THESIS

STAND STRUCTURE AND WOOD PRODUCTION EFFICIENCY IN BLACK HILLS PONDEROSA PINE

Submitted by

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ABSTRACT

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Contemporary North American forestry has moved away from management primarily for fiber production toward management for a suite of priorities, including aesthetics, forest health, wildlife habitat, and restoration of pre-settlement conditions. Multi-aged forest stands are better suited to contemporary management priorities than even-aged stands in many instances, largely because stand density can be held in check and regeneration initiated without wholesale removal of the overstory. However, competitive interaction between trees of varying size and inherent physiological differences between small and large trees make it unclear that multi-aged stands produce stemwood volume as efficiently as even-aged stands. In South Dakota’s Black Hills National Forest, fiber production remains an important management objective, which raises questions regarding potential impacts to wood production associated with creating multi-aged structures.

We used stemwood volume production per unit leaf area as a metric of production efficiency to compare productivity of different sized trees and cohorts of trees within multi-aged stands, as well as to compare productivity of multi-aged to even-aged stands of pure *Pinus ponderosa var. scopulorum*. Leaf area is a good measure of resource acquisition for productivity analysis both because it is closely related to light capture, and because multi-aged silvicultural systems can use leaf area per unit ground area (leaf area index) as a stocking tool to regulate density of individual cohorts within a stand. Direct measurement of leaf area is currently unfeasible in the context of daily forestry operations. Consequently, an explicit relationship between leaf area and a standard forestry metric is needed to allow managers to allocate leaf area among cohorts within multi-aged stands using available inventory data. A widely-used stocking tool called stand density index (SDI) is highly correlated with leaf area and has been suggested for this purpose. Yet, it is unclear that the relationship between SDI and leaf area is unbiased across cohorts within multi-aged stands.

This work sampled 1,824 trees in 21 multi-aged and 10 even-aged stands to address questions of production efficiency and implementation of multi-aged silviculture. We found trees in the smallest cohort in multi-aged stands produced stemwood on average 20% less efficiently than trees in larger cohorts. Growth dominance analysis showed efficiency increased with increasing size for the smallest trees in multi-aged stands, but this relationship was inverted for larger trees. Despite size related efficiency differences between trees in multi-aged stands, there was no statistical difference in production efficiency between stand structures. SDI explained almost 90% of leaf area variation in multi-aged stands, with no statistical difference in the relationship across cohorts. Results suggested no penalty in terms of production efficiency for multi-aged stands compared to their even-aged counterparts. Furthermore, SDI provided an unbiased estimate of leaf area in multi-aged stands, supporting its use as a stocking tool for management of complex stand structures.

TABLE OF CONTENTS

ABSTRACT…………………...…………………………………...…………………………….....ii

TABLE OF CONTENTS…………………...………………………………………………..iv

INTRODUCTION……………………………………...…………………………..………1

METHODS……………………………………………………………………………….....5

Study Area…………………………………………………………………………………5

Evaluation of Leaf Area Estimators……………………………………………………….6

Production Efficiency Analysis……………………………………………………………7

RESULTS…………………………………………………………………………..……..14

Evaluation of Leaf Area Estimators………………………………………………………14

Production Efficiency Analysis……………………………………………………..……14

DISCUSSION…………………………………………………………………………….20

CONCLUSION…………………………………………………………………………...28

REFERENCES…………………………………………………………………………...29

INTRODUCTION

The relative productivity of different-sized trees in multi-aged forest stands is a matter of ongoing debate (O'Hara and Nagel, 2006; Binkley *et al.*, 2010). Multi-aged stands have curried favor as of late because their structural complexity is often better suited than even-aged stands to accommodate multiple, diverse management objectives (Maguire, 2005). In the Black Hills of South Dakota and Wyoming, USA, multi-aged silviculture is a means to restore diverse pre-settlement structural conditions in pure ponderosa pine (*Pinus ponderosa* C. Lawson var. *scopulorum* Engelm.) stands, most of which were converted to even-aged structure during the 20th century (Shepperd and Battaglia, 2002; Brown and Cook, 2006).When, as in the Black Hills, multi-aged silviculture is considered where even-aged methods have traditionally been used for fiber production, it is important to quantify potential costs or benefits in terms of stemwood growth. Identifying more or less productive cohorts within multi-aged stands also allows silviculturists to create prescriptions that maximize productivity.

Stemwood production is a function of quantity of resources acquired by trees, efficiency with which resources are used, and proportion of ensuing product allocated to stemwood growth (Smith and Resh, 1999). In comparative studies of stemwood production, efficiency is often represented as production per unit leaf area, where leaf area represents resource acquisition, while periodic stemwood volume increment integrates resource use efficiency and proportional allocation to stemwood (Waring, 1983). Leaf area is a good measure of resource acquisition at the tree level because it is closely related to light capture and thus photosynthetic capacity (Binkley *et al.*, 2010). At stand and cohort levels, leaf area index (projected leaf area per unit ground area, hereafter LAI) approximates a holistic measure of resource acquisition, often conceptualized as occupied growing space (Oliver and Larson, 1996; Smith *et al.*, 1997). Silvicultural methods seek to manipulate growing space in stands, so efficiency quantified in terms of stand or cohort level LAI is highly translatable to management (Long *et al.*, 2004; O'Hara and Gersonde, 2004).

In multi-aged stands, stemwood production efficiency is almost certainly influenced both by inherent functional differences between trees of varying age and size, and competitive interaction between neighbors (Seymour and Kenefic, 2002). Prior research suggests stemwood production efficiency generally declines as trees grow old and large. This decrease has been attributed to increased needle turnover in lodgepole pine (*Pinus contorta* Dougl.) (Smith and Resh, 1999), and reduced hydraulic conductance in ponderosa pine (Ryan *et al.*, 2000). Without explicitly identifying causal agents, numerous empirical studies in North American conifer stands support the notion that efficiency generally decreases as tree age and size increase. Work in balsam fir (*Abies balsamea* (L.) Mill.) and red spruce (*Picea rubens* Sarg.) found stemwood production efficiency of dominant and co-dominant trees was negatively correlated with crown size (DeRose and Seymour, 2009), while in multi-aged stands of red spruce, production efficiency was negatively correlated with age and crown size, holding height (and consequently canopy position) constant (Maguire *et al.*, 1998)**.** Seymour and Kenefic (2002) isolated the effect of age on production efficiency, concluding reduced efficiency was negatively correlated with age but not crown size in multi-aged stands of red spruce and eastern hemlock (*Tsuga Canadensis* (L.) Carrière).

While stemwood production efficiency decreases as trees grow old and large, in multi-aged stands efficiency decreases are at least partly offset by improved canopy position. Woodall et al. (2003a) modeled stemwood production efficiency as a function of intraspecific competition in multi-aged ponderosa pine stands, concluding light competition from larger neighbors reduced efficiency of the smallest trees. These findings are consistent with results from O’Hara (1996), which showed stemwood production efficiency generally increased with cohort age and size (and consequently canopy position) in multi-aged ponderosa pine stands. Similarly, Kollenberg and O'Hara (1999) found production efficiency increased with cohort age in multi-aged lodgepole pine stands. The authors concluded canopy position was a more important factor than tree age or size in predicting stemwood production efficiency of multi-aged lodgepole pine stands. Similar patterns appear in even-aged stands with complex canopy structure. Roberts et al. (1993) asserted improved canopy position accounted for a peak in stemwood growth efficiency relative to crown size for trees in even-aged subalpine fir (*Abies lasiocarpa* Hook.) stands compared to a steady decline for trees in even-aged lodgepole pine stands. The authors maintained the difference between species in production efficiency relative to crown size resulted from differential shade tolerance, with shade tolerant subalpine fir forming multi-strata canopies in even-aged stands, and shade-intolerant lodgepole pine forming a single canopy stratum.

Although the patterns described above are appealingly intuitive, recent work in structurally complex, irrigated and fertilized clonal plantations of eucalyptus (*Eucalyptus saligna* Sm.) suggest they may not be general to all trees and forest types. Binkley et al. (2010) found biomass production per unit of absorbed light increased with tree size, and that small trees intercepted as much light per unit leaf area as larger neighbors. These results appear contradictory to the bulk of empirical findings from North American conifer systems, implying in some systems, canopy position is relatively unimportant, and there is a net efficiency benefit associated with increased tree size.

Prior work on ponderosa pine found the oldest and largest cohorts of trees in multi-aged stands produced stemwood more efficiently than younger and smaller cohorts (O'Hara, 1996; O'Hara and Nagel, 2004), and multi-aged stands were marginally more efficient than their even-aged counterparts (O'Hara and Nagel, 2006). However, leaf area in these studies was estimated as a linear function of breast-height (1.37 m) sapwood area, which could have biased efficiency calculations by over estimating leaf area of the largest trees (Dean *et al.*, 1988). In addition, Seymour and Kenefic (2002) identified potential extrapolation bias in O’Hara (1996), noting the leaf area estimator used was developed using a substantially narrower range of tree sizes (O'Hara and Valappil, 1995) than that which was analyzed in the later work. Consequently, there is value in revisiting stemwood production efficiency of multi-aged ponderosa pine stands using refined methodology. The current work uses data from Black Hills ponderosa pine stands to address three questions critical to implementation of multi-aged silviculture: 1.) does a linear function of breast-height sapwood area offer an unbiased estimate of leaf area, 2.) does stemwood production efficiency change with tree size or canopy position in multi-aged stands, and 3.) is there a difference in average stemwood production efficiency between even- and multi-aged stands?

METHODS

Study Area

The Black Hills of northwest South Dakota and northeast Wyoming are a unique topographic feature in the Great Plains of the Midwestern United States. These mountains formed several million years ago when underlying granite was forced upward through sedimentary rock, creating a rugged landscape composed variously of limestone, shale, sandstone, sandy clay, siltstone, dolomite, and granite, among other substrates (Hoffman, 1986). The Black Hills climate is continental, with freezing winter temperatures and warm summers (Shepperd and Battaglia, 2002). Average annual precipitation is in excess of 50 cm, most of which falls during the growing season (Shepperd and Battaglia, 2002). Temperature generally decreases along increasing gradients of elevation (approximately 1,000 to 2,200 m) and latitude (approximately 43° 20' to 44° 50' N), while precipitation increases along the same gradients (Hoffman, 1986). The Black Hills National Forest encompasses about one-third of the Black Hills, covering approximately 5,000 km^2 (DeBlander, 2002). Of the 92% of the Black Hills National Forest that is forested, 85% is primarily ponderosa pine, while the remaining 15% consists of white spruce (*Picea glauca* (Moench) Voss), quaking aspen (*Populous tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh) and burr oak (*Quercus macrocarpa* Michx.) (DeBlander, 2002). Pre-settlement ponderosa pine stand structures were diverse, encompassing open stands of large, widely-spaced trees, dense second-growth forest, and multi-aged stands (Brown and Cook, 2006). However, well over a century of even-aged silviculture for fiber production has greatly simplified stand structures in most areas (Shepperd and Battaglia, 2002).

Evaluation of Leaf Area Estimators

Two previously-published leaf area estimation model forms were compared in this analysis. A linear predictor based solely on breast-height sapwood area (A_s) was evaluated on the strength of its recommendation for use in multi-aged ponderosa pine stands by O'Hara and Valappil (1995). The linear estimator was compared to a nonlinear model form based on A_s and distance from breast height to center of live crown (D). The nonlinear estimator was recommended for use in even-aged stands of lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.) and subalpine fir because it was found unbiased with respect to stand structure and site quality, while a linear estimator was not (Dean *et al.*, 1988; Long and Smith, 1989).

Data to compare leaf area estimators were collected in 2006 from 80 trees in 16 stands of pure ponderosa pine spanning a range of density and average tree size in the South Dakota portion of the Black Hills National Forest. Five trees in each stand were felled for precise measurement of A_s and whole tree leaf area (A_l), although 12 trees were eventually removed from analysis because of missing data or measurement error. Crowns of felled trees were divided vertically into 10 equal sections, and green mass of foliage was obtained for all sections. For more detailed explanation of field methods and summary data, see Keyser and Smith (2010). Oven-dry mass was obtained for a foliage sample from one representative section near the bottom, middle, and top of the crown for each tree. A_l was obtained by first measuring one-sided leaf area of oven-dry foliage samples using an optical scanner and the digital image analysis program ImageJ (Rasband, 1997-2008) to establish specific leaf area (SLA, area per unit mass) for the bottom, middle, and top sections of crowns. Whole tree oven-dry foliage mass was calculated from green foliage mass using the ratio of green to oven-dry mass obtained from oven-dry foliage samples. A_l was then calculated by applying SLA values obtained from the oven-dry samples to calculated whole tree oven-dry foliage mass. There were small, yet significant differences in mean SLA between crown thirds (alpha = 0.05, df = 211), so same-tree top section SLA values were used to calculate leaf area for the upper three sections of each tree, middle section SLA values were used for the middle four sections, and bottom section SLA values were used for the bottom three sections. A_s for each tree was calculated by subtracting heartwood area from inside-bark basal area. Areas were calculated using the average of two diameters from breast-height stem cross-sections.

Both leaf area estimators were fit using SAS software (Version 9.2 for Windows. Copyright, SAS Institute, Inc.). The linear model form (Model 1) was fit using the 'proc reg' procedure, while the nonlinear form (Model 2) was fit using the 'proc nlin' procedure. Parameter estimates from Dean *et al*. (1988) were used as starting values for non-linear regression.

Model 1: $A_l = A_s$

Model 2: $A_l = \beta_0 * A_s^{\beta 1} * D^{\beta 2}$

Both estimators explained > 90% of the variation in A_l, so model selection was primarily based on bias in residual error relative to crown base height.

Production Efficiency Analysis

Data for stemwood production efficiency analyses were collected in 2010 from 1,824 trees in 21 three-cohort (hereafter multi-aged) and 10 even-aged stands of pure ponderosa pine in the South Dakota portion of the Black Hills National Forest (Fig. 1, Table 1). Eight trees were eventually removed from analysis as a result of missing data. We evaluated numerous multi-aged stands prior to selecting stands for sampling. Stands were sampled if they satisfied four criteria: 1) fully stocked (defined here as basal area > 60 ft^2 ac^{-1} (13.77 m^2 ha^{-1})), 2) pure ponderosa pine (one white spruce was present in each of four stands, and a few stands had isolated quaking aspen or paper birch in the understory), 3) no evidence of recent disturbance, and 4) three clearly identifiable cohorts of trees with sufficient trees in small cohorts for replacement of the largest

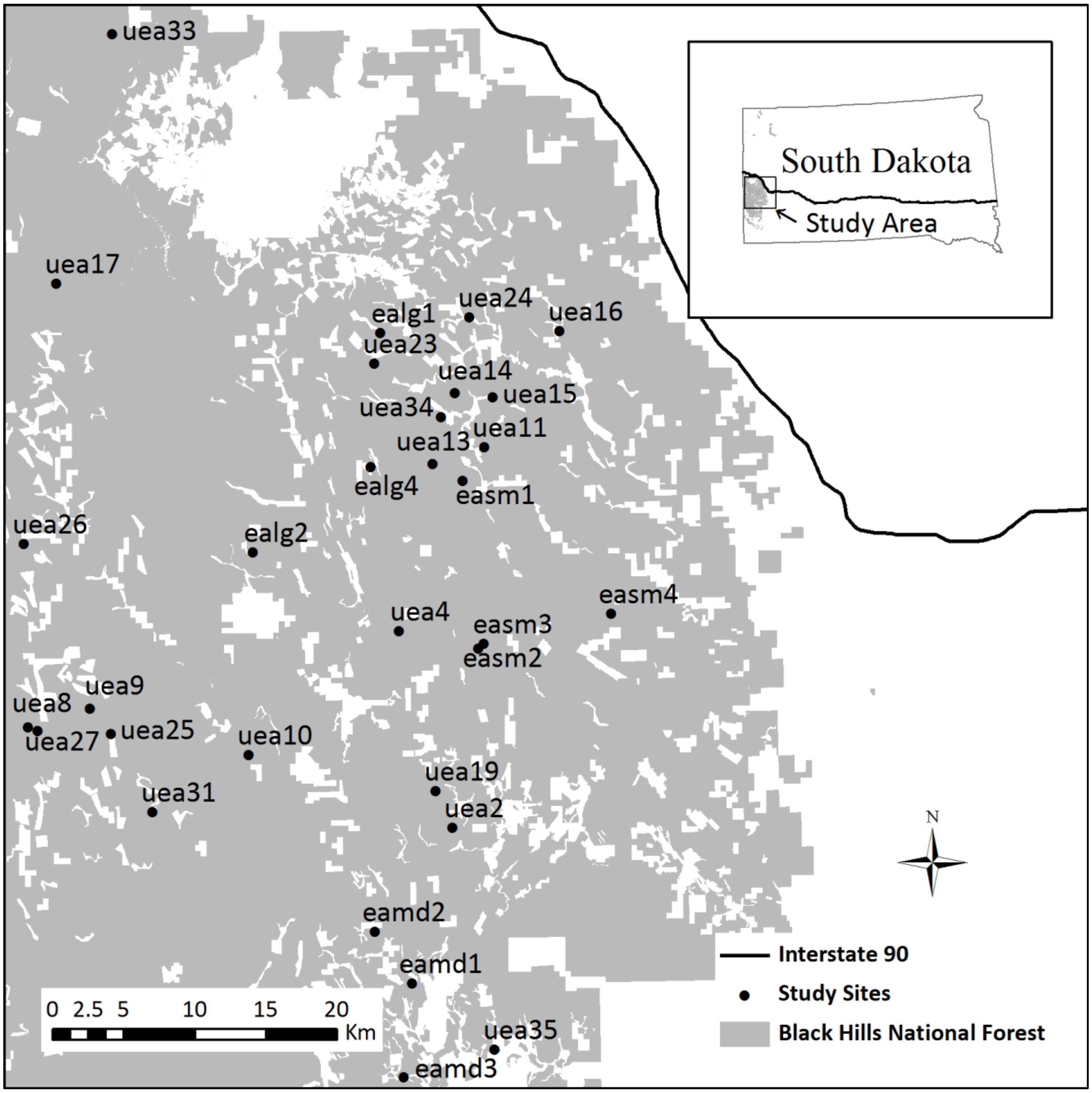

Fig. 1. Location of study plots in the Black Hills National Forest. Plot names beginning with 'u' denote multi-aged stands; names beginning with 'e' denote even-aged stands.

cohort (Table 2). Cohorts in this work were defined as discrete tree size classes and canopy strata within multi-aged stands. In managed Black Hills ponderosa pine stands, where regeneration is rapid and prolific (Shepperd and Battaglia, 2002), these size classes of trees almost certainly resulted from discrete regeneration events following management intervention. Even-aged stands were selected using criteria 1-3 such that the average tree size of three even-aged stands (ealg1, 2 and 4) roughly corresponded to the largest cohorts in multi-aged stands, three stands (eamd1, 2

Table 1. Summary data for all stands sampled in 2010 (n = 31). Metric stand density index (SDI; Reineke, 1933) was calculated using the summation method: SDI = $\sum$ (DBH cm / 25)$^{1.6}$ (Shaw, 2000). SI is site index in m (Smith *et al.*, 1997, p. 52), base age 50, from USDA Forest Service inventory data (B. Cook, pers. comm., 11 May 2011). Eff. is average five year periodic annual stem volume increment (mL) per unit leaf area (m^2). Volume increment is five year periodic annual stem volume increase (m^3) per ha. Ages are breast-height; standard errors follow in parentheses.

*Increment cores used to determine age were estimated to have missed > 20 years for some trees.

	Plot ID	n	SDI	LAI	SI	Eff.	Vol. inc.	Mean age
Even-aged stands	ealg1	29	421	2.33	18.6	139.10	3.32	107 (1)
	ealg2	33	418	1.98	13.7	168.92	3.14	110 (23)
	ealg4	34	323	1.66	20.4	179.36	3.06	113 (4)
	eamd1	44	764	3.11	16.2	129.14	4.17	91 (4)
	eamd2	33	455	2.04	14.3	241.19	5.10	106 (5)
	eamd3	37	797	3.21	17.1	160.65	5.26	128 (55)
	easm1	30	465	2.10	13.4	80.51	1.77	68 (10)
	easm2	28	505	2.47	18.0	98.49	2.41	54 (6)
	easm3	30	443	2.14	18.0	65.97	1.43	58 (2)
	easm4	33	555	2.56	16.8	64.41	1.72	73 (5)
Multi-aged stands	uea10	52	368	2.25	25.0	164.78	3.66	79 (49)
	uea11	81	373	1.84	17.4	182.92	3.82	71 (54)
	uea13*	78	520	2.59	16.5	145.84	3.99	93 (52)
	uea14	77	463	2.28	19.8	146.81	3.42	91 (59)
	uea15	71	493	2.72	17.4	123.05	3.34	94 (65)
	uea16	78	408	2.39	17.7	198.10	4.97	61 (42)
	uea17	70	340	2.12	19.2	177.79	4.20	61 (43)
	uea19*	54	254	1.46	16.8	159.49	2.43	97 (76)
	uea2*	54	424	2.41	19.5	136.88	3.46	117 (124)
	uea23	75	491	2.42	18.9	135.14	3.11	88 (39)
	uea24	86	356	2.04	19.8	164.48	3.34	63 (33)
	uea25*	63	304	2.02	23.8	153.88	3.30	99 (67)
	uea26*	61	420	2.71	19.2	152.14	3.80	77 (38)
	uea27	75	370	2.29	20.1	166.22	3.95	78 (43)
	uea31	91	399	2.39	20.4	160.02	3.84	64 (38)
	uea33*	67	336	1.92	20.7	184.25	3.63	94 (73)
	uea34	96	581	2.70	17.1	187.52	5.40	91 (55)
	uea35*	70	400	2.24	19.8	150.45	3.51	79 (43)
	uea4	49	512	2.64	21.0	142.32	3.41	102 (76)
	uea8	58	315	2.00	20.4	198.56	3.88	68 (22)
	uea9	87	357	2.13	19.2	155.34	3.53	77 (35)

Table 2. Cohort level summary data for all multi-aged stands (n = 21). TPH is trees per ha. Standard errors follow mean values in parentheses.

Cohort	**SDI**	**TPH**	**Age**	**DBH (cm)**
Small	87 (8)	221 (21)	40 (19)	14 (0.9)
Medium	156 (12)	138 (15)	84 (26)	28 (0.6)
Large	158 (13)	55 (4)	140 (54)	49 (0.2)

and 3) corresponded to medium sized cohorts, and four stands (easm1, 2, 3 and 4) corresponded to the smallest cohorts (Table 1).

Three nested fixed-radius plots were established in each multi-aged stand to sample at least 20 trees from the smaller two size cohorts, and at least 10 trees from the largest cohort. Nested plots were necessary because tree density varied widely between cohorts. Using a single plot in each stand would have required extreme over-sampling to obtain adequate numbers of trees from all cohorts. Plot sizes ranged from 0.08 ha to 0.5 ha. Fewer trees were sampled from the largest cohort because trees in this cohort were typically widely-spaced, which made establishing fixed-radius plots of sufficient size to sample more trees unfeasible. Trees were assigned to cohorts using diameter at breast height (DBH). Cohort DBH bounds were chosen separately for each stand based on the observed DBH range of trees in each canopy stratum. Approximately 30 trees were sampled from each even-aged stand using a single fixed-radius plot, which ranged in size from 0.03 ha to 0.2 ha.

Overall height, crown base height, crown top height (for trees with dead tops), DBH, and species were recorded for all trees. For calculation of A_s and periodic stemwood volume increment, one breast-height increment core was collected from each tree, and bark thickness was measured using a bark gauge. Where trees leaned perceptibly or grew on sloping ground, increment cores and bark thicknesses were collected perpendicular to the direction of lean or slope. The boundary between heartwood and sapwood was identified in the field by backlighting increment cores with the sun, which made sapwood appear translucent, while heartwood was opaque. Sapwood radius was marked and measured in the field, before increment cores dried and shrunk. A subsample of trees was bored to the pith to obtain breast-height age. In multi-aged stands, ages were recorded for every third tree in the largest size class and every fifth tree in smaller classes to yield at least three ages per size class for averaging. Every seventh tree was aged in even-aged stands.

A_s (cm^2) was obtained by subtracting heartwood area from inside-bark basal area. A_l (m^2) was calculated using an equation generated from Model 2 (Equation 2). Cohort and stand-level LAI were obtained by multiplying A_l by the inverse of fixed plot size, summing over all trees, and dividing by 10,000 to obtain leaf area (m^2) / ground area (m^2). Stem volume (m^3) was calculated using the ‘calcTotCubic’ function in the Excel Volume Functions application (USDA, 2011) for Microsoft Excel software (version 2010 for Windows). This application calculates total stem volume from DBH and tree height using a two point Flewelling profile model (Flewelling and Raynes, 1993) specific to species, region, and National Forest. Breast-height age was determined by counting growth rings. Where increment cores missed the pith or tree centers were rotten, missed growth rings were estimated using techniques adapted from Duncan (1989). Missed rings were estimated using the height to length ratio of the arc of the earliest available ring and the mean width of the earliest three rings. Increment cores estimated to have missed > 20 growth rings were excluded from analysis, except where they were needed to ensure at least three ages per size class for averaging (Table 1).

We analyzed tree level stemwood production efficiency in multi-aged stands as a function of tree size relative to neighbors (within-stand percentile leaf area rank). In addition to linear regression of efficiency on relative tree size, we adapted techniques described in Binkley et al. (2006) to develop a growth dominance curve and calculate a corresponding dominance coefficient. Binkley et al. (2006) created dominance curves by first ranking trees by stem mass, then plotting cumulative periodic stem mass increment (%) as a function of cumulative stem mass (%). The resulting curve falls on the 1:1 line if every tree contributes to periodic mass increment proportional to its share of cumulative stand mass. If small trees contribute less than expected based on their proportion of stand mass, the curve falls below the 1:1 line (growth dominance), while if large trees contribute less than expected based on their mass, the curve falls above the 1:1 line (reverse growth dominance). A corresponding growth dominance coefficient is calculated by subtracting the area below the growth dominance curve from the area below the 1:1 line, yielding a positive value when large trees contribute disproportionately to stand growth, a negative value when the opposite is true, and returning a value of zero when trees of all sizes contribute to stand growth proportional to their stem mass. As dominance increases, the dominance coefficient moves farther from zero toward a maximum value of 1 (-1 for reverse dominance). We modified the techniques described above by substituting leaf area for stem mass, both for ranking trees and for plotting cumulative leaf area against cumulative volume increment, and by substituting stem volume increment for stem biomass increment. Leaf area offers a more direct analogue for resource acquisition than stem mass because stem mass includes non-transpiring heartwood, which steadily accumulates as trees grow. Consequently, using stem mass to approximate resource acquisition potentially introduces a negative bias for stemwood production efficiency of large trees because the relationship between stem mass and leaf area, and by extension photosynthetic capacity, may be different for small and large trees.

In addition to the tree level analyses described above, we compared average stemwood production efficiency both between cohorts in multi-aged stands, and between even- and multi-aged stands. Grouping trees by cohort in multi-aged stands served two purposes: 1.) it helped reduce the influence of spatial heterogeneity within cohorts by using average efficiency of trees with a common canopy position as the unit of analysis, and 2.) it produced results that were directly applicable to the scale of silvicultural intervention in multi-aged stands, that of individual cohorts. Similarly, comparing mean stemwood production efficiency between even- and multi-aged structures at the stand scale produced results relevant to the scale of silvicultural decision making in the absence of a predefined stand structure (e.g. comparing even- and multi-aged management alternatives for a given stand).

RESULTS

Evaluation of Leaf Area Estimators

Linear regression of A_l on A_s using Model 1 yielded Equation 1 ($r^2 = 0.9189$, $n = 68$).

Equation 1: $A_l = -0.2424 + 0.1345\ (A_s)$

Despite the high proportion of variation in leaf area explained by Equation 1, the linear model displayed significant bias with respect crown base height, a variable which generally varies across cohorts in multi-aged stands. Equation 1 under-predicted leaf area for trees with short lengths of crown-free bole, and over-predicted leaf area for trees with long length of crown-free bole (Fig. 2a).

Non-linear regression of A_l on A_s and D using Model 2 yielded Equation 2 (pseudo-$r^2 = 0.9787$, $n = 68$).

Equation 2: $A_l = 0.1748\ (A_s^{\ 1.2152})\ (D^{-0.6642})$

Equation 2 explained a higher proportion of the variation in leaf area than Equation 1 while eliminating the bias detected in the linear estimator (Fig. 2b). Accordingly, we used Equation 2 to estimate leaf area for stemwood production efficiency analysis.

Production efficiency analysis

Linear regression of stemwood production efficiency on within-stand percentile leaf area rank indicated a weak yet significant positive relationship between production efficiency and tree size relative to neighbors in multi-aged stands (Fig. 3). However, despite the statistical significance of

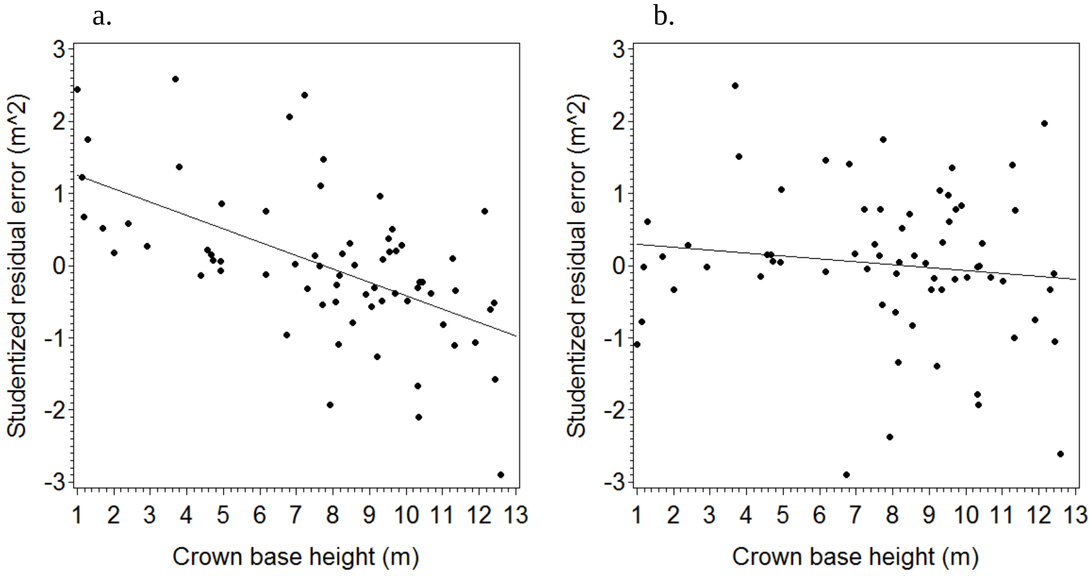

Fig. 2. There was significant bias in linear leaf area estimation with respect to crown base height (a). The fitted trend line is residual error (m^2) / standard deviation = 1.4418 – 0.1854 * D ($r^2 = 0.3276$, df = 66). Both intercept and slope parameters were significant ($p < 0.0001$). This bias was eliminated by the nonlinear estimator (b). Neither slope nor intercept of the trend line were significantly different from zero ($p > 0.3$). Symbols in both figures represent individual trees.

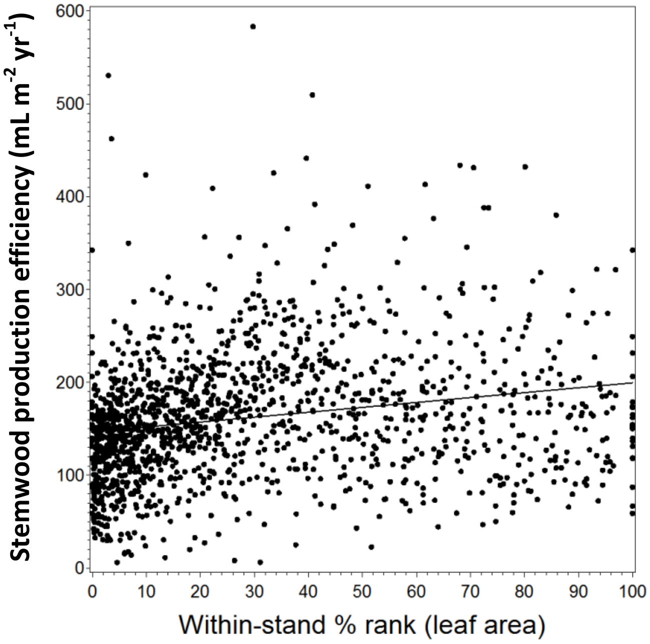

Fig. 3. Five year periodic annual stemwood volume increment per unit leaf area (mL m^{-2} yr^{-1}) as a function of within-stand percentile leaf area ranking. Symbols represent individual trees. The fitted trend line is: stemwood production efficiency = 146.6364 + 0.52621 * within-stand percentile leaf area rank (r^2 = 0.0433, df = 1484). Both intercept and slope parameters were highly significant ($p < 0.0001$). Two outliers were dropped before fitting the regression line.

this relationship, it explained less than five percent of variation in tree level stemwood production efficiency.

While the significant positive relationship between leaf area and stemwood production efficiency described above suggested growth dominance in multi-aged stands, we found slight evidence of reverse growth dominance. The absolute magnitude of the dominance coefficient was small (-0.0132), however, which was reflected in the nearness of the cumulative leaf area dominance curve to the 1:1 line (Fig. 4). The trend indicated by growth dominance analysis was of a positive

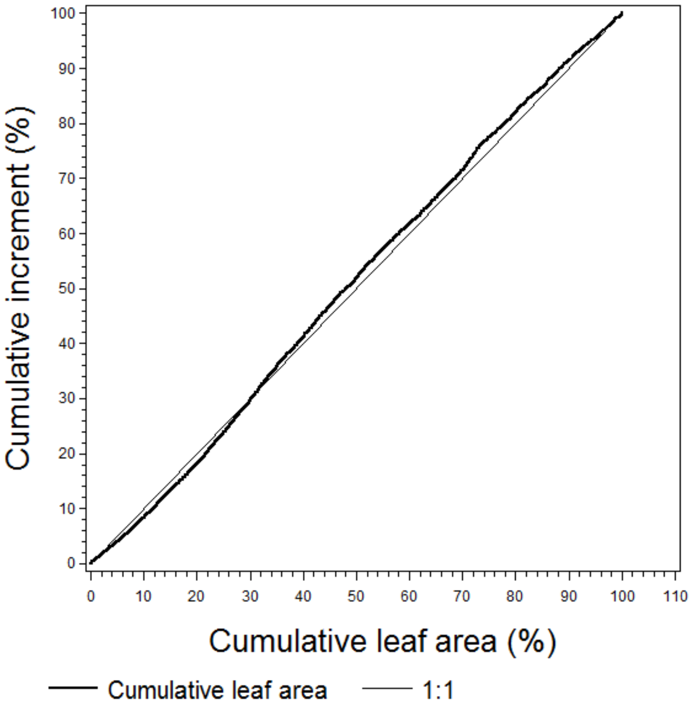

Fig. 4. Dominance curve for all 1,483 trees in the 21 multi-aged stands. The heavy line describes cumulative volume increment as a function of cumulative leaf area. The light line is 1:1. The point at which the dominance curve crosses 1:1 (~30th percentile tree by leaf area) can be interpreted as the point at which increasing leaf area no longer leads to increased stemwood production efficiency and instead results in declining efficiency.

relationship between leaf area and growth efficiency for the smallest ~30% of trees, which shifted to a negative relationship for the largest ~70% of trees.

Growth dominance analysis results were generally consistent with trends in proportional leaf area and volume increment across cohorts (Fig. 5). The smallest cohort of trees in multi-aged stands, on average, carried ~14% of stand leaf area, but contributed only ~11% of periodic annual stem volume increment. By contrast, the medium-sized cohort carried ~36% of leaf area compared to ~40% of growth, while the largest cohort carried ~50% of leaf area compared to ~49% of growth. A Ryan-Einot-Gabriel- Welsch-Q-adjusted least significant difference means comparison of stemwood production efficiency across cohorts in multi-aged stands showed trees in the smallest cohort were significantly less efficient than trees in larger cohorts (alpha = 0.05, df = 60) (Fig. 6). Trees in the smallest cohort produced, on average, 137 mL of stemwood per m^2 leaf area

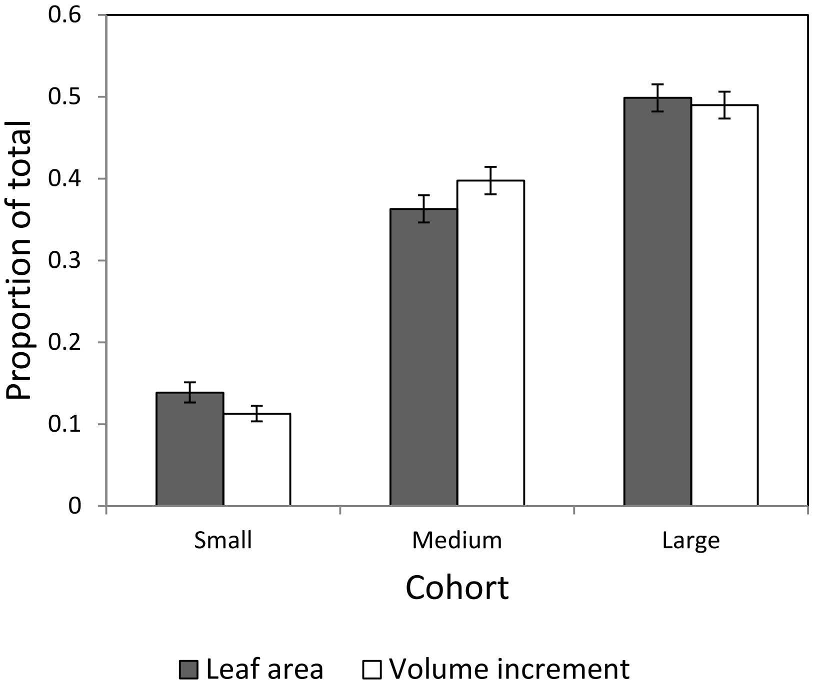

Fig. 5. Average proportion of total stand leaf area and five year periodic annual stem volume increment by cohort in multi-aged stands. Error bars represent 95% confidence interval of means.

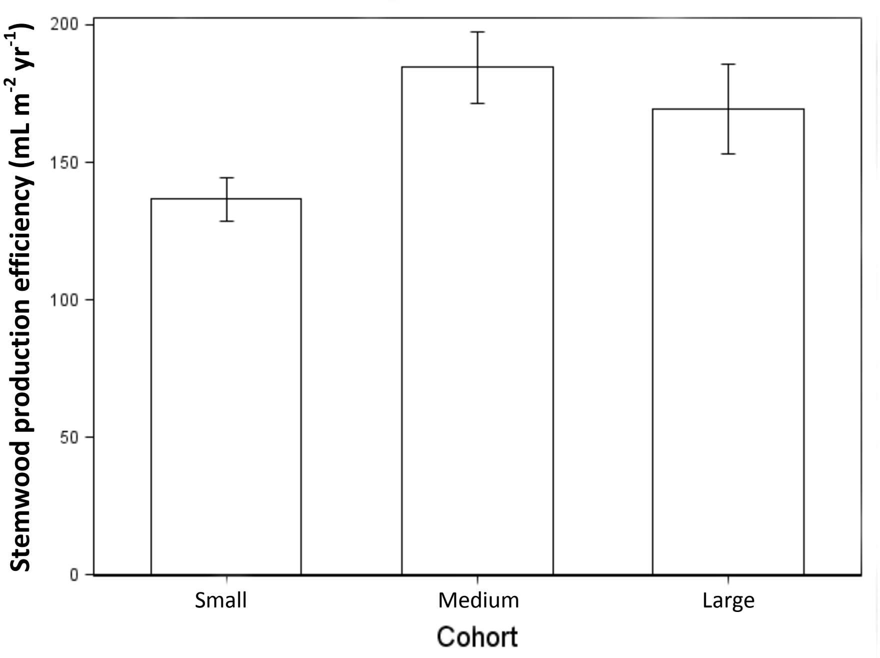

Fig. 6. Five year periodic annual stemwood volume increment per unit leaf area (mL m^{-2} yr^{-1}) by cohort for multi-aged stands. On average, trees in the largest two cohorts produced significantly more stemwood per unit of leaf area than trees in the smallest cohort (alpha = 0.05). Error bars represent 95% confidence intervals of means.

annually, compared to 185 mL for trees in the medium cohort and 169 mL for trees in the large cohort (Table 3).

Table 3. Five year periodic annual volume increment per unit leaf area (mL m^{-2} yr^{-1}) by cohort and stand type. Standard errors follow group means in parentheses; letters denote statistical grouping (alpha = 0.05).

Cohort	**Efficiency**	**n**
Large	169 (7.85) a	21
Medium	185 (6.23) a	21
Small	137 (3.75) b	21
Stand type	**Efficiency**	**n**
Even-aged	132 (17.74) a	10
Multi-aged	161 (4.55) a	21

On average, stand level production efficiency in multi-aged stands was ~20% greater than in even-aged stands (Fig. 7, Table 3). However, comparison of even- and multi-aged stands using Satterthwaite's approximate t-test showed no statistical difference between stand structures

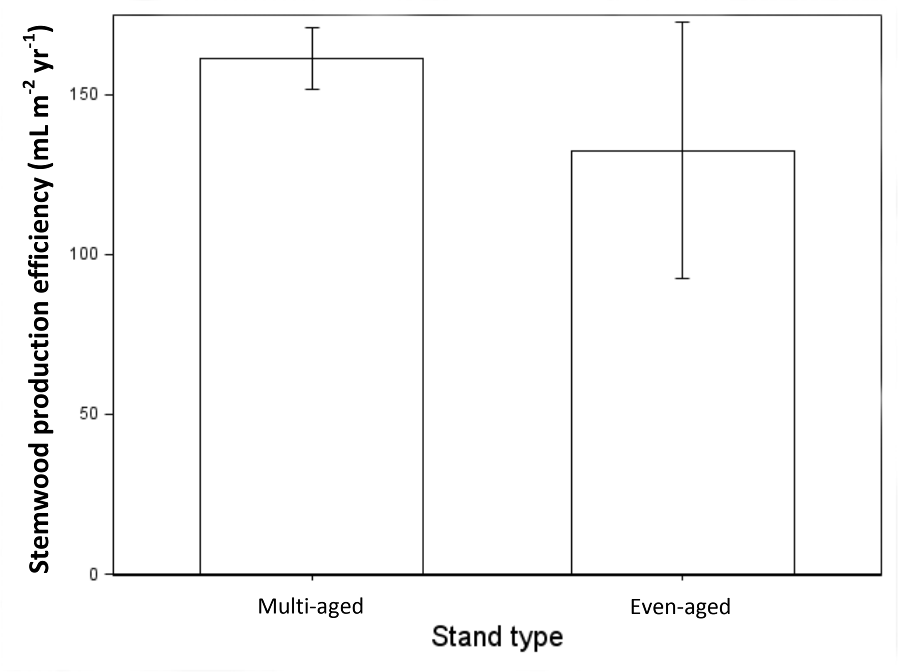

Fig. 7. Despite an average of ~20% greater stemwood production efficiency (mL m^{-2} yr^{-1}) in multi-aged stands, there was no statistical difference in mean efficiency between multi-aged and even-aged stands (alpha = 0.05). Error bars represent 95% confidence intervals of means.

(t = 1.57 p = 0.1465 df = 10.21). It was necessary to compare structures using a conservative means test to account for large variation in efficiency across relatively few even-aged stands. Wide variation in even-aged stands came from uniformly low stemwood production efficiency among stands consisting of small trees (Table 1).

DISCUSSION

Prior work in multi-aged ponderosa pine stands concluded stemwood production efficiency generally increased with tree size, and that multi-aged stands were as or marginally more efficient than even-aged stands (O'Hara and Nagel, 2006). This study corroborated prior results while correcting for a potentially important source of bias by estimating leaf area as a non-linear function of A_s and D instead of as a linear function of A_s alone. Simple linear regression of stemwood production efficiency on relative within-stand leaf area revealed a statistically significant positive relationship between efficiency and relative size in multi-aged stands, yet explained little variation in tree level efficiency (Fig. 3). Growth dominance analysis suggested efficiency increased with tree size for the smallest ~30% of trees before decreasing with tree size for the largest ~70% of trees (Fig. 4). Size related efficiency differences in multi-aged stands were also perceptible in cohort-level analysis, often the unit of interest in multi-aged silviculture (Long and Daniel, 1990; Smith *et al.*, 1997; O'Hara and Gersonde, 2004; Loewenstein, 2005). Proportion of stand leaf area relative to proportion of stand volume growth decreased from the smallest cohort to the two larger cohorts (Fig. 5). We found, on average, stemwood production efficiency of trees in medium and large cohorts in multi-aged stands was significantly greater than efficiency of trees in small cohorts (Fig. 6, Table 3). In contrast to prior work, however, we found efficiency plateaued after trees were recruited out of the youngest and most subordinate cohort, instead of continuing to increase as trees transitioned into the oldest and most dominant cohort (Fig. 6). Diminished stemwood production efficiency of the smallest cohort in multi-aged stands did not reduce stand level efficiency relative to even-aged stands. Instead, multi-aged stands were on average more efficient than even-aged stands, although the difference was not statistically significant (Fig. 7, Table 3).

Our first research question asked if a linear function of A_s constituted an unbiased estimation of leaf area for multi-aged ponderosa stands. Ecological theory suggested a linear estimator would be biased. The ‘pipe model theory’ (Shinozaki *et al.*, 1964) says cross-sectional sapwood area is proportional to distal leaf area for a given location on the stem. Because sapwood is in-effect a cluster of pipes carrying water to transpiring leaves, sapwood area reflects required fluid transport capacity and thus distil transpiring biomass. Waring et al. (1982) applied the pipe model theory to predict one-sided leaf area of conifers using sapwood area, concluding sapwood area and leaf area were directly proportional if sapwood area was measured at or above the base of the live crown, but that it was necessary to account for sapwood taper to predict leaf area from sapwood area below the crown. Successive work in various North American conifer types generally validated the importance of accounting for sapwood taper in leaf area estimation (Dean and Long, 1986; Long and Smith, 1988, 1989; Gilmore *et al.*, 1996; Maguire and Batista, 1996; Kenefic and Seymour, 1999), but see Coyea and Margolis (1992). Sapwood taper appears sensitive to stand density and site quality, leading Dean and Long (1986) and Long and Smith (1988, 1989) to include a term accounting for taper (D) in non-linear one-sided leaf area predictors for lodgepole pine and subalpine fir that were otherwise based on A_s. D is the distance from breast-height to center of leaf area, which reflects two physical characteristics of trees that are sensitive to growing conditions: length of crown-free bole, and crown ratio. In contrast to the majority of studies referenced above, O’Hara and Valappil (1995) found A_s was directly proportional to all-sided crown leaf area in multi-aged ponderosa pine stands. In the current study, estimating leaf area using a linear function of A_s (Equation 1) biased estimates with respect to crown base height (Fig. 2a), while a non-linear estimator including D (Equation 2) removed the bias (Fig. 2b). We maintain Equation 2 performed better because it accounted for physical effects of growing conditions (sapwood taper), whereas Equation 1 did not. The largest size class of trees measured by O'Hara and Valappil (Table 1,1995) had a mean DBH of 11.5 cm, which is smaller than the average DBH of the smallest cohort of trees measured in the current work (Table 2). It is likely the earlier work did not sample an adequate number of trees with substantial lengths of crown-free bole above breast height to detect the influence of sapwood taper on the A_s: leaf area relationship.

The bias detected in Equation 1 would over estimate leaf area for trees with substantial lengths of crown-free bole, resulting in under estimation of stemwood production efficiency for these trees (Dean *et al.*, 1988). Prior work on stemwood production efficiency of multi-aged ponderosa pine stands relied on a leaf area estimator functionally equivalent to Equation 1, yet still concluded efficiency generally increased with canopy position and tree size (O'Hara, 1996; O'Hara and Nagel, 2004), despite the apparent likelihood that efficiency of larger, taller trees was underestimated. This suggests potential bias in the earlier work introduced by linear estimation of leaf area from A_s was small relative to the magnitude of efficiency differences in multi-aged stands.

While bias from linear estimation of leaf area from A_s did not appear to substantially influence efficiency analysis, it has important implications for implementation of multi-aged silviculture. Density management in multi-aged stands seeks to allocate resources among cohorts within a stand; contemporary methods use LAI as an index of occupied growing space (O'Hara and Valappil, 1999; Long *et al.*, 2004). However, leaf area is difficult to measure directly, so a suitable proxy is required for LAI allocation to be operational. LAI is highly correlated with SDI (Table 1), which has been suggested for this purpose (Long, 1995). However, Woodall et al. (2003b), using A_s as a proxy for leaf area, found the relationship between SDI and leaf area changed across size classes in multi-aged ponderosa pine stands, ultimately concluding a local conversion factor was required to estimate LAI using SDI. The current study found no difference in the SDI: LAI relationship across cohorts in multi-aged ponderosa pine stands when LAI was estimated using Equation 2 (Fig. 8), but found significant differences between all cohorts using

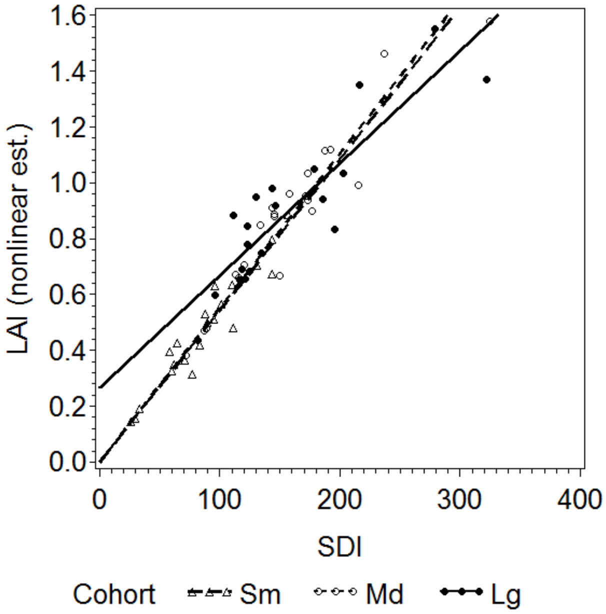

Fig. 8. There were no statistically significant differences across size cohorts in the slope of regression lines describing LAI as a linear function of SDI when LAI was calculated using Equation 2. A multiple regression of LAI on SDI and cohort showed no significant interaction between independent variables (F = 2.04, p = 0.1388, df = 57). Regression lines are forced through the origin for small and medium cohorts because intercepts were not significantly different from zero. Regression equations are as follows: LAI_{Lg} = 0.2542 + 0.0040 *SDI, LAI_{Md} = 0.0055 *SDI, LAI_{Sm} = 0.0054 * SDI. Symbols represent size class means.

Equation 1 (Fig. 9). We suspect Woodall et al.’s (2003b) findings reflect bias introduced by assuming a linear relationship between A_s and leaf area. The implication is that, contrary to prior findings, SDI offers an unbiased estimate of LAI across cohorts in multi-aged ponderosa pine stands. In the current work, a single linear function of SDI accounted for almost 90% of the variation in LAI for all cohorts in multi-aged stands (LAI = 0.0870 + 0.0050 * SDI, r^2 = 0.8937, df = 61).

Our second research question asked whether stemwood production efficiency changed with tree size or canopy position in multi-aged stands. A simple linear relationship between efficiency and relative tree size was positive and statistically significant, but lacked explanatory power (Fig. 3).

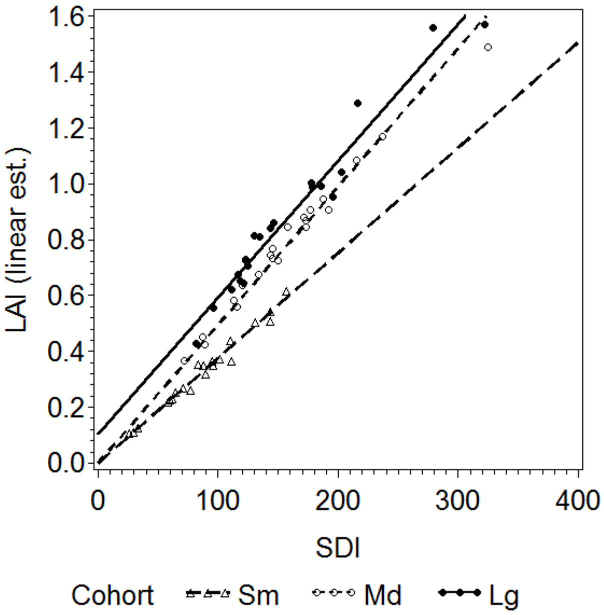

Fig. 9. A multiple regression of LAI on SDI and cohort showed significant interaction between independent variables when LAI was calculated using Equation 1 (F = 7.49, p = 0.0013, df = 57). Regression line slopes were significantly different between all cohorts (alpha = 0.05). Regression lines are forced through the origin for small and medium cohorts because intercepts were not significantly different from zero. Regression equations are as follows: $LAI_{Lg} = 0.1030 + 0.0049 * SDI$, $LAI_{Md} = 0.0050 * SDI$, $LAI_{Sm} = 0.0038 * SDI$. Symbols represent size class means.

Growth dominance analysis offered a clearer picture of the effect of relative tree size on efficiency in multi-aged stands. Dominance analysis using leaf area as an index of resource acquisition showed the largest ~70% of trees in multi-aged stands produced a larger proportion of total periodic annual stemwood volume increment per unit of leaf area than the smallest ~30% of trees, although efficiency decreased with increasing size for these large trees (Fig. 4). Our use of leaf instead of stem biomass both for ranking trees by size and as a metric of resource acquisition strongly influenced the results of growth dominance analysis. When stem volume (a linear function of biomass, assuming constant wood density) was used instead of leaf area, we detected substantial reverse growth dominance (Fig. 10), resulting in a negative dominance coefficient of relatively large absolute magnitude (-0.2847). This probably reflected over-estimation of resource acquisition for large trees by including non-transpiring heartwood in the efficiency calculation. Because tree level leaf area is closely related to light capture (Binkley *et al.*, 2010), and is an

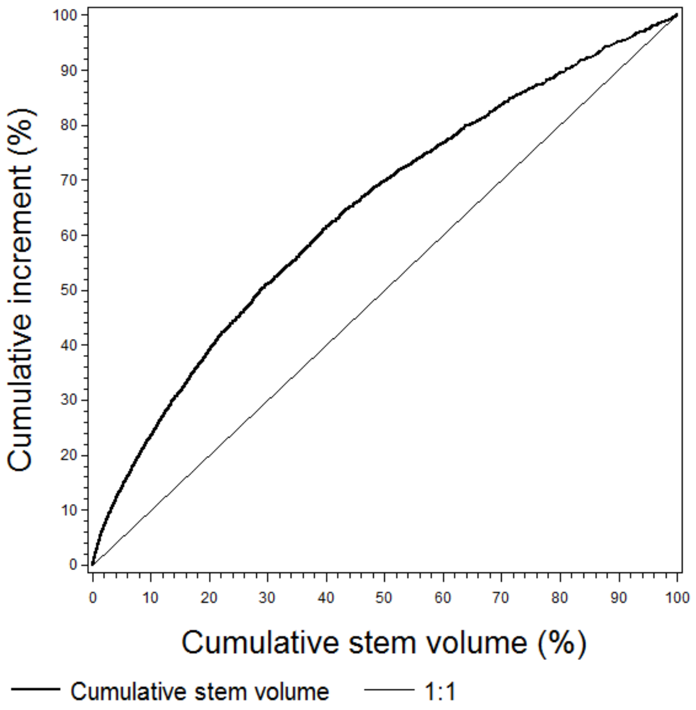

Fig. 10. Dominance curve derived from stem volume instead of leaf area. The heavy line describes cumulative volume increment as a function of cumulative stem volume. The light line is 1:1. When stem volume is used to represent both tree size (for ranking) and resource acquisition, the pattern in multi-aged stands is of strong reverse growth dominance for all tree sizes.

accepted index of growing space occupancy (O'Hara and Valappil, 1999; Long *et al.*, 2004), we believe the results of dominance analysis using leaf area are both ecologically relevant and readily translatable to management. Results of cohort level stemwood production efficiency generally corroborated tree level growth dominance analysis. Regardless of methodology or analysis unit, it was clear the most subordinate trees in multi-aged stands produced stemwood less efficiently than larger, more dominant trees, yielding ~20% less stemwood per unit leaf area at the cohort level (Table 3).

Stemwood production is the product of resource acquisition, efficiency with which resources are used to convert atmospheric carbon and water to carbohydrate, and proportion of carbohydrate allocated for stemwood growth (Smith and Resh, 1999). Any or all of these factors could be responsible for inefficient stemwood production of small trees compared to larger neighbors in multi-aged stands. Because small trees were in unfavorable canopy positions, the most obvious explanation for reduced growth is that small trees intercepted less light than large trees as a result of shading. This seems especially likely given prior work that showed growth of small trees in multi-aged ponderosa pine stands was sensitive to neighbor height (Woodall *et al.*, 2003a). A non-significant trend of declining stemwood production efficiency from medium to large cohorts may reflect a shift from net efficiency increase with tree size resulting from improved canopy position to net decrease as improved access to sunlight is offset by detrimental physiological changes associated with increasing age or size (Seymour and Kenefic, 2002).

Our final research question asked whether there was a difference in stemwood production efficiency between even- and multi-aged stand structures. Despite greater average efficiency in multi-aged stands than in even-aged stands, there was no significant difference between structures (Fig. 7). Average stemwood production efficiency of even-aged stands was highly variable compared to multi-aged stands, which limited scope for statistical comparison. The source of wide variation in even-aged stands was uniformly low efficiency among stands with average tree size corresponding to the smallest cohort of trees in multi-aged stands (Table 1). The most obvious explanation for this was that in attempting to select even-aged stands consisting of small trees, we inadvertently chose stands on poor sites. This was not supported by summary data, however, as the stands in question were both markedly younger than other even-aged stands, and comparable in terms of site index (Table 1). Mean SDI was also similar for even-aged stands of small trees, and even-aged stands of medium and large trees ($p = 0.7399$, $df = 8$). It is possible even-aged ponderosa pine stands in the Black Hills pass through a period of diminished production efficiency before trees grow large, though a large body of work suggests this would be a unique finding (e.g. Assmann, 1970; Ryan *et al.*, 1997; Smith and Long, 2001; Binkley *et al.*, 2002). It is more likely the apparent inefficiency of even-aged stands of uniformly small trees reflects the influence of one or more unmeasured variables. For example, there could be a substantial difference in wood density between even-aged stands of small trees and stands of larger trees, so efficiency analysis using biomass instead of stem volume might have produced wholly different results. When stand level efficiency of multi-aged stands was compared to efficiency of only even-aged stands of medium and large trees, the even-aged stands were ~5% more efficient, although this difference was nowhere near significant (p = 0.5041, df = 25). The important outcome of stand-level efficiency comparisons is that this work found no evidence of a penalty in terms of periodic annual volume increment for multi-aged silviculture compared to even-aged methods.

CONCLUSION

Outcomes of leaf area estimation and productivity analyses were extremely sensitive to methodology. In this study, we found SDI offered an unbiased estimate of LAI when leaf area was estimated using a nonlinear model form, while prior work that used sapwood as a surrogate for leaf area concluded the relationship between SDI and LAI changed across size classes in multi-aged stands (Woodall *et al.*, 2003b). Similarly, growth dominance analysis using leaf area suggested a complex relationship between tree size and stemwood production efficiency in multi-aged stands, where increasing tree size was associated with increased efficiency of small trees, but was associated with decreased efficiency of larger trees. However, when stem volume was used instead of leaf area, stemwood production efficiency appeared to decrease with increasing size for all trees. Our data showed the smallest cohorts of trees in multi-aged ponderosa pine stands produced stemwood volume less efficiently than larger cohorts, probably because of shading by larger trees, but that this apparent benefit of improved canopy position did not translate to greater efficiency of the largest cohorts of trees compared to medium-sized cohorts. This may reflect physiological differences between small and large trees. Despite efficiency differences between trees and cohorts in multi-aged stands, we found no evidence of inherent efficiency differences between even and multi-aged structures.

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