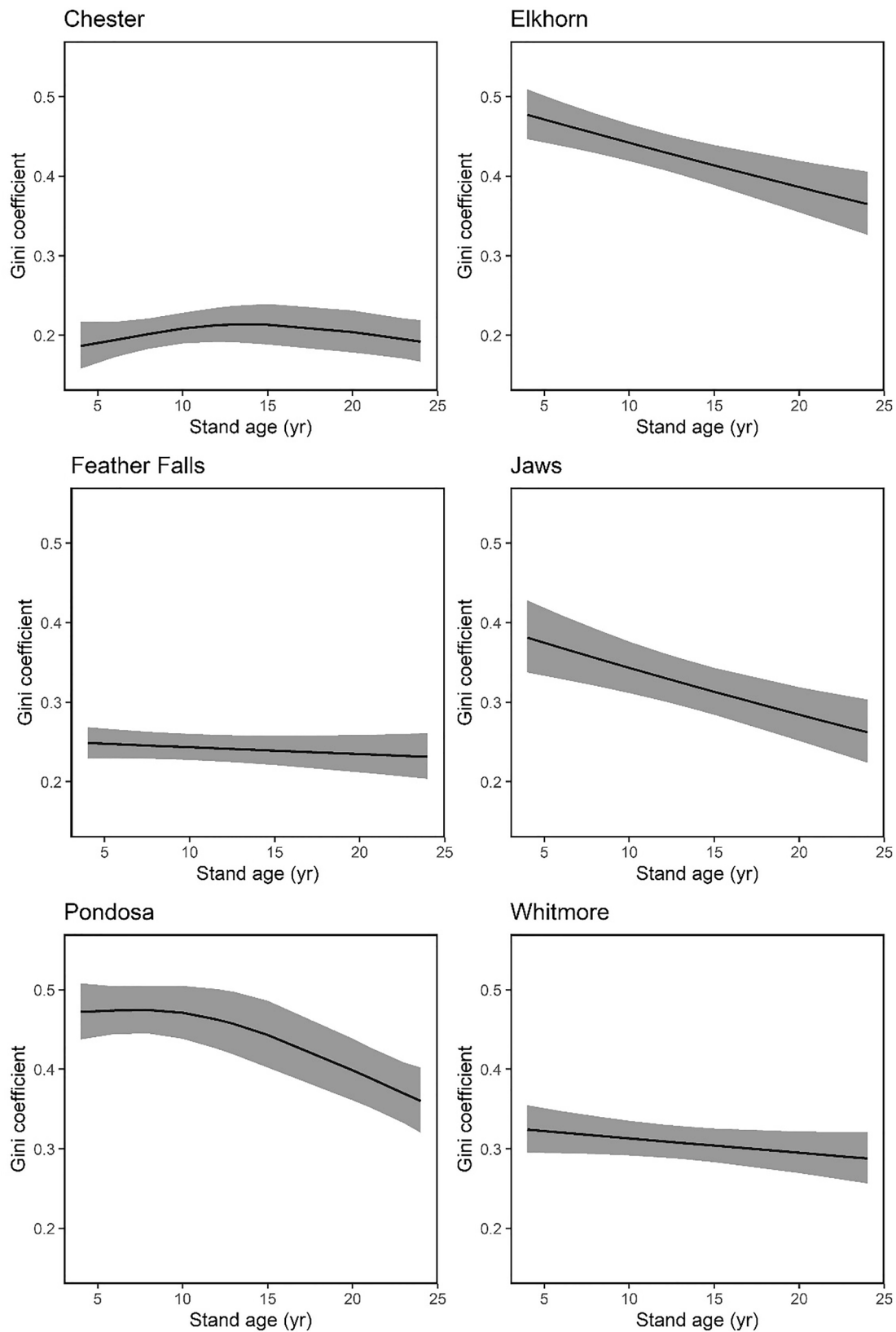


Fig. A.2. . Predicted values of the Gini coefficient of basal area for six Garden of Eden sites over time, based on generalized additive mixed model results.

Under the treatment $\times$ site interaction, the H and F treatments had lower GD than the control at Pondosa, while the F treatment had lower GD than the H treatment at Whitmore (Fig. 1). Treatments were not consistently distinct at other sites. Age-related trends in GD simplified to

simple linear trends in GAMM (Fig. A.1), revealing negative site-specific trends at Jaws and Pondosa and positive trends at Feather Falls and Whitmore. Treatments did not otherwise vary consistently over time at any other site. No other model was plausible based on AICc (Fig. 2).

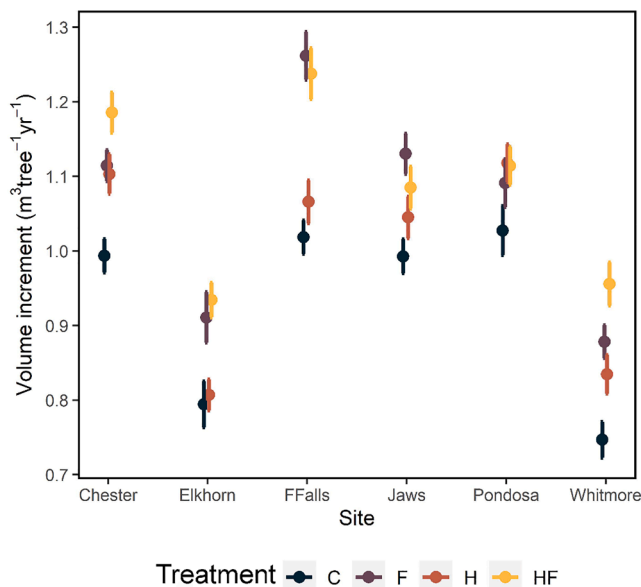


Fig. A.3. . Estimated marginal mean ($\pm 95\%$ C.I.) individual tree volume increment at age 20 by treatment for 6 Garden of Eden study sites, with initial DBH, growth dominance, and the Gini coefficient of inequality held constant at their average value.

3.2. Structural complexity

The GC ranged from a nearly equal distribution of plot basal area among trees (0.05, corresponding with low structural complexity) to highly unequal plot basal area (0.78, corresponding with high structural complexity), with study-wide values averaging 0.25 (SD = 0.13). The best-approximating model of GC (GC3 in Table 3) included the effects of treatment, site, the treatment $\times$ site interaction, smoothed age, and the smoothed age $\times$ site interaction. Under the site $\times$ treatment interaction, treatments were more distinct and covered a wider range of GC at Elkhorn, Pondosa, Jaws, and Whitmore compared to Chester, and Feather Falls (Fig. 3). In general, H and HF treatments had lower GC compared to other treatments. The.

F treatment had the highest GC at Chester, Elkhorn, and Jaws, while the C treatment had the highest GC at Feather Falls, Pondosa, and Whitmore. GC declined linearly over time at Elkhorn and Jaws, while declining after age 10 in most treatments at Pondosa (Fig. 4). At Chester, GC rose slightly to peak at age 15, then declined. Changes in GC over time at both Feather Falls and Whitmore were similar to Chester. Age-related trends simplified to simple linear relationships in GAMM at all sites except Chester and Pondosa, where the decline was curvilinear (Fig. A.2). No other model had substantial AICc support.

3.3. Individual-tree volume increment responses

The best-approximating model of individual-tree volume increment at approximately age 20 included the main effects of smoothed GD and GC, the GC $\times$ DBH interaction, and the null model terms of site, treatment, treatment $\times$ site, smoothed initial DBH, and smoothed BAL (Table 4). Because treatment and site-level growth responses have already been reported for this study (Zhang et al., 2022), we focus our reporting of results on GD and GC main effects and interactions. (Please see Fig. A.3 for summary of treatment and site effects.) Volume increment followed a curvilinear relationship with GD, highest at neutral (size-symmetric) values and lower at both strongly positive (size-asymmetric) and strongly negative (reverse size-symmetric) values (Fig. 5). Volume increment varied little up to a GC of 0.2, declined steeply between GC = 0.2 and GC = 0.35, and declined only slightly with further increases in structural complexity on the most structurally

complex plots. Under the GC $\times$ DBH interaction, the volume increment of trees growing in low GC (structurally simple) plots was consistently higher than that of trees in high GC (structurally complex) plots up to approximately 18 cm DBH, above which tree growth under high and low GC converged (Fig. 5). Increment declined with BAL (Fig. A.4). No other volume increment model was plausible.

4. Discussion

4.1. Treatment, site, and age influences on the development of growth dominance

Despite dramatic treatment effects on stand-level growth and growth efficiency (Zhang et al., 2022), our results suggest treatment did not consistently predict individual-tree contributions to growth efficiency. Substantial variation was visible among treatments and years within a given site, but these patterns were highly inconsistent across sites and years, contributing to a low amount of model variance explained (10%). We nevertheless found support for a treatment $\times$ site interaction, with evident treatment effects at Pondosa, where GD declined in response to vegetation control. This finding for the Pondosa site confirms negative GD-vegetation control relationships previously reported in southern pine systems (Campoe et al., 2013; Martin and Jokela, 2004). Elsewhere, the lack of an herbicide effect on GD agrees with Ferreira et al. (2020) and McGown et al. (2015), who found no effect of competing vegetation control on GD in loblolly and ponderosa pine plantations, respectively.

Given positive effects of site quality and moderate levels of N deposition on tree size-growth relationships (Looney et al., 2021; Pretzsch and Dieler, 2010), we expected to find higher GD under fertilization. Instead, fertilization had no apparent influence on GD, either in isolation or in conjunction with herbicide. Previous studies of fertilization in isolation of competing vegetation control in loblolly pine plantations have found both positive (Campoe et al., 2013) and neutral effects (Ferreira et al., 2020) on GD. Fertilization treatments largely ceased prior to canopy closure, and the LAI of fertilized and unfertilized plots may have quickly converged to limit any intensification in light competition that would have increased GD in our study. Another possibility is that fertilization compounded abiotic stress, which can negatively impact tree size-growth relationships (Castagneri et al., 2012; Pretzsch and Dieler, 2010). The application of fertilizer in salt form resulted in visible drought stress and seedling mortality (Powers and Ferrell, 1996).

Despite our study plots spanning a wide gradient of site index, there was no discernable role of site quality in driving variation in GD. Site quality is positively correlated with GD in *Populus tremuloides* stands (Pothier, 2017), while the similar size-growth relationship also increases with site index in a study of *Fagus sylvatica* L. and *Picea abies* (L.) Karst stands (Pretzsch and Dieler, 2010). However, our stands were generally much younger than those examined in either of these studies.

In Binkley's (2004), Binkley et al. (2002) model, growth dominance is predicted to shift as stands age, with size-symmetric (neutral) values during stand initiation becoming size-asymmetric (positive) during canopy closure and self-thinning, before returning to neutral or negative (reverse-size asymmetric) later in stand development. The development of size-asymmetric growth dominance may be particularly consequential for stand-level productivity, as the monopolization of stand growth by large trees is theorized to account for age-related growth decline as small-tree growth efficiency falls (Binkley, 2004; Ryan et al., 1997). In agreement with a previous study of young ponderosa pine (McGown et al., 2015), growth dominance across the range of young stand ages in this study varied little over time, with values close to 0 indicating that growth was generally proportional to tree size. Our stands achieved canopy closure by approximately age 6 at Feather Falls and ages 10–12 elsewhere, at which point GD should be expected to increase as trees transition from open growth to competition for light (Binkley et al., 2006). However, model results did not support a consistent increase in

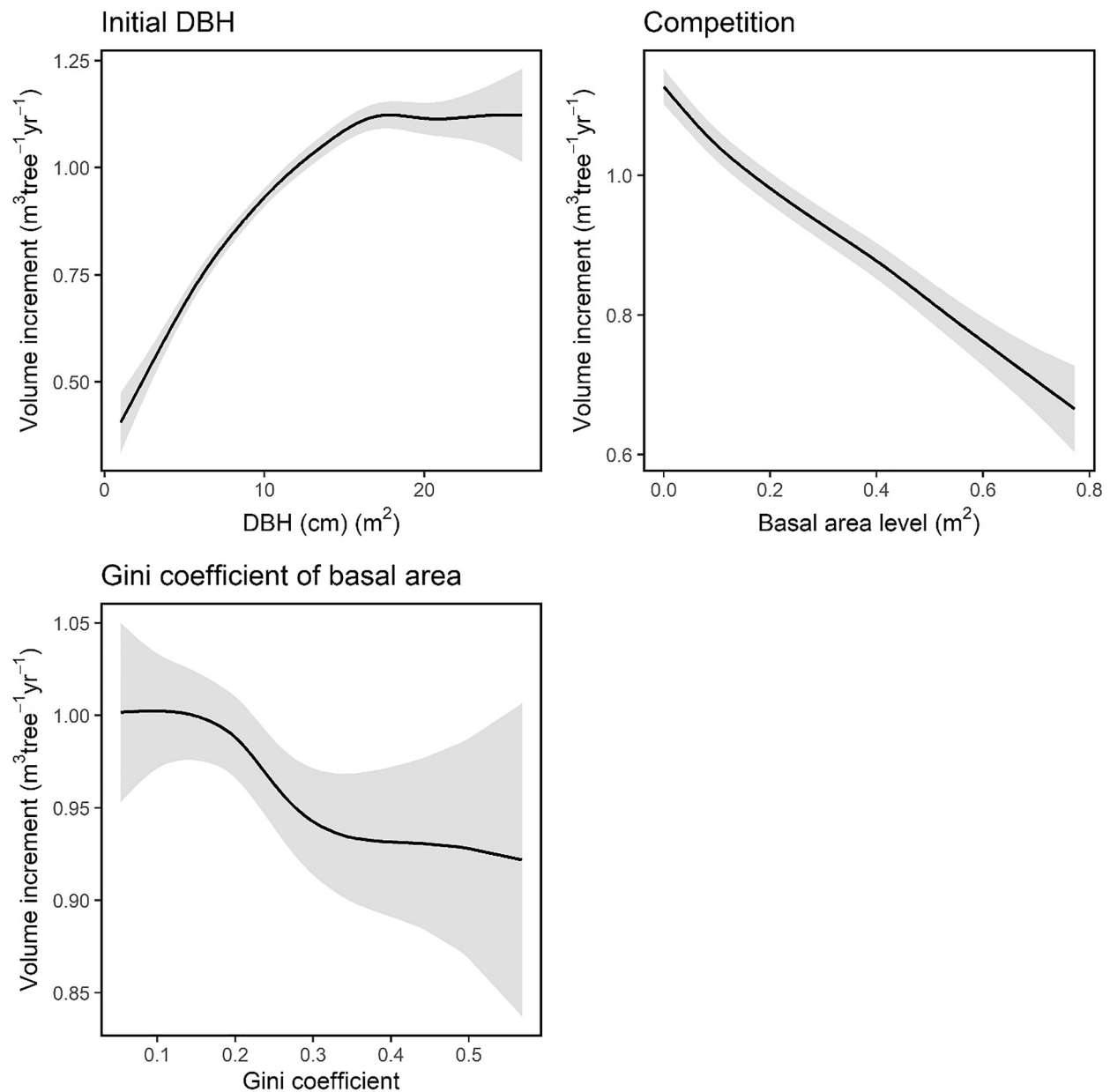


Fig. A.4. . Predicted values of individual-tree periodic annual volume increment at age 20 as functions of three continuous predictors: diameter at breast height (DBH), basal area level, and the main effect of the Gini coefficient of basal area.

GD with age across the study, nor was there evidence of a temporary increase around ages 6–12 in the raw data. Although strongly apparent in *Eucalyptus* plantations (Doi et al., 2010), shifts from size-symmetry to size-asymmetry are subtler in pine systems (Bradford et al., 2010; Martin and Jokela, 2004), particularly ponderosa pine (Binkley et al., 2006; Fernández et al., 2011; McGown et al., 2015). A caveat of our study is that longer measurement intervals after age 10 may have obscured upward trends in GD, as longer integration periods reduce estimates of similar size-growth relationships (Dye et al., 2019). Furthermore, our stands had not entered the self-thinning phase during which GD is hypothesized to peak (Binkley, 2004; Binkley et al., 2006).

4.2. Treatment, site, and age influences on the development of structural complexity

Treatment and site strongly interacted to influence GC across the study, and treatment effects remained consistent over time. Herbicide

and HF treatments had substantially lower GC, indicative of lower structural inequality, compared to C and F treatments. Our findings of generally lower structural complexity in response to competing vegetation control correspond with two previous studies of conifer plantations (Ferreira et al., 2020; Harrington et al., 1991). However, our results were in contrast to those of Nilsson and Allen (2003), who found that higher-intensity site preparation was more influential in reducing size variation in planted loblolly pine than subsequent herbicide treatments. Ferreira et al. (2020) noted that tree size distributions were right-skewed in plots with competing vegetation, whereas ours remained normally distributed. Compared to the southeastern U.S. coastal plain where planted pines may compete with large hardwood trees, competing vegetation species in this study were of generally small stature, such as shrub-form *Manzanita* spp. While our Feather Falls site formerly supported tree-form tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) Manos, C.H. Cannon, & S. Oh and Pacific madrone (*Arbutus menziesii* Pursh), these species were uncommon even in non-H

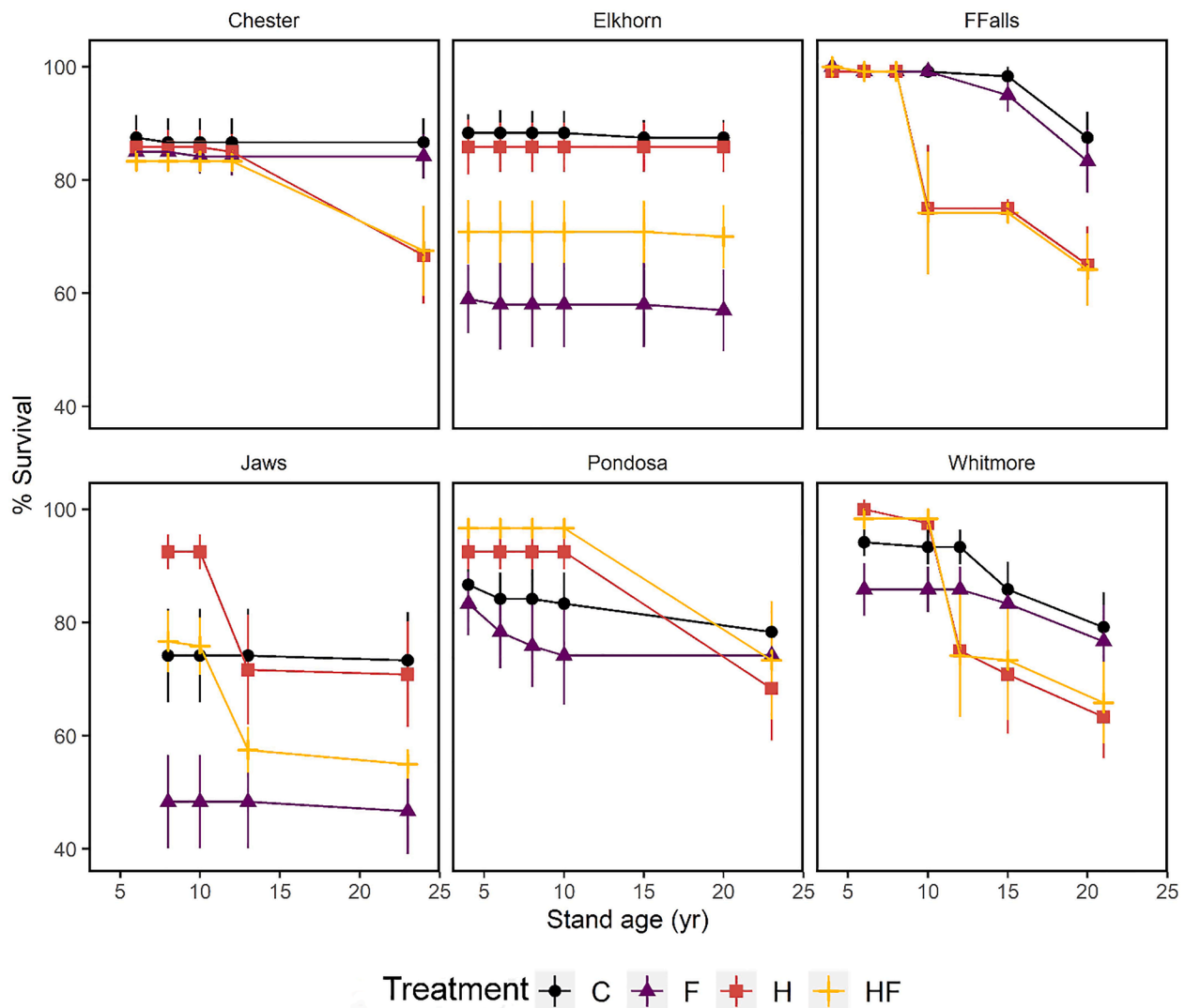


Fig. A.5. . Percent ponderosa pine survival ($\pm$ S.E) by treatment and measurement period for 6 Garden of Eden study sites.

plots following study establishment. The reduction in structural complexity with competing vegetation control was greatest on poorer-quality sites (Pondosa) or those with metasedimentary parent materials (Elkhorn and Jaws), suggesting the evenness of soil resources may be a key driver of size differentiation in this study. Whether competition for soil resources or light drives distinctly different patterns of planted tree size variation among ecoregions would be an interesting topic for future research.

Fertilization effects on GC were contingent on site, with Elkhorn and Jaws showing the strongest changes in F treatment GC relative to other treatments. While H treatment effects consistently reduced GC relative to the control group, the F and HF treatment effects showed nuanced effects among sites. At Elkhorn, the F treatment increased GC relative to the C group, while at Jaws the F treatment increased GC relative to the H and HF treatments. The lack of support for an interaction between treatment and stand age suggested these treatment differences arose during stand establishment and remained distinct over time. In contrast to our results, fertilization decreased structural complexity relative to control treatments in loblolly pine, but this effect was only apparent under more intensive site preparation practices than applied in our study and was not evident until stands were well-established (Nilsson and Allen, 2003). In a study of western red-cedar (Harrington and Devine, 2011), fertilization increased structural complexity relative to the control, which the authors attributed to reduced small-tree mortality

and more rapid large-tree growth. Higher stand leaf area under fertilization could ultimately accelerate the self-thinning of smaller trees, given the shade intolerance of ponderosa pine (Long et al., 2004). However, self-thinning was negligible over the duration of this study. Instead, soil properties may better explain our results, as Elkhorn and Jaws had metasedimentary parent materials where salt-form fertilizers exacerbated drought stress (Powers and Ferrell, 1996). Higher structural complexity under F treatments at these metasedimentary sites may, therefore, reflect adverse conditions during seedling establishment. There was otherwise little indication that overall site quality, as indicated by site index, drove the interaction between treatment and site. Treatment effects were weakest at Chester and Feather Falls, although these sites widely contrasted in site index. Porcupine damage during the first few years of plantation establishment at Chester may have confounded results at that site. Climatic conditions during planting and seedling establishment would have varied among sites and years of establishment.

Structural complexity, as indicated by GC, generally declined with age across the study. These declines are consistent with our finding that size-symmetric GD was prevalent across the study, as improved small-tree growth efficiency would be expected to lead to converging tree sizes over time (Forrester, 2019). While our results are also consistent with declining structural complexity during the stem exclusion phase of stand development (Oliver and Larson, 1996), our stands had not yet

experienced considerable self-thinning by the conclusion of the study. There was no clear correspondence between tree survival and structural complexity, with the most dramatic changes in survival emerging during seedling establishment rather than later in the study (Fig. A.5). The poorest sites, Elkhorn and Pondosa, had relatively high levels of structural complexity from the time of stand initiation. In contrast, structural complexity remained consistently low at the highest quality site, Feather Falls. Poor site quality may reflect a combination of lower overall growth potential, as well as greater within-site heterogeneity in growing conditions.

4.3. The influences of growth dominance and structural complexity on growth

The age-related growth decline in forest stands is thought to partly reflect shifts in growth efficiency among tree size classes (Smith and Long, 2001). Particularly during the self-thinning phase of stand development, size-asymmetric competition is hypothesized to concentrate stand growth on large trees at the expense of small-tree growth efficiency, reducing overall stand-level production (Binkley, 2004; Binkley et al., 2006). We would expect that size-asymmetric growth at the stand level should correspond with relatively low small-tree growth efficiency, a pattern that has been previously reported for both Canadian boreal forests (Baret et al., 2017) and conifer-dominated forest inventory plots in the western United States (Looney et al., 2021). Instead, we found that GD effects were not dependent on tree size. The greater monopolization of stand growth by large trees may accelerate rates of self-thinning (Looney et al., 2021; Pretzsch and Dieler, 2010), censoring the slowest-growing small trees from plots with high GD, yet stands did not display substantial self-thinning over the course of this study. Rather than interacting with tree size to influence growth, we found that both extremes of size-asymmetry, therefore, appear to evenly reduce the growth of all trees in a stand. Although there is no clear explanation for this pattern, extremes of GD could potentially drive rapid changes in stand structure (Forrester, 2019).

In agreement with previous studies, higher structural complexity reduced PAI in these young stands (Bourdier et al., 2016; Cordonnier and Kunstler, 2015; Liang et al., 2007). At age 20, an average-sized tree growing at the lowest observed GC plot (0.05) would have grown approximately 7% more rapidly compared to the highest GC plot (0.56). This effect size is weaker compared the results of tree and stand-level studies of shade-intolerant *Eucalyptus* spp. plantations (Luu et al., 2013; Soares et al., 2016), suggesting that the structural complexity effect on shade-intolerant conifer growth is subtler but also negative. Our results contrast with a stand-level study of ponderosa pine-dominated stands spanning a large range of ages, which did not detect a structural complexity effect (Long and Shaw, 2010). Complexity-productivity relationships can shift from negative to positive as stands mature (Zeller and Pretzsch, 2019), which may have rendered this negative complexity-PAI relationship clearer in our young ponderosa pine data compared to Shaw and Long's (2010) analysis of inventory data.

Several mechanisms may account for growth increases under decreasing structural complexity. We found that at age 20, small-moderate sized trees grew faster under low structural complexity, while large tree growth did not benefit. These findings are opposite those of Luu et al. (2013), who found that low structural complexity was most beneficial for large tree growth. In a study of mature, structurally complex ponderosa pine stands, Mainwaring and Maguire (2004) found that growth efficiency improved with tree size. Instead, the growth efficiency of densely planted young ponderosa pine may more closely resemble dense stagnating stands of lodgepole pine (*Pinus contorta* Douglas), where efficiency declines with tree size (Mainwaring and Maguire, 2004). Structural complexity can also reduce light use efficiency if large trees do not benefit from a marginal increase in sun exposure in more heterogeneous canopies at the same time that small

trees are adversely impacted by greater shading (Bourdier et al., 2016). Another possibility is that size differences could foster variation in competition intensity, and spatial complexity has been previously linked to local variation in growth rates (Fraver et al., 2014). Whereas we investigated structural complexity in terms of the distribution of tree sizes, we did not consider tree spatial patterns given that trees were row planted in a uniform distribution. Another factor could be crown shyness from wind-driven crown abrasion between neighboring trees, which is an important driver of declining leaf area during the age-related growth decline (Meng et al., 2006; Smith and Long, 2001). In more irregular forest canopies, taller trees might have adversely impacted smaller neighbors through crown abrasion. Lastly, plot-level variation in structural complexity could signal unevenness in site preparation or treatment effectiveness within a given study plot. However, this possibility appeared less plausible given a comparative lack of evidence for an interaction between structural complexity and treatment.

5. Conclusions

Our study of trends in growth dominance, structural complexity, and individual-tree growth across a gradient of ponderosa pine site productivity had three main conclusions. In support of previous studies, the average trend for ponderosa pine growth dominance was nearly size-symmetric, although there was considerable variation within study sites. Growth dominance did not consistently vary with site quality, time, or treatment, suggesting that intensive silvicultural treatments in the stand initiation stage do not leave a lasting, predictable legacy on ponderosa pine growth efficiency or mode of competition. High site quality and competing vegetation control promoted lower structural complexity, which generally tended to decline over time across all sites. Simpler stand structures benefitted the growth of small-medium trees, while larger trees grew similarly in both complex and simple structures.

Our results have important management implications. As climate-change driven wildfires increase in frequency and extent worldwide, researchers have advocated for manipulating the spacing of plantings during reforestation as a means of enhancing structural complexity to improve stand resistance and resilience against reburns (North et al., 2019; Stephens et al., 2010). Particularly on public lands where intermediate treatments, such as precommercial thinning, may not be feasible, slower small-tree growth in complex young stands would impede the recruitment of larger trees critical to enhancing survival during fire (Johnston et al., 2019). Because neither site nor treatment had consistent influences on GD, private land managers might focus instead on intermediate treatments such as thinning, to optimize the distribution of growth within a stand. Finally, an anachronism of the Garden of Eden study is that the design's 2.4 m initial tree spacing has since been largely abandoned in favor of wider spacings in California. Managers could generally delay the rate of tree size differentiation through planting at wider spacing.

CRediT authorship contribution statement

Christopher E. Looney: Conceptualization, Methodology, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Jianwei Zhang:** Conceptualization, Data curation, Visualization, Writing – original draft, Writing – review & editing.

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.

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Appendix A

See Table A.1 and Figs. A.1–A.5.

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