Leaf area and tree increment dynamics of even-aged and multiaged lodgepole pine stands in Montana

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Abstract: Age structure and distribution of leaf area index (LAI) of even and multiaged lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) stands were examined on three study areas in western and central Montana. Projected leaf area was determined based on a relationship with sapwood cross-sectional area at breast height. Stand structure and LAI varied considerably between individual plots. LAI and stand stem volume increment were significantly higher in multiaged than even-aged stands with the exception of one study area, which had higher volume increment in even-aged stands. Older cohorts and higher canopy strata generally had greater LAI than younger cohorts and lower strata. Ratios of stem volume increment to leaf area were used to assess stand, cohort, and individual tree vigor or growing space efficiency (GSE). Even-aged stands had significantly higher GSEs in individual study areas and overall than multiaged stands. Cohort GSE generally increased with increasing age of the cohort. Stand increment was weakly associated with stand LAI. Individual tree volume increment was strongly related to projected leaf area when stands were divided by age-classes or canopy strata. These results suggest separating these stands into components, such as age classes or canopy strata, and summing predicted increment for each component may provide more accurate prediction of stand increment than using whole-stand LAI.

Résumé : Nous avons examiné la structure d'âge et la distribution de l'indice de surface foliaire (ISF) de peuplements équiennes et inéquiennes de pin lodgepole (*Pinus contorta* var. *latifolia* Engelm.) sur trois sites expérimentaux dans le centre et l'ouest du Montana. La surface foliaire projetée a été déterminée à partir d'une relation avec la surface d'une coupe transversale du bois d'aubier à hauteur de poitrine. La structure et l'ISF des peuplements variaient beaucoup d'une parcelle à l'autre. L'ISF et l'accroissement en volume des tiges étaient significativement plus élevés dans les peuplements inéquiennes, à l'exception d'un site expérimental dans lequel l'accroissement était supérieur dans les peuplements équiennes. Les cohortes d'arbres les plus vieilles et les étages les plus élevés avaient un ISF supérieur à celui des cohortes les plus jeunes et des étages les plus bas. Nous avons utilisé le rapport entre l'accroissement en volume des tiges et la surface foliaire pour évaluer l'efficacité spatiale de croissance (ESC) ou la vigueur des peuplements, des cohortes et des arbres individuels. L'ESC des peuplements équiennes était significativement plus élevé que celui des peuplements inéquiennes, tant à l'échelle des sites individuels que de l'étude au complet. L'ESC des cohortes d'arbres s'accroissait généralement avec un accroissement de l'âge de la cohorte. L'accroissement à l'échelle du peuplement n'était que faiblement relié à l'ISF du peuplement. L'accroissement en volume des tiges individuelles était fortement relié à leur surface foliaire projetée quand nous divisions les peuplements en classes d'âge ou en étage de dominance. Ces résultats suggèrent que nous pouvons mieux relier l'ISF à l'accroissement du peuplement si nous stratifions ces peuplements sur la base de leurs composantes, telles que les classes d'âge ou les étages, et si nous faisons la somme des accroissements prédits pour chaque composante.

[Traduit par la rédaction]

Introduction

A number of studies have reported lodgepole pine (*Pinus contorta* var. *latifolia* Englem.) stands consisting of several age classes (Tande 1979; Stuart 1984; Muir 1993; Arno et al. 1993) suggesting this structure is more common than previously believed (Arno 1980; Agee 1993). Apparently the disturbance dynamic associated with bark beetles, dwarf mistletoe, and fire that commonly results in even-aged stands can also produce multiaged stands. Multiaged lodgepole stands present a potential management alternative to even-aged stands, which might avoid many of the aesthetic and environmental concerns associated with even-aged management. However, managers need information on the dynamics of these multiaged stands and how available growing space, as represented by leaf area, might be allocated to different age-classes or canopy strata.

Previous work with leaf area dynamics in multiaged ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) stands indicated leaf area index (LAI) and volume increment are nearly equal in comparable even-aged and multiaged stands (O'Hara 1996). O'Hara also found younger cohorts and lower canopy strata generally had less LAI than older cohorts and upper

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strata. Tree increment was strongly related to its all-sided leaf area within cohorts and provided the basis for reasonably accurate predictions of stand increment from the sum of predicted increments from each cohort in a stand. Similar results were observed in mixed Scots pine (*Pinus sylvestris* L.) – Norway spruce (*Picea abies* (L.) Karst.) stands in Finland (O'Hara et al. 1999).

A number of studies have examined leaf area dynamics in lodgepole pine stands. Keane and Weetman (1987) document LAI for very dense lodgepole stands in British Columbia. Pearson et al. (1984) examined LAI in the Rocky Mountains of Canada, and Kaufmann and Ryan (1986) and Kaufman and Watkins (1990) have examined individual tree relationships. A series of studies in the central Rocky Mountains have documented a number of production ecology relationships for lodgepole pine (Long and Smith 1988, 1990, 1992; Smith and Long 1989; Dean et al. 1988 and others). These studies indicate lodgepole pine stands increase in LAI with stand density, have strong relationships between stand or tree volume increment and LAI, and strong relationships between individual tree increment and leaf area.

This study uses projected leaf area to represent occupied growing space (O'Hara 1988, 1996) and reports leaf area, stem volume increment, and growing space efficiency relationships for even-aged and multiaged lodgepole pine stands from three study areas in Montana. An additional objective was to quantify relationships between volume increment and leaf area using stand components such as age classes or canopy strata for subsequent development of stocking control models (O'Hara and Valappil 1999)

Methods

Sites were sampled in three general study areas: the Bitterroot National Forest and the University of Montana's Lubrecht Experimental Forest in western Montana, and Tenderfoot Creek Experimental Forest in central Montana. Bitterroot National Forest sites ranged from 1829 and 2134 m elevation, Lubrecht at approximately 1250 m, and Tenderfoot Creek from 2103 and 2377 m. All plots sampled were between 46°33′ and 46°50′N and longitudes 111°15′ and 113°49′W. Precipitation in the Bitterroot ranges from 550 to 600 mm/year. Average annual precipitation at Lubrecht is 455 mm, half of which is in the form of snow (Goetz 1996). Tenderfoot Creek also has a continental climate and receives an average precipitation of 880 mm/year (McCaughey 1996).

Stands were selected on the basis of being pure (90% or greater) lodgepole pine, and having experienced no major disturbance within the past 15 years. Other minor species present included subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), and whitebark pine (*Pinus albicaulis* Englem.) in the Bitterroot and Tenderfoot forests, and interior Douglas-fir, ponderosa pine, western larch (*Larix occidentalis* Nutt.) at Lubrecht. Recently disturbed areas were avoided so as not to include stands where leaf area might be less than potential. Plots were established in both even-aged and multiaged stands. Approximately half of the sampled stands were even-aged to provide a comparison with multiaged stands for basic stand increment, site quality, and physiological relationships.

Areas encompassing a range of different site variables such as slope, aspect, elevation, and soils were sampled. Site index was determined for the even-aged lodgepole pine plots using curves for lodgepole pine in western Montana (Milner 1992) (Table 1). These site index values were determined to provide some reference to site quality independent of measurements of LAI. Many of the multiaged plots were purposely located near even-aged plots for which site index was known. This study did not use site quality as an independent variable but instead used LAI as an independent variable through its relation to site quality (McCleod and Running 1988; Long and Smith 1990).

Most of the stands sampled in the Bitterroot National Forest were within the *Abies lasiocarpa* climax series (Pfister et al. 1977), with one stand within the *Pseudotsuga menziesii* climax series (Table 1). Stands sampled in Lubrecht Experimental Forest included habitat types within the *Abies lasiocarpa* and the *Pseudotsuga menziesii* climax series. All sampled stands at Tenderfoot were classified within the *Abies lasiocarpa* climax series (Table 1).

A total of 35 fixed-radius circular plots were constructed and measured. Thirteen plots were measured on the Bitterroot National Forest, eight at Lubrecht Forest, and 14 on the Tenderfoot Forest. Initially, the plot size was 400 m^2 in size, but later reduced to 200 m^2 size plots since the variability of the stand was still encompassed with the smaller plot size

Within each plot, the diameter at breast height (DBH; 1.37 m) and total height of every tree were measured. Each tree was assigned a stratum and a crown class within each stratum (Oliver and Larson (1996). In even-aged stands the main canopy was classified as the B stratum.

Each tree was cored on the north and east sides at breast height. The sapwood radius was measured to the nearest millimeter on each core in the field immediately after the core was extracted. Holding the core up to the sunlight while in the field delineated the sapwood–heartwood boundary. The growth rings of the cores that intercepted, or nearly intercepted, the pith of the tree were counted (usually to the nearest 5 years for cores that missed the pith) using a dissecting scope in the laboratory. Every tree in the multiaged plots was aged, and on average, 74% of the trees were aged in the even-aged plots. Bark thickness was measured on every tree using a bark gauge at breast height adjacent to where the tree was cored.

Every tree sampled in this study was assigned to a cohort or age-class (Oliver and Larson 1996). Assignment of an individual tree to a cohort was primarily based on tree age and other physical characteristics such as bark thickness, height, fire scars, crown class, and diameter. In some plots there did not appear to be discrete disturbance events that led to distinct clusters of trees or cohorts; therefore, the assignment of the trees on these plots was more subjective. These plots may have been the result of windthrow events occurring at such magnitudes as to create openings large enough to facilitate regeneration. The plots without discrete differences in ages of the trees may also have been the result of bark beetle damage and resulting tree mortality or a combination of windthrow disturbances and infestation of trees by bark beetles. In such stands, evidence of multiple disturbances such as fire scars was studied as well as the age-distribution graphs of the stand. If the age distribution had a strong bimodal pattern, and disturbance evidence suggested multiple, frequent disturbances, then cohorts with less than a 20-year difference in age may have been designated. Cohort designations were based on breast height age rather than base age. This is the source of some error in cohort assignment if years to breast height is highly variable. Trees were assigned to cohorts 1, 2, or 3; cohort 1 being the oldest. No plot contained more than three cohorts.

Leaf area estimation

Projected leaf area for individual trees was estimated using an equation developed by Long and Smith (1988) for lodgepole pine in southeastern Wyoming. This equation was chosen over others because it was developed in a similar environment to that of western and central Montana. Long and Smith (1988) sampled in climatic regions receiving precipitations between 400 and 900 mm/year, the same range of precipitation received in the various plots sampled in this study. This equation also included the

Table 1. Characteristics of sampled stands: location, habitat type, age structure, number of age classes, plot size, site index (from even-aged stands only), and projected LAI (leaf area index).

Plot	Location	Habitat type*	Structure	Cohorts	Plot size (m^2)	Site index (m at 50 years)	LAI
1	Bitterroot	ABGR/XETE	Even-aged	1	400	16.2	1.5
2	Bitterroot	ABLA/VACA	Even-aged	1	400	11.9	1.6
3	Bitterroot	ABLA/VACA	Even-aged	1	400	14.3	1.6
4	Bitterroot	ABLA/XETE	Even-aged	1	400	21.6	2.1
5	Bitterroot	ABLA/VACA	Multiaged	2	200		3.3
6	Bitterroot	ABLA/VACA	Multiaged	3	200		3.0
7	Bitterroot	ABLA/XETE	Multiaged	3	200		3.0
8	Bitterroot	ABLA/VACA	Multiaged	3	200		2.9
9	Bitterroot	ABLA/VACA	Multiaged	3	200		3.7
10	Bitterroot	ABLA/XETE	Even-aged	1	200	22.9	2.5
11	Bitterroot	ABLA./XETE	Multiaged	3	200		2.0
12	Bitterroot	PSME/VAGL	Multiaged	2	200		1.3
13	Bitterroot	ABLA/XETE	Multiaged	2	200		1.8
14	Lubrecht	PSME/LIBO	Even-aged	1	200	16.5	2.2
15	Lubrecht	PSME/CARU	Even-aged	1	200	20.7	1.4
16	Lubrecht	ABLA/CACA	Even-aged	1	200	13.7	1.8
17	Lubrecht	PSME/VACA	Even-aged	1	200	21.0	2.2
18	Lubrecht	PSME/VACA	Multiaged	2	200		2.2
19	Lubrecht	PSME/VACA	Even-aged	1	200	21.6	1.2
20	Tenderfoot	ABLA/VAGL	Even-aged	1	200	13.7	2.2
21	Tenderfoot	ABLA/VAGL	Multiaged	2	200		2.5
22	Tenderfoot	ABLA/VAGL	Multiaged	3	200		3.1
23	Tenderfoot	ABLA/VAGL	Multiaged	3	200		2.4
24	Tenderfoot	ABLA/VAGL	Multiaged	3	200		1.7
25	Tenderfoot	ABLA/VAGL	Even-aged	1	200	11.3	1.8
26	Tenderfoot	ABLA/VAGL	Multiaged	2	200		2.5
27	Tenderfoot	ABLA/VAGL	Even-aged	1	200	15.2	1.9
28	Lubrecht	PSME/SYAL	Even-aged	1	200	18.6	0.9
29	Lubrecht	PSME/SYAL	Even-aged	1	200	19.2	1.8
30	Tenderfoot	ABLA/VASC	Multiaged	2	200		2.8
31	Tenderfoot	ABLA/VAGL	Multiaged	2	200		2.8
32	Tenderfoot	ABLA/VASC	Even-aged	1	200	13.1	3.1
33	Tenderfoot	ABLA/VASC	Even-aged	1	200	11.3	2.0
34	Tenderfoot	ABLA/VAGL	Even-aged	1	200	16.8	1.9
35	Tenderfoot	ABLA/VASC	Multiaged	2	200		2.6

*Species abbreviations: ABGR, *Abies grandis*; ABLA, *Abies lasiocarpa*; PSME, *Pseudotsuga menziesii* var. *glauca*; XETE, *Xerophyllum tenax*; VACA, *Vaccinium caespitosum*; VAGL, *Vaccinium globulare*; LIBO, *Linnaea borealis*; CARU, *Calamagrostis rubescens*; CACA, *Calamagrostis canadensis*; SYAL, *Symphoricarpos albus*; VASC, *Vaccinium scoparium*.

distance from breast height to the center of a tree's crown (D, in m) (Long and Smith 1988). The actual equation was

$$\text{Projected leaf area} = (0.064 A_S^{1.43} D^{-0.73}) \times 1.24 \text{ (the correction factor for fresh needles)}$$

where A_S was the sapwood cross-sectional area of the tree in centimetres.

Sapwood cross-sectional area of the tree at 1.37 m was calculated from the DBH and bark thickness measurements and from the sapwood measurements from the two increment cores extracted from every tree on every plot. Stand LAI was determined by summing the leaf areas (m^2) of all the trees in the stand and dividing by the plot size (m^2).

Tree and stand volume calculation

Cubic volume for the whole tree including the stump was calculated for every tree in the sampled plots. Species-specific, unpublished, stemwood volume equations developed by Champion International Corporation (Rocky Mountain Operations, Milltown, Mont.) for Montana conifers were used (Table 2). Volumes were estimated in English units and converted to metric units.

Radial increment for the previous 5 years was measured to the nearest 0.5 mm using a dissecting microscope from the two cores extracted from each tree. Five-year height growth was measured on a subsample of windthrown and felled trees by counting five budscars from the tip of the terminal. Five-year height increment (HGTINC) was then estimated for all other trees using a multiple regression equation derived from the subsample. This model used DBH (m) and 5-year radial increment (m) (RADINC) as independent variables and explained 76% of the variation in 5-year height growth (m). The actual equation was

$$\text{HGTINC} = 0.471 + [6.401 \times \text{DBH} + (-0.00044 \times \text{RADINC}^{-1})]$$

Table 2. Coefficients for Champion International Corporation (Rocky Mountain Operations, Milltown, Montana) volume equations used in this study.

	a	*b*	*c*
Lodgepole pine ≤ 80 years old	–2.537 58	1.877 65	1.033 12
Lodgepole pine > 80 years old	–2.003 00	1.656 14	0.884 91

Note: The equations were $CVTS = (10^a)(DBH^b)(HGT^c)$ and $CVT = CVTS(0.9679 - 0.1051 \times 0.5523^{(DBH - 1.5)})$, where CVTS is the cubic-foot volume of the total tree, including the top and stump; CVT is the cubic-foot volume, excluding stump volume; HGT is total height in feet; DBH is diameter at 4.5ft (1.37 m) in inches; and *a*, *b*, and *c* are species- and age-specific coefficients.

Table 3. Mean projected LAI (leaf area index) for even-aged and multiaged stands in Montana.

	Bitterroot		Lubrecht		Tenderfoot		All stands	
	LAI	*n*	LAI	n	LAI	*n*	LAI	*n*
Even-aged	1.8 (0.19)*a*	5	1.6 (0.19)	7	2.2 (0.19)*c*	6	1.9 (0.12)*e*	18
Multiaged	2.6 (0.28)*b*	8	2.2	1	2.5 (0.14)*d*	8	2.6 (0.15)*f*	17
All stands	2.3 (0.21)	13	1.7 (0.18)	8	2.4 (0.12)	14	2.2 (0.11)	35

Note: Values are means, with SE given in parentheses. Values with the same letter are not significantly different between even-aged and multiaged stands within study areas using *t* tests ($\alpha = 0.05$). It was not possible to use *t* tests for Lubrecht data because only one multiaged stand was sampled.

The height of each tree in 1991 was estimated by subtracting the estimated 5-year height growth from the height measured in the field. Using the radial increment measurements and assuming the bark growth increased by the same percentage that diameter increased, the DBH of the tree in 1991 was estimated. Cubic volume for each tree 5 years previous (1991) was estimated using the Champion volume equations. Volume increment for the past 5 years was the difference between volume in 1991 and 1996. Individual tree vigor or growing space efficiency (GSE) was expressed as ratios of volume increment of LAI or leaf area for stands, cohorts, and individual trees.

Statistical analysis

Student's *t* tests were used to compare the differences in total LAI, standing volume, volume increment, and GSE between even-aged and multiaged stands and between the different cohorts. One way analysis of variance (ANOVA) was used to test the differences in mean stand LAI, mean stand volume growth, mean stand density, and mean stand GSE among different habitat types and study locations. Linear regression was used to determine the relationship between stand volume increment and LAI, and tree volume increment and leaf area among the canopy strata, overstory, and understory trees. Evaluation of the regression models was based on residual plots, standard errors, adjusted coefficients of determination (r^2), and their biological justification.

Results

Evaluation of growing space per stand

Projected LAI of study plots sampled in Montana ranged from 0.9 to 3.7 (Table 1). LAI ranged from 1.3 to 3.7 on the Bitterroot National Forest sites, from 0.9 to 2.2 on the Lubrecht sites, and from 1.7 to 3.1 on the Tenderfoot Creek sites (Table 1). Mean LAI at Tenderfoot Creek was significantly higher than at Lubrecht ($p = 0.046$) but not significantly higher than the mean LAI of the Bitterroot stands (Table 3). Mean LAI of the multiaged (two or three cohorts) stands was significantly higher than mean LAI of even-aged (one cohort) stands over all plots sampled ($p = 0.001$) (Table 3). There were no significant differences in mean LAI across the different habitat types sampled.

In multiaged stands, cohort LAI was unequally distributed among cohorts and generally decreased with decreasing cohort age (Table 4). Only plots 5, 7, 18, 22, and 23 had higher LAI in cohort 2 than in the cohort 1. Cohort 3, when present, always had less LAI than the older cohorts. Mean LAI of cohort 1 in multiaged stands was significantly higher than the mean LAI of cohorts 2 and 3 ($p \leq 0.002$) (Table 5). The distribution of trees per cohort was also unequal within the multiaged stands and varied considerably between plots (Table 4). Plots with greater numbers of trees in cohort 2, also had large amounts of the plot LAI in cohort 2. Many plots had fewer trees in cohort 2 than cohort 1 and these plots usually had 10% or less of plot LAI in cohort 2. Only plots 22 and 24 had distributions of trees per cohort that resembled the reverse J-shaped curve typically associated with uneven-aged stands.

Overstory trees (A and B strata trees) had significantly greater LAI than trees in the understory (C and D strata trees) ($p < 0.001$) (Table 6). In multiaged stands, the overstory included a mean LAI of 2.3 (or 90% of plot LAI) as compared with a mean LAI of only 0.3 for the understory.

Total standing stemwood volume ranged from 79.5 $m^3 \cdot ha^{-1}$ on plot 4 in the Bitterroot National Forest to 711.5 $m^3 \cdot ha^{-1}$ on plot 34 in the Tenderfoot Creek. Stands at Tenderfoot had significantly higher mean standing volume per hectare than those from Lubrecht ($p = 0.005$) (Table 7). Stands from the Bitterroot National Forest had volumes intermediate between the other two study areas. Multiaged stands had greater standing volume than even-aged stands at Lubrecht and Bitterroot, but not Tenderfoot. The Tenderfoot study area contained older trees at a significantly higher mean density per hectare than the Lubrecht Forest study area. There were no significant differences in mean standing volume among plots with one, two, or three cohorts present.

Stand volume increment ($m^3 \cdot ha^{-1}$ per year) ranged from 5.7 to 15.8 at the Bitterroot, from 3.7 to 10.1 at Lubrecht,

Table 4. Number of trees, percent of stand LAI (leaf area index) per cohort, and cohort GSE (growing space efficiency) in multiaged stands.

Plot	Plot size	Trees (ha^{-1})			Percent LAI/cohort			Cohort GSE ($cm^3 \cdot m^{-2}$)			Plot LAI
		Cohort 1	Cohort 2	Cohort 3	Cohort 1	Cohort 2	Cohort 3	Cohort 1	Cohort 2	Cohort 3	
5	200	40	270		38.5	61.4		387.9	262.0		3.3
6	200	40	100	85	51.4	45.5	3.1	336.1	318.9	182.0	3.0
7	200	50	145	115	32.2	48.6	19.2	377.3	304.8	266.8	3.0
8	200	90	70	90	69.0	25.0	6.0	351.5	296.5	139.9	3.0
9	200	45	10	95	75.6	6.2	18.1	295.7	344.8	175.0	3.7
11	200	20	75	215	41.3	35.9	21.6	423.4	344.9	266.3	2.0
12	200	35	295		65.8	34.2		580.8	536.7		1.3
13	200	195	50		95.4	4.6		449.1	254.5		1.8
18	200	40	125		47.5	52.5		424.6	355.8		2.2
21	200	95	35		89.7	10.3		407.0	408.5		2.5
22	200	15	160	180	35.8	49.9	14.3	326.3	258.3	161.0	3.1
23	200	5	130	25	11.7	87.3	0.9	554.7	287.4	100.6	2.4
24	200	30	45	85	64.9	30.4	4.7	566.8	320.7	86.2	1.7
26	200	285	30		98.8	1.3		383.9	309.6		2.5
30	200	140	90		97.6	2.4		401.0	96.8		2.8
31	200	230	85		98.4	1.6		348.6	124.5		2.8
35	200	165	85		96.6	3.4		318.2	114.5		2.6
Mean		89	106	111	65.3	29.4	11.0	407.8	290.5	172.2	2.5

Table 5. Mean LAI (leaf area index) for the different age-classes in multiaged stands.

Cohort	LAI		n
	Mean	SE	
1	1.6	0.20	17
2	0.8	0.17	17
3	0.3	0.09	8

and from 2.4 to 12.8 at Tenderfoot. Multiaged stands had greater increment than even-aged stands at Bitterroot and Lubrecht but not Tenderfoot (Table 7). Stand volume increment increased with increasing stand LAI, but the relationship was not strong (Fig. 1). There was no difference in the mean stand volume increment among stands with one, two, and three cohorts present or among the stands in the three different study areas.

Stand GSE varied widely across the sample plots ranging from 133.1 $cm^3 \cdot m^{-2}$ per year for plot 25 to 693.3 $cm^3 \cdot m^{-2}$ per year for plot 34. There was no difference in mean stand GSE between habitat types sampled. Even-aged stands had significantly higher GSE at Bitterroot, Tenderfoot, and overall. The differences in mean stand GSE between stands with one, two, and three cohorts present were not significant.

The mean stand GSE in even-aged stands (Table 7) was higher but not significantly higher than the mean GSEs of cohort 1 in two- and three-cohort stands (Table 4). Mean GSE of cohort 1 was significantly greater than the mean GSE of cohort 2 and cohort 3, and mean GSE of cohort 2 was significantly greater than the mean GSE of cohort 3 (Table 4). Cohort GSE decreased with decreasing age of cohort in every plot except plot 21 where GSE was nearly equal (Table 4).

Individual tree GSE ($cm^3 \cdot m^{-2}$ per year) ranged from 25.2 to 3431.3 for trees in cohort 1, from 11.2 to 3612.7 for trees in cohort 2, and from 23.4 to 665.4 for trees in cohort 3 (Fig. 2). Trees in the understory had a significantly lower mean GSE than trees in the overstory (Fig. 3). Mean individual tree GSE of cohort 1 was significantly higher than that of cohorts 2 and 3 ($p < 0.001$), and GSE of cohort 2 was significantly higher than that of cohort 3 ($p < 0.001$) (Fig. 2). There was no relationship evident between individual tree GSE and age for even-aged or multiaged stands (Fig. 4).

Mean individual tree GSE was significantly higher at Lubrecht and the Bitterroot than at Tenderfoot ($p \leq 0.001$) (Fig. 2). This may be due to differences in tree age, density, and stand structure in the different study areas. Stands

Fig. 1. Volume increment in relation to leaf area index for multiaged lodgepole pine stands from three study areas. VI = 5.994 + 1.179 × LAI; r^2 = 0.34, standard error of estimate = 0.93 $m^3 \cdot ha^{-1}$ per year. (VI, volume increment in $m^3 \cdot ha^{-1}$ per year; LAI, leaf area index).

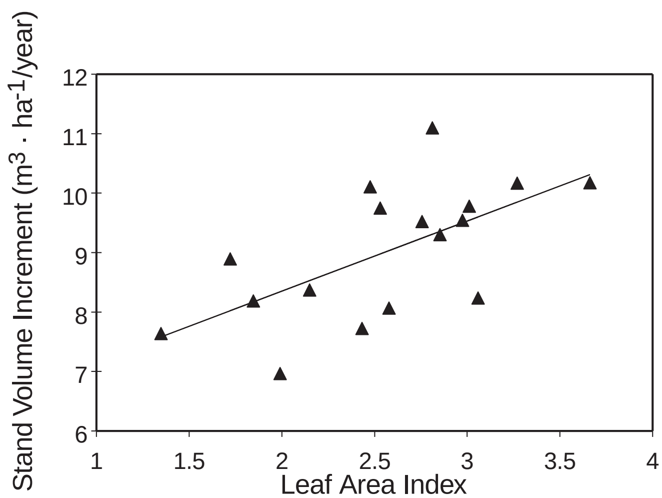


Table 6. Number of trees and percent of stand LAI (leaf area index) by canopy strata in multiaged stands.

Plot	Trees/canopy strata (ha^{-1})		Percent LAI/canopy strata		LAI		Plot LAI
	Overstory	Understory	Overstory	Understory	Overstory	Understory	
5	180	130	96	4	3.1	0.1	3.3
6	140	85	97	3	2.9	0.1	3.0
7	260	50	97	3	2.9	0.1	3.0
8	175	75	97	3	2.8	0.1	3.0
9	55	95	98	2	3.6	0.1	3.7
11	105	215	82	18	1.6	0.4	2.0
12	45	285	70	30	1.0	0.4	1.3
18	110	55	97	3	2.1	0.1	2.2
21	95	35	94	6	2.3	0.1	2.5
22	115	240	78	22	2.4	0.7	3.1
23	115	45	96	4	2.3	0.1	2.4
24	30	125	56	44	1.0	0.4	1.7
26	255	60	96	4	2.4	0.1	2.5
30	105	125	93	7	2.6	0.2	2.8
31	120	195	78	22	2.2	0.6	2.8
35	85	165	78	22	2.0	0.6	2.6
Mean	124.3	123.8	87.7	12.3	2.3	0.3	2.5

Table 7. Standing volume, volume increment, and growing space efficiency for even-aged and multiaged stands across three different study sites.

	Bitterroot		Lubrecht		Tenderfoot		All Stands	
	Mean	*n*	Mean	*n*	Mean	*n*	Mean	*n*
Standing volume ($m^3 \cdot ha^{-1}$)								
Even-aged	295.6 (85.5)*a*	5	221.8 (45.8)	7	517.3 (51.0)*b*	6	340.8 (45.0)*d*	18
Multiaged	342.9 (23.8)*a*	8	361.7	1	368.9 (30.4)*c*	8	356.2 (17.8)*d*	17
All stands	324.7 (34.4)	13	239.3 (45.9)	8	432.5 (33.6)	14	348.3 (24.4)	35
Volume increment per year ($m^3 \cdot ha^{-1}$)								
Even-aged	7.2 (0.6)*e*	5	6.8 (1.1)	7	9.8 (1.6)*g*	6	7.9 (0.7)*h*	18
Multiaged	8.9 (1.0)*f*	8	8.4	1	9.2 (0.4)*g*	8	9.0 (0.5)*i*	17
All stands	8.3 (0.7)	13	7.0 (0.9)	8	9.5 (0.7)	14	8.5 (0.5)	35
Growing space efficiency per year ($m^3 \cdot m^{-2}$)								
Even-aged	4.2 (0.7)*j*	5	4.3 (0.6)	7	4.6 (0.8)*l*	6	4.3 (0.4)*n*	18
Multiaged	3.6 (0.4)*k*	8	3.9	1	3.7 (0.3)*m*	8	3.7 (0.2)*o*	17
All stands	3.8 (0.3)	13	4.2 (0.5)	8	4.1 (0.4)	14	4.0 (0.2)	35

Note: Values given in parentheses are SE. Values with the same letter are not significantly different between even-aged and multiaged stands within study areas using *t* tests (α = 0.05). Using *t* tests was not possible for Lubrecht data because only one multiaged stand was sampled.

sampled at Lubrecht included only one two-aged stand and no three-aged stands. The Tenderfoot plots contained the oldest trees sampled. Many trees were over 150 years old, the age at which a noticeable decline in vigor occurred. The Tenderfoot plots also had the highest mean density of trees per hectare of all three sites sampled, but the difference was not significant at the 0.05 level.

To assess the relationship between volume increment and tree leaf area, all trees from a single cohort were combined from multiaged stands for all three of the study areas. For example, all trees from cohort 1 from both two- and three-cohort stands were grouped together. This grouping was used because little or no differences were observed when the cohorts were grouped by the age structure of the stand (e.g., two- or three-cohorts) or by study area.

Tree volume increment was strongly related to leaf area in the multiaged plots for individual cohorts and canopy strata. Linear equations provided a strong fit for the second cohort and the understory (Figs. 5 and 6). Nonlinear equations provided a stronger fit for the first and third cohorts and the overstory. All regression equations had a r^2 of 0.75 or higher. Equations for the older cohorts and overstory predicted greater increment per unit of leaf area than equations for younger cohorts and the understory. For example, a tree with a leaf area of 40 m^2 from the oldest cohort would be predicted to have an increment of 0.015 m^3/year as compared with 0.011 m^3/year for a tree from the second cohort.

Discussion

The projected LAI results in this study were similar to results reported by others for lodgepole pine in the central

Fig. 2. Mean individual tree growing space efficiency (GSE) by cohort and study area. All means were significantly different ($p < 0.001$).

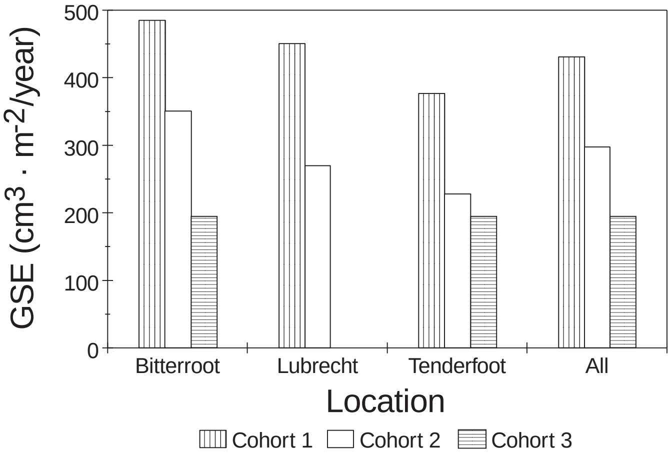
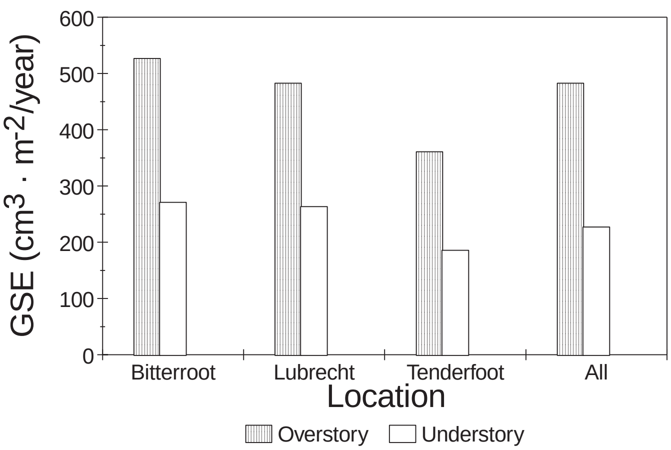


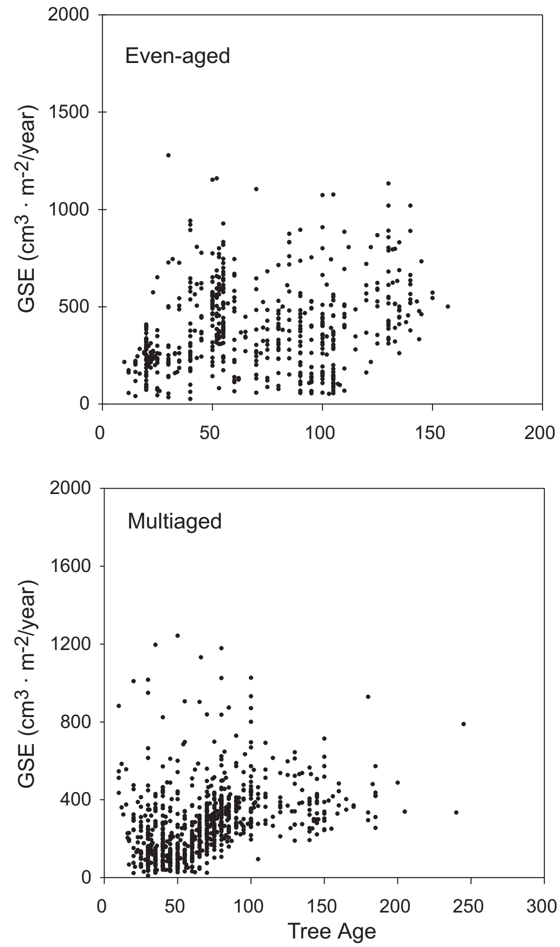
Fig. 3. Mean individual tree growing space efficiency (GSE) by canopy strata and study area. All means were significantly different ($p < 0.001$).



Rocky Mountains, which have ranged from 1.2 to 6.5 (Smith and Long 1989; Jack and Long 1991; Long and Smith 1992). These results were lower than the 8.8 to 13.4 range published by Keane and Weetman (1987) for all-sided LAI in even-aged stands in British Columbia. These differences in LAI were probably related to comparing projected with all-sided LAI, and variations in sapwood – leaf area prediction equations. For example, LAIs calculated using two alternate equations (Pearson et al. 1984; Keane and Weetman 1987) were two to three times greater than the LAIs calculated using the Long and Smith (1988) equation used in this study.

Multiaged stands had higher LAI than even-aged stands in this study. This is in contrast to the results for even-aged and multiaged ponderosa pine stands (O'Hara 1996) but may be related to the higher stand densities observed in the multiaged lodgepole pine stands. Cohort LAI generally decreased with decreasing cohort age with a few exceptions in individual plots. These exceptions appeared to have resulted from relatively severe disturbances, which left very few trees in the oldest cohort.

Fig. 4. Mean individual tree growing space efficiency (GSE) by tree age for even-aged stands and multiaged stands.



The volume increment results of this study (Table 7) were comparable with results from other studies in lodgepole pine forests. In southern Wyoming and northern Utah, Smith and Long (1989) and Long and Smith (1990, 1992) reported lodgepole pine stand increment ranging from 1.4 to 17.7 $m^3 \cdot ha^{-1}$ per year with a mean stand volume increment ranging between 5 and 7 $m^3 \cdot ha^{-1}$ per year. Binkley et al. (1995) found periodic annual increment to range from 3.9 to 8.8 $m^3 \cdot ha^{-1}$ in lodgepole pine in southeastern Wyoming. Multiaged stands had higher volume increment except at Tenderfoot where the older cohort was relatively old as compared with the other study areas.

A weak relationship was found between stand volume increment and stand LAI for the multiaged lodgepole pine stands (Fig. 1). O'Hara (1996) also found only weak relationships between stand volume increment and LAI in multiaged ponderosa pine. O'Hara attributed this to the inability of LAI to represent stand structure in multiaged stands and found more variation in increment could be explained if the location of LAI, or the stand structure, were considered along with total LAI. A similar relationship may apply to lodgepole pine. Volume increment – LAI relationships for even-aged lodgepole pine stands have generally been stronger than those observed in this study for multiaged stands (Dean et al. 1988; Smith and Long 1989; Long

Fig. 5. Tree volume increment/leaf area relationships by cohort for multiaged stands from all study areas combined. The equations were VI = –0.001 523 + 0.001 135 × $LA^{0.719\ 964}$ (r^2 = 0.822) for cohort 1, VI = 0.000 120 + 0.000 280 × LA (r^2 = 0.889) for cohort 2, and VI = 0.000 126 + 0.000 045 × $LA^{1.745\ 506}$ (r^2 = 0.888) for cohort 3 (VI, volume increment in m^3/year, LA, tree leaf area in m^2).

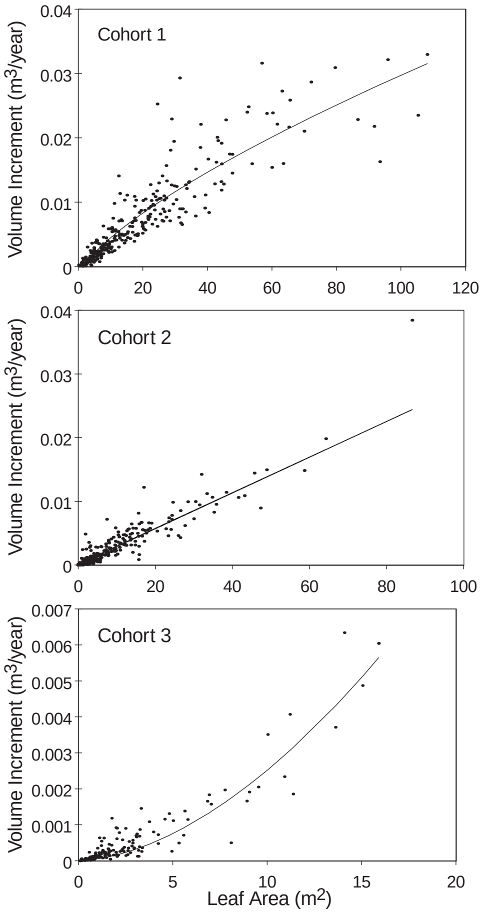
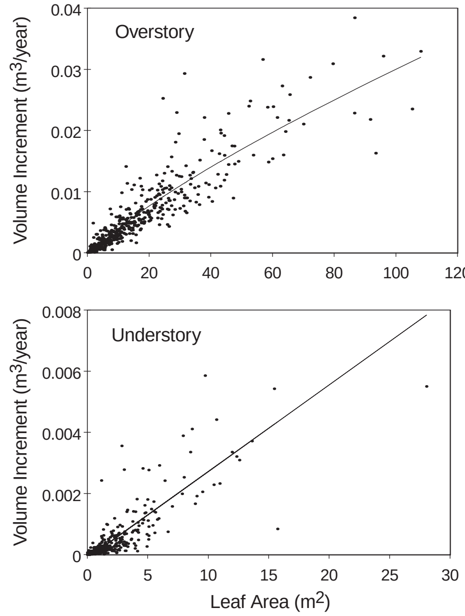


Fig. 6. Tree volume increment/leaf area relationships by canopy strata for multiaged stands from all study areas combined. The equations were VI = –0.001 167 + 0.000 835 × $LA^{0.786\ 051}$ (r^2 = 0.804) for the overstory, and VI = –0.000 121 + 0.000 284 × LA (r^2 = 0.755) for the understory (VI, volume increment in m^3/year, LA, tree leaf area in m^2).



and Smith 1990). Smith and Long (1989) have noted, however, the importance of vertical arrangements of LAI in affecting stand increment.

Strong relationships were found between individual tree leaf area and individual tree volume increment for the different cohorts and strata. This is consistent with other studies of even-aged lodgepole pine (Long and Smith 1990) and multiaged ponderosa pine (O’Hara 1996). This indicates the potential to predict stand increment using individual trees within components such as age-classes or cohorts, canopy strata, or species. If increment could be successfully predicted with a component, then components could then be summed to determine stand increment thereby integrating stand structure variability into increment prediction using LAI. O’Hara (1996) found using cohorts as components greatly improved increment prediction over using only LAI. Similar results are likely with lodgepole pine (Kollenberg 1997).

Age did not appear to be an important factor affecting GSE for trees growing in even-aged structures (Fig. 4). Previous studies have found tree vigor or GSE to be strongly influenced by tree age (Kaufman and Ryan 1986; Kaufmann and Watkins 1990; Long and Smith 1992; Ryan and Waring 1992; Binkley et al. 1995; Kaufmann 1996). GSE decreased slightly with age in the trees growing in multiage structures, particularly for trees older than approximately 150 years (Fig. 4). This indicates that GSE might not decline before 150–160 years of age. Trees in even-aged stands ranged from very high to very low in GSE (Fig. 4) but included no trees older than 160 years. In the multiaged stand structures, GSE approached zero among some younger trees (ages 20–70), but none of the trees 80 years and older had such low GSEs. This may indicate younger, less vigorous trees in multiage structures may be released and become more vigorous over time. The less vigorous trees in the even-aged stands may not be released and remain less vigorous and suppressed for longer time spans. Conversely only the more vigorous younger trees may survive to an older age. Kaufmann and Watkins (1990) found that vigorous young trees became low vigor trees later at an older age and that older trees that were vigorous had lower vigors when they were younger. O’Hara (1996) also found that mean cohort GSE decreased with decreasing cohort age in ponderosa pine. The highest cohort GSE in ponderosa pine was cohort 1 in multiaged stands, whereas the highest cohort GSE in this lodgepole pine study was in the even-aged stands.

Although a strong relationship between GSE and age was not apparent over all study areas combined (Fig. 4), the significant differences between average GSE for individual cohorts and canopy strata (Figs. 2 and 3) suggests crown canopy position may be a more important determinant of efficiency than age. Cohorts, of course, are based on age, but in these stands they were generally found in strata and always with the oldest cohort in the uppermost canopy position.

When trees from different stands and study areas are combined as in Fig. 4, canopy positions are intermingled in stands of diverse age structure.

Conclusions

Multiaged lodgepole pine stands have higher LAI but lower GSE than comparable even-aged stands. The considerable variation that was found between stands and between study areas suggests different results might be found in multiaged stands with a younger overstory or different density histories. Stand volume increment was poorly related to stand LAI, but individual tree increment was strongly related to tree leaf area. GSE declined with tree age in multiaged stands but not in even-aged stands. These results indicate the poor relationship between stand volume increment and stand LAI may be due to differential leaf area or growing space efficiencies related to canopy position or age-class.

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