Management, Morphological, and Environmental Factors Influencing Douglas-Fir Bark Furrows in the Oregon Coast Range

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ABSTRACT

Many land managers in the Pacific Northwest have the goal of increasing late-successional forest structures. Despite the documented importance of Douglas-fir tree bark structure in forested ecosystems, little is known about factors influencing bark development and how foresters can manage development. This study investigated the relative importance of tree size, growth, environmental factors, and thinning on Douglas-fir bark furrow characteristics in the Oregon Coast Range. Bark furrow depth, area, and bark roughness were measured for Douglas-fir trees in young heavily thinned and unthinned sites and compared to older reference sites. We tested models for relationships between bark furrow response and thinning, tree diameter, diameter growth, and environmental factors. Separately, we compared bark responses measured on trees used by bark-foraging birds with trees with no observed usage. Tree diameter and diameter growth were the most important variables in predicting bark characteristics in young trees. Measured environmental variables were not strongly related to bark characteristics. Bark furrow characteristics in old trees were influenced by tree diameter and surrounding tree densities. Young trees used by bark foragers did not have different bark characteristics than unused trees. Efforts to enhance Douglas-fir bark characteristics should emphasize retention of larger diameter trees' growth enhancement.

Keywords: bark furrow depth, cavity-nesters, experimental thinning, model selection

Large diameter Douglas-fir (*Pseudotsuga menziesii*) trees with well-developed bark structure are a key structural component of forested ecosystems in western states (Minore 1979, Spies and Franklin 1991, Van Pelt 2007). Douglas-fir bark is formed by flaky patches of thick outer cork layers, bound together in furrows by a fibrous secondary phloem (Ross and Kahmer 1971). This thick bark insulates trees (van Mantgem and Schwartz 2003) and influences postfire mortality patterns (Ryan and Reinhardt 1988, Fowler et al. 2004). Douglas-fir tree bark is also a key component of late-successional structure as it provides microhabitat for a host of species; these habitat features increase in number and quality with increasing bark structural development (Michel and Winter 2009). Epiphytes on tree boles show marked variation with respect to bark surface, stem diameter, tree microclimate, and height in the canopy (McCune et al. 2000, Thomas et al. 2001). Invertebrate density and diversity are positively related to complexity of bark structure, and arthropod densities are significantly and positively associated with Douglas-fir bark furrow depth (Mariani and Manuwal 1990). Twelve species of bats occur in Douglas-fir forests of the Pacific Northwest, of which eight roost in bark structures such as bark crevices, flakes, and cavities (Christy and West 1993, Wunder and Carey 1996). Oregon Coast Range Douglas-fir supports at least six species of bark-gleaning birds (Carey et al. 1991), including the brown creeper (*Certhia americana*) that shows strong preference for larger bark furrows (Mariani and Manuwal 1990, Weikel and Hayes 1999). Because of its role in support of various ecosystem functions, the amount and variability of bark microhabitat features has been suggested as an indicator of forest biodiversity (Michel and Winter 2009, Winter and Möller 2009). Despite its documented role in supporting microhabitat and species diversity in forested ecosystems, the importance of environmental factors in Douglas-fir bark furrow development remains unclear. The ability of forest management to enhance microhabitat features such as bark furrows is also unknown.

Previous studies mainly linked Douglas-fir bark furrow depth positively to tree diameter (Mariani and Manuwal 1990, Michel et al. 2011). However, other factors also likely affect the development of bark structures. Douglas-fir bark in older trees has been observed to vary based on tree environment and position, with different sides of trees exhibiting different bark characteristics depending on exposure, orientation, and proximity of neighboring trees (Van Pelt 2007). Michel and Winter (2009) found that management history and tree age, in addition to tree diameter, influenced the density of Douglas-fir bark microhabitat features such as bark pockets and

This article uses metric units; the applicable conversion factors are: centimeters (cm): 1 cm = 0.39 in.; square centimeters (cm²): 1 cm² = 0.155 in.²; hectares (ha): 1 ha = 2.47 ac; kilometers (km): 1 km = 0.6 mi.

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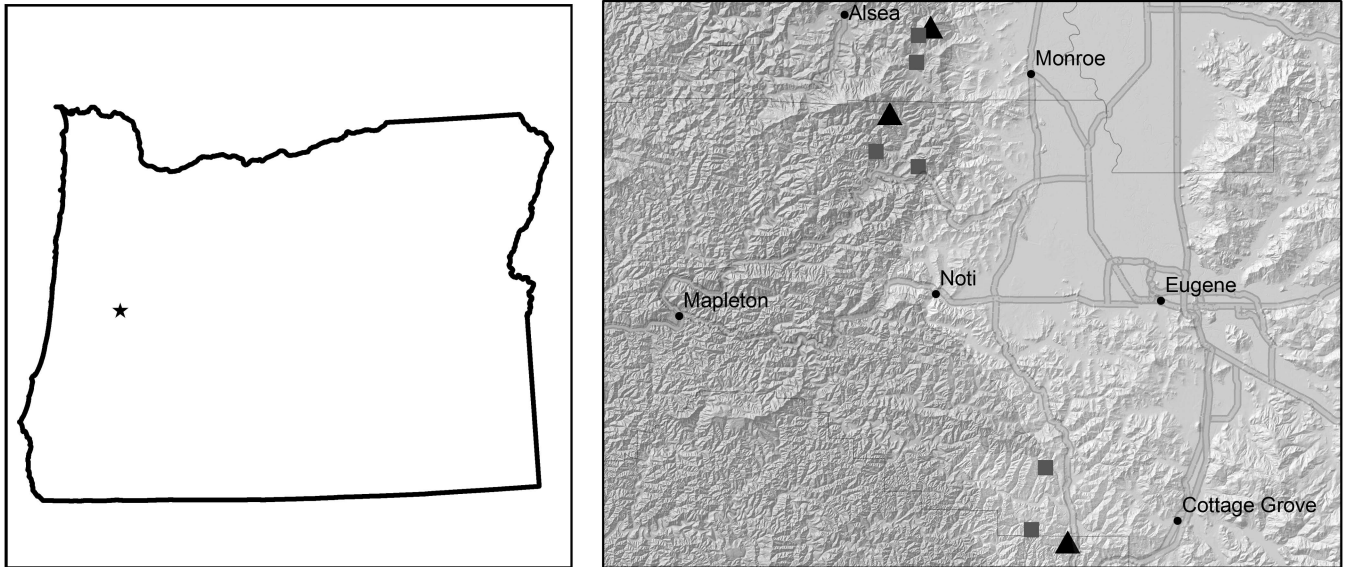
Figure 1. Study location including Young sample sites (triangles) and Old sample sites (squares) in the Coast Range of Oregon.

cavities, but their study did not evaluate the response of bark furrows or bark roughness. Bark furrowing in northern hardwood species was found to be related to tree growth rate and age as well as tree diameter (MacFarlane and Luo 2009).

Silvicultural practices designed to support diverse plant and animal forest communities and incorporate objectives for wildlife are crucial for multiple-use forest management (Hayes 1997), and a basic principal of ecologically sustainable forestry (Lindenmayer and Franklin 2002). Maintenance of forest biodiversity is mandated on federal forests (USDA Forest Service 2011) and a priority for many other public and private landowners. Silvicultural treatments supporting these goals include variable thinnings and other treatments designed to accelerate the development of late-successional forest structures in young stands (Cissel et al. 2006, Poage and Anderson 2007, Bauhus et al. 2009). Previous approaches to enhance forest structure in young even-aged stands have emphasized increasing spatial variability, thinning to increase tree diameters and growth rates (Tappeiner et al. 1997, Garman et al. 2003), and creating snags and downed wood (Rose et al. 2001). Although deeply-furrowed bark is a defining structural characteristic of mature and old Douglas-fir trees, enhancement of bark structures has not been among targeted forest management goals. Silvicultural approaches to promote deep, furrowed bark have not been developed or empirically tested (FEMAT 1993, Hayes et al. 1997, Hunter 2001). If one goal of multiple-use forest management is to promote the development of late-successional ecosystems, including the maintenance of diverse microhabitats associated with single-tree structures (Michel and Winter 2009), then a greater understanding of the effects of silviculture on bark development is needed.

Assessing management or environmental factors that influence Douglas-fir bark furrow development also requires an understanding about the range of bark furrow conditions to which fauna respond. For example, bark-foraging birds such as the brown creeper (*C. americana*) have well-documented ties to bark furrow characteristics, including furrow depth. Brown creepers select conifers with deeper bark furrows (Weikel and Hayes 1999) and are consequently more abundant in areas with very large (>100 cm dbh) trees. This is presumably due to trees with large diameters having larger furrows

and, thus, higher arthropod density (Mariani and Manuwal 1990). Identifying a range of furrow depths that support use by bark-foraging birds would provide an indicator of biological significance that managers could use to assess attainment of late-successional structural goals.

The goal of our study was to increase the understanding of management effects and environmental conditions on Douglas-fir bark furrow characteristics. Specific objectives included: (1) to investigate the importance of thinning treatment, tree diameter, diameter growth, surrounding tree density, and local tree environment on Douglas-fir bark furrow characteristics in young forests; (2) to compare Douglas-fir bark characteristics and factors influencing them in trees in young stands with those in older stands; and (3) to determine whether trees used by bark-foraging birds had distinctive bark characteristics.

Methods

Study Area and Sample Size

We conducted our study at three young forest sites and at six adjacent older forested reference sites (Figure 1). Young forest sites (62–73 years old, the Young sample) were part of a large-scale silvicultural experiment (Cissel et al. 2006, Poage and Anderson 2007, Dodson et al. 2012), selected to be representative of young forest conditions in the Oregon Coast Range (Figure 1). Management history for Young sites included regeneration harvest (1939–1946), replanting, precommercial thinning, and an experimental thinning treatment roughly one decade prior to the initiation of our study. The Old sample was developed using current vegetation survey (CVS) plots (USDA Forest Service 2012). Two CVS plots were selected randomly from the set of existing plots established in stands greater than 195 years old within 6.2 km of each of the three Young sample sites (Figure 1). Old site plant associations, sandstone-derived soils, elevations, and range in aspects were similar to Young sites. Conditions in Young and Old sample sites are summarized in Table 1.

At each Young site, we sampled trees from two treatments: a heavily thinned treatment retaining approximately 100 trees per ha

Table 1. Sample sizes for Young Unthinned ("Unt"), Young Thinned ("Thin"), and Old reference sites. Number of forager observations in Unthinned and Thinned treatments. Site characteristics for Young and Old sample sites, including maximum elevation (m), north latitude, west longitude, stand initiation year (Init yr) and year of experimental thinning (Thin yr).

| | Sample sizes | | | Foragers | | Site characteristics | | | | |
Site	Unt	Thin	Old	Unt	Thin	Elev	Latitude	Longitude	Init yr	Thin yr
Young sites										
Bottomline	40	42		2	1	360	43° 46′ 20.0″	123° 14′ 11.0″	1939	1997
Green Peak	44	42		7	1	765	44° 22′ 00.0″	123° 27′ 30.0″	1935	1999
Ten High	40	41		3	3	647	44° 16′ 50.0″	123° 31′ 06.0″	1946	2000
Old sites										
2078078			17			396	43° 46′ 56.2″	123° 20′ 14.66″	1747	–
2081082			23	1		320	43° 51′ 22.9″	123° 16′ 11.1″	1678	–
2095070			15			299	44° 12′ 2.0″	123° 28′ 36.3″	1795	–
2096066			10			457	44° 13′ 2.0″	123° 32′ 43.60″	1539	–
2100070			16			383	44° 19′ 25.3″	123° 28′ 39.89″	1769	–
2101070			15			332	44° 20′ 54.0″	123° 28′ 40.61″	1659	–
Totals	124	125	96	13	5					

Table 2. Response and explanatory variables used in this study. Nested model levels for data.

Variable	Full name	Units	Description
Response			
FDPTH	Furrow depth	cm	Depth of the single largest furrow per tree. Quantified by: (1) creating an outline of the single-largest furrow per tree using a contour gauge, similarly to Jackson (1979); (2) digitizing and rectifying bark furrow outline in Arc GIS (9); and (3) calculating rectified polygon height using Arc GIS (9).
AREA	Furrow area	cm^2	Cross-sectional area of the single largest furrow per tree. Quantified similarly to FDPTH but by calculating rectified polygon area in Arc GIS (9).
BROUGH	Bark roughness	unitless	Bark roughness was calculated as $1{,}000*((C_a - C_t)/C_t)$, following Glitzenstein and Harcombe (1979), where C_t was tree circumference measured traditionally using a diameter tape, and C_a traced outer bark, including all furrows using 1.25 mm gauge electrical wire conformed to the tree bole at BH, similarly to Mariani and Manuwal (1990).
Explanatory			
DBH	Tree diameter at breast height	cm	Taken on bark exterior at 1.37 m, as typical silvicultural measure. Measured using established DBH nails for trees in both Young and Old sample plots.
PAI	Tree periodic annual increment	cm^2/yr.	PAI measures the growth in tree cross-sectional area at BH, calculated similarly to Poage and Tappeiner (2002), but measured using changes in outside bark diameter between measurement periods (3–9 yr), normalized to one year.
RD	Relative density	unitless	Calculated as BA/QMD$^{0.5}$, as per Curtis (1982). RD was calculated using all trees in fixed area plots surrounding individual sample tree, both for Young and Old plots. Young plots had 17.9 m radii; Old plots had 15.6 m radii.
HTLD	Plot heatload	unitless	Calculated similarly to McCune and Keon (2002), using regression equations with the folded aspect, slope, and latitude of the surface in which the tree was rooted.
FASP	Folded furrow aspect	0°–180°	Direction (azimuth, in degrees) which the single largest furrow faces away from the tree bole, folded about a southwest-northeast line similarly to McCune and Dylan (2002) such that 0° represents NE-facing furrows and 180° represents SW-facing furrows.
UP	Uphill orientation	0°–180°	Quantified as the absolute difference between folded plot aspect (McCune and Dylan (2002)) and folded furrow aspect (FASP). UP ranges from 0° or downhill-facing (furrow aspect same as plot aspect) to 180° or uphill-facing (furrow aspect opposite of plot aspect).
CC	Furrow-side overstory cover	%	Measured using a spherical densiometer (Lemmon 1956), held 1 m from furrow, perpendicular to breast height, similarly to Fiala et al. (2006).
FORAGER	Observed use by bark-foraging bird	categ	A categorical variable with two levels: used by a bark-foraging bird, or not used. Furrow responses were assigned to the FORAGER class if bark foraging was observed for that tree during opportunistic surveys.
Model levels			
PLOT	Fixed radius plot	categ	Young sample plots had 17.9 m radii; Old plots had 15.6 m radii.
TRT	Treatment	categ	Treatment was also included as a categorical explanatory variable.
SITE	Site	categ	Three independent Young sites; six independent Old sites.

(Thinned), and an unthinned treatment retaining 495–866 trees per ha (Unthinned). Old reference sites did not have a treatment level.

The Young sample consisted of 40–44 Douglas-fir trees from each treatment at each site, selected randomly from trees >40 cm dbh (DBH) sampled in the previous silvicultural experiment (Cissel et al. 2006). The Old sample included a minimum of 10 and up to 25 sample trees from each CVS plot based on availability, selected randomly from all previously sampled Douglas-fir trees >40 cm DBH. Data collection in both Young and Old samples occurred in dry conditions in 2008–2009.

Bark Furrow Responses and Explanatory Variables

Three bark furrow responses were measured for each sample tree in Young and Old sites (Table 2). Bark response variables were correlated and considered to represent different ways of quantifying a similar bark response. Except where noted, all response and explanatory variables were measured at 1.37 m above the uphill interface between the tree and the ground surface (breast height (BH)). Bark furrow depth and area were measured for the single largest furrow in each tree, using methods similar to those in Jackson (1979). A contour gauge was used to create a furrow outline in the field. This outline was scanned, digitized, rectified, and was closed as

a polygon in ArcGIS (ESRI 2010); furrow area was calculated as rectified polygon area and furrow depth as rectified polygon width, the length of the axis perpendicular to the bark surface. Bark roughness was calculated as the difference between tree circumference, measured using a malleable 1.25 mm diameter wire conformed to outer bark and furrow surfaces, and traditional tree circumference measured using a steel tape (Table 2). This difference was standardized to traditional circumference and multiplied by 1,000, following Glitzenstein and Harcombe (1979).

Eight factors were measured as potential explanatory variables influencing development of Douglas-fir bark furrow responses (Table 2). Thinning treatment (TRT) was assigned as a categorical variable (Thinned, Unthinned) at the treatment scale for the Young sample only. Relative density of surrounding trees (RD) was measured at the plot scale following Curtis (1982), using data from fixed area plots in Young and Old samples. Three factors were measured at the tree scale: tree diameter, tree diameter growth, and heatload. Tree diameter (DBH) was measured using a steel diameter tape. Tree growth was measured as periodic annual increment (PAI) in tree cross-sectional area since last measurement, using changes in outside bark diameter between measurement periods (3–9 years), normalized to one year. Heatload (HTLD), a variable used to represent the effects of annual direct incidental radiation received by the geomorphic surface in which the tree was rooted, was estimated following McCune and Keon (2002). Three factors were measured at the scale of the single largest furrow on each sampled tree: canopy cover directly above the individual furrow (CC), furrow aspect (FASP), and furrow orientation with respect to hillslope (UP). CC was quantified using a curved mirror densiometer; FASP and UP were measured using a compass (Table 2).

Foraging Bird Sample

In addition to randomly selected trees in our Young and Old samples, we measured the bark responses of trees we observed being used by bark-foraging birds in the Green Peak and Ten High Young sample sites on three days (36 person hours) each in late winter of 2009. Use was defined as presence on a tree bole for greater than 10 seconds of the most commonly observed species of bark-foraging birds, the brown creeper (*C. americana*).

Analysis

We developed competing hypotheses positing that Douglas-fir bark furrow responses were a function of tree diameter, diameter growth, environmental conditions, thinning treatment, or some combination of these drivers, and populated independent, a priori competing models supporting these broad hypotheses with our explanatory variables (Table 3, 4). Models were based on ecology, tree physiology, parsimony, and careful consideration (Burnham and Anderson 1998). Model sets were limited to 43 models with a maximum of four minimally correlated ($r < 0.5$) variables. DBH was included in most models due to its observed relationship with bark characteristics in previous studies. Quadratic terms for DBH, growth, and plot density were included to represent nonlinear responses where tree physiology and mechanics made such effects seem plausible. In some models, the effect of DBH was allowed to interact with tree growth, treatment, or heatload. A null model without fixed effects was included in each model set tested to determine if any of the measured factors were related to bark furrow characteristics. Individual bark furrow observations were nested within plots, treatments (in the Young sample), and sites. Nested, hierarchical model structures were developed to address this grouped data and were included in the parameterization of all models.

We used AIC model selection and multimodel inference (Burnham and Anderson 2004) to compare models. Model sets for bark furrow depth, furrow area, and roughness responses in Young and Old samples were compared separately, resulting in six independently ranked model sets. Models involving furrow-scale explanatory variables (UP, FASP, and CC) were excluded from bark roughness model sets since roughness incorporates multiple furrows. Models involving the TRT categorical variable were excluded from Old model sets. Log transformation of bark furrow responses satisfied model assumptions of normality and constant variance with one exception. Normality of residuals for models of bark roughness in the Young sample was violated (Shapiro–Wilk's W = 0.97, P < 0.01), due to two outliers. While removal of these outliers led to roughly normally distributed residuals, no meaningful differences in results occurred, so the outliers were retained.

We used the small sample size corrected Akaike's information criterion (AICc: Burnham and Anderson 1998) to select the most likely and parsimonious models, and to illustrate the importance of individual variables. Model support was judged by AICc, model rank, residuals, and generalized R_p^2 (Nagelkerke 1991). Due to the measurement of RD as a tree-scale variable and the inclusion of quadratic and interaction terms in some models, model-averaged parameter estimates were considered inappropriate for quantifying the effects of individual variables on bark furrow response (Burnham and Anderson 2002). Instead, model-weighted predictions of bark furrow response were used for quantifying magnitude and direction of effect of individual explanatory variables. Response curves of model-weighted predictions (with unconditional 95% prediction envelopes) were investigated for the full range of explanatory variables in Young and Old samples. Effects of variables with high model weights were illustrated by setting explanatory variables at contrasting mean values for Thinned and Unthinned levels in the Young sample or at contrasting levels relevant to management for the Old sample. Model variables other than the variables of interest were set to their mean values for the sample: TRT was set at Unthinned level when not testing Thinning treatment effects. Results were depicted across an illustrative range of diameters (45–75 cm) for both the Young and Old samples.

We compared bark furrow depth, area, and bark roughness measured on trees used by bark-foraging birds with those not observed to have been used in two Unthinned Young stands. Although many bark-foraging birds were heard in Young and Old sample stands, only 18 observations of bark-forager use were made (Table 1). To avoid an unbalanced design, only the 12 late-winter 2009 observations of trees with foraging brown creeper made in Unthinned treatments in Green Peak and Ten High sites were analyzed and compared to all measured Unthinned treatment trees in these two sites. Data were fit to a mixed-effects model with site, treatment, and plot as random effects and Forager as a binary fixed effect with two states: use by bark-foraging birds (defined above) and nonuse.

Results
Effects of Thinning, Tree Diameter, Diameter Growth, and Environmental Factors

Trees in the Thinned treatment showed a weak trend in increased furrow depth, area, and bark roughness a decade following

Table 3. Models of hypothesized relationships between three separate bark furrow responses and tree, environmental and thinning treatment factors in the Young sample. Size (S) models hypothesize that bark responses are a function of tree size; growth (G) models hypothesize that bark responses are a function of tree growth; environment (E) models hypothesize that bark responses are a function of various environmental factors; thinning (T) models hypothesize that bark responses are a function of thinning treatment or surrounding tree density. K is number of parameters estimated in the model, including random effects; AICc is the small sample size adjusted Akaike Information Criterion; ΔAICc is the difference in AICc relative to the best model; Wt is AICc model weight; R_p^2 is Nagelkerke's generalized R^2; rank is the rank order of the model based on AICc, for all models with ΔAICc < 4.0.

Hyp	Model	K	Furrow depth AICc	ΔAICc	Wt	R_p^2	#	Furrow area AICc	ΔAICc	Wt	R_p^2	#	Bark roughness AICc	ΔAICc	Wt	R_p^2	#
S	DBH	6	2.1	0	0.11	0.30	1	232.7	1.8	0.07	0.33	4	227	9.24	0.00	0.10	
	DBH + DBH2	7	2.5	0.4	0.09	0.30	2	230.9	0	0.16	0.34	1	229	11.23	0.00	0.10	
G	PAI	6	97.3	95.2	0.00	0.06		347	116.1	0.00	0.02		234.9	17.15	0.00	0.08	
	PAI + PAI2	7	99.3	97.2	0.00	0.06		349	118.1	0.00	0.00		236.9	19.08	0.00	0.08	
E	HTLD + FASP + UP + CC	9	111.1	109	0.00	0.03		366.1	135.2	0.00	0.00		0				
	HTLD + UP	7	116.6	114.5	0.00	0.00		370.8	139.9	0.00	0.06		0				
T	TRT	6	114.6	112.5	0.00	0.00		369.2	138.4	0.00	0.01		259	41.22	0.00	0.02	
	RD	6	114.3	112.2	0.00	0.01		369.2	138.4	0.00	0.00		262.4	44.64	0.00		
	RD + RD2	7	114.8	112.7	0.00	0.01		370	139.1	0.00	0.00		263.6	45.78	0.00		
SG	DBH + PAI	7	4.2	2	0.04	0.30		234.1	3.2	0.03	0.33	11	218.2	0.42	0.22	0.13	2
	DBH + PAI + DBH*PAI	8	5.4	3.3	0.02	0.30		236	5.1	0.01	0.33		220	2.22	0.09	0.13	5
	DBH + DBH2 + PAI	8	4.5	2.3	0.03	0.30		232.7	1.9	0.06	0.33	5	220	2.19	0.09	0.13	4
	DBH + DBH2 + PAI + PAI2	9	6.5	4.3	0.01	0.30		234.1	3.3	0.03	0.34	12	222	4.22	0.03	0.13	
	DBH + DBH2 + PAI + DBH*PAI	9	5.4	3.3	0.02	0.30		234.7	3.9	0.02	0.33	16	221.7	3.91	0.04	0.13	7
SE	DBH + HTLD + UP + CC	9	7	4.8	0.01	0.30		236.7	5.8	0.01	0.06		0				
	DBH + HTLD + UP	8	5.2	3.1	0.02	0.30		234.7	3.8	0.02	0.33	14	0				
	DBH + HTLD + DBH*HTLD	8	4.6	2.5	0.03	0.30		235.9	5.1	0.01	0.33		230.1	12.34	0.00	0.10	
	DBH + DBH2 + HTLD	8	4.4	2.3	0.04	0.30		232.7	1.8	0.07	0.34	3	230.4	12.58	0.00	0.10	
	DBH + HTLD	7	4	1.9	0.04	0.30		234.5	3.6	0.03	0.33	13	228.4	10.60	0.00	0.10	
	DBH + UP	7	3.3	1.2	0.06	0.30	4	232.8	2	0.06	0.33	6	0				
	DBH + CC	7	4	1.8	0.04	0.30	8	234.7	3.8	0.02	0.33	15	0				
	DBH + FASP	7	3.2	1.1	0.06	0.30	3	233.7	2.9	0.04	0.33	9	0				
ST	DBH + TRT	7	3.7	1.6	0.05	0.30	7	234	3.2	0.03	0.33	10	223.1	5.28	0.02	0.12	
	DBH + TRT + DBH*TRT	8	5.4	3.3	0.02	0.30		236	5.1	0.01	0.33		224.6	6.81	0.01	0.12	
	DBH + RD	7	3.7	1.6	0.05	0.30	6	233.3	2.4	0.05	0.34	8	225.7	7.93	0.01	0.11	
	DBH + RD + DBH*RD	8	5.7	3.6	0.02	0.30		235.1	4.2	0.02	0.33		227.7	9.91	0.00	0.11	
	DBH + DBH2 + RD	8	4.2	2	0.04	0.30		231.6	0.7	0.11	0.33	2	227.7	9.94	0.00	0.11	
	DBH + DBH2 + RD + RD2	9	5.7	3.6	0.02	0.30		233.2	2.3	0.05	0.33	7	227.8	10.02	0.00	0.11	
GE	PAI + HTLD + FASP + UP	9	98.7	96.6	0.00	0.07		347.4	116.5	0.00	0.02		0				
	TRT + HTLD + FASP + UP	9	114.5	112.4	0.00	0.02		368	137.1	0.00	0.00		0				
	RD + HTLD + FASP + UP	9	114.8	112.7	0.00	0.02		368.6	137.7	0.00	0.00		0				
	RD + RD2 + HTLD + UP	9	118.2	116.1	0.00	0.01		372.4	141.6	0.00	0.00		0				
	RD + HTLD	7	115.6	113.5	0.00	0.01		370.1	139.2	0.00	0.00		263.5	45.72	0.00		
SGE	DBH + PAI + HTLD + UP	9	7.3	5.1	0.01	0.30		236.1	5.2	0.01	0.33		0				
	DBH + PAI + HTLD + CC	9	7.9	5.7	0.01	0.30		237.8	7	0.00	0.03		0				
	DBH + PAI + DBH*PAI + HTLD	9	7.3	5.2	0.01	0.30		237.8	6.9	0.01	0.06		220.5	2.70	0.07	0.13	6
	DBH + PAI + HTLD + FASP	9	7.1	5	0.01	0.30		237	6.2	0.01	0.08		0				
SGT	DBH + PAI + TRT	8	5.6	3.4	0.02	0.30		235.8	5	0.01	0.33		217.8	0.00	0.27	0.13	1
	DBH + PAI + RD	8	5.5	3.4	0.02	0.30		235.2	4.4	0.02	0.33		219.4	1.66	0.12	0.13	3
SET	DBH + TRT + HTLD + UP	9	7	4.9	0.01	0.30		236.3	5.5	0.01	0.33		0				
	DBH + TRT + HTLD	7	3.7	1.5	0.05	0.30	5	236	5.1	0.01	0.33		224.5	6.73	0.01	0.12	
	DBH + RD + HTLD + UP	9	6.9	4.8	0.01	0.30		235.5	4.6	0.02	0.33		0				
	DBH + RD + HTLD	8	5.7	3.5	0.02	0.30		235.3	4.4	0.02	0.33		227.3	9.54	0.00	0.11	
	DBH + RD + HTLD	8	5.7	3.5	0.02	0.30		235.3	4.4	0.02	0.33		227.3	9.54	0.00	0.11	
Null		5	113.9	111.7	0.00	0.00		369.1	138.3	0.00	0.00		262.3	44.51	0.00	0.0	

thinning; tree diameter and diameter growth, both influenced by thinning, had much stronger relationships with bark responses (Table 3, Table 5). DBH was the most important variable in predicting furrow responses; PAI was also useful in predicting bark roughness (Table 3). Models describing furrow depth and furrow area as a function solely of DBH had the lowest AICc values and accounted for >16% of cumulative model weight, although the full set of competing models (those with AICc < 4.0) included each of the seven explanatory variables. Models without DBH had little support (none with >1% model weight). The best models describing bark roughness all included DBH and PAI, with a summed model weight of 94% (Table 3); no other variables clearly added explanatory power. Other than its effects on tree diameter and diameter growth, thinning had negligible effect on bark structure. The best models for

furrow depth, area, and roughness included TRT or RD (a surrogate for treatment) in addition to DBH and PAI; however, these variables provided no increase in generalized R_p^2 (Table 3). Models including TRT or RD without DBH had <1% model weight and provided <1.5% R_p^2 above null models.

We found no evidence that environmental conditions influenced bark-furrow responses in the Young sample. Models including only environmental variables (CC, FASP, UP, HTLD) had <1% cumulative model weight and provided only 0–3.5% generalized R_p^2 above nested models without fixed effects (Table 3).

Model-weighted predictions illustrated the positive relationship between DBH and bark responses in the Young sample. Predicted median furrow depth and furrow area almost doubled over the range of tree diameters in the Young sample (Figure 2, 3). Predicted

Table 4. Models of hypothesized relationships between bark furrow responses and tree and environmental factors in the Old sample. Size (S) models hypothesize that bark responses are a function of tree size; growth (G) models hypothesize that bark responses are a function of tree growth; environment (E) models hypothesize that bark responses are a function of various environmental factors; density (D) models hypothesize that bark responses are a function of surrounding tree density. K is number of parameters estimated in the model, including random effects; AICc is the small sample size adjusted Akaike Information Criterion; ΔAICc is the difference in AICc relative to the best model; Wt is AICc model weight; R_p^2 is Nagelkerke's generalized R^2; rank is the rank order of the model based on AICc, for all models with ΔAICc < 4.0.

| Hyp	Model	K	Furrow depth					Furrow area					Bark roughness				
			AICc	ΔAIC	Wt	R_p^2	#	AICc	ΔAIC	Wt	R_p^2	#	AICc	ΔAIC	Wt	R_p^2	#
S	DBH	5	77.7	2.5	0.05	0.60	7	163.3	7.4	0.01	0.58		81	7.1	0.01	0.53	
	DBH + DBH2	6	76.5	1.3	0.09	0.61	3	161	5.1	0.02	0.60		75.5	1.6	0.15	0.56	3
G	PAI	5	173.5	98.3	0.00	0.16		247.4	91.5	0.00	0.19		141.3	67.4	0	0.18	
	PAI + PAI2	6	174.7	99.5	0.00	0.16		248.3	92.5	0.00	0.20		143.3	69.4	0	0.18	
E	HTLD + FASP + UP + CC	8	195.2	120.1	0.00			275.5	119.6	0.00							
	HTLD	5	192.4	117.2	0.00			270.7	114.8	0.00			160.4	86.5	0		
	HTLD + UP	6	194.4	119.2	0.00			272.7	116.9	0.00							
D	RD	5	192	116.8	0.00			269.5	113.6	0.00			159.9	86	0		
	RD + RD2	6	194	118.8	0.00			271.6	115.7	0.00			161.7	87.8	0		
SG	DBH + PAI	6	79.7	4.5	0.02	0.60		163.7	7.8	0.01	0.59		82.6	8.7	0	0.54	
	DBH + PAI + DBH*PAI	7	81.5	6.3	0.01	0.60		165.8	9.9	0.00	0.59		84.4	10.5	0	0.54	
	DBH + DBH2 + PAI	7	78.5	3.3	0.03	0.61	11	161.9	6	0.01	0.60		77.3	3.4	0.06	0.57	4
	DBH + DBH2 + PAI + PAI2	8	79.7	4.5	0.02	0.61		163.6	7.7	0.01	0.60		79.1	5.2	0.02	0.57	
	DBH + DBH2 + PAI + DBH*PAI	8	77.8	2.6	0.05	0.62	8	163	7.1	0.01	0.60		78.9	5	0.03	0.57	
SE	DBH + HTLD + UP + CC	8	82.3	7.1	0.00	0.61		164.7	8.8	0.00	0.60						
	DBH + HTLD + UP	7	81	5.8	0.01	0.60		166.1	10.3	0.00	0.59						
	DBH + HTLD + DBH *HTLD	7	80.8	5.7	0.01	0.61		166.2	10.3	0.00	0.59		82.2	8.3	0.01	0.55	
	DBH + DBH2 + HTLD	7	77.7	2.5	0.05	0.61	6	162	6.1	0.01	0.60		77.4	3.5	0.06	0.57	5
	DBH + HTLD	6	78.9	3.7	0.03	0.60	13	164.1	8.2	0.00	0.59		82.4	8.5	0	0.54	
	DBH + UP	6	79.7	4.6	0.02	0.60		165.3	9.4	0.00	0.58						
	DBH + CC	6	79.3	4.1	0.02	0.60		162.9	7.1	0.01	0.59						
	DBH + FASP	6	79.3	4.2	0.02	0.60		165.3	9.4	0.00	0.58						
SGD	DBH + RD	6	75.9	0.7	0.12	0.61	2	157.4	1.5	0.13	0.61	4	78.2	4.3	0.04	0.55	
	DBH + RD + DBH*RD	7	77.9	2.8	0.04	0.61	9	158.5	2.6	0.08	0.61	5	80.3	6.4	0.01	0.55	
	DBH + DBH2 + RD	7	75.2	0	0.17	0.62	1	155.9	0	0.28	0.62	1	73.9		0.34	0.58	1
	DBH + DBH2 + RD + RD2	8	77.3	2.1	0.06	0.62	5	157.2	1.3	0.15	0.62	2	74.8	0.9	0.22	0.58	2
GE	PAI + HTLD + FASP + UP	8	179.8	104.7	0.00	0.16		253.4	97.5	0.00	0.19						
	RD + HTLD + FASP + UP	8	197.3	122.1	0.00			275.5	119.6	0.00							
	RD + RD2 + HTLD + UP	8	198.2	123	0.00			275.8	119.9	0.00							
	RD + HTLD	6	194	118.8	0.00			271.6	115.7	0.00			161.8	87.9	0		
SGE	DBH + PAI + HTLD + UP	8	82.9	7.7	0.00	0.61		166.6	10.7	0.00	0.59						
	DBH + PAI + HTLD + CC	8	82	6.8	0.01	0.61		163.1	7.2	0.01	0.60						
	DBH + PAI + DBH*PAI + HTLD	8	82.7	7.5	0.00	0.61		166.7	10.8	0.00	0.59		85.8	11.9	0	0.54	
	DBH + PAI + HTLD + FASP	8	82.3	7.1	0.00	0.61		166.7	10.8	0.00	0.59						
	DBH + PAI + RD	7	78	2.8	0.04	0.61	10	159.1	3.2	0.06	0.61	6	80.3	6.4	0.01	0.55	
	DBH + RD + HTLD + UP	8	78.6	3.4	0.03	0.62	12	159.2	3.3	0.05	0.61	7					
	DBH + RD + HTLD	7	76.5	1.4	0.09	0.62	4	157.4	1.5	0.13	0.61	3	79	5.1	0.03	0.56	
Null	Nested structure	4	190.3	115.2	0.00	0.00		268.6	112.8	0.00	0.00		158.4	84.5	0	0.00	

Table 5. Means and 95% confidence intervals for tree size (DBH), growth (PAI), and bark responses for each treatment, incorporating nested (site, treatment in Young sample, and plot) model structure.

| Variable	Unthinned	Thinned	Old
Tree DBH (cm)	52.97 (51.33–54.61)	55.58 (53.9–57.26)	102.6 (93.27–111.93)
Tree PAI (cm²/yr)	40.36 (24.94–55.78)	64.64 (49.02–80.26)	59.1 (48.86–69.34)
Furrow depth (cm)	1.87 (1.52–2.3)	2.05 (1.66–2.52)	6.79 (5.09–8.49)
Furrow area (cm²)	6.54 (4.78–8.96)	7.49 (5.46–10.27)	57.37 (37.22–77.52)
Bark roughness (unitless)	50.52 (36.56–69.8)	64.37 (46.48–89.15)	136.19 (117.93–154.45)

median bark roughness in the Young sample increased almost 50% (25 units) across this DBH range (Figure 4). In comparison to DBH, tree growth (PAI) had a smaller impact on bark responses. Predicted bark roughness when PAI was 65.5 cm²/yr. (average Thinned PAI) was only slightly higher than when PAI was 38.2 cm²/yr. (average Unthinned PAI) (Figure 5). Model-weighted predicted median furrow depth, furrow area, and bark roughness did not vary significantly (<5%) across the full range of RD and environmental variables in the Young sample, singly or in combination.

Comparison of Young and Old Tree Bark Furrows and Roughness

Bark furrows were more developed in trees in the Old sample than trees in the Young sample (Table 5), but Old sample bark responses were influenced by similar factors, principally tree diameter. The major difference in influential factors was the negative effect of local stem densities surrounding individual trees in Old stands. Models of Old sample trees that included tree size (DBH) and plot-scale stem density (RD) in combination accounted for 40,
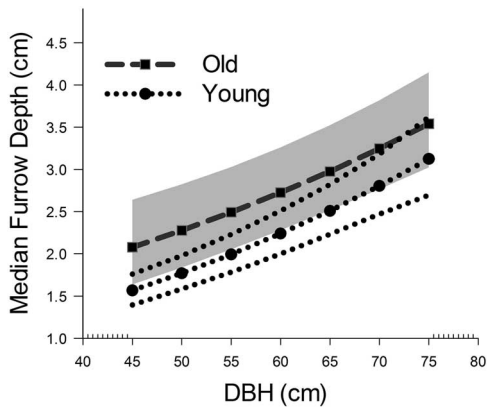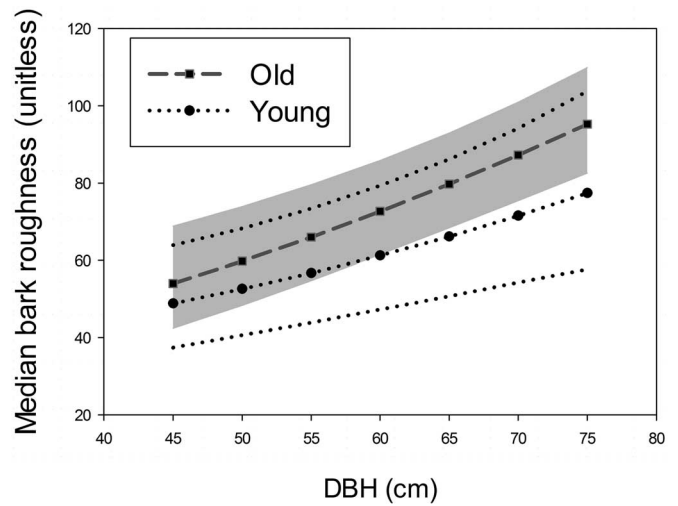
Figure 2. Model-averaged prediction results for predicted median furrow depth for Young and Old samples, with unconditional 95% confidence envelopes. Young sample and Old sample predictions are displayed together but were modeled independently.
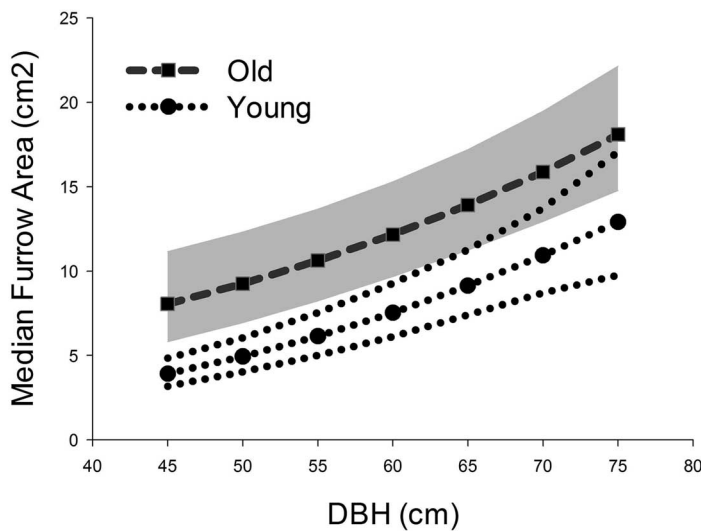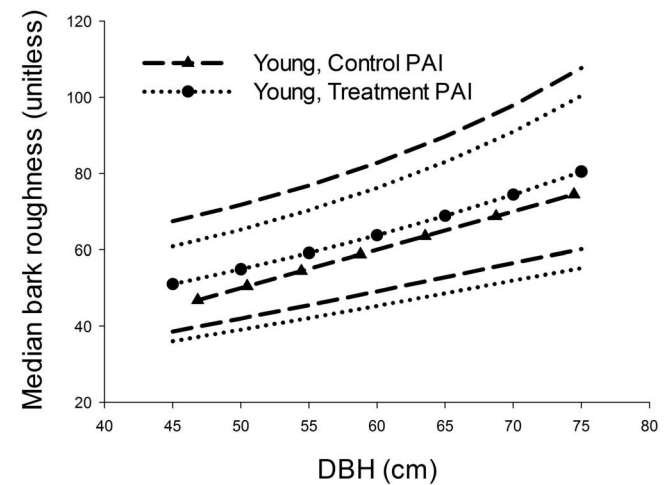

Figure 3. Model-averaged prediction results for predicted median furrow area for Young and Old samples, with unconditional 95% confidence envelopes. Young sample and Old sample predictions are displayed together but were modeled independently.

Figure 4. Model-averaged prediction results for predicted median bark roughness for Young and Old samples, with unconditional 95% confidence envelopes. Young sample and Old sample predictions are displayed together but were modeled independently.

Figure 5. Model-averaged prediction results for predicted median bark roughness for Young sample trees with low (38.2 cm²/yr) and high (65.5 cm²/yr) growth, with unconditional 95% confidence envelopes.

64, and 61% of the model weight for furrow depth, area, and bark roughness models (Table 4). All models including DBH and RD were included in competing models for furrow depth and area (ΔAICc $<$ 4.0). Competing models describing bark roughness also included growth (PAI) and heatload (HTLD). Although RD was included in competing models, it added $<$ 1.9% R_p^2 to a model with DBH and DBH^2 alone.

Model-weighted predictions illustrate the strong positive increase in all Old sample bark responses with increasing tree diameter as well as the negative effect of relative density on furrow area. Model-weighted predictions of bark responses in the Old sample almost doubled over the range of tree diameters observed in the Young sample (Figures 2, 3, 4), and more than quadrupled across the full range of Old sample tree diameters. Model-weighted predicted median furrow area in open conditions (RD = 20) was approximately twice that in dense conditions (RD = 75; Figure 6). Furrow depth and bark roughness had similar negative relationships with RD. However, open and dense cases were not significantly different for these two responses. Model-average predicted bark re-

sponses changed $<$10% across the range ingrowth (PAI), heatload (HTLD), and other environmental variables (alone or in combination) in the Old tree sample.

Bark Characteristics of Trees Used by Bark-Foraging Birds

Bark-foraging birds did not appear to discriminate among trees in Young Unthinned stands based on bark furrow depth, area, or roughness (Table 6). Trees with observed use by bark foragers in the Young Unthinned treatment did not have significantly different bark responses than the rest of the Young Unthinned sample (all $P > 0.44$).

Discussion

Experimental thinning in our study led to residual stands with significantly higher tree diameter growth and a trend in larger diameter trees a decade following thinning; larger, faster-growing trees had more-developed bark roughness, deeper furrows, and larger
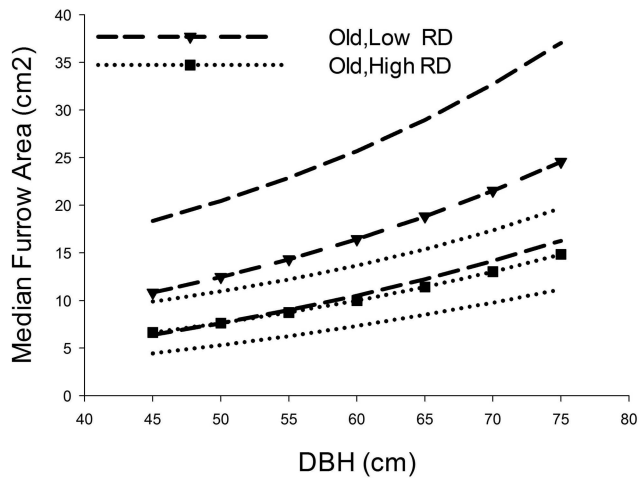
Figure 6. Model-averaged prediction results for predicted median bark furrow area for the Old sample, for open (RD = 20) conditions and dense (RD= 75) conditions, with unconditional 95% confidence envelopes.

Table 6. Characteristics of trees with observed use by brown creepers and with no observed use by creepers in two Unthinned Young stands. Means and 95% confidence intervals for furrow responses, including furrow depth (FDPTH), furrow area (AREA) and bark roughness (BROUGH).

	Forager use	No observed use
Sample size	12	84
Bark response		
FDPTH	1.81 (1.28, 2.34)	1.86 (1.74, 1.98)
AREA	5.50 (3.18, 7.82)	5.50 (4.90, 6.11)
BROUGH	42.20 (29.83, 54.57)	49.39 (44.74, 54.05)

furrow areas. Our results support Mariani and Manuwal's (1990) and Michel et al.'s (2011) findings on the importance of tree diameter in determining Douglas-fir bark characteristics. The influence of forest management on bark characteristics in our study was weaker than management effects found by Michel and Winter (2009) studying different Douglas-fir bark microhabitat features, or MacFarlane and Luo (2009) studying bark furrows in northern hardwoods. Surrounding tree densities had a strong negative association with Douglas-fir bark furrow characteristics in trees in our sampled Old stands, similar to results for northern hardwoods found by MacFarlane and Luo (2009). Trees in our Young sites showed a nonsignificant negative trend between furrow characteristics and local tree density, which may have been attributable to the relatively short time since thinning (10 years). In contrast to observations by Van Pelt (2007), results in our Young and Old stands did not suggest other environmental variables as important influences on bark characteristics.

Tree age was not included in our models as a factor since trees from our Young, even-aged stands varied less than 12 years in age (Table 1). *A posteriori* observations suggested some correlation between tree age and bark characteristics in our more variable Old stands. Although age was not included as an explanatory variable in our analyses, comparisons between bark characteristics in Young and Old samples and the relative importance of different factors influencing bark characteristics in these samples provides a qualitative gauge of the importance of age. Trees in our Old stands had more developed bark furrows, even for a DBH range comparable to

young trees. As trees age, they produce and accumulate outer bark that is incapable of expanding in response to diameter growth, and cracks to form furrows. Thus, older trees should have thicker bark and deeper furrows than younger trees with similar diameters, as noted by Clausen and Goodman (1969) and Glitzenstein and Harcombe (1979). Older Douglas-fir bark also undergoes conformational changes, becoming flaky over time (Van Pelt 2007). Tree aging, including bark accumulation and conformational changes, may represent a constraint on the rate of Douglas-fir bark furrow development that cannot be overcome by management. This is consistent with findings suggesting late-successional tree structures generally begin to develop only after age 80 (Franklin et al. 2002, Michel and Winter 2009).

The only previous study that investigated whether brown creepers select trees based on bark furrow characteristics in young stands found a positive relationship between odds of tree selection and average furrow depth (Weikel and Hayes 1999). Our study did not detect a relationship between selection by bark-foraging birds and depth of deepest furrow. In addition to low forager sample size in our study, difference in observed relationships between foragers and bark characteristics could be attributable to:

(1) Different measures used to represent the response: Weikel and Hayes (1999) calculated average bark furrow depth from four locations at BH while our study measured depth of single largest furrow, similarly to Michel et al. (2011).

(2) Different measurement seasons: Our observations were made in late winter whereas Weikel and Hayes (1999) measured in spring. Brown creepers have been shown to exhibit seasonal variability in diet and in selection of foraging substrates (Wilson 1970, Adams and Morrison 1993, Hejl et al. 2002). Deep furrows may be less conducive to successful foraging in winter if they allow arthropod prey to overwinter beyond reach of avian predators (Moore and Lee 1991).

(3) Different stand histories: Stands used in our study were initiated through harvest. Stands studied by Weikel and Hayes (1999) were initiated by fires and may have represented a greater range of bark structural development by including residual trees with more biologically meaningful furrow structure.

Although bark furrows on trees selected by brown creepers were not significantly different than on other unthinned trees, trees in our Young sites included a range in bark furrow conditions that might have biologically meaningful differences for this species, as indicated by typical prey sizes. Brown creeper abundance is positively correlated with the abundance of spiders sized 0.6–1.1 cm in length using Douglas-fir bark (Mariani and Manuwal 1990). Measured bark furrow depths in our Young sites had a range greater than this prey size (Table 5); large trees in Young stands would be predicted to have higher carrying capacity for these prey items than smaller trees. Thinning treatment, growth conditions, and environmental variables in Young stands were associated with differences in furrow depth substantially smaller than this prey size. In contrast, differences in mean furrow depth between trees in our Old sites and Young thinned sites were three times larger than the size of this preferred prey.

We believe our results should apply to Douglas-fir trees in the Coast Range of Oregon, but general principals may apply to other tree species and regions as well. The study sites used were chosen to be broadly representative of young stand conditions in the Coast

Range of Oregon (Cissel et al. 2006). Similarly, plots in old stands were established as part of a regular grid across Bureau of Land Management (BLM)-managed landscapes with the goal of representing the range of environmental conditions and disturbance histories present in Oregon Coast Range stands.

Management Implications

In response to regulatory pressure (FEMAT 1993, USDA Forest Service 2011) and the desire to provide late-successional structures (Lindenmayer and Franklin 2002), support biodiversity (Michel and Winter 2009) and wildlife (Hayes 1997), significant effort has been expended developing silvicultural treatments that accelerate development of late-successional forest characteristics compared to natural development patterns (Busing and Garman 2002, Muir et al. 2002, Poage and Anderson 2007). Variable density harvesting (Cissel et al. 2006, Gustafson et al. 2012) retains larger trees and sustains tree growth and open growing conditions, enhancing a suite of late-successional characteristics, including tree microhabitat features (Michel and Winter 2009). Our study suggests that Douglas-fir bark furrows and bark roughness are two of the suite of late-successional characteristics advanced by these silvicultural thinning treatments. Our results predict that trees in young thinned stands achieve a given bark roughness at DBHs approximately 5 cm lower than unthinned trees, equivalent to developing a given bark roughness 8 years faster.

Where enhancement of stand biodiversity and accelerated development of single-tree bark furrow structures is a management goal, active management directly focused on these structures should be beneficial. Specifically, in younger stands bark development is enhanced by the retention of larger diameter trees and practices that lead to higher growth rates such as maintenance of open growing conditions and fertilization. Our Young sample of even-aged trees had variation in furrow depth over twice as large as bark-forager prey length, and older stands have larger variation (Ross and Kahmer 1971). Thinnings designed to retain trees with already deep furrows could provide significantly more of these structures in residual stands.

The benefit of experimental thinning on accelerating bark development toward late-successional habitat conditions a decade after harvest was modest: a trend of approximately 10% increase in bark furrows. Comparison to trees in older stands makes clear that thinning in young stands has produced only minimal advancement toward late-successional bark furrow structure. Trees in older stands have much deeper furrows than trees in young thinned stands, and these furrows have significant, positive relationships with bark-foraging bird use. Development of deep furrows and their associated fauna may require many decades and may not be physiologically possible in young trees. This highlights the importance of retaining trees in final harvest operations. Retained trees provide structural legacies for future stands, including deep bark furrows that are relatively slow to develop in young trees, even with management. Legacy bark furrow structures can provide a life-boat function for arthropods and associated bark-foraging birds (Rosenvald and Lohmus 2008). While initial results regarding the effects of thinning on Douglas-fir bark are promising, more research is needed to determine if the accelerated development of Douglas-fir bark furrows and roughness after thinning continue through stand development and if other techniques including approaches targeted at bark development can further enhance bark furrow development in young stands.

Literature Cited

ADAMS, E.M., AND M.L. MORRISON. 1993. Effects of forest stand structure and composition on red-breasted nuthatches and brown creepers. *J. Wildl. Manage.* 57:616–629.

BAUHUS, J., K. PUETTMANN, AND C. MESSIER. 2009. Silviculture for old-growth attributes. *For. Ecol. Manage.* 258:525–537.

BURNHAM, K.P., AND D.R. ANDERSON. 1998. *Model selection and inference: A practical information-theoretic approach.* Springer-Verlag, New York. 353 p.

BURNHAM, K.P., AND D.R. ANDERSON. 2002. *Model selection and multimodel inference: A practical information-theoretical approach.* Springer-Verlag Press, New York. 488 p.

BURNHAM, K.P., AND D.R. ANDERSON. 2004. Multimodel inference: Understanding AIC and BIC in model selection. *Sociolog. Meth. and Res.* 33:261–304.

BUSING, R.T., AND S.L. GARMAN. 2002. Promoting old-growth characteristics and long-term wood production in Douglas-fir forests. *For. Ecol. Manage.* 160:161–175.

CAREY, A.B., M.M. HARDT, S.P. HORTON, AND B.L. BISWELL. 1991. Spring bird communities in the Oregon Coast Range. P. 123–144 in *Wildlife and vegetation of unmanaged Douglas-fir forests*, Ruggiero, L.F., K.B. Aubry, A.B. Carey, and M.H. Huff (tech. eds.). USDA For. Serv., Gen. Tech. Rep. PNW-GTR-285, Pacific Northwest Research Station, Portland, OR. 533 p.

CHRISTY, R.E., AND S.D. WEST. 1993. *Biology of bats in Douglas-fir forests.* USDA For. Serv., Gen. Tech. Rep. PNW-GTR-308, Portland, OR. 28 p.

CISSEL, J.H., P.D. ANDERSON, S. BERRYMAN, S.S. CHAN, D.H. OLSON, K.J. PUETTMANN, AND C. THOMPSON. 2006. *BLM density management and riparian buffer study: Establishment report and study plan.* US Geological Survey Scientific Investigations Report 2006–5087, Reston, VA. 144 p.

CLAUSEN, K.E., AND R.M. GOODMAN. 1969. *Bark characteristics indicate age and growth rate of yellow birch.* USDA For. Serv., Res. Note NC-75. 3 p.

CURTIS, R.O. 1982. A Simple Index of Stand Density for Douglas-fir. *For.Sci.* 28(1):92–94.

DODSON, K.E., A. ARES, AND K.J. PUETTMANN. 2012. Early responses to thinning treatments designed to accelerate late successional forest structure in young coniferous stands of western Oregon, USA. *Can. J. For. Res.* 42(2):345–355.

ESRI. 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, CA.

FOREST ECOSYSTEM MANAGEMENT ASSESSMENT TEAM (FEMAT). 1993. *Forest ecosystem management: an ecological, economic, and social assessment.* US Department of Agriculture, US Department of the Interior [and others]. Portland, OR. 139 p.

FIALA, A.C., S.L. GARMAN, AND A.N. GRAY. 2006. Comparison of five canopy cover estimation techniques in the western Oregon Cascades. *For. Ecol. Manage.* 232:188–197.

FOWLER, J.F., AND C.H. SIEG. 2004. *Postfire mortality of ponderosa pine and Douglas-fir: A review of methods to predict tree death.* USDA For. Serv., Gen. Tech. Rep. RMRS-GTR-132, Fort Collins, CO. 25 p.

FRANKLIN, J.F., T.A. SPIES, R. VAN PELT, A.B. CAREY, D.A. THORNBURGH, D.R. BERG, D.B. LINDENMAYER, ET AL. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manage.* 155:399–423.

GARMAN, S.L., J.H. CISSEL, J.H. MAYO, AND H. JAMES. 2003. *Accelerating development of late-successional conditions in young managed Douglas-fir stands: A simulation study.* USDA For. Serv., Gen. Tech. Rep. PNW-GTR-557, Portland, OR. 57 p.

GLITZENSTEIN, J., AND P.A. HARCOMBE. 1979. Site-specific changes in the bark texture of *Quercus falcata* Michx. (Southern red oak). *Am. J Bot.* 66:668–672.

GUSTAFSSON, L., S.C. BAKER, J. BAUHUS, W.J. BEESE, A. BRODIE, J. KOUKI, D.B. LINDENMAYER, ET AL. 2012. Retention forestry to maintain multifunctional forests: A world perspective. *BioScience* 62(7):633–645.

HAYES, J.P., S.S. CHAN, W.H. EMMINGHAM, J.C. TAPPEINER, L.D. KELLOGG, AND J.D. BAILEY. 1997. Wildlife response to thinning young forests in the Pacific Northwest. *J. For.* 95(8):28–33.

HEJL, S.J., K.R. NEWLON, M.E. MCFADZEN, J.S. YOUNG, AND C.K. GHALAMBOR. 2002. Brown creeper (*Certhia americana*). Webpage in *The Birds of North America Online*, Poole, A. (ed.). Cornell Lab of Ornithology, Ithaca, NY. Available online at bna.birds.cornell.edu/bna/species/669/articles/introduction; last accessed Aug. 27, 2012.

HUNTER, M. 2001. Communiqué No. 3: Management in young forests. Cascade Center for Ecosystem Management, Corvallis, OR. 28 p. Available online at andrewsforest.oregonstate.edu/research/related/ccem/pdf/Comque3.pdf; last accessed Aug. 27, 2012.

JACKSON, J.A. 1979. Tree surfaces as foraging substrate for insectivorous birds. P. 115–130 in *The role of insectivorous birds in forest ecosystems*, Dickson, J.G., R.N. Connor, R.R. Fleet, J.C. Kroll, and J.A. Jackson (eds.). Academic Press, New York. 394 p.

LEMMON, P.E. 1956. A spherical densiometer for estimating forest overstory density. *For. Sci.* 2:314–320.

LINDENMAYER, D.B., AND J.F. FRANKLIN. 2002. *Conserving forest biodiversity: A comprehensive multiscaled approach.* Island Press, Washington, DC. 351 p.

MACFARLANE, D.W., AND A. LUO. 2009. Quantifying tree and forest bark structure with a bark-fissure index. *Can. J. For. Res.* 39(10):1859–1870.

MARIANI, J.M., AND D.A. MANUWAL. 1990. Factors influencing brown creeper (*Certhia* Americana) abundance patterns in the southern Washington Cascade Range. *Stud. Avian Biol.* 13:53–57.

MCCUNE, B., R. ROSENTRETER, J.M. PONZETTI, AND D.C. SHAW. 2000. Epiphyte habitats in an old conifer forest in western Washington, U.S.A. *The Bryologist* 103(3):417–427.

MCCUNE, B., AND D. KEON. 2002. Equations for potential annual direct incident radiation and heat load. *J. Veg. Sci.* 13:603–606.

MICHEL, A.K., AND S. WINTER. 2009. Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, U.S.A. *For. Ecol. Manage.* 2577:1453–1464.

MICHEL, A.K., S. WINTER, AND A. LINDE. 2011. The effect of tree dimension on the diversity of bark microhabitat structures and bark use in Douglas-fir (*Pseudotsuga menziesii* var. menziesii). *Can. J. For. Res.* 41(2):300–308.

MINORE, D. 1979. Comparative autecological characteristics of northwestern tree species: A literature review. USDA For. Serv., Gen. Tech. Rep. PNW-GTR-87. 72 p.

MOORE, M.V., AND R.E. LEE. 1991. Surviving the big chill: Overwintering strategies of aquatic and terrestrial insects. *Am. Entomologist* 37:111–118.

MUIR, P.S., R.L. MATTINGLY, J.C. TAPPEINER II, J.D. BAILEY, W.E. ELLIOTT, J.C. HAGAR, J.C. MILLER, E.B. PETERSON, AND E.E. STARKEY. 2002. *Managing for biodiversity in young Douglas-fir forests of western Oregon.* US Geological Survey, Biological Resources Division, Biological Science Report USGS/BRD/BSR–2002–0006. 76 p.

NAGELKERKE, N.J.D. 1991. A note on a general definition of the coefficient of determination. *Biometrika* 78(3):691–692.

POAGE, N.J., AND J.C. TAPPEINER. 2002. Long-term patterns of diameter and basal area growth of old-growth Douglas-fir trees in western Oregon. *Can. J. For. Res.* 32(7):1232–1243.

POAGE, N.J., AND P.D. ANDERSON. 2007. *Large-scale silviculture experiments of western Oregon and Washington.* USDA For. Serv., Gen. Tech. Rep PNW-GTR-713, Portland, OR. 44 p.

ROSE, C.L., B.G. MARCOT, T.K. MELLON, J.L. OHMANN, K.L. WADDELL, D.L. LINDLEY, AND B. SCHEIBER. 2001. Decaying wood in Pacific Northwest forests: Concepts and tools for habitat management. P. 580–623 in *Wildlife habitat relationships in Oregon and Washington,* Johnson, D.H., and T.A. O'Neill (eds.). Oregon State University Press, Corvallis, OR. 768 p.

ROSENVALD, R., AND A. LOHMUS. 2008. For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. *For. Ecol. Manage.* 255(1):1–15.

ROSS, W.D., AND R.L. KRAHMER. 1971. Some sources of variation in structural characteristics of Douglas-fir bark. *Wood Fiber* 3(1):35–46.

RYAN, K.C., AND E.D. REINHARDT. 1988. Predicting postfire mortality of seven western conifers. *Can. J. For. Res.* 18:1291–1297.

SPIES, T.A., AND J.F. FRANKLIN. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. P. 91–109 in *Wildlife and vegetation of unmanaged Douglas-fir forests,* Ruggiero, L.F., K.B. Aubry, A.B. Carey, and M.H. Huff (tech. eds.). USDA For. Serv., Gen. Tech. Rep. PNW-GTR-285, Pacific Northwest Research Station, Portland, OR. 533 p.

TAPPEINER, J.C., D. HUFFMAN, D. MARSHAL, T.A. SPIES, AND J.D. BAILEY. 1997. Density, ages and growth rates in old-growth and young-growth forests in coastal Oregon. *Can. J. For. Res.* 27:638–648.

THOMAS, S.C., D.A. LIGUORI, AND C.B. HALPERN. 2001. Corticolous bryophytes in managed Douglas-fir forests: Habitat differentiation and responses to thinning and fertilization. *Can. J. Bot.* 79(8):886–896.

USDA FOREST SERVICE. 2011. 36 CFR Part 219. National Forest System land management planning; proposed rule. USDA For. Serv., Federal Register vol. 76, No. 30. Part III. February 14, 2011.

USDA FOREST SERVICE. 2012. Current vegetation survey. Available online at www.fs.fed.us/r6/survey/index.htm; last accessed Apr. 13, 2012.

VAN MANTGEM, P., AND M. SCHWARTZ. 2003. Bark heat resistance of small trees in Californian mixed conifer forests: Testing some model assumptions. *For. Ecol. Manage.* 178:341–352.

VAN PELT, R. 2007. *Identifying old trees and forests in eastern Washington.* Washington State Department of Natural Resources, Olympia, WA. 166 p.

WEIKEL, J.M., AND J.P. HAYES. 1999. The foraging ecology of cavity-nesting birds in young forests of the northern coast range of Oregon. *The Condor* 101:58–66.

WILSON, M.F. 1970. Foraging behavior of some winter birds of deciduous woods. *The Condor* 72:169–174.

WINTER, S., AND G. MÖLLER. 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. *For. Ecol. Manage.* 255:1251–1261.

WUNDER, L., AND A.B. CAREY. 1996. Use of the forest canopy by bats. *Northw. Sci.* 70:79–85.