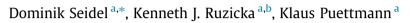
Forest Ecology and Management 363 (2016) 31-38

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Canopy gaps affect the shape of Douglas-fir crowns in the western Cascades, Oregon



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ARTICLE INFO

Article history: Received 21 October 2015 Received in revised form 14 December 2015 Accepted 17 December 2015 Available online 24 December 2015

Keywords: Terrestrial laser scanning Tree crown Forest management Complexity

ABSTRACT

Silvicultural regimes that aim at an increased stand structural diversity typically promote small-scale heterogeneity in horizontal and vertical structures, e.g. through the creation of gaps. We used terrestrial laser scanning (TLS) to investigate impacts of altered growing conditions on trees adjacent to artificial gaps as compared to responses of trees in a regularly spaced, thinned forest interior. Based on the TLSbased point clouds we calculated a number of structural tree crown properties that were hypothesized to be sensitive to spatial variability in growing conditions. We found several significant differences between structural properties of trees in the two growing conditions. Compared to trees in regular spacing, border trees near gaps had a lower crown base height (CBH) and a lower height of maximum crown projection. Crown surface area and crown volume of border trees were significantly larger than those of trees growing in a regular spacing. Also, the asymmetry of entire tree crowns of border trees, and in particular of the lower third of crowns, was directed towards the gap center, reflecting the increased light level in the gap. Our results raise concerns that the economic value of border trees is negatively affected by gap creation. These trees had shorter branch free boles and additionally, due to horizontal branch elongation, larger knots. Conversely, the overall increase in structural variability contributed by the border trees in stands with artificial gaps is likely to positively affect several ecosystem functions as well as biodiversity.

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1. Introduction

Over the last several decades, plantations managed for timber production have replaced natural forests in many regions of the United States (Williams, 1989) and other parts of the world (e.g. Wagner et al., 2006). Such monocultures often have lower levels of variety or are lacking key attributes, such as standing deadwood. These key attributes can be of great importance for ecosystem services and functions, such as habitat diversity, aesthetics for recreation purposes or ecosystem resilience and stability (e.g. Haynes et al., 1996; Bauhus et al., 2009, 2010). Increasing knowledge about the ecological consequences of large scale conversions has been a key development leading to the rethinking of traditional silviculture (Kohm and Franklin, 1997; Bauhus et al., 2010; Kuuluvainen, 2009). Today, silviculture on many ownerships worldwide is undergoing a management paradigm shift which includes a new focus on providing a wider range of ecosystem services while

* Corresponding author. E-mail address: dominik.seidel@oregonstate.edu (D. Seidel). ensuring ecosystem resilience and adaptability at the same time (e.g. Puettmann et al., 2013).

New silvicultural approaches have been proposed to accelerate the development of old-growth like composition and structures in planted forests (e.g. Bauhus et al., 2009) and better prepare these forests for an uncertain future (Messier et al., 2013). One of the key features of these approaches includes increasing the horizontal and vertical heterogeneity within stands. Typically, this goal is modelled after conditions in old-growth forests, such as irregular tree distributions and multiple canopy layers (Franklin and van Pelt, 2004). Bauhus and colleagues (2009) collected a number of structural attributes typically associated with "old-growth conditions" and suggested silvicultural operations that could result in the development of desired attributes. They highlight the creation of gaps in even-aged monocultures to simulate natural disturbances such as small-scale mortality through diseases or tree falls (Lutz and Halpern, 2006; Wilson et al., 2009; Schliemann and Bockheim, 2011). Interestingly, simulation studies suggested that stand productivity may not necessarily be negatively affected by gap creation when compared to standard plantation management (Barbour et al., 1997; Busing and Garman, 2002), even though







management costs are higher. Even for mixed-aged, mixed-species forests the creation of canopy gaps was found to reduce the forest growth rates considerably less than gap area indicates (Pedersen and Howard, 2004).

Increased heterogeneity in horizontal and vertical structures through gap creation implies changing growing conditions for trees and other vegetation. It is well documented that gaps have a strong influence on growing conditions for trees in their vicinity due to changed light conditions and belowground resource levels (e.g. Ammer and Wagner, 2002; Harper and Macdonald, 2002; Harper et al., 2005; Gray et al., 2012). Creation of man-made gaps in even-aged stands also results in significantly changed belowground resource availability (e.g. Thiel and Perakis, 2009). In the past, research has addressed the response of understory vegetation (e.g. Fahey and Puettmann, 2007, 2008), seedling growth (York et al., 2007: York and Battles, 2008) and growth of surrounding canopy trees (e.g. Dodson et al., 2012) to gap formation. Gap closure rates were derived from a combination of height growth of trees, in-growth in gaps, and lateral branch extension of trees adjacent to gaps (e.g. Runkle, 1981, 1998; Schliemann and Bockheim, 2011). Mean turn-over rates of canopy trees and gap formation rates are a key factor in understanding forest stand dynamics and have been derived for forests all over the world (Pickett and White, 1985; Oliver and Larson, 1996; Henbo et al., 2004).

The spatial variability in growing conditions after gap creation causes trees directly adjacent to the opening's "edges" (i.e., border trees) to respond with higher diameter growth than trees in the interior of homogenously spaced even-aged stands (Dodson et al., 2012). This response is partially due to the changes in structural development of tree crowns. For example, crown asymmetry increased towards gaps (e.g. Young and Hubbell, 1991; Muth and Bazzaz, 2002) and the increased number of epicormic branches due to increased radiation reaching the bark (Franklin and van Pelt, 2004). Even in small gaps, diameters of the largest branches (larger), height of the lowest living branch (lower), taper (higher), and other branch and stem characteristics of Norway spruce (*Picea abies* (L.) H. Karst) edge trees showed significant trends compared to trees growing in evenly spaced conditions (Pfister et al., 2008). Besides their impact on tree growth, crown characteristics are an important ecological indicator for wildlife and other aspects of diversity (e.g. Muir et al., 2002). We study these phenomena in Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) because this species is especially flexible in terms of crown shape (Ishii and Wilson, 2001; Ishii and McDowell, 2002) and managing for variability in crowns shapes, such as those typically found in old-growth trees is of great interest in the region (Cissel et al., 2006; Kohm and Franklin, 1997).

Qualitative and quantitative assessments of tree and crown shape responses to gaps have been difficult in the past. Accurate measurements were difficult to obtain due to methodical constraints of measuring the three-dimensional structure of tree canopies surrounding gaps (Seidel et al., 2011a) or even the gap dimensions itself (Seidel et al., 2015a). For this reason, past research on indirect methods has focused mainly on modelling approaches that relate thinning regimes to wood properties as affected by crown dynamics (Barbour et al., 1997; Busing and Garman, 2002). Recent advances in measurement technologies, such as terrestrial laser scanning (TLS) provide an opportunity to investigate morphological aspects of crown response to forest management practices, including gaps. A number of laser scans from different perspectives can be combined into a single point cloud offering comprehensive 3D- geometry of the scanned trees and forest structure (e.g. Watt et al., 2003).

In our study, we used terrestrial laser scanning to investigate the effects of a change in growing conditions on trees adjacent to artificially created gaps as compared to the response of trees in the regularly spaced, thinned forest interior. Understanding the changes in tree and crown shapes can provide new insights into effects of silvicultural practices on tree stability, timber quality, and habitat suitability for a variety of species.

2. Methods

2.1. Study sites

Our study area was located in the Willamette National Forest on the western slopes of the Cascade mountain range in Oregon, USA (Fig. 1). This area experiences a Mediterranean climate with cool, wet winters and warm, dry summers. The site, Christy Flats, receives an average 1680 mm of precipitation falling primarily as rain from November to May and was part of the Young Stand Thinning and Diversity Study (YSTDS). In this larger silvicultural experiment options for accelerating the development of late-seral conditions in young forests are investigated (for more detail about the study, see Davis et al., 2007). The site is 122 ha, mostly flat, and at an elevation of about 898 m. Although the exact history is unknown, the site was clear-cut sometime in the 1950s, broadcast-burned and planted to Douglas-fir. The plantation was pre-commercially thinned to 4 m spacing about 10-15 years after planting. Consequently, Douglas-fir was the dominant overstory tree species with only minor components of western hemlock (Tsuga heterophylla Raf.) and hardwoods, such as bigleaf maple (Acer macrophyllum Pursh.).

In 1997, the stand was fairly homogeneous in terms of the structural properties of trees in the study area (Davis et al., 2007). Before treatments it was dominated by 35-45 year-old Douglas-fir with an average density of 855-871 trees per ha and a basal area of 39.5 m² per ha. For our study we examined trees in the 'light thinning' and trees adjacent to the gaps in the 'light thinning with gaps' treatment. The light thinning treatment (32 ha) involved the removal of smaller diameter trees (low thinning) to achieve a target density of 275 trees per ha with fairly regular spacing. The thinned with gaps treatment (39 ha) was thinned using the same prescription as the light-thin treatment, but in addition 20 percent of the area was cut into 0.2 ha fairly circular gaps. In these gaps all trees were removed except a few hardwoods that were left to encourage species diversity. Treatments were completed in 1997 with harvester-forwarders. After harvest, the gaps were planted at a density of 500 seedlings per ha with a mix of conifer species. Some of the seedlings reached heights of up to 7 m at the time of our measurements (height measurements taken from the scan data from 2015) but the gap area was still easily distinguishable from the surrounding forest.

2.2. Study trees and terrestrial laser scanning

2.2.1. Trees adjacent to a gap

Within the light thinning with gaps treatment we identified 18 Douglas-fir trees growing directly adjacent to gaps. The selected trees (from here on named 'border trees') had no other tree (or any portion of another tree's crown) between the stem and the gap center in a cone with an angle of 45° (Fig. 2). Trees were only selected if they were vigorous codominant trees, at least 30 m in height, and greater than 40 cm in diameter at breast height (DBH; measured at 1.3 m above ground). We only selected healthy looking individuals with abundant foliage in good color and fairly straight stems (i.e., without crooks or forks).

In early April 2015 we used a Faro Focus 3D 120 terrestrial laser scanner (Faro Technologies Inc., Lake Marry, USA) to scan all border trees from six to ten different perspectives and with varying distances to the stem (10–20 m). These perspectives, or scanner positions, were chosen in the field to ensure a good visibility of the

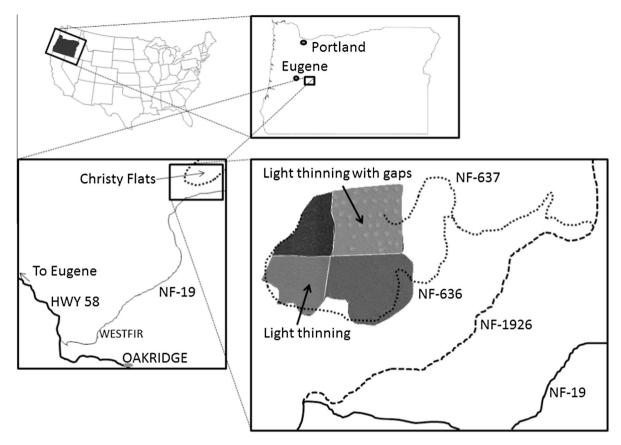


Fig. 1. Map of the study site locations within the national boundaries (upper left), within the State of Oregon (upper right) and locally (lower images). In this study we only focused on tree individuals growing in the 'light thinning' and in the 'light thinning with gaps' treatments (lower right).

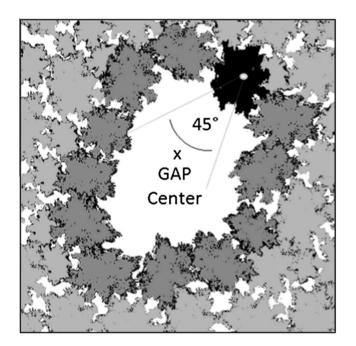


Fig. 2. A study tree (black) selected from the available border trees (darker gray) based on its height, DBH and growth conditions. No neighbor tree should have any above-ground element between the study tree and the gap center in an angle of 45°.

study trees from all sides. All scans of an individual tree were later combined into a single point cloud based on artificial chessboard targets fixed in the tree's vicinity for registration purposes. The scanner was set to capture a field of view of 310° vertical and 360° horizontal direction. The instrument operated with an angular step with of 0.035° (~45 million measurements per scan) and used laser light with a wavelength of 905 nm. All scans were performed during calm, dry weather with no snow remaining on the trees or ground.

2.2.2. Interior trees

To compare the three-dimensional appearance of the border trees with trees managed conventionally, i.e. with regular spacing, we selected 20 interior Douglas-firs from the adjacent treatment area in which a "light thinning" (without gaps) was conducted. This treatment was considered the control in our study. The sample trees were chosen to have at least 10 m distance to each other's crown margins. Again, to qualify as a study tree a tree needed to be vigorous, at least 30 m in height and 40 cm in DBH and without crooks or forks. All trees were scanned (7–12 scans per tree) using the same procedure as applied to the border trees described above and during the same week of favourable weather conditions in early April 2015.

At time of the thinning study establishment in 1997/98 the border group trees had an average live crown ratio of 47.5% (mean in crown base height: 10.7 m; mean in tree height: 26.2 m) and the interior group 45.6% (mean in crown base height: 11.9 m; mean in tree height: 28.0 m), respectively (see YSTDS establishment report; available online at http://ecoshare.info/projects/centralcascade-adaptive-management-partnership/forest-studies/youngstand-thinning-and-diversity-study/).

These data suggest that individuals of both groups had relatively open growing condition at treatment initiation, and more importantly, that crown conditions between the groups did not differ.

2.3. Point cloud processing

Each scan file was filtered for erroneous measurement points using the standard settings for filtering as provided by Faro Scene (Faro Technologies Inc., Lake Marry, USA). We semi-automatically referenced all scans for the study trees to each other based on the artificial targets using the Faro Scene referencing functionality. The resulting combined point clouds of each study tree and its surroundings had reference errors (displacement errors) of less than 2 cm in all cases. We then imported the point clouds as pts.-files into Leica Cyclone (Leica Geosystems AG, Heerbrugg, Switzerland) and manually separated the points representing the study tree from the surrounding trees and understory vegetation.

The point clouds of all study trees were imported into Mathematica (Wolfram Research, Champaign, USA) as xvz-files and several structural parameters were calculated automatically by an algorithm using the original point clouds as well as a 10 cm voxel representation of the trees obtained as described in Seidel et al. (2011b). We calculated a number of structural properties that we hypothesized to be affected by the spatial variability in growing conditions, i.e., by different growing conditions in the forest interior versus conditions adjacent to gaps. We calculated and tested the following variables: total tree height (TTH; in m), diameter at breast height (DBH; in cm), maximum crown projection area in a single height layer (CPA; in m²), the height of the maximum crown projection area (HCPA; in m), and crown length (CL; in m) as presented in Seidel et al. (2011b). In addition we determined crown volume (CV; in m³), crown base height (CBH; in m), crown surface area (CSA; in m²) according to Metz et al. (2013), mean crown radius (CR_{mean}, in m) and maximum crown radius (CR_{max}, in m) according to Seidel et al. (2015b). We also calculated the live crown ratio (LCR) as the ratio between crown length (CL; as derived from the scan data) and tree height (TTH; as derived from the scan data) expressed in percent.

To identify possible asymmetric growth of the border trees towards the gap center we determined the relative asymmetry (ASYM%) of all trees. ASYM% was defined as the ratio between a trees' absolute asymmetry and the height of the maximum crown projection area (Hmaxarea; in m). Absolute asymmetry (ASYM) was defined as the horizontal distance between the center of the crown at the height of maximum crown projection area and the stem-location on the ground-level (in accordance to Seidel et al., 2011b; in m). Here, we calculated relative asymmetry (percent) to avoid bias due to differences in absolute tree sizes.

One of our objectives was to test if the trees' relative asymmetry was directed towards gap centers. Therefore we measured the angle between the line from gap centers to the stem base and the direction of crown displacement. Both directions, expressed as vectors, should be counter-directional (angle: 180°) if the trees grew towards the available canopy space in the gap. We determined the average angle between the two directions of all study trees and calculated the probability of such an average value to occur as a result of random asymmetry. Therefore we performed 1000 simulations using random directions obtained from the RANDBETWEEN-function in Microsoft Excel (random directions between 0° and 180° for each tree).

To quantify changes in branch length induced by the increased resource levels available to border trees we focused on crown parts directly above CBH (lowermost third of crown). Since more open grown trees retain branches longer we expected to detect a stronger effect for the lower crown. We determined the direction between the stem base position (none of the trees had a noticeable lean) and the center coordinate (arithmetic mean of x and y) of the

entire point cloud of the crown section from CBH to one third of the distance between CBH and Hmaxarea (Fig. 3). Finally, we measured the Euclidean distance between the stem base's x and y coordinates and the x and y coordinate of the outermost tip of the longest branch in this crown area (Fig. 3, box). This was considered a conservative measure of branch length as it does not account for the curvature of branches, and hence it is biased towards shorter lengths. We compared the length of branches in the lowermost third of the crown between the two groups of trees.

To test whether branch growth in lower crowns was directed towards gaps, we measured the angle between the direction from the gap center to the trees' stem base position and the direction from the tree stem base position to the *xy*-center of the point cloud in the lowermost third of the crown. Again we expected counterdirectional pattern (angle: 180°) if the trees lowest branches grew towards the available growing space in the gaps. Based on 1000 simulations with random directions (Excel) we determined the probability of the average angle between the two directions as a result of pure chance.

2.4. Statistical analysis

All structural properties of the border trees were compared to the corresponding properties of the trees growing in the forest interior with a two-sided Welch *t*-test using R (R Development Core Team, 2008). We considered *p*-values smaller than 0.05 to indicate significant differences between the two groups of trees.

3. Results

The growing conditions during the last 18 years affected the tested tree crowns and stem properties. Welch *t*-tests revealed significant changes in the spatial dimensions of tree crowns (see Table 1). Compared to trees growing in regular spacing, gap creating resulted in border trees to have significantly lower crown base heights (CBH) as well as lower heights of maximum crown projection (HCPA). As a consequence of the lower CBHs of border trees but similar total tree heights, crown length (CL) and live crown ratio (LCR) were significantly higher for border trees.

The crown surface area (CSA) and crown volume (CV) of border trees were also significantly larger than those of interior trees. All other tested parameters were not significantly different between the groups. Fig. 4 visualizes the observed differences in tree shapes based on one exemplary tree per group.

The relative asymmetry (ASYM%) was not significantly different between the two groups. However, border trees had a direction of asymmetry that was on average only 62° off from the direction towards gap centers. The probability to observe such directional patterns by chance was determined to be 8/1000, i.e. only eight of one thousand simulations with random directions achieved the same or a lower deviation. Hence the chance that the border trees showed asymmetric growth towards the center of the gaps due to random is less than 1 percent (p < 0.01).

The simulation with random directions for the lowermost crown portions (lower third) revealed that the probability that the observed directions of growth were random was less than $1/1000 \ (p = 0.001)$. Thus, lower crown portions of border trees showed a statistically significant growth shift towards gap centers. The average deviation of the growth direction from the perfect counter direction (from the center of the gap to the tree) was 53.67°. The length of the longest branch in the lowermost third of crowns was not significantly different between border and interior trees (5.39 m and 4.96 m, respectively).

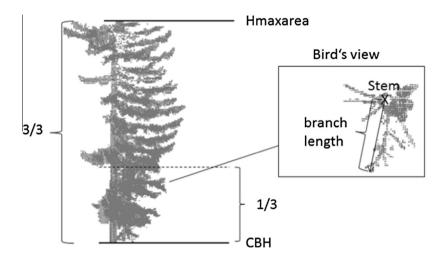


Fig. 3. Side-view on the point cloud (centers of 10-cm voxels) in which the lowermost third of the crown between CBH and Hmaxarea is highlighted. In the box: bird's view of the lowermost third of the crown in which the distance measurement between the stem base position and the tip of the longest branch is visualized.

Table 1

Comparison of structural properties of trees growing adjacent to gaps (border trees) and in regularly spaced thinned forests (interior trees). Variables that were not significantly different between the groups are marked with n.s. (not significant).

Parameter	Mean of group 'border tree'	Mean of group 'interior tree'	p-value
CBH (m)	9.83	15.59	<0.001
HCPA (m)	20.70	24.41	< 0.001
LCR (%)	73.66	58.98	< 0.001
CL (m)	27.50	22.52	<0.01
$CSA(m^2)$	608.70	484.23	0.01
CV (m ³)	544.10	407.13	0.02
CR (m)	4.29	4.05	0.18 (n.s.)
CRmax (m)	4.24	4.04	0.20 (n.s.)
ASYM%	0.33	0.42	0.23 (n.s.)
CPA (m ²)	52.59	47.19	0.24 (n.s.)
DBH (cm)	60.17	57.63	0.40 (n.s.)
TTH (m)	37.32	38.10	0.45 (n.s.)

4. Discussion

One of our most intriguing results was the missing effect of gap creation on horizontal crown extension. The lack of a significant difference in lateral crown extension suggested that individuals of both groups must have been able to expand their crowns to a similar extent since 1997. This is reflected in our decision to investigate the impact of spatial arrangement only (i.e., not confound spatial arrangement and density by using trees in unthinned areas) and use trees in thinned stands as controls. Both stands were thinned to reduce competition and apparently this provided sufficient room and resources for similar lateral branch extension. Also, border trees would have experienced an increase (although not as much as from the gap) in resource availability in the thinned matrix away from the gap. Rather than develop completely one sided crowns, trees expanded in both directions, reducing the development of asymmetry due to a gap effect. Furthermore, Muth and Bazzaz (2002) found that the growth towards light is generally low for coniferous species. The combination of these factors, might explain why the lateral extension of branches, and hence the increase in maximum crown radius, was very similar for both tree groups, even though the border trees had access to more light and below-ground resources in the gaps. This trend may not hold in the future, as competition for interior trees is likely

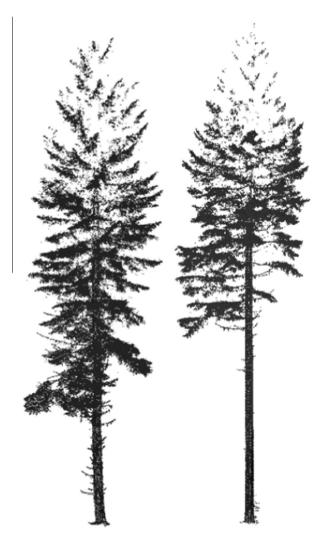


Fig. 4. Graphical visualization of 3D point clouds of one exemplary tree of each of the two groups (in scale). Trees were selected to illustrate the most prominent differences among trees growing in the settings. The left tree (gap is to the left of tree) shows a typical border tree with low CBH and high LCR. The right tree depicts an interior tree growing in regular spaced thinned forest with higher CBH and lower LCR).

to increase faster than for border trees. Further monitoring would therefore provide more insight into potential trajectories the tree groups will follow. The investigated trees grew approximately 40 years or the first two thirds of their lives in similar conditions. Thus, any difference today is due to the last 18 years in which growing conditions were different between the groups. Therefore, current conditions are the result of a combination of both time periods, whereby post-treatment growth also includes an adjustment or "carry over" phase. Consequently, our results have to be viewed in this temporal context. For example, if the growing conditions would have been altered earlier and/or the trees had more time to respond, we possibly would have found more differences in crown and tree structures (Wilson and Oliver, 2000).

However, several crown structural attributes responded more dynamically or were more sensitive to growing conditions. We observed a foraging processes to areas with increased resource availability (light and space) expressed by asymmetric crown growth towards the center of the gaps. This effect was statistically significant for the entire crown and particularly strong for the lower crown. Earlier studies observed the similar effects for a variety of tree species, including maple, birch, ash, oak (Muth and Bazzaz, 2003), and European beech (Seidel et al., 2011b).

The most prominent differences among the tested tree groups were related to the vertical dimension of the tree crown, more specifically crown base height (CBH) and height of the maximum crown projection area (HCPA). The vertical crown extension of border trees also included a shift in crown shape towards a lower center of gravity. This may indicate a shift in crown dynamics towards "old-growthness" as such bottom-loaded crowns are typical for old forest (e.g. Franklin and van Pelt, 2004). For Norway spruce Pfister et al. (2008) also found significantly lower heights to the first living branch for trees growing on the edge of gaps.

The thinning treatments lead to the expectation that trees in both groups would have reduced crown lifting, as branch mortality is halted due to sufficient growing space (e.g. Davis et al., 2007). In fact we detected that regularly spaced trees experienced crown lift, but not the border trees. A similar effect of the increased growing space availability has been observed for other tree species, e.g. Scots pine (Hynynen, 1995). Due to similar tree heights, the lower crown base of the border trees also indicated larger crown sizes, as quantified in crown length, crown surface area, and crown volume. Such crown size differences are already reflected in higher diameter growth (Dodson et al., 2012) and will likely exaggerate growth and vigor differences in the future as well as increasing the speed of development of several microhabitat features (Michel and Winter, 2009), such as bark fissures (Sheridan et al., 2013).

While increased crown sizes may be viewed desirably in terms of future growth and development of old-growth crown structures, larger crowns can have negative effects on tree value. The lower log is the most valuable part of the stem and its quality is directly influenced by the height of the crown base as it determines the branch free length of the bole (e.g. Spiecker and Hein, 2009). Also the branch length and the related knot size reduces the value of a log (e.g. Macdonald and Hubert, 2002; Macdonald et al., 2009). The TLS data was not sufficient to compare branch diameters directly, but the trend towards increased branch length (albeit not statistically significantly different), in particular in the lowermost part of the crown, provides an indication that gaps reduce log values in the long term. Earlier studies also found larger branches in the lower crown of trees in thinned stands when compared to unthinned stands, for example for Eucalypthus nitens H. Deane & Maiden (Medhurst and Beadle, 2001) or Pinus taeda L. (Yu et al., 2003).

Using the allometric equation by Ishii et al. (2000) for coastal Douglas-fir (branch length = $1.198 * branch diameter^{0.567}$)

suggested that the average increase in the longest branch of the border trees investigated in our study corresponds to a branch diameter that was 0.16 cm larger on average than in trees growing in regular spaced thinned stands. Whether the increase in branch diameter is sufficient to actually lead to lower log grades, thus reduced economic values of border trees, is likely a function of how long trees can expand their branches into open gap areas. Our data suggest that 18 years are not likely sufficient for branch diameters to reach thresholds that would result in major economic losses compared to evenly spaced thinnings. However, foresters planning longer rotation ages should consider this economic impact carefully when deciding the timing of gap creation.

Changes in tree and crown shape and associated impacts on canopy layering also have ecological effects (Angelstam, 1992; North et al., 1999: Michel and Winter, 2009). Thus, increasing the small scale, within-stand spatial variability through gap creation will increase the habitat diversity in formerly fairly homogenous stands (e.g. Barbeito et al., 2009). Trees in the stand interior will develop under conditions of a more regular spacing. In contrast, those facing the gaps will develop larger, more one-sided crowns and branches. This variety in crown structures is likely to result in larger diversity of resources and environmental conditions and hence larger diversity in species that utilize these resources (e.g. McElhinny et al., 2005; Hinsley et al., 2009). The longer and more bottom-loaded crowns of trees facing the gaps have increased ecological values, in particular their lower branches (e.g. Muir et al., 2002), e.g., for bryophyte (Rosso et al., 2001) and lichen development (Lesica et al., 1991).

5. Conclusions

As foresters increasingly understand the ecological value of spatial variability in stands, it is important to gain knowledge on the effects of such management goals on a variety of aspects, including the growth and architecture of individual trees. Our study of Douglas-fir forests in western Oregon showed that gap creation as a tool to increase structural old-growthness of forests has a noticeable effect on crown growth and shape of the remaining trees. It also showed that pre-treatment conditions have a buffering and lingering effect, suggesting that treatments of younger stands may be more efficient in achieving the goal of higher variability in tree and crown conditions. In summary, Douglas-fir trees growing adjacent to canopy gaps of about 0.2 ha in size developed a bottom-loaded crown architecture, which has been reported for other species as well as a reaction to thinning. Douglas-fir trees also foraged towards available growing space and increased light levels within the gaps.

The economic value of the border trees was potentially negatively affected by gap creation, especially when trees grow near gaps for extended periods. In contrast, the overall increase in structural variability contributed by the border trees in otherwise fairly homogenous stands is likely to positively affect several ecosystem functions as well as biodiversity within stands.

The choice of the different management practices (regular thinning versus gap creation) in regards to crown development has to be viewed in a long-term management context. For example, without further thinning the regularly spaced stands will close in, resulting in smaller, shorter crowns. In contrast, even without further entries the gaps will remain "open" for longer. Whether crowns of border trees will follow the development of interior trees with a delay (Wilson and Oliver, 2000) or have room for a continuous expansion depends on the gap size and the specific location of border trees in regards to their neighbors. Thus, the likelihood of future management opportunities is an important factor to consider when deciding whether to create gaps in thinned stands and when selecting gap densities and sizes.

Acknowledgements

This work was funded through a research scholarship granted to Dominik Seidel by the German Research Foundation (reference number: Se 2383/1-1) and the Edmund Hayes Professorship in the Department of Forest Ecosystems and Society, College of Forestry, Oregon State University.

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