

Silvicultural implications from analyzing light induced height growth development of eight North American juvenile tree species in mixed-conifer forests

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Modern silviculture is based on simulating natural disturbance regimes on the one side and reducing their impact on the other side. Disturbances modify light regimes of forests along complex spatial patterns, and species participating in the ecosystem tend to have unique adaptations to the multitude of light conditions found in forests. We studied the height growth reaction of saplings from eight native North American tree species to different light availabilities in a Sierra Nevada mixed conifer forest. Large height growth differences occurred between species. Height growth increased for most species with increasing light availability. However, black oak but also incense cedar and tanoak reached an optimal value or saturation point of light availability at intermediate light levels, above which their growth stayed the same or slightly declined on average. A variety of stand conditions, representing the range from early to late successional stages, are beneficial to maintain tree species diversity across stands. Such a gradient of conditions can be achieved by diversifying silvicultural regimes and using regeneration approaches that mimic a range of disturbance intensities. The results add to knowledge on the species' ecology by specifying their height growth in dependence of a quantified light environment. The quantification of the light environment can directly be linked to % canopy cover and a range of regeneration methods, respectively. With this, the results may help achieve a more precise and target-oriented management of Sierra Nevada mixed conifer forests.

Introduction

The natural disturbance regimes of western forests in North America display great variation in time and space, resulting in a complex of mixed-severity disturbance effects on vegetation structure (Oliver and Larson, 1996). Disturbances caused by fire, insects, and disease result in the mortality of single trees, smaller groups of trees, whole forest stands, and even watersheds (Stephens et al., 2018). As a consequence, the understory light regime of these forests are highly variable, and tree species show different adaptations and capabilities to establish and grow under a wide range of disturbance intensities (Pickett and White, 1986).

A key component of an ecosystem-based management approach (e.g. Grumbine, 1994; Coates and Burton, 1997; Kuuluvainen, 2009; North et al., 2009) is the recognition of such disturbances as ecosystem-inherent processes, which are to be accounted for in 'close-to-nature' forest management decisions (Messier et al., 2013). This accounting can come from applying silvicultural approaches that as much as possible approximate the natural disturbance regime in time, space, and intensity

(e.g. through creating competition and light environments in the understory to which species are adapted). By using the natural disturbance regime as a guide, the desired outcome is to create a high variety of forest structures, species compositions, as well as microclimatic conditions and light regimes (e.g. Reilly and Spies, 2015; Stiers et al., 2018; Ehbrecht et al., 2019). In forests with mixed severity disturbances, such an approach requires a high diversity of silvicultural methods. Instead of assuming that one silvicultural system is best adapted to a certain forest, a disturbance regime-guided approach in mixed severity forests would likely incorporate a variety of basic silvicultural systems.

Next to the soil and climatic conditions, a strong driver for the individual growth performance of trees in the understory is local light availability (e.g. Pacala et al., 1994; Claveau et al., 2002; Ammer, 2003; Ammer et al., 2008). Basically, every disturbance changes the light regime at the forest floor (Bigelow et al., 2011) and hence the resource availability for tree regeneration. However, in view of light availability, species requirements follow an optimal curve, meaning that more light does not necessarily improve every species performance (e.g. Annighöfer,

2018) and individual responses of species will vary (e.g. Canham, 1988; Belair *et al.*, 2018).

Differing requirements to regenerate and grow also characterize species associated with mixed-conifer forests in the western parts of North America (Burns and Honkala, 1990). In addition to affecting absolute growth (e.g. height and diameter growth), light availability also affects allocation patterns within plants (Hofman and Ammer, 2008; Annighöfer *et al.*, 2017), i.e. under light limitation, growth ratios shift (Lüpke, 2004). Hence, light availability finally also affects, for example, height-diameter ratios (H/D) and the resulting individual plant stability (Wonn and O'Hara, 2001).

This study evaluates height growth performance of eight North American tree species occurring across light gradients in the Sierra Nevada mixed conifer forest for one full vegetation period. The high diversity of light regimes in the study area, as a result of applying various silvicultural treatments, is rare to this region, as landowners generally tend to use either one method or another (i.e. clear-cut or single tree selection). Deepening the understanding of co-occurring species' growth requirements should increase the success of management efforts that seek to emulate natural disturbances that create favorable conditions considering species-specific growth requirements (e.g. Walker *et al.*, 2012). Efficient new measuring techniques, as applied here, now allow re-assessing and specifically quantifying relative light requirements of co-existing species.

The hypotheses of this study are directed towards the effect of light environment on sapling dimensions and biomass allocations (H1) as well as the effect of light environment on height growth (H2). The specific hypotheses of this study were:

H1.1: Root-collar diameter is a significant predictor for sapling height.

H1.2: Height-diameter ratios significantly differ between broadleaved and conifer species.

H1.3: Height-diameter ratios generally decrease with increasing light availability.

H2.1: Light availability significantly affects absolute height growth.

H2.2: Differences in light requirements result in significant height growth differences between species along the light gradient.

H2.3: Within species height growth increases with increasing light availability.

Methods

Study area

The study was conducted in mixed-conifer forests with single broadleaf individuals at Blodgett Forest (38°540 N, 120°390 W), near Georgetown, California, in the northern Sierra Nevada. Blodgett Forest is a research forest of the University of California, USA. The study sites were located at about 1200 to 1500 m a.s.l. The climate of the area is a hot dry-summer Mediterranean climate (Csa, Köppen climate classification) with an average precipitation of about 1600 mm year⁻¹, falling mainly between September and May. Summer temperatures range from 14°C to 27°C and winter temperatures from 0°C to 9°C. The soils are very deep and well drained. The soils are considered productive conifer Californian forest sites and classified as Holland, Piliken-variant and Musick soils (USDA Soil Series Description), derived from granodiorite parent materials (Dore *et al.*, 2016). Conifers grow heights of up to 70 m and more on

these soils. Since Blodgett forest is a research forest, stands within the different compartments at Blodgett forest are managed using a wide variety of silvicultural practices. Due to alternating management strategies, this results in a wide range of light availabilities in the understory.

Study sites

Data were collected in three compartments at Blodgett forest, namely 240 (38.906 °N, 120.667 °W), 270 (38.903 °N, 120.659 °W), and 420 (38.893 °N, 120.642 °W). Naturally regenerated saplings were sampled on unmanaged control sites that have been undisturbed for over 20 years (Blodgett Forest, in compartment 240). This compartment has a size of 13 ha. To expand the light gradient, saplings of comparable age range (5 – 10 years for naturally regenerated saplings) were also sampled that had been planted in compartments with clear-felled areas and group selections with retention (Blodgett Forest, in compartments 270 and 420). The compartment 270 has a size of 27 ha, the compartment 420 of 18 ha. Clear-felled areas were discrete canopy openings, ranging from 0.1 to 0.5 ha in size. This canopy opening is large enough to maximize full sunlight availability (York *et al.*, 2004). Group selections with retention were created at the same time as the clear-felled sites. Trees retained included all trees with dbh greater than 76 cm. Harvesting and planting activities date back to 2013. Climatic and soil conditions can be considered constant throughout the sampling locations, demonstrated by a uniform productivity across Blodgett Forest. The overstory on the control units mainly consists of incense-cedar (*Calocedrus decurrens* (Torr.) Florin), ponderosa pine (*Pinus ponderosa* P. Lawson & C. Lawson), sugar pine (*Pinus lambertiana* Dougl.), and white fir (*Abies concolor* (Gord. et Glend.) Lindl. ex Hildebr.) with fewer Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), and single individuals of California black oak (*Quercus kelloggii* Newb.) and tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) Rehder).

Data collection

All data were collected in the first weeks of July 2018. For naturally regenerated stands in the compartment 240, data were collected along transect lines through the stands, respectively, which were North-South oriented and spaced at about 20 m from one another. Starting point of the first transect line was randomly placed along the southern border of compartment 240. All other transect lines were systematically placed relative to the first. This resulted in a total of 30 transect lines, with an average length of about 250 m in North-South direction. Transects were chosen to assure sampling objectivity and covering a variety of stand situations. Saplings within 1 m to both sides of the transect line were sampled, if they fulfilled the selection criteria (comp. below). Whenever the transect line intersected with a group of naturally regenerated saplings ($n \leq 5$ per species), all saplings were measured. For groups consisting of more individuals ($n > 5$), also up to five individuals per species were measured. The individuals chosen per species were then the ones that dominated the group in terms of height. The clearing and group selection with retention sites were artificially regenerated. On these sites, saplings were recorded by following the planting rows. More details on the planting sites can be found in York *et al.* (2004). This study focused on eight species, which were California black oak, incense-cedar, Douglas-fir, ponderosa pine, sugar pine, giant sequoia (*Sequoiadendron giganteum* (Lindl.) J.Buchholz), tanoak, and white fir (Table 1). Main criteria for selection was that the individual sapling was vital (free of apparent damage) and in the age range of 5 to 10 years (counting internodes) to assure comparability. In tree and also other plant species, biomass allocation and plant growth are strongly affected by ontogeny but also size (Coleman *et al.*, 1994; Poorter *et al.*, 2012), which we both tried to control for as far as possible in the field (comp. dimensions presented in Table 1). For each sapling, root-collar diameter (measured with a

Table 1 Overview and summary of recorded species and their dimensions; n = number of observations; minimum, maximum and mean (in brackets) values shown for RCD = root-collar diameter (cm) and H = height (cm).

Species	n	RCD (cm)			H (cm)		
Black oak	75	0.40	05.02	(2.19)	38	524	(205)
Douglas-fir	102	0.83	07.58	(3.02)	48	408	(157)
Giant sequoia	70	0.90	12.02	(5.84)	46	426	(199)
Incense-cedar	96	0.91	08.81	(3.85)	59	322	(162)
Ponderosa pine	69	0.92	12.24	(4.33)	52	456	(175)
Sugar pine	109	1.02	08.00	(3.21)	49	400	(153)
Tanoak	31	1.34	07.29	(3.20)	106	306	(212)
White fir	147	0.80	07.58	(2.67)	49	373	(137)

caliper 5 cm above ground) and total height (measured with a tape measure or meter stick) were recorded. From these measurements the height-diameter ratios (H/D) were calculated. Additionally, the full height growth for 2017 was measured. Annual height growth for 2017 was measured as distance between the two consecutive annual internodes. Internodes could be visually identified with high precision for all species, aside of incense-cedar. Therefore, the results for this species must be considered with caution, because transition zones for this species are not as pronounced. Measurements for incense-cedar were conducted where coloring contrasts suggested an annual internode. A total of 699 saplings were measured, most of which were white firs ($n = 147$), followed by sugar pines ($n = 109$). The fewest individuals were recorded for tanoak ($n = 31$) (Table 1). The root-collar diameter ranged from 0.40 – 12.24 cm and the height from 38 – 524 cm, with 534 individuals larger than 100 cm (Table 1).

At each sampling location, the light environment was measured using an automated measuring device equipped with a fisheye lens (Solariscope, Behling SOL300), which calculates values for indirect site factor (ISF), direct site factor (DSF), total site factor (TSF), openness (opn), gap fraction (GapF), and leaf area index (LAI) by analyzing hemispherical photographs according to seven threshold values (Pryor 2010). For single saplings, all Solariscope measurements were conducted directly above the highest point of the sapling. For sapling groups, the Solariscope measurements were conducted in the center of the regeneration group, at the height of the highest sapling. This was possible up to a height of 2.5 m. Recorded saplings above 2.5 m were bent to the side as far as possible and light was measured at 2.5 m height. The results of this study are based on the ISF as measure of the light environment for each sapling. The ISF stands for the proportion of indirect or diffuse radiation reaching the measurement point and is considered as standard measure for the light availability in the understory (Annighöfer, 2018). Furthermore, the ISF is strongly correlated with many of the other variables describing the light environment (Supplementary data 1). However, since some species react sensitively to sun flecks, especially under low light levels (Chazdon and Percy, 1991), and because LAI is a measure often found in scientific literature (e.g Barr et al., 2004; Jonckheere et al., 2004; Wang et al., 2005), results for the LAI can be found in the appendix (Supplementary data 2). The LAI is the ratio of the summed one-sided leaf surface area of all leaves above a defined area, to the same area. We also included GapF, which is the fraction of uncovered 'gaps' in a circular solid angle section around the zenith (Supplementary data 2). The angle was set to 60°, in reference to the search cone method (Pretzsch, 1995; Pretzsch et al., 2002). Unlike direct field measurements, model assumptions to calculate LAI from fisheye images only allow a broad classification, which is why LAI values from fisheye images should be compared to field measurements with caution (Behling, 2015).

Data analysis

To model the diameter-height relationships we fit a 2nd order polynomial linear model passing through the origin ($0/0$) of the type $f(x) = 0 + a_1x + a_2x^2$. Polynomials were expected to be appropriate to model the relationship between diameter and height for saplings.

Mean group comparisons of growth ratios with $\mu = 0$ were conducted with a one sample t-test and normal distributions of the data were tested with Shapiro-Wilk normality test. For data not normally distributed a Wilcoxon Rank Sum test (Mann-Whitney U test) was applied.

To analyze the relationship between the height growth as response (y) and the light availability as explanatory (x) variable, non-linear Generalized Additive Modeling (GAM) techniques were applied (Wood, 2017). One advantage of these techniques is that the relationship between response and explanatory variable is not required to be specified in advance (Otto et al., 2014). This allows an unbiased detection of trends in the data themselves, here as induced by light availability. The effective degrees of freedom (EDF) were limited to a maximum of 3 (number of knots = 4), to avoid over-fitting the data. The amount of smoothing was chosen automatically through generalized cross-validation (Ciannelli et al., 2004). The data family was set to Gaussian type with an identity-link function (Wood, 2011). Model evaluation occurred through interpreting the parametric estimate for intercept. As the splines of the models are centered at zero, the intercept measures the overall mean of the height growth. Furthermore, the EDF value as complexity of smoothing function (values of 1 indicate linearity) was evaluated. P-values show the statistical significance of the intercept, as difference to zero and of the explanatory to the response variable, tested by F -test. Both, explained deviance ($DE = 1 - (\text{residual deviance} / \text{null deviance})$) and adjusted R^2 (Adj. R^2) as robust measure against over-fitted models were also extracted from the GAM models.

Growth comparisons between species and different levels of light availability were conducted with analysis of variance models, with growth values for each class assumed to stem from a normal distribution, verifying homoscedasticity with the Bartlett test. As post-hoc analysis for pairwise comparisons between the species and the different light levels Tukey's HSD (honestly significant difference) test was applied.

The significance level for this study was $P < 0.05$. All statistical analyses, model fitting, and graphs were processed using the free software environment R, version 3.4.0 (R Core Team, 2017).

Results

Diameter and height relationships for different species

The root-collar diameter to height relationships revealed a very close regression for each species (Figure 1) and were generally well described using a 2nd order polynomial linear model, with R^2 values all above 0.94 (Table 2). For black oak and sugar pine, the second parameter estimate (a_2) was not significantly different from zero, indicating a non-polynomial relationship ($y = 0 + a_1x$) between root-collar diameter and height for the data range considered (Table 2).

From the root-collar and height measurements we calculated the H/D ratio as stability indicator. Both broadleaf species (black oak, tanoak) had the highest H/D ratios on average with 97.6 and 70.8, respectively. These H/D ratios were significantly higher than the ratios of the conifers ($P < 0.001$). The conifer species all had H/D ratios around 50, with Douglas-fir reaching the highest value of 54.2 and giant sequoia the lowest with 38.1. Both firs had higher average values than pines, and pines were higher than incense-cedar and giant sequoia. So generally, the broadleaf species were thinner than the conifer species at

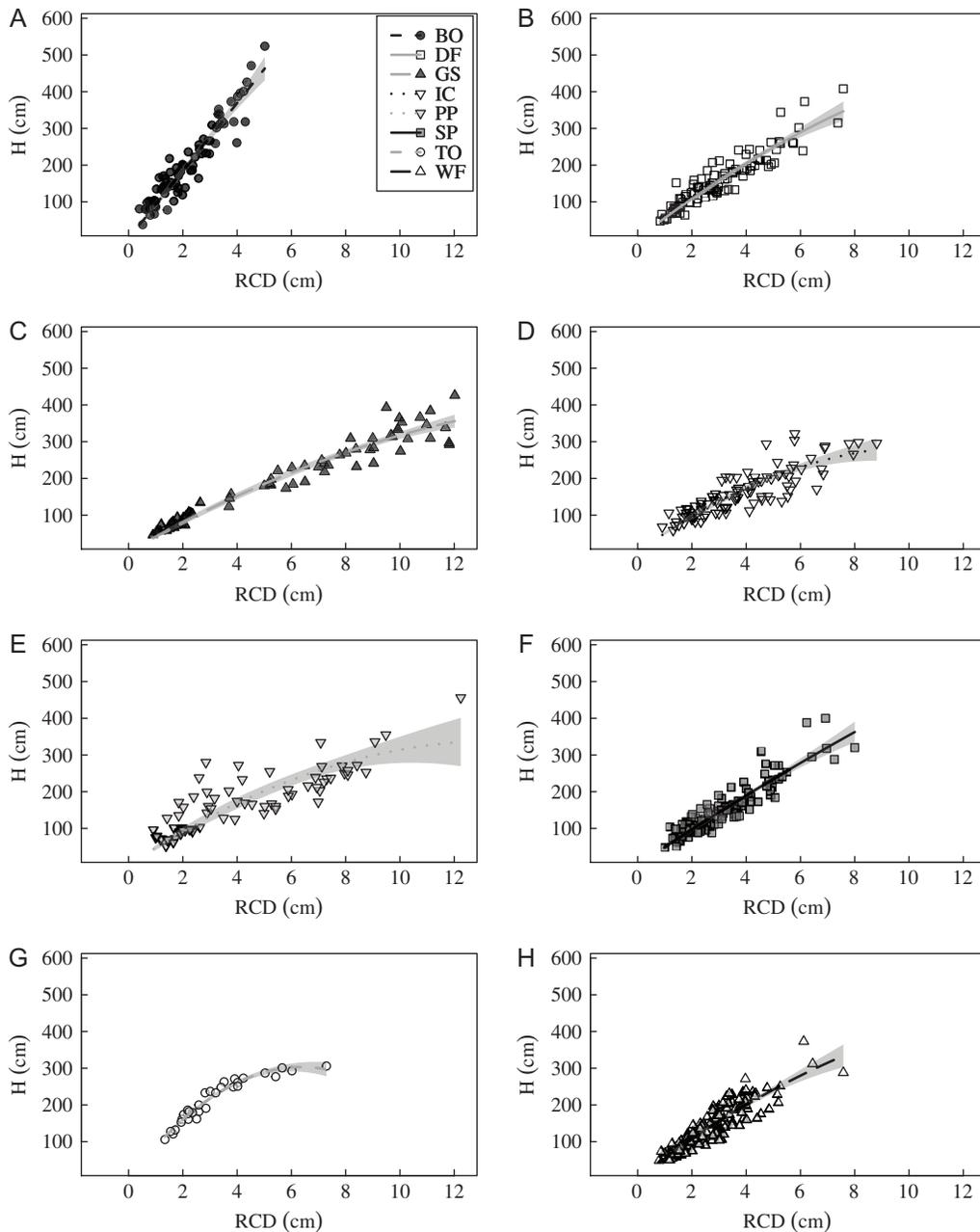


Figure 1 Diameter (RCD, cm) to height (H, cm) relationships for the different sapling species considered, with BO = black oak (A), DF = Douglas-fir (B), GS = giant sequoia (C), IC = incense-cedar (D), PP = ponderosa pine (E), SP = sugar pine (F), TO = Tanoak (G), WF = white fir (H). Shaded gray band shows the 95 per cent confidence interval.

the same height. When aggregating all species within each light class (ISF_{class}), the H/D ratio significantly decreased along the light gradient (Figure 2).

Light dependent height growth

Height growth patterns for different levels of light availability were compared for the completed growth period of 2017 to exclude effects of incomplete growth in 2018. Under the

premise of not significantly changed light availabilities between the years 2017 and 2018, significant differences within the growth patterns of the species were detected (Figure 3).

Ignoring giant sequoia (GS), the GAM models show two distinct species groupings of growth response trends: a more or less steady increase of height growth with increasing light availability for ponderosa pine, Douglas-fir, sugar pine, white fir (in decreasing order of maximal height growth), and an almost flat or slightly humped (meaning declining above a certain light level) height growth for black oak, tanoak, and incense-cedar

Table 2 Parameter estimates (a_1 , a_2) for the polynomial functions of the diameter-height relationships with significance of the parameter estimates and R^2 for the different sapling species considered. Relationships modeled as 2nd degree polynomial function, forced through the origin (0/0).

Species	a_1	$p(a_1)$	a_2	$p(a_2)$	R^2
Black oak	92.219	<0.001	0.008	0.996	0.98
Douglas-fir	57.409	<0.001	-1.537	0.003	0.98
Giant sequoia	42.240	<0.001	-1.051	<0.001	0.99
Incense-cedar	52.996	<0.001	-2.426	<0.001	0.96
Ponderosa pine	49.325	<0.001	-1.792	<0.001	0.94
Sugar pine	49.528	<0.001	-0.528	0.251	0.97
Tanoak	94.887	<0.001	-7.426	<0.001	0.99
White fir	56.633	<0.001	-1.665	0.001	0.97

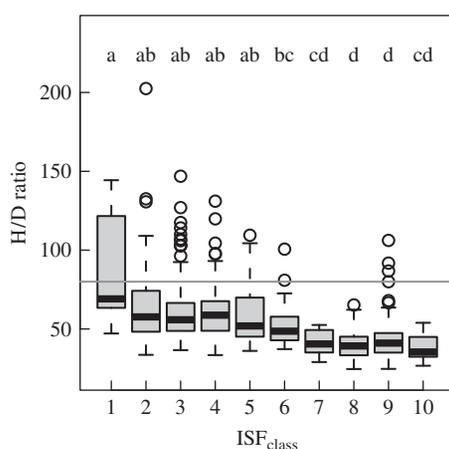


Figure 2 Height-diameter ratios (H/D ratio) for all saplings along the light gradient (ISF_{class}), with 1 = (0, 10], 2 = (10, 20]... 10 = (90, 100] % indirect site factor. Boxes sharing a letter are not significantly different at the 5 per cent level. Horizontal line makes an H/D ratio of 80, which is considered to be a threshold for stability.

along the gradient of light availability (Figure 3). For Douglas-fir and white fir, the GAM models even suggest a linear increase (EDF = 1, comp. Table 3). For black oak, incense-cedar, and tanoak the ISF values for the maximal height growths derived from the GAM models are 54.7 per cent (LG₂₀₁₇ = 28.9 cm), 64.1 per cent (LG₂₀₁₇ = 23.6 cm), and 46.6 per cent (LG₂₀₁₇ = 23.2 cm), respectively (comp. Figure 4 for estimation of % canopy cover). Giant sequoia height growth increased most steeply at first and then leveled off to an asymptote at highest light availabilities (Figure 3C). Also, no naturally regenerated or planted giant sequoia saplings were found below an ISF value of 39 per cent. The ISF significantly affected all species (p -value significant for all EDF values, comp. Table 3, differences among light classes within species, Table 4). The amount of deviance explained exceeded 50 per cent for the two pine species, whereas the lowest amount of explained deviance was found for incense-cedar (34.5 per cent). No significant difference was found between species for the light levels ranging from 0.5 ≤

0.6 and 0.6 ≤ 0.7 (Table 4), whereas no plots were recorded with ISF values ranging from 0.57 – 0.68 (comp. Figure 3).

Discussion

The diameter to height relationships showed considerable inter-specific variation. The morphological traits of black oak especially stand out, with individuals being much taller for a given diameter than the other species. However, the relationships for some of the conifers (e.g. Ponderosa pine and giant sequoia) suggest that it might be possible to model the allometry of morphologically more similar tree species with less equations than there are species (comp. O'Brien *et al.*, 1995). The close diameter-height regressions and high R^2 values of the models suggest that the efficiency of field measurements can be increased by refraining from the more time-consuming diameter measurements and using models to predict the diameter for juvenile tree species from height. The opposite is true for mature trees, where diameter measurements are widely used as predictors for tree heights (e.g. Temesgen and Gadaw, 2004). However, the inter-specific variation and the general lack of equations for juvenile tree species suggests the need for continued expansion of models to predict diameter, height and also biomass allometries for juvenile trees (Annighöfer *et al.*, 2016). These results have confirmed the first hypothesis (H1.1), namely that the diameter is a significant predictor of juvenile tree height.

The significantly higher height-diameter (H/D) ratios for the broadleaf species also confirm the second hypothesis (H1.2). The higher H/D ratios for the black oak and tanoak suggest a reduced allocation to diameter growth compared to the conifer species in a juvenile stage, which is in line with conventional descriptions of hardwoods (e.g. Burns and Honkala (1990)). The highest average H/D values (>95) found for black oak suggest a possible pronounced vulnerability when exposed to strong winds or snow pressure (Röhrig *et al.*, 2006). York and DeVries (2013) were able to show this for about 30 year old stands in the study area, in which the stem-snapping frequency of black oak was significantly higher compared to conifer species, following a winter with high snow-fall. So even though black oak sheds its leaves during the winter season and hence reduces snow pressure, it is more vulnerable than the conifer species. On the other hand, black oak, but also tanoak, are able to resprout, so a snapped stem is not necessarily mortal for species that are able to resprout, compared to the conifer species considered here. The reduced biomass allocation towards secondary diameter growth and hence higher H/D ratios could be characteristic for the juvenile stage of tree species that are able to resprout. However, a higher H/D ratio could also be the characteristic response of a more shade intolerant species. Pooling all species together showed the expected decrease of the H/D ratio along the light gradient, indicating that a higher light availability generally allows a stronger allocation towards diameter growth as also found for other juvenile tree species (e.g. Annighöfer, 2018). These results confirm the third hypothesis (H1.3), stating that the H/D ratio generally decreases with increasing light availability across all species.

As expected, light availability significantly affected height growth (H2.1). The relationships between light and height

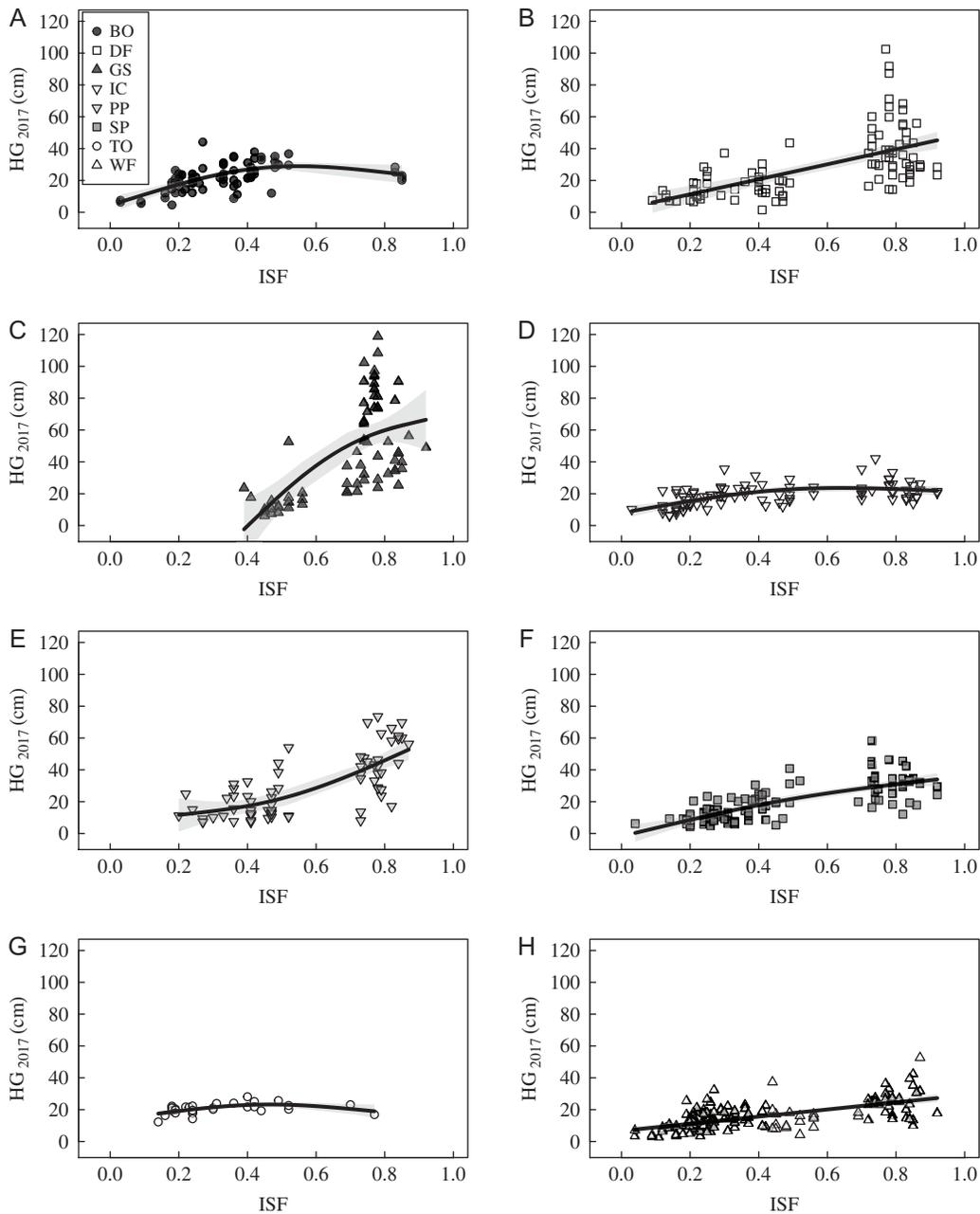


Figure 3 Recorded height growth measurements for 2017 (HG_{2017}) of individual saplings in dependence of indirect site factor (ISF). Black solid lines show modeled GAM functions of height growth. Shaded gray band is an approximated 95 per cent point-wise confidence interval. Species are BO = black oak (A), DF = Douglas-fir (B), GS = giant sequoia (C), IC = incense-cedar (D), PP = ponderosa pine (E), SP = sugar pine (F), TO = Tanoak (G), WF = white fir (H).

growth revealed a pronounced interspecific difference for juvenile trees (comp. H2.2). General trends for the species are in line with their traditional classifications of shade tolerance (e.g. Baker, 1949; Burns and Honkala, 1990). More recently the concept of tolerance has been expanded, incorporating combinations of persistence (survival) (Snyder, 2010), growth (e.g. Pallardy and Kozlowski, 2008), and morphology or physiology (e.g. Hutchings and Kroon, 1994; Kitajima, 1994). Shade tolerance remains to be a more qualitative concept with different facets and uniform quantification is still pending. Against this

background, this study does not assign or verify shade-tolerance levels as found in the literature, but rather contributes to increasing the understanding of species-specific growth reactions to different light levels and silvicultural implications that might be derived from these.

The strongest reaction to increasing light availability by far was found for giant sequoia. It was not present in the study area at lower light levels (ISF < 35 per cent), but with light levels above about 55 per cent ISF, its height growth quickly exceeded that of most other species, slightly more than twofold. At

Table 3 Summary of the GAM models estimating height growth in 2017 from the indirect site factor, showing the parametric estimate for intercept (Intercept), its significance (p Intercept), the effective degrees of freedom for the GAM models (EDF), the significance of the smoothing term (p smooth), a pseudo R² estimate (Pseudo R²), and the proportion of the deviance explained by the GAM models (Dev.exp.).

Species	Intercept	p Intercept	EDF	p smooth	Pseudo R ²	Dev.exp.
Black oak	22.15	<0.001	1.963	<0.001	0.404	0.42
Douglas-fir	28.53	<0.001	1	<0.001	0.371	0.377
Giant sequoia	46.69	<0.001	1.645	<0.001	0.382	0.397
Incense-cedar	19.12	<0.001	1.919	<0.001	0.331	0.345
Ponderosa pine	29.42	<0.001	1.727	<0.001	0.526	0.538
Sugar pine	18.91	<0.001	1.679	<0.001	0.571	0.577
Tanoak	20.58	<0.001	1.912	0.0025	0.318	0.361
White fir	15.81	<0.001	1	<0.001	0.404	0.408

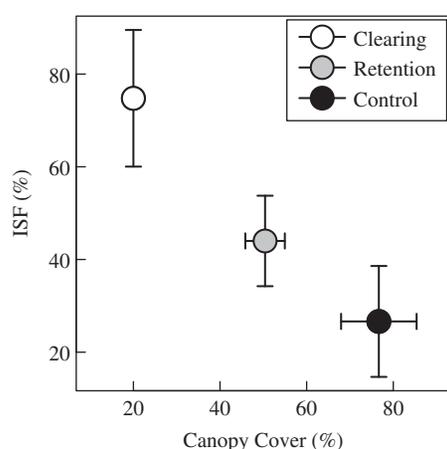


Figure 4 Mean values \pm SD of canopy cover (%) measurements from 2013 and 2016 compared to indirect site factor (ISF %) measurements from 2018, as reference for silviculturalists using canopy densities. Values need to be treated carefully, however, since they were recorded at different points in time, the measurement locations were close but not identical, and the number of observations differs ($n = 15$ for canopy cover, $n = 76$ for ISF). For ‘clearing’ there was only one canopy cover measure, which is why SD could only be calculated for ISF, not for canopy cover

around 70 per cent ISF the average increase in height growth became slightly more asymptotic, which is in line with previous findings from the study area by York *et al.* (2011) but also with other studies (e.g. Coates, 2000). The other two tree species showing relatively sensitive height growth responses to increasing light availability were Douglas-fir and ponderosa pine, reflecting an opportunistic behavior towards increasing light availability. This is not surprising, both species are considered to preference full sunlight for their growth (Burns and Honkala, 1990), even though Douglas-fir is classified to be intermediately shade tolerant (Minore, 1979) and contradictory findings can also be found in literature (Bigelow *et al.*, 2011). The height growth of sugar pine similarly increased along the light gradient, but not as pronounced as for the other mentioned species. This is in line with other publications that have found the early growth of sugar pine to be slow compared to other pines, although the species becomes one of the tallest trees after

giant sequoia in its native range (Burns and Honkala, 1990). White fir is commonly considered to be relatively shade-tolerant and a strong competitor in a shaded environment versus more light-demanding species (Harvey, 1980). As mentioned, shade tolerance does not necessarily mean that the species’ height growth does not benefit from increased light availability, as also stated by Kuhns and Rupp (2000). This was verified here, as white fir showed a positive trend towards light availability. Only the two broadleaf tree species (black oak, tanoak) and incense-cedar showed a different trend. Interestingly, the height growth of these three species also initially increased, reached a maximum average height growth at intermediate light levels of 40–60 per cent ISF and stayed stable or decreased slightly (black oak) on average beyond this point. Although shade tolerance of oak varies with age, it is most often classified as intolerant (Edwards, 1957). We found that black oak grew surprisingly well under lower light conditions, and a clear positive height growth reaction towards full sunlight was not found in this study. On the contrary, black oak outgrew all other species on average for light levels around 30–50 per cent ISF. Above these values, its height growth was smaller on average and it was especially surpassed by giant sequoia, ponderosa pine, and Douglas-fir. However, its high H/D ratios (comp. above), also at lower light levels, might indicate a lower shade tolerance, independent of the average height growths. For incense-cedar, the height growth trend we found is in line with its classification as a shade tolerant species, but not as an intermediate shade tolerant species as found in Arno (1973), and it even seemed to be at the low end of the tolerance scale. However, we could also not find that full sunlight generally favors height growth of this species (Burns and Honkala, 1990). However, the same authors also state that browsing pressure by deer might mask the species’ ability to respond to increased light and measuring height growth is not as precise for incense cedar, because internodes cannot be detected as well (comp. methods). Since incense-cedar was not protected from browsing in the research area and browsing is known to be heavy on incense-cedar, this could have impacted our results. Finally, differences in height growth along the light gradient were also not very pronounced for this species, compared to black oak. Even though a slightly humped shaped height growth could also be detected for tanoak, its ability to growth under a wide range of stand situations (Tappeiner *et al.*, 1986) manifests itself in height growth. Thus,

Table 4 Cross table of column-wise differences (small letters) of the height growth in 2017 between indirect site factor light levels (LL) (1 = (0, 10], 2 = (10, 20]... 10 = (90, 100] % indirect site factor) per species, and row-wise differences (capital letters) of the height growth in 2017 between the species (SP) within each light level. Cells per column sharing a letter are not significantly different at the 5 per cent level. Asterisk under species name shows significant differences within the species, asterisk next to light level shows significant differences between species; n.s. = non-significant.

SP/LL		Black oak	Douglas-fir	Giant sequoia	Incense-cedar	Ponderosa pine	Sugar pine	Tanoak	White fir
	ALL	*	*	*	*	*	*	*	*
1	*	a	ab		abc	ab	abc		a
		AB	AB		B		AB		A
2	*	ab	b		a	b	b	a	ab
		CD	AB		BD	ABC	A	C	AB
3	*	bc	b		c	b	bd	ab	ab
		D	AD		BD	ABC	A	CD	AC
4	*	bc	b	ac	bc	b	bc	b	b
		B	AB	AB	AB	AB	A	AB	A
5	*	c	b	a	ac	ab	c	ab	b
		B	A	A	AB	A	AB	AB	A
6	n.s.	c		ab	abc		bce	ab	ab
		A		A	A	A	A	A	A
7	n.s.			ab	bc		bce	ab	abc
				A	A		A	A	A
8	*		a	c	b	ac	e	ab	c
			B	A	BC	BC	BC	ABC	C
9	*	bc	a	bc	bc	c	ae		c
		AB	BC	CD	A	D	AB		AB
10	*		ab	ac	abc		cde		abc
			A	B	A		A		A

the differences in height growth were least pronounced for this species, according to the differences in light availability, respectively (average height growth values for tanoak were nearly the same for light levels around 10–20 per cent ISF and around 70–80 per cent ISF).

Based on these findings, this study confirms the fifth hypothesis (H2.2) that there are significant height growth differences within and between species at given light availabilities. However, a general height growth increase with increasing light availability (comp. H2.3) as well as clear threshold values of optimal growth performance could only be partially derived from the results and generally also might require repeated observations throughout several vegetation periods and differed by ontogeny. For height growth, the general rule of ‘the more light the better’ seems to be true for most species considered here (giant sequoia, Douglas-fir, ponderosa pine, sugar pine, and white fir). Only black oak, incense-cedar, and tanoak, however, had their maximal height growth values at intermediate light levels (40–60 per cent ISF). Under low light levels (10–20 per cent ISF) height growth of these three species was significantly higher than that of the other species occurring under similar light conditions (comp. Table 4). Against this background, the sixth and last hypothesis (H2.3) of the study assuming a within species increasing height growth with increasing light availability could not be confirmed for all species. The results also showed that the scatter within the data increased significantly for some species with increasing light availability. In forest stands, there could be different reasons for this related to other growth site factors, mainly

presumably water and temperature. The less limiting the light availability becomes, the stronger effects of interacting environmental factors become (Chapin *et al.*, 1987). These results generally support the idea that tolerance is a relative term and different species adapt differently to shade, (height) growth is only one measure of the multi-faceted adaption process of plants to their environment (Hutchings and Kroon, 1994). The results also emphasize the importance of precise management of the light regime in forests, to regulate mixture, abundance but also individual growth of species in view of the management objectives. For example, wildlife habitat value could be increased by creating light conditions amenable to recruitment of black oak, which produces acorns. Or by creating conditions for slow-growing incense-cedar, which supports the development of sooty mold (*Arthrobotryum spongiosum* Hoerl), which are required for overwintering song birds (Morrison *et al.*, 1989).

Conclusion and silvicultural implications

The results highlight the wide variety of individual evolutionary adaptations of these co-occurring species to different light conditions, possibly as an adaptive response to a complex, mixed severity disturbance regime. From a silvicultural perspective this opens up a variety of ways to make use of these adaptations to control species composition and sustain high species diversity. However, the results once again reiterate the necessity for management decisions adapted to the needs of each species, by not

emulating one disturbance pattern, but the variety of disturbances that can occur in forests of the northern Sierra Nevada.

The results for giant sequoia demonstrate the necessity of maintaining high light availability levels, not only for the initiation of seedling cohorts (e.g. York *et al.*, 2011), but also during establishment and recruitment phases to counteract the replacement of the giant sequoia by more shade tolerant species, like white fir or incense-cedar (comp. Harvey, 1980). Similar to giant sequoia, the results for ponderosa pine confirm the necessity of higher light levels in the understory, if the species is to be added or maintained in an existing stand. The concept of 'low-impact silviculture,' suggests mainly low levels of canopy disturbance would likely exclude ponderosa pine and definitely giant sequoia. Moderate levels of light availability (30–40 per cent ISF) were sustaining most of the species in this stage of regeneration. But since height growth varied, a prognosis of the species dominating and managing to grow into the canopy layer as future next generation, is challenging. This suggests that a gap-based silvicultural approach can be appropriate to sustain many tree species of the mixed conifer forest, but requires a large gradient of gap sizes and careful light regime management to regulate abundances and desired future tree mixtures.

A species performing comparably well, but being of low commercial importance currently is black oak. Selectively promoting this species by improving its competitive situation could increase its role in these forests and allow the growing high quality oak timber for commercial use, since its wood properties are comparable to, e.g. eastern red oak. This species also adds to the wildlife habitat value for the forest.

Our work suggests that multiple species can be sustained by managing for a wide range of structural and light availability conditions. By this not only a variety of tree species but also high overall plant diversity may be promoted (Battles *et al.*, 2001). This is not only important on the level of forest stands, but also on the scale of landscapes for conserving biodiversity (Nolet *et al.*, 2018; Schall *et al.*, 2018). To create a diversity of stand conditions, forest managers have to make use of the variety of regeneration methods, ranging from single tree selection to group selection-with retention to clearings. Upfront, such an approach requires determining what proportion different tree species are desirable. To improve the adaptability and resilience towards global change-related stress in the future, maintaining or increasing species diversity in forests is considered to be advantageous (e.g. Holling and Meffe, 1996; Messier *et al.*, 2013). Against this background, more studies are required not only focusing on currently valuable commercial species, but also on other tree species participating in the ecosystems to improve the precision with which forests can be managed.

Supplementary data

Supplementary data are available at *Forestry* online.

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Conflict of interest statement

None declared.

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