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Whoa on the wobble! Stem sinuosity in juvenile Douglas-fir across levels of genetic gain, silvicultural treatments, site conditions, and climatic variables in the Pacific Northwest

Michael Premer [a,*], Eric Turnblom [b], Aaron Weiskittel [c]

[a] School of Forest Resources, University of Maine, United States
[b] College of the Environment, University of Washington, United States
[c] Center for Research on Sustainable Forests, University of Maine, United States

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ABSTRACT

Managed forests serve as a natural climate change solution through sequestration of C and long-term storage in harvested wood products, in addition to providing ecosystem services and wildlife habitat. Specifically, commodity products such as dimensional lumber and building materials, utilized from high-quality, defect free trees, provide greatest economic return and long-term C reservoir. Stem sinuosity is a noted deformity in juvenile coastal Douglas-fir (*Pseudotsuga menziesii var. menziesii* (Mirb.) Franco) and can result in loss of value and degraded economic end-product. While the causal mechanisms have been of interest for decades, relatively little is known regarding the influence of tree improvement, silviculture, and local growing conditions. A network of experimental plots ($n = 132$) across six installations in the Pacific Northwest (PNW) were assessed to determine the effects of tree spacing, vegetation control, genetic gain, soil, site, and climate variables on stem sinuosity 10 years since planting. Sinuosity presence was greatest in wild genetic sources and on sites with low soil C and A horizon thickness. Severity increased with stem size and declined with concomitant gains in stand density and local windspeed. Findings suggest that site-specific deployment of genetic resources and silvicultural treatments may enhance Douglas-fir stem form in the PNW.

1. Introduction

Private industrial forestlands in the United States have long been utilized for production of commodity timber goods. These settings are increasingly recognized as a natural solution to climate change through long-term C storage and provision of alternatives to fossil-fuel derived materials, commonly in the form of dimensional lumber, building supplies (Meyer et al., 2022; Singh et al., 2022), and emerging applications of biomaterials (Lamm et al., 2020). With continued land fragmentation and expansion of the wildland urban interface (Mockrin et al., 2022), evolving pest outbreaks (Anderegg et al., 2015), and regeneration challenges (Dey et al., 2019), innovative approaches to enhancing forest production on a decreasing operational land base are needed. Tree improvement through genetic selection and intensive silviculture offer attractive solutions to increase harvestable yield, shorten rotations, and increase C sequestration, that can be refined by site-specific conditions (Allen et al., 2005).

In addition to species-specific market demand, the timber value and associated C storage interval of wood products are dependent upon stem form (e.g., branching, straightness), and structural defects (Middleton et al., 1989) for utilization. Wood products, including furniture, veneer, and building materials, are generated from the highest quality tree stems and have the greatest potential for long-term C storage and economic return (Li et al., 2022; Daigneault et al., 2022). As wood quality decreases, market value and C residence time generally decline in parallel. In turn, increased recovery of high value commodity goods on managed forestlands has been a central focus of applied research programs across multiple regions.

Across the Pacific Northwest of North America, planted Douglas-fir (*Pseudotsuga menziesii var. menziesii* (Mirb.) Franco) forests provide timber supply to the domestic housing sector and resource for export markets (Flora et al., 1993), due the unique characteristics such as specific gravity, strength, and stiffness (i.e., modulus of rupture, modulus of elasticity) (Cline and Knapp, 1911). Since the 1960 s, there

* Corresponding author.
E-mail address: michael.premer@maine.edu (M. Premer).

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have been ongoing applied research efforts to enhance timber yields of Douglas-fir through intensive management. To date, there have been notable gains in productivity and utilization through genetic improvement and silvicultural treatments, including site preparation, fertilization, variability in planting densities (Talbert and Marshall, 2005), and remote sensing applications. Much of this progress can be attributed to regional research cooperatives and associated long-term replicated field trials that serve to facilitate collaboration among industrial, academic, and government research scientists (Homyack et al., 2022).

Genetic and environmental factors that result in stem defects in Douglas-fir stands have been of interest to forest managers in the PNW for decades (Campbell, 1965; Carter et al., 1986; Temel and Adams, 2000). Specifically, stem sinuosity, defined here as any internodal stem crookedness and associated displacement from original direction of growth (Campbell, 1965), can result in reductions of usable volume due to the formation of compression wood, increase in lignin content, and associated slope of grain (Middleton et al., 1989). Early work to discern the influence of genetic effects on stem form and growth were based in progeny tests at the Pacific Northwest Tree Improvement Cooperative (NWTIC) which is based at Oregon State University. While these efforts were successful in identifying seed sources with lower heritability of sinuosity, the effects of stand structure, stem dimensions, and environmental conditions were not explicitly tested or inconclusive (Adams and Howe, 1985). In the early 2000 s, the NWTIC, Stand Management Cooperative (SMC) at the University of Washington, and U.S. Forest Service, collaboratively established a genetics and silvicultural experimental research network in Western Washington, referred to as the Type IV project. Previous findings from this work have alluded to the role of local environmental conditions on stem form and growth, yet questions remain regarding the influence of site factors, genetics, and silviculture on sinuosity of Douglas-fir.

The primary goal of this work was to evaluate the influence of seed source, planting density, chemical vegetation control, site, and climatic factors on stem sinuosity in planted Douglas-fir forests. The specific objectives include: [*i*] quantifying the presence and severity of stem sinuosity; [*ii*] relating these trends to potential influences of genetic, tree, stand, site, and climate covariates; and [*iii*] outlining key management recommendations to strategically allocate genetic resource and silvicultural activities to enhance stem form and utilization of planted Douglas-fir forests. It was expected that sinuosity occurrence and severity would decrease with concurrent gains in genetic improvement. It was further assumed that the inclusion of soil and physio-climatic variables would capture variability across the study network and enhance predictive model performance.

2. Methods

2.1. Site descriptions and study design

The Type IV project is a multi-factorial, replicated experimental network with six installations across Western Washington, USA, on land traditionally occupied by the Chehalis and Clatskanie Indigenous peoples, and the Quinault Nation (Fig. 1). Installations cover a range of environmental conditions near the Pacific Ocean. The climate of the

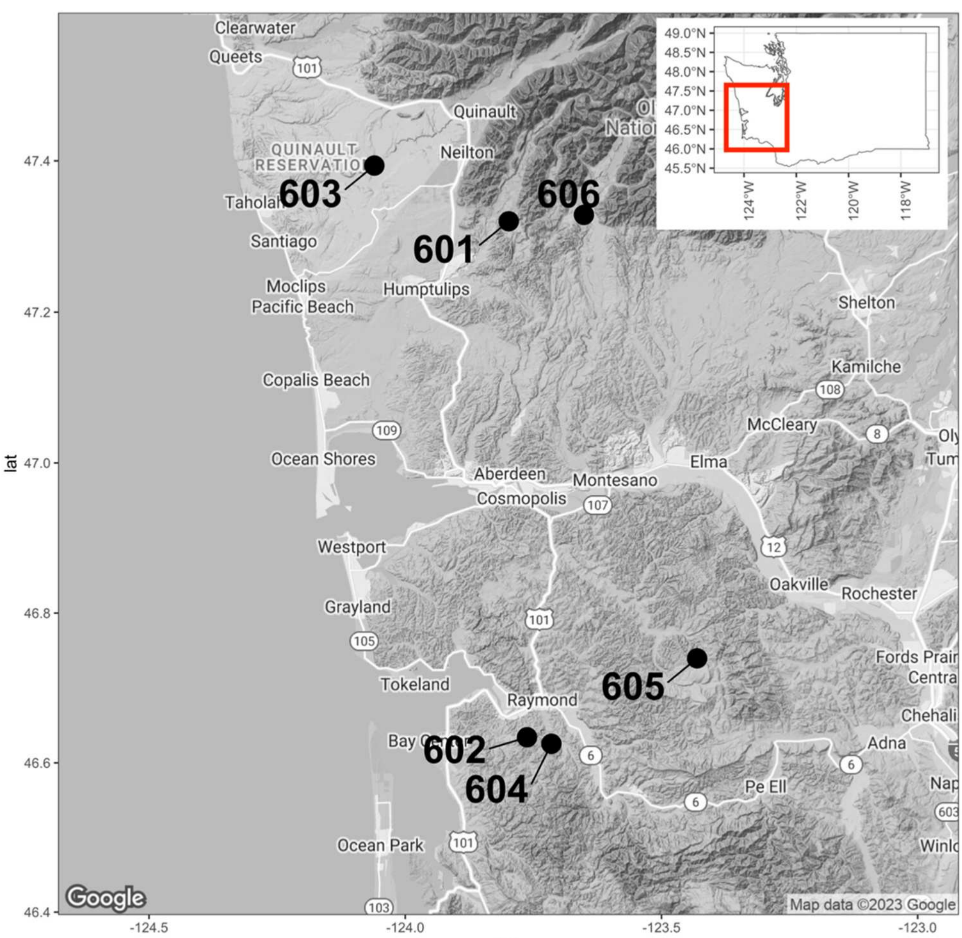

Fig. 1. Locations of the SMC Type IV Plot Network (Installations, $n = 6$; 601–606) in Pacific and Grays Harbor Counties, Washington, USA, and the Quinault Nation. Background image provided by Google in 1984 WGS coordinates. Washington State polygon generated with the spData package (Biven et al., 2021) and inset created with the ggplot2 (Wickham et al., 2022) and cowplot (Wilke 2022) packages.

study area is classified as Oceanic and Warm-Summer Mediterranean, and monthly mean temperatures span from 4.9 to 15.1^{o} C in the winter and summer, respectively, with most of the annual precipitation (219–350 cm) occurring in the winter season (PRISM 2023). Geologic provinces include the Southern Olympic Mountains and Willapa Hills. Parent materials include alluvium over unconsolidated glacial deposits, glacial till, and residuum from weathered basalt and sandstone, that result in high variability of soil chemistry, texture, and drainage class (McKee, 1972; NRCS, 1999). Across the study sites, elevation ranges from 54 to 237 m above sea level on gentle to moderate slopes of 0–15% (Table 1).

All sites were planted in 2005 and 2006 with Douglas fir 1–0 plug stock types at 3 levels of initial density (476, 1076, 2195 trees per hectare), with plots ranging from 0.09 to 0.1 ha, respectively. Three levels of genetic gain were tested across planting densities: (*i*) unimproved sources from a random selection of wild trees; (*ii*) medium gain from selected pairs of 20 intermediate parent trees; and (*iii*) high gain from crossing selected pairs of 20 best performing parents. Two levels of competing vegetation control (1 – pre-planting chemical site preparation only, 2 – pre-planting chemical site preparation and <20% competitor cover estimated ocularly until crop tree crown closure) were further evaluated against a no treatment reference, for a total of 22 plots per installation (132 total plots). Individual trees were measured annually on all plots for the first 5 years after planting, then on a 4-year recurring cycle during the dormant season. In 2016–17 (10 years since planting), all trees (n = 13,250) were recorded by diameter at breast height (1.37 m) to the nearest 0.1 cm, total height to the nearest 0.1 m, and visually assessing the degree of misalignment and offset of apical growth from the initial stem direction along the entirety of the stem. Sinuosity ratings were determined by counting the number of 0.5 stem diameter unit internodal crooks offset from where the main stem would have been growing given no sinuosity. (greater degree of internodal offset from the main stem, the greater the sinuosity value – please see Adams and Howe (1985) for an illustration). The mean stem sinuosity rating was 0.94 and the data exhibited high variability (Standard deviation; SD = 1.97, range 0–60) across the plots and installations. Trees ranged in size from 0.1 to 9.7 cm DBH and 0.25 – 9.20 m in height, across densities of 307–2223 trees per hectare (tph). Standard metrics of density and stand structure including basal area per hectare, quadratic mean diameter, and relative density (%, Curtis, 1982) were calculated from the raw tree list data (Table 2).

Table 1
Topographic, soils, climatic, and meteorologic variables derived from the digital elevation model, the PRISM climate network, NRCS, and GWA, across all plots (n = 132) of the Type IV Installations (n = 6).

Site Variable	Mean and range
Topographic	
Aspect (0–359^{o})	166.03 (2.68 – 344.87)
Elevation (meters above sea level)	150.12 (54.02 – 237.02)
McNab's Index	0.00 (−0.11 to 0.10)
Bolstad's Index	0.04 (−0.01 to 0.19)
Planform Curvature	66.70 (−12277.49 to 4035.95)
Slope (%)	5.23 (0.00 – 15.56)
Forest soils	
Soil C (Mg ha)	19.04 (14.37 – 21.77)
Soil N (Mg ha)	1.00 (0.79 – 1.90)
Total depth (cm)	84.45 (42.17 – 114.41)
Thickness of A horizon (cm)	10.93 (2.60 – 22.24)
Clay % in A Horizon	9.22 (7.21 – 11.74)
Thickness of B horizon (cm)	38.97 (23.99 – 52.79)
Clay % in B Horizon	13.59 (5.73 – 19.50)
Soil Water Capacity (mm m2)	99.49 (50.13 – 203.27)
pH	4.73 (4.29 – 4.96)
Exchangeable Ca (Mg ha)	0.87 (0.50 – 1.51)
Exchangeable K (Mg ha)	0.12 (0.06 – 0.21)
Exchangeable Mg (Mg ha)	0.44 (0.24 – 0.75)
Cation exchange capacity (cmol$_c$ kg)	35.79 (27.53 – 41.28)
Climatic and meteorologic	
Mean Annual Dew Point (C)	5.89 (5.64 – 6.23)
30-year Average Maximum Annual Temperature (C)	14.51 (13.86 – 15.13)
30-year Average Mean Annual Temperature (C)	9.82 (9.49 – 10.18)
30-year Average Minimum Annual Temperature (C)	5.12 (4.86 – 5.53)
30-year Average Maximum Vapor Pressure Deficit (h Pa)	7.97 (7.33 – 8.60)
30-year Average Minimum Vapor Pressure Deficit (h Pa)	0.39 (0.30 – 0.42)
30-year Mean Annual Precipitation (mm)	2709.27 (213.95 – 3502.75)
Mean windspeed (meters per second)	2.63 (1.58 – 3.57)
Mean daily solar insolation (kW h m^2)	5.21 (0.58 – 8.06)

2.2. Data curation and processing

All data processing, analysis, graphics, and reporting were conducted in the R software environment, version 4.2.2 (Core Team, 2022). Individual plot locations were overlaid with a region wide 30 m digital elevation model (DEM) from the United States Geologic Survey 3D Elevation Program (3DEP) sourced through the elevatr package (Hollister et al., 2021). The DEM resolution was chosen to match plot dimensions and avoid potential errors when calculating topographic metrics. Aspect (0–360^{o}) and slope (%) were calculated with the raster package (Hijmans, 2022). Planform curvature, Bolstad's topographic index (Bolstad and Lillesand, 1992), and McNab's topographic index (McNab, 1993), were calculated with the spatialEco package (Evans, 2021). Forest soils data, including parent material, soil series, and physical and chemical characteristics, were accessed from the Natural Resource Conservation Service (NRCS) through the soilDB (Beaudette et al., 2023a) and sharpshootR (Beaudette et al., 2023b) packages (Table 1; Appendix 1). Regional climatic records of 30-yr normal (1984–2014) temperature (minimum, mean, maximum), vapor pressure deficit, dew point, and precipitation data were accessed from the PRISM (2023) database. Considering the link between wind exposure, translocation of growth hormones, and resulting formation of reaction wood noted by Kozlowski and Pallardy (1996) and others (Jacobs, 1954; Campbell, 1965), estimates of local wind speed (meters per second) at 10 m above the terrestrial surface were acquired from the Global Wind Atlas (Global Wind Atlas 3.0, 2023). The GWA estimates utilize a topographically derived downscaling process to account for the effects of terrain and landform on variation in local velocity. The System for Automated Geoscientfiic Analysis software (Conrad et al., 2015) was accessed through the rsaga package (Brenning, 2008) to calculate the annual mean daily incoming solar insolation (kW h m^2). All geospatial products were re-scaled to 20 m resolution for processing and spatial compatibility with field measurement plots.

2.3. Statistical Analysis

To model the occurrence and severity (count) of stem sinuosity, several distribution families were tested, including the Poisson (P) and Negative Binomial (NB), with zero-inflated (ZI) and zero-adjusted (ZA) variations. As noted in other works (Li et al., 2011; Russell, 2015), while the ZI and ZA variations of the Poisson distributions can model excessive zeros in a dataset, they may not adequately capture overdispersion of

Table 2
Mean and range of tree (n = 13,250) and plot-level (n = 132) structural attributes from the SMC Type IV Plot Network across all installations (n = 6) used in this analysis. SD corresponds to the standard deviation.

Tree and stand attribute	Mean, SD, and range
DBH (cm)	3.72, 1.99 (0.10 – 9.65)
Height (m)	3.27, 1.46 (0.25 – 9.20)
Trees per hectare	1271, 538 (307–2223)
Basal area per hectare (m^2 ha^{-1})	1.64, 0.93 (0.20 – 4.20)
Quadratic mean diameter (cm)	4.16, 2.1 (2.40 – 5.74)
Relative Density (%)	5.94, 4.13 (0.98 – 13.76)
Stem sinuosity rating	0.94, 1.97 (0.00 – 20.00)

non-zero count data due to the assumption of equal mean and variance. Preliminary analysis revealed a high frequency of zeros and overdispersion of the count data. Model comparisons and performance were evaluated using Akaike Information Criteria (AIC; 1973), Bayesian Information Criteria (BIC; Schwarz 1978), and − 2 log-likelihood metrics, where lower values indicate comparatively better model performance. Likelihood ratio tests were used to test the addition of the overdispersion parameter between the standard Poisson and NB models, and examine the binomial component of the ZIP, ZAP, ZINB, and ZANB models. Goodness of fit was assessed with Pearson's chi-square statistics (χ^2) by comparing log-likelihoods of each model with an intercept-only approach. The ZA distribution consistently underestimated the frequency of zero occurrences, thus, the ZINB was the superior model. The base NB model is estimated through a gamma function and can be defined as,

$$fNB(y) = \frac{\Gamma\left(y+\frac{1}{\alpha}\right)}{\Gamma\left(\frac{1}{\alpha}\right)\Gamma y+1}\left(\frac{1}{\lambda\alpha+1}\right)^{1/\alpha}\left(\frac{\lambda\alpha}{\lambda\alpha+1}\right)^{y} \tag{1}$$

Where y is the observed stem sinuosity score, λ is the mean sinuosity score, and α is the overdispersion parameter, with a defined variance of $\mu + \alpha\,\mu^2$. When $\alpha = 0$ the shape takes the properties of a Poisson distribution. To account for excessive zeros in the dataset, the ZINB partitions the approach through estimating the occurrence of zeros through a binomial mechanism and Poisson process that can be expressed as

$$fZINB(y) = \begin{cases} \pi + (1-\pi)\left(\frac{1}{\lambda\alpha+1}\right)^{1/\alpha} & y = 0 \\ (1-\pi)fNB(y) & y > 0 \end{cases} \tag{2}$$

Where π indicates the probability of a zero occurrence (i.e., stem with no sinuosity), and f_{NB} refers to the NB probability mass function defined above in Eq. 1. The λ parameter is estimated through a linear prediction approach with a log-link function, in this case using the suite of explanatory variables outlined in Tables 1 and 2.

Tree, stand, site, and climatic covariates were assessed using a random forest selection procedure with the VSURF package (Genuer et al., 2015), following recommendations of Speiser et al. (2019). Multicollinearity of predictor variables were assessed with variance inflation factors using the performance package (Lüdecke et al., 2021). Variables with VIF> 5 were omitted as outlined by James et al. (2014). To compare the relative improvement in model quality through the addition of covariates across scales (tree – climate) and increasing model complexity, the best ranked variables of each category were added in a stepwise manner, taking the form,

$$\ln(\lambda) = \beta_0 + \beta_n X_{n\ \mathrm{TREE}} + \beta_n X_{n\ \mathrm{STAND}} + \beta_n X_{n\ \mathrm{SITE}} + \beta_n X_{n\ \mathrm{CLIM}} \tag{3}$$

Where TREE, STAND, SITE, and CLIM correspond to the best ranked tree, stand, site, and climatic variables, respectively. Similarly, the π parameter indicating the probability of a zero occurrence through a binomial process in Eq. (2) is estimated through a logistic equation with the approach,

$$\pi = \frac{1}{1+\exp-(\gamma 0+\gamma nXnTREE+\gamma nXnSTAND+\gamma nXnSITE+\gamma nXnCLIM)} \tag{4}$$

using the same set of potential explanatory features. Variables were standardized with z-scores and transformed to odds ratios for interpretation. Variability within installations not explicitly captured was tested using a specified random effect in the intercept of each tested model with the glmmTMB package (Brooks et al., 2017) and assumed to follow a normal distribution ($b_i \sim N(0, \sigma^2)$), where b_i is the random installation effect. Final candidate models were compared using Akaike information criterion (AIC) values and Akaike weights, implemented with the MuMIn package (Bartón, 2023). Model performance and uncertainty as defined by coefficient of determination (R^2), root mean square error (RMSE), mean bias (MB), and mean absolute bias (MAB) were used as additional metrics of goodness of fit.

3. Results

Of the 13,250 individual live tree observations across the experimental network, a total of 9290 zeros (no sinuosity) were present in the dataset (66.3%) (Fig. 2), ranging from 21% at Installation 601–97% to Installation 606 (Fig. 1; Table 3). For stems with a noted occurrence of sinuosity, the mean severity score (count) was 2.88 (SD=2.50) and ranged from 1 to 20. Sinuosity scores ranged from 2.6 to 4.6. Installations with low proportions of stems with sinuosity reported greater severity when presence was detected. The overall variance to mean ratio was 2.17, indicating overdispersion in sinuosity count scores (Table 3).

The stepwise model comparison results indicate consistent gains in relative model performance with the addition of stand and site characteristics. However, including the best ranked climatic variables resulted in a marginal gain in model quality, as indicated by AIC scores and weights (Table 4). Results from the zero-inflated model component (γ_0-γ_9) suggest the probability of sinuosity is lowest in the high and medium genetic gain seed sources and in stands with greater basal area, yet increases with asymmetric tree competition (BAL), tree DBH, and height (Table 5). Trees in the standard vegetation control exhibited a lower probability of sinuosity compared to the intensive treatment. At the site level, probability of sinuosity declined with corresponding gains in soil C and depth of the mineral A horizon (Fig. 3; Table 5).

The conditional component of the ZINB model (β_0- β_8) indicates that when trees exhibit sinuosity, severity increases with tree DBH, and asymmetric competition as indicated by BAL, and is greatest in the unimproved genetic sources and on sandstone parent materials (Table 5). The addition of mean windspeed as a predictor variable improved model quality and corresponded with a decrease in sinuous severity (Fig. 4; Table 5). The R^2 of the final model was 0.266, with a RMSE of 1.80, 0.383 and 0.833 for MB and MAB, respectively (Table 6).

4. Discussion

The results suggest, (*i*) multiple factors influence stem sinuosity

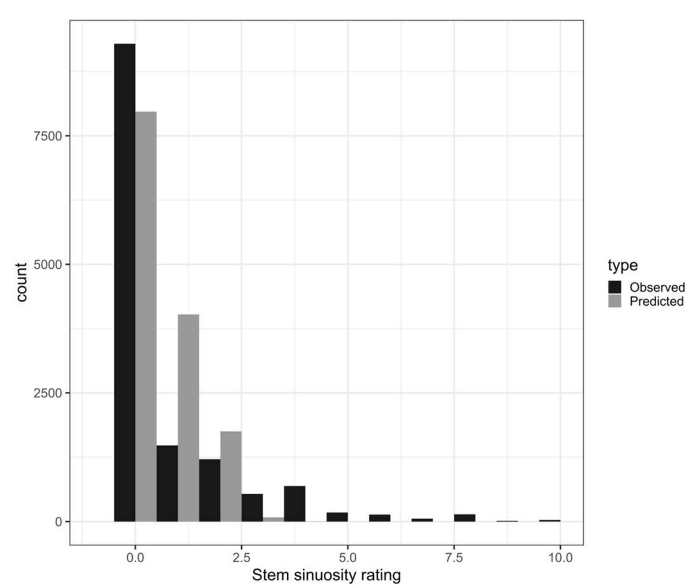

Fig. 2. Frequency of observed (black) and predicted values (dark gray) of Douglas-fir sinuosity rating for the zero inflated negative binomial (ZINB) model.

Table 3
Summary of stand structure and stem sinuosity occurrence by Installation (n = 6) of the Type IV SMC Plot Network. Values indicate the mean followed by standard deviations in parenthesis.

Installation	601	602	603	604	605	606
Parent Material	Loess and Alluvium	Basalt	Glacial Till	Sandstone	Sandstone	Glacial Till
DBH (cm.)	5.04 (1.36)	3.84 (1.57)	3.75 (1.78)	4.06 (1.98)	3.04 (2.04)	2.67 (2.1)
Height (m)	4.17 (0.88)	3.38 (1.02)	3.38 (1.27)	3.49 (1.39)	2.8 (1.63)	2.45 (1.68)
Height:Diameter	7.01 (1.77)	7.50 (2.81)	7.46 (3.45)	6.99 (3.57)	6.56 (4.24)	6.09 (4.86)
Sinuosity rating	2.60 (2.13)	2.62 (2.39)	2.67 (2.43)	4.66 (2.84)	4.57 (3.51)	4.55 (3.31)
Proportion non-sinuous stems	0.31	0.48	0.43	0.85	0.94	0.97
Sinuosity mean:variance	1.74	2.18	2.22	1.73	2.69	2.4
Relative Density (%)	1.17 (0.47)	0.75 (0.28)	0.81 (0.34)	1.04 (0.46)	0.67 (0.26)	0.63 (0.24)
QMD (cm)	5.22 (0.25)	4.14 (0.31)	4.13 (0.43)	4.51 (0.32)	3.62 (0.54)	3.37 (0.43)
Basal area (m^2 ha^{-1})	2.67 (1.05)	1.53 (0.55)	1.65 (0.71)	2.22 (1.03)	1.28 (0.52)	1.16 (0.45)

Table 4
Akaike Information Criterion (AIC) ranking of the candidate models including stand, site, and climate variables. LL indicates log likelihood, Delta and w_i indicate the relative differences and conditional probabilities of the compared models.

Model form	LL	AIC	Delta	w_i
TREE, STAND, SITE, CLIM	-12939.57	25923.21	0.00	0.80
TREE, STAND, SITE	-12941.97	25926.01	2.80	0.20
TREE, STAND	-13790.20	27610.43	1687.22	0.00
TREE	-15233.96	30489.95	4566.74	0.00

Table 5
Parameter estimates for zero inflated (γ_0-γ_9 and conditional (β_0-β_8) parameters of the zero inflated negative binomial (ZINB) (Eqs. 3 and 4) model, exp(γ_n , β_n) is the transformed odds ratio of the parameter estimate.

Parameter	Variables	Estimate	SE	P value	exp (γ_n , β_n)
γ_0	Intercept	0.922	1.412	0.514	2.581
γ_1	DBH (cm)	-0.345	0.074	0.000	0.504
γ_2	Height (m)	-0.966	0.101	0.000	0.244
γ_3	Genetics $_{medium}$	0.096	0.116	0.408	1.101
γ_4	Genetics $_{wild}$	-0.467	0.097	0.000	0.627
γ_5	Stand basal area (m^2 ha^{-1})	0.502	0.094	0.000	1.594
γ_6	Basal area larger (m^2 ha^{-1})	-0.339	0.126	0.007	0.756
γ_7	Soil A layer depth (cm)	0.078	0.029	0.007	1.302
γ_8	Total Soil Carbon (Mg ha^{-1})	0.165	0.046	0.000	1.310
γ_9	Vegetation Control $_{Site\ prep}$	0.278	0.123	0.024	1.320
β_0	Intercept	0.590	0.255	0.021	1.432
β_1	DBH (cm)	0.107	0.017	0.000	1.236
β_2	Genetics $_{medium}$	0.042	0.040	0.297	1.043
β_3	Genetics $_{wild}$	0.211	0.034	0.000	1.235
β_4	Basal area larger (m^2 ha^{-1})	-0.104	0.027	0.000	0.917
β_5	Glacial Till Parent Material	0.230	0.167	0.464	1.259
β_6	Loess Alluvium Parent Material	0.157	0.189	0.407	1.170
β_7	Sandstone Parent Material	0.906	0.181	0.000	2.473
β_8	Windspeed (m s^{-1})	-0.192	0.087	0.029	0.889

across genetic, tree, stand, site, and subregional climatic scales; (*ii*) these effects can be quantified by integrating field records and emerging geospatial variables; and (*iii*) tree improvement programs, site-specific genetic deployment, and precision silvicultural practices may reduce sinuosity occurrence, and thus, has potential to increase value of planted Douglas-fir forests in the PNW. This agrees with prior research that found that intensive silvicultural practices like vegetation control, thinning, and fertilizer did not adversely affect Douglas-fir simulated lumber yield or quality from a wide range of conditions in the coastal Pacific Northwest similar to the research installations assessed in this analysis (Weiskittel et al., 2006).

Assessment of stem form in tree improvement programs and soil nutrition studies commonly utilize heritability scores (Jayawickrama and Ye, 2021) or least square means to test for differences among groups (Gartner and Johnson, 2006; Littke and Zabowski, 2007; Ye et al., 2009; Dwivedi et al., 2019). While informative for relative comparisons, group level mean values may result in misleading interpretations given high frequencies of zeros in a dataset. For example, in a subset of the sites and field data tested here, Dwivedi et al. (2019) report relativized plot level sinuosity scores from approximately 0.02 to 0.08 across genetic sources. This range of values obscures the high proportion of trees with no occurrence of defect, and suggests that all trees have some, although minimal, degree of sinuosity, which is clearly not the case. The approach to estimate occurrence and severity of sinuosity at the individual tree level parallels past work with cavity tree and snag abundance (Eskelson et al., 2009; Russell, 2015), regeneration ingrowth, and recruitment (Li et al., 2011; Zhang et al., 2012), using variations of the NB distribution form. As noted, high frequency of zeros and moderate overdispersion is common in these types of forest inventory datasets.

The influence of tree, stand, site, and climatic effects are complex, difficult to model, and are not entirely captured by the covariates utilized in this analysis. While the ZINB was the best approach tested here for quantifying sinuosity occurrence and severity within the SMC type IV dataset, the final prediction model only partially explained the overall variance and exhibited a slight bias, with the MB and MAB revealing a systematic overprediction of sinuosity severity. These trends may be attributed to the wide range in occurrence and severity of sinuosity by individual experimental installation across a relatively limited replicated sampling network ($n = 6$). Therefore, while the approach is useful for investigating correlations with stem form within the study area of the SMC Type IV project, extrapolation of these findings beyond the narrow climatic range of this portion of the Washington Coast should be applied with caution. Nonetheless, the results reveal an effect of genetic seed source and stem size on stem sinuosity, with lower occurrences and severity scores in the medium and high groups and increasing stem dimensions. While the effect of genetics on tree size was not explicitly tested here, Dwivedi et al. (2019) reported greater stem height in the high and medium gain groups when compared with the unimproved sources on a subset of plots on 3 of the installations analyzed in the current study. Similarly, simulation work by Joo et al. (2020) and Isaac-Renton et al. (2020) consistently forecasts increased yield of high gain seed sources using Douglas-fir genetic gain trials in Northern Oregon and British Columbia, respectively. Collectively, the results indicate that the use of improved genetic Douglas-fir seed sources in the PNW can result in a greater volume recovery and marketability at rotation, in line with other working forest regions (Homyack et al., 2022) yet stem form can vary across site types.

Stand density has been noted to have effects on branch size, and low densities can result in large knots and defects in Douglas-fir (Carter et al., 1986; Lowell et al., 2018). Alternatively, high planting densities

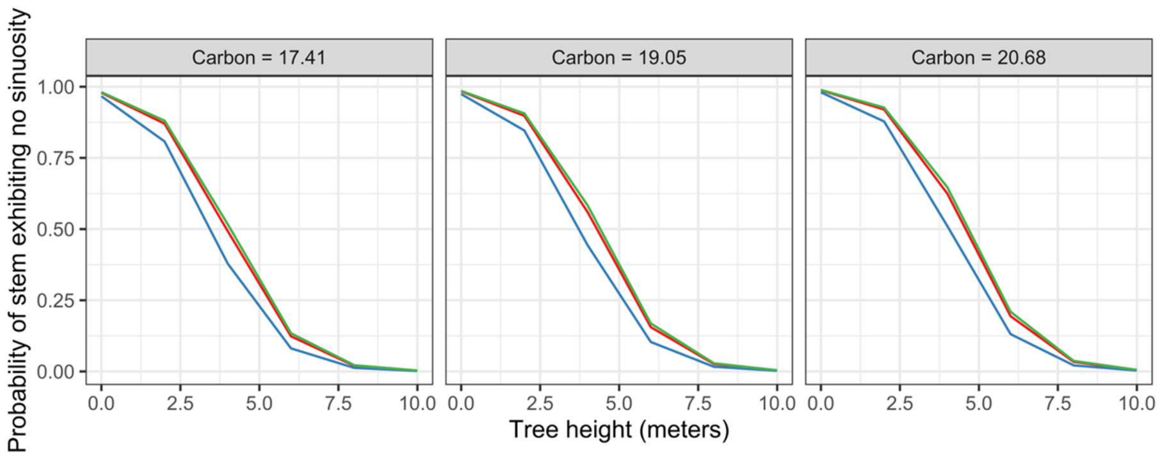

Fig. 3. Predicted probability of stem exhibiting no sinuosity (Y Axis) by tree height (X Axis) across levels of genetic gain (lines - red – high gain, green – moderate gain, blue – unimproved) and site-specific estimates of total soil C (Mg ha – 17.41 Mg ha^{-1} left panel; 19.05 Mg ha^{-1} center panel; 20.68 Mg ha^{-1} right panel).

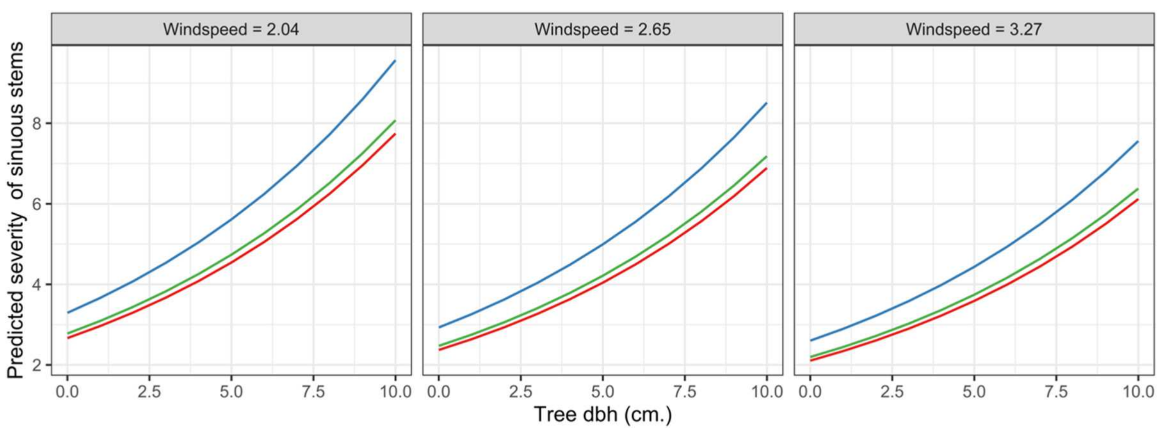

Fig. 4. Predicted sinuosity severity rating (Y Axis) according to level of genetic gain (red – high gain, green – moderate gain, blue – unimproved) and tree DBH (cm; X Axis) across site-specific estimates of mean windspeed (meters per second – 2.04 m s^{-1} left panel; 2.65 m s^{-1} center panel; 3.27 m s^{-1} right panel).

Table 6
Uncertainty and Goodness of fit metrics of the candidate models with hierarchical subsets. RMSE is root mean square error, MB is mean bias, MAB is mean absolute bias, and R^2 is the coefficient of determination.

Model form	RMSE	MB	MAB	R^2
Tree, Stand, Site, Climate	1.805	0.383	0.835	0.266
Tree, Stand, Site	1.804	0.385	0.834	0.207
Tree, Stand	1.802	0.365	0.864	0.205
Tree	1.798	0.391	0.851	0.198

can eliminate lower branches through tree self-pruning and have been noted to result in increased leader elongation and height growth in juvenile plantations ("crossover effect" – Scott et al., 1998). However, as noted by Gartner and Johnson (2006), rapid leader growth may ultimately result in higher occurrence of sinuosity, or "speed wobble". While the data reported here suggest greater sinuosity with tree height and diameter, sinuosity appeared to decline with increases in stand basal area. While a causal mechanism remains elusive, lower initial inter-tree spacing at planting may provide an attractive solution to capture stand growing space, enhance early growth performance, and minimize sinuosity.

Soil nutrient availability and local environmental factors have long been recognized as influential to stem sinuosity across several commercial conifer species. Both Ca and N can be limiting to tree cell growth and maintenance (Kozlowski and Pallardy, 1996), yet nutrient amendments through fertilization have mixed results. In juvenile *Pinus taeda* forests of the SE region of the U.S., additions of N without Ca have been found to increase sinuosity (Espinoza et al., 2012). Hopmans et al. (1995) applied urea and sodium nitrate to young *Pinus radiata* stands of SE Australia and found no effect on stem sinuosity and deformity. Likewise, Littke and Zabowski (2007) tested the addition of Ca in form of gypsum and lime to young Douglas-fir PNW plantations but failed to detect a decrease in sinuosity over the 1-year study period. Results from the work of Dwivedi et al. (2019) on a subset of the installations reported here show that foliar N and Ca can be significantly greater in the high gain seed sources. This could suggest improved nutrient uptake capacity/use efficiency/translocation, which could partially explain the comparatively low sinuosity occurrence and severity in the medium and high gain genetic seed sources, yet the direct mechanisms remain speculative.

As physical samples of soil chemistry data were only collected for a subset of the installations in the Type IV network, (Dwivedi et al., 2019), they were not included in this study. It is reasonable to expect that the addition of measured soil variables would improve overall model performance and predictive ability. Yet, given that soil characteristics are driven in part by climate and topography (Jenny, 1941), the use of open-access remote sensing data (e.g., digital terrain models and high spatial resolution climatic records), coupled with existing publicly available forest soils data, can be an attractive solution when field sampling opportunities are limited. The effect of soil C and depth of the soil A horizon on sinuosity detected here may reflect an underlying influence of soil organic matter on root architecture and, subsequently, aboveground growth form. As noted by Gatch et al. (1999) and Harrington et al. (1999) in the Southeastern U.S., bent taproots of juvenile *Pinus taeda*, caused by either poor planting quality or impenetrable soil hardpan layers, was consistently related to stem sinuosity. While the mapping products by the NRCS can be utilized for testing as reviewed here, future efforts to generate high resolution digital soil maps could increase predictive model quality and serve a variety of additional applications.

The decrease of sinuosity count with concomitant gains in windspeed was unanticipated, as greater windspeeds would presumably increase formation of compression wood in the leader as reported by Turvey et al. (1993) in *Pinus radiata* stands of Australia. However, as noted by Jacobs (1954) and Campbell (1965) in *Pinus radiata* and Douglas-fir, respectively, stem movements caused by wind can result in a shift of carbohydrate allocation to diameter growth along upper sections of the stem at the expense of leader extension. In turn, this could result in less taper along internodal sections of the stem and greater recoverable volume at rotation. As illustrated by the Global Wind Atlas tool (Appendix 1), mean windspeed is highly variable across the region and is strongly influenced by topography, where windspeeds increase with gains in elevation. Coincidentally, forest research installations are commonly situated in lowlands and river valleys for ease of access (Bruce, 1977). Upon review, the Type IV installations may be limited in covering the range of windspeeds and located in areas with the increased susceptibility to sinuosity. Given the trends reported here, more work on the influences of windspeed and environmental variables on Douglas-fir stem form is warranted. It should be noted that the original sampling design of the Type IV did not intend to provide a full coverage of environmental variables that are influential to Douglas-fir stem form.

The results from this work represent only a single measurement in time, and there is conjecture regarding the long-term effects of sinuosity in young plantations on volume recovery at rotation (40 years), and whether stems can “grow out of” the sinuosity phase with incremental radial growth. Both Temel and Adams (2000) and Spicer et al. (2000) observed that Douglas-fir with high sinuosity scores at age 12 were more likely to be sinuous in following years due to greater amounts of compression wood near the pith and developed more slope of grain defect, resulting in a 15% loss in log volume. To corroborate these trends, future measurements in the Type IV should follow-up with sinuosity scoring across all trees and conduct wood quality sampling to quantify potential long-term losses in harvestable volume.

5. Conclusion

The collective findings suggest that genetic improvement, density management, and local growing conditions can influence Douglas-fir sinuosity occurrence and severity. Unimproved, wild seed sources exhibited consistently greater occurrences and severity of sinuosity when compared with medium and high gain families. The continued use of open-source physio-climatic datasets, public soil survey data, and field measurements can prove useful when testing the influence of abiotic conditions on stem form and species-site interactions. Future efforts to capture the influence of site and climatic conditions of stem sinuosity and defects could utilize continuous forest inventory programs with georeferenced plot locations and/or tracking of seedling planting quality across out-planting conditions to assess root form on aboveground stem quality.

CRediT authorship contribution statement

Michael Premer: Conceptualization, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Eric Turnblom**: Data curation, Resources, Validation, Writing – review & editing. **Aaron Weiskittel**: Resources, Validation, Writing – review & editing.

Declaration of Competing Interest

The authors declare no competing interests in the generation of this work.

Data availability

The authors do not have permission to share data.

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Appendix A. Site variables across experimental installations of the SMC Type IV Experimental Network

	601	602	603	604	605	606
DBH (cm.)	5.04 (1.36)	3.84 (1.57)	3.75 (1.78)	4.06 (1.98)	3.04 (2.04)	2.67 (2.1)
Height (m)	4.17 (0.88)	3.38 (1.02)	3.38 (1.27)	3.49 (1.39)	2.8 (1.63)	2.45 (1.68)
Sinuosity	1.8 (2.14)	1.37 (2.17)	1.52 (2.26)	0.7 (2)	0.28 (1.41)	0.12 (0.91)
Elevation (m)	201.05 (1.14)	108.31 (17.08)	55.21 (0.5)	119.19 (11.1)	220.03 (12.96)	190.56 (2.05)
Topo. Roughness Index	0.52 (0.26)	3.21 (0.64)	0.09 (0.1)	3.02 (0.66)	3.83 (1.02)	0.88 (0.5)
Topo Position Index	0.09 (0.1)	0.03 (0.75)	-0.02 (0.07)	0.44 (0.51)	0.51 (0.34)	-0.03 (0.35)
Roughness	1.68 (0.8)	10.06 (1.78)	0.33 (0.3)	9.46 (2.35)	12.44 (3.09)	3.14 (1.73)
Slope (%)	1.41 (0.73)	8.67 (1.87)	0.26 (0.27)	8.21 (1.96)	10.59 (2.78)	2.42 (1.37)
Aspect	263.46 (78.11)	168.75 (21.4)	194.67 (53.74)	120.69 (137.6)	186.99 (49.9)	69.96 (22.39)
McNab’s Index	0.01 (0.01)	-0.05 (0.02)	0 (0)	0.05 (0.04)	-0.03 (0.06)	-0.01 (0.01)
Bolstad’s Index	0.02 (0.02)	0.01 (0.19)	-0.01 (0.02)	0.11 (0.13)	0.12 (0.08)	-0.01 (0.09)
Planform Curvature	241.81 (535.95)	326.88 (303.02)	-670.21 (2323.71)	495.41 (733.29)	250.03 (347.57)	-246.94 (1384.67)
PPT (cm)	3292.98 (8.21)	2376.57 (15.75)	2649.83 (5.93)	2203.95 (6.03)	2206.14 (2.34)	3487.34 (8.77)
Minimum Temperature (Celsius)	5.12 (0.01)	4.91 (0.03)	5.53 (0)	5.03 (0.01)	5.14 (0.01)	4.98 (0)
Mean temperature (Celsius)	9.5 (0.01)	9.61 (0.04)	10.18 (0)	10.05 (0.01)	9.95 (0.01)	9.58 (0.01)

(*continued on next page*)

(*continued*)

	601	602	603	604	605	606
Maximum Temperature (Celsius)	13.88 (0.02)	14.31 (0.06)	14.83 (0)	15.07 (0.03)	14.76 (0.02)	14.18 (0.02)
Solar insolation (kW h m^{-2})	5189.91 (303.04)	4795.47 (2416.96)	4780.77 (65.42)	7050.71 (523.97)	4426.92 (395.52)	4922.93 (426.19)
Dew Point	5.77 (0.01)	5.85 (0.01)	6.23 (0)	5.92 (0.01)	5.93 (0)	5.65 (0)
Max VPD	7.34 (0.01)	8.04 (0.02)	7.99 (0)	8.29 (0)	8.58 (0.01)	7.62 (0.01)
MIN VPD	0.39 (0)	0.39 (0)	0.3 (0)	0.41 (0)	0.41 (0)	0.4 (0)
Soil Depth	89.96 (2.92)	100.94 (9.63)	49.1 (29.33)	119.29 (3.24)	103.44 (2.5)	99.45 (6.11)
% Clay A horizon	7.9 (0.34)	9.19 (0.42)	7.63 (4.5)	9.94 (0.71)	10.43 (0.63)	7.9 (0.41)
A horizon thickness (cm.)	6.63 (0.54)	9.89 (0.93)	11.55 (7.16)	13.45 (0.97)	13.04 (1.61)	8.16 (1.25)
Base saturation	1.8 (0.19)	3.55 (0.17)	0.87 (0.53)	4.93 (0.72)	5.49 (0.59)	1.9 (0.24)
% Clay in B horizon	12.01 (0.51)	14.21 (0.87)	5.02 (3.05)	17.84 (0.86)	17.83 (0.65)	11.05 (0.63)
B horizon thickness (cm.)	31.21 (2.15)	40.06 (4.74)	20.47 (12.32)	48.85 (2.48)	41 (3.33)	41.63 (4.45)
Carbon (Mg ha)	19.96 (0.88)	19.39 (1.84)	14.85 (8.7)	19.65 (0.82)	16.26 (0.78)	19.35 (0.52)
Exchangeable Ca (Mg ha)	0.65 (0.05)	0.76 (0.15)	0.91 (0.54)	0.86 (0.09)	1.2 (0.13)	0.64 (0.04)
Cation Exchange capacity (cmol$_c$ kg)	35.66 (1.41)	37.01 (1.52)	24.22 (14.32)	36.32 (1.99)	35.28 (1.3)	37.1 (2.21)
Carbon:Nitrogen	17.51 (0.21)	17.85 (0.38)	11.5 (6.74)	16.36 (0.3)	16.28 (0.31)	16.46 (0.2)
Exchangeable K (Mg ha^{-1})	0.08 (0.01)	0.14 (0.02)	0.09 (0.05)	0.15 (0.02)	0.19 (0.01)	0.08 (0.01)
Soil water capacity (mm m^{2})	102.28 (5.48)	160.6 (15.79)	43.12 (25.42)	85.81 (4.37)	105.21 (7.48)	81.28 (4.35)
Exchangeable Magnesium (Mg ha^{-1})	0.3 (0.02)	0.51 (0.06)	0.29 (0.17)	0.61 (0.08)	0.55 (0.07)	0.28 (0.02)
Nitrogen (Mg ha^{-1})	0.9 (0.04)	0.97 (0.05)	1.17 (0.7)	0.97 (0.06)	0.93 (0.05)	0.83 (0.04)
pH	4.8 (0.05)	4.77 (0.03)	3.27 (1.91)	4.74 (0.12)	4.82 (0.05)	4.77 (0.05)
Exchangeable Na (Mg ha^{-1})	0.07 (0)	0.08 (0.01)	0.03 (0.02)	0.08 (0.01)	0.07 (0)	0.06 (0.01)
Windspeed (meters per second)	3.04 (0.07)	2.23 (0.3)	2.04 (0.04)	3.42 (0.1)	3.1 (0.22)	1.89 (0.14)
Relative Density (%)	8.15 (3.27)	5.24 (1.92)	5.64 (2.36)	7.21 (3.22)	4.65 (1.8)	4.38 (1.69)
Height:Diameter	7.01 (1.77)	7.5 (2.81)	7.46 (3.45)	6.99 (3.57)	6.56 (4.24)	6.09 (4.86)
Quadratic mean diameter (cm)	5.22 (0.25)	4.14 (0.31)	4.13 (0.43)	4.51 (0.32)	3.62 (0.54)	3.37 (0.43)
Basal area (m2 ha^{-1})	2.67 (1.05)	1.53 (0.55)	1.65 (0.71)	2.22 (1.03)	1.28 (0.52)	1.16 (0.45)

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