Establishment Histories and Structural Development of Mature and Early Old-growth Douglas-fir Forests of Western Washington and Oregon

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Abstract

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Regeneration of tree populations following stand-replacing wildfires is an important process in the multi-century development of Douglas-fir—western hemlock forests. Temporal patterns of tree establishment in naturally regenerated, mid-aged (100- to 350-year) Douglas-fir-dominated forests have received little study in comparison with the abundance of research on regeneration in older Douglas-fir stands (>400 years of age). Increment cores were obtained from 1455 trees in 18 mature and early old-growth forests in western Washington and northwestern Oregon USA in order to determine temporal patterns of natural Douglas-fir regeneration following stand-replacing wildfire. Continuous regeneration of Douglas-fir for many decades following initiating fire was evident in all of the stands. The establishment period averaged 60 (range 32 to 99) years. The pattern observed contrasts both with the view of rapid (one- to two-decade) regeneration of Douglas-fir portrayed in early forestry literature and with reports of establishment periods

exceeding 100 years in older (>400 year) Douglas-fir—western hemlock stands. Current intensive production forestry practices directed toward rapid and uniform stand closure following logging have no precedent in the historic natural patterns of Douglas-fir regeneration documented in this study. Conversely, results of this study provide evidence that early seral ecosystems persisted for several decades following wildfires.

Patterns of structural development in mid-successional Douglas-fir dominated forests – a period in which forest structures evolve from the relatively simple conditions found in young forests to the complex old forests – is poorly understood. Stand structure and composition was analyzed in nine early old-growth (200- to 350-year-old) Douglas-fir-dominated stands in western Washington and Oregon, all of which originated following a single stand-replacement wildfire. Structure and composition of live tree populations (density, diameters, and heights) as well as dead tree structures (snags and logs) were quantified and compared with conditions in previously reported studies of older (400-600-year old) forests. Stand-level attributes were analyzed using descriptive statistics, nonlinear regression, principal components analysis, and two old-growth indices. Variability among stands in specific structural features was large but consistent with the current conceptual model of Douglas-fir forest development. Diameter distributions generally exhibited a reverse-J shape, a characteristic of >450-year-old forests. Douglas-fir populated the tallest height classes and shade-tolerant species (e.g., western hemlock and Pacific silver fir) were present in lower (co-dominant and intermediate) canopy positions. Coarse woody debris was abundant in early old-growth stands in the form of both snags (42-140 m^3 ha^{-1}) and logs (172-584 m^3 ha^{-1}). Scores for early old-growth stands calculated using existing old-growth structural indices were comparable to those in older (400- to 600-year-old) forests.

The structural conditions and variability in these early old-growth forests are useful guides for managers seeking to accelerate development of complex structures in young Douglas-fir forests.

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CHAPTER 1: INTRODUCTION

Importance of succession and structural development

Forest succession and stand structural development are fundamental processes involved in directional, long-term changes in the structure and composition of forest communities (Larson 2008). Hence, thorough knowledge of these related processes is critical to understanding and predicting long-term change (Larson 2008). Structural development involves progressive changes in physical elements of the forest (e.g. trees, snags, logs) and their spatial arrangement following the initiation of a forest ecosystem, often following a disturbance (Franklin et al. 2002).

Knowledge of forest succession and structural development is of particular importance in forest ecosystems that are subject to periodic stand- replacement disturbances because significant changes in ecosystem processes and biological diversity are typically associated with succession, particularly where long-lived tree species are involved (Lindenmayer and Franklin 2002). For example, major changes may occur in the provision of habitat for threatened and endangered species and socially valued ecological services, such as provision of domestic water supplies, sequestration of carbon, and wood production (Costanza et al. 1997).

Forests of long-lived tree species, such as Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) may change compositionally and structurally for many centuries but comprehensive understanding of compositional and structural changes is rarely complete (e.g., Franklin and Spies 1991, Spies and Franklin 1991). Two possible reasons for the lack of comprehensive descriptions may be that: (1) plant ecologists have focused primarily on changes in plant community composition (Daubenmire 1968); and (2) silviculturalists have focused primarily on the early stages of forest development (<100 years) (Oliver and Larson 1996) because of their interest in wood production. Building a richer, more comprehensive understanding of succession and structural development requires studies that will fill gaps in existing knowledge. Two such gaps in our knowledge of long-lived Douglas-fir forests are the focus of this dissertation: the post-disturbance period of tree regeneration and re-establishment of closed-canopy forest and the transitional period between mature and old forests that occurs at 200 to350 years.

Douglas-fir—western hemlock ecosystems

Naturally developing Douglas-fir are forests that undergo centuries of development (Figure 1.1), experiencing both compositional (Halpern 1988, Halpern and Lutz 2013) and structural (Franklin et al. 2002) change. Wildfire is the most important category of natural disturbance initiating seres in most of the Douglas-fir region. A wide variety of forest age classes have been initiated by wildfires over the last millennium (Morrison and Swanson 1990, Agee 1993) providing a diversity of stands in differing stages of compositional and structural change. There is substantial variability in fire severity associated with a regional, south-to-north climatic gradient, with mixed-severity wildfires occurring more commonly in southern latitudes (Impara 1997, Weisberg 1998, Tepley 2010). However, fires with a dominantly high-severity behavior appear most common in northern, moister areas of the Douglas-fir region (e.g., Hemstrom and Franklin 1982).

Numerous conceptual models have been developed of forest successional processes. Models in which ecosystem development moves toward a steady state of composition and structure are characteristic of many early theoretically-focused models including one developed for northeastern hardwood forests (Bormann and Likens 1979). Many forester-created models of forest development have a silvicultural and management orientation and are relatively simple.

For example, Oliver and Larson (1996) provide a model with four structural stages: regeneration, stem exclusion, understory reinitiation, and old growth.

Extensive research on the structure, function, and composition of old-growth Douglas-fir forests (e.g., Franklin et al. 1981, Franklin and Spies 1991, Spies and Franklin 1991) has made it possible to develop more quantitative descriptions of succession and, especially, structural development of northwestern forests (e.g., Spies and Franklin 1996, Franklin et al. 2002, Spies 2009, Tepley et al. 2013). Moreover, the process-based successional models help link structure and function much more directly with benefits in setting targets for active or passive management (Spies and Franklin 1996, Franklin et al. 2002).

Conceptual Framework

The most comprehensive conceptual model of structural development in Douglas-fir forests was developed by Franklin et al. (2002) (Tables 1.1 and 1.2) and is extensively cited in this dissertation as a framework and point-of-reference. The eight elements (two events and six stages) of this model are described in the following paragraphs.

1. Disturbance and Legacy Creation

Disturbances and the legacies that they create initiate a stand-development cycle or sere. Large and severe disturbances are commonly referred to as stand-replacement events because the majority of the overstory tree population typically is killed. Also, these disturbances usually include significant areas of low and intermediate disturbance levels and undisturbed areas within their larger boundaries. Individual disturbance events may affect many thousands of hectares and occur at infrequent intervals of several centuries or even a millennium (Hemstrom and Franklin 1982.)

These natural stand-replacement disturbances leave behind significant physical and biological legacies that play important ecological roles in the post-disturbance landscape (Franklin et al. 2002). Biological legacies include: 1) living organisms; 2) organic matter, much of it in the form of structures (standing dead trees or snags, logs, and other woody debris); and 3) biologically-derived patterns, such as in soil physical, chemical and biological properties. Much of the organic matter is in the form of snags or standing dead trees, logs, and other woody debris; such structures are very important because they can function as habitat and substrate as well as modify physical conditions and processes (Harmon et al. 1986; Maser et al. 1988).

2. Cohort establishment

During cohort establishment trees begin regenerating in the post-disturbance landscape. It has been postulated that during this stage tree regeneration can vary widely. Some reasons for the proposed variation relate to seed source limitations, size and severity of initiating disturbance, repeat disturbances, severe environmental conditions, and/or intense competition from shrubs. As cohort establishment progresses, many stands attain tree densities high enough where canopy closure and intense intra-tree competition will begin. The model describes this period as usually lasting for 25 years. However, the typical period of tree regeneration following wildfire remains an unclear issue with evidence which supports both extended (>150 year) and attenuated (<25 year) establishment.

The importance of the early seral ecosystem that occupies the disturbed site during this stage has recently been recognized. This is a distinct stage characterized by dominance of diverse plant life forms (cryptograms, herbs, shrubs) and not just trees. In fact, this early seral stage has been identified as the most biologically diverse of all six developmental stages and provides critical habitat for many animals, including birds and butterflies (Swanson et al. 2010).

3. Forest canopy closure

Canopy closure is the most dramatic event in the development of a stand and one in which major changes occur in ecosystem structure, function, and biodiversity second only in significance to those associated with the disturbance event that initiated the sere. With the onset of canopy closure trees assume dominance of the site, significantly altering the resources available to other plant life forms.

Consequences of canopy closure include major changes in environmental conditions and in biological diversity. Interior portions of the forest undergo greatly reduced light levels and greatly moderated microclimatic conditions in comparison with those found in open areas. Nutrients may be more strongly conserved but the potential for nitrogen fixation probably decline, except where trees that can serve as hosts for nitrogen-fixing species, such as red alder, are present in the stand.

The degree of canopy closure attained by trees depends upon the density and composition of the forest stand and the uniformity of the tree regeneration. Factors influencing the rate of canopy closure include availability of tree seed, seedling banks, environmental conditions, competing plant life forms, pests and pathogens, climatic events (e.g., intense ice and snow storms), wind, and herbivory. These fine scale-disturbances can introduce heterogeneity into otherwise uniformly dense young stands (e.g., Lutz and Halpern 2006).

4. Biomass accumulation/competitive exclusion

Biomass accumulation and competitive exclusion are the important developmental processes that are dominant in the young post-canopy-closure forest. Other classifications of structural development have referred to this period as the competitive exclusion, stem exclusion, or biomass accumulation stage. Biomass accumulation is the most consistent feature of the young post-canopy-closure forest: trees are utilizing most of the site's resources and are in an exponential growth phase.

Competitive processes are an important feature of this developmental stage. High tree stem densities contribute to intense competition among trees, which is most pronounced in height growth. Trees that fall behind in height growth are quickly suppressed by the taller individuals within the stand. Consequently, mortality is predictably in the smaller trees. Mortality rates are also density dependent. Competitive processes also result in elimination of most understory vegetation because of the low light levels.

Distinctive functional attributes of the biomass accumulation stage relate to the dense, rapidly growing young forest. High rates of primary productivity and biomass accumulation, primarily wood, are prominent and essentially all of the resources of the site are being channeled to this outcome. Woody debris is being generated, primarily in the form of competitively-killed standing dead trees and branches. Biodiversity is at its lowest level during this stage.

The biomass accumulation stage does vary substantially in the intensity of its expression, as a result of either the density of the trees or the dominant tree species or both. Plantations tend to produce an intense representation of the stage because they are uniformly planted at high density. The duration of this stage can vary from 60 to 100 years. Much of the variability is associated with site productivity with productive sites moving through the stage more rapidly than low productivity sites. For example, dense stands on low productivity sites may stagnate because trees have difficulty expressing dominance.

5. Maturation

Competitive processes and biomass accumulation begin to decline as the forest transitions into the maturation stage. The forest is still dominated by a relatively even-aged cohort of trees but the density is sufficiently reduced so that light and other resources are now available for establishment of understory communities, including reproduction and growth of shade-tolerant trees. The maturing forest will undergo significant shifts in structure, causes and patterns of tree mortality, and begin experiencing important development processes, such as increased decadence and spatial heterogeneity. The maturation stage may begin at 80-100 years and persist for up to 150 years.

During maturation the cohort of dominant trees will attain the majority of its ultimate height and crown spread. The dominant trees will continue to exhibit the classic tree crown growth form with defined growing tips (Van Pelt and Sillett 2008) but will have essentially completed most of their height growth by the end of this stage. Dominant Douglas-fir trees will begin expanding old and generating new epicormic branch systems, thereby extending their crowns downward in response to improved light conditions within the stand.

Mass of coarse woody debris in the stand – including snags and logs -- reaches minimal levels during the mature stage of development (Maser et al. 1988, Spies et al. 1988). Most of the dead wood legacy inherited from the previous forest has decomposed and it is only during the last half of the maturation phase that replenishment of the coarse wood will begin to occur as a result of mortality in overstory trees. Improved understory light and moisture conditions allow for re-establishment of understory plant communities and establishment and more rapid growth of shade-tolerant tree associates, such as western hemlock (*Tsuga heterophylla)*, western redcedar (*Thuja plicata*), and Pacific silver fir (*Abies amabalis*).

Generally, mortality processes transition from competition/density-dependent to agent-based causes of mortality duration the maturation stage. Key agents include root and butt rots, bark beetles, and wind (true uprooting and stem breakage not mechanical breakage due largely to rots). The agent-based mortality is notable because much of it affects the overstory dominant and co-dominant trees and it tends to be spatially aggregated, rather than occurring as isolated trees. Canopy gaps are created in the forest as a consequence, providing significant additional light and moisture resources for development of shade-tolerant tree seedlings and saplings as well as creating more spatially heterogeneous stands.

6. Vertical diversification

The vertical diversification stage represents a phase of forest development where late successional characteristics begin to become expressed especially as it relates to tree size distributions and the establishment of canopy continuity. This stage often occurs from 200-350 years in development. Vertical variability in forest canopies is a dimension of spatial heterogeneity where canopies are typically continuous from the ground to the tops of the tallest trees. Vertical development is related to both the presence of multiple generations of shade-tolerant trees species and the regeneration of epicormic branch systems on the shade-intolerant Douglas-fir.

The period of vertical diversification describes characteristics and structural processes of the early old-growth stage, but these descriptions are lacking validation because they are largely based on inferences made from younger and older forests. Consequently, it remains unknown whether forests undergoing development from 200-350 years are represented by increasing old-growth characteristics. Specifically, it is unclear whether (1) the size distributions are starting to resemble old-growth, (2) if vertical diversification of foliage is actually occurring, (3) and levels of coarse woody debris are rebounding from the lowest levels of the mature stage.

7. Horizontal diversification

The horizontal diversification stage represents a phase of forest development where stands evolve much heterogeneity as a result of canopy gaps. This period of forest development generally begins after 300 years and primarily occurs as a result of several interacting agent-based mortality processes associated with laminated root rot, velvet top fungus (*Phaeolus schweinitzii* [Fr.] Pat.), Douglas-fir bark (*Dendroctonus pseudotsugae* Hopkins) beetles, and small wind events. The horizontal diversification stage is also characterized by development of complex crown features (e.g. broken tops, reiterations, large epicormic branches), and further reductions in the densities of Douglas-fir.

8. Pioneer cohort loss

The pioneer cohort loss stage of development is characterized by the continued mortality of the shade-intolerant pioneering cohort of Douglas-fir that is no longer able to establish under shade or in small gaps. Pioneer cohort loss may occur as rapidly as 800 years on productive sites, yet may be more protracted on lower productivity last until 1300 years. The loss of pioneering cohort of Douglas fir can be highly influential on the remaining forest as many functional processes are closely tied to this species (e.g. wildlife habitat, structure for tree establishment, biogeochemical cycling).

Dissertation research

The 8-stage conceptual framework outlined in the previous section is supported by data sets and analyses at both ends of the developmental sequence, albeit the majority of analyses exist for old-growth forests. However, both the early establishment period and the intermediate stages of stand development (maturation through the vertical diversification stages of development) are not well documented. Furthermore, current understanding is complicated by the fact that many of the old-growth stands previously studied experienced multiple disturbances and largely underwent different developmental pathways (Tepley et al. 2013).

The studies reported in this dissertation represent my attempt to clarify some key processes in Douglas-fir stand development, specifically:

1) Rates and patterns of establishment of the new tree cohort, persistence of the early seral ecosystem, and eventual tree canopy closure; and

2) Patterns of structural development in forests during their shift from the mature to old forest stages.

In pursuing this effort I focused on forests that appeared to represent single-cohort stands – i.e., stands that showed no evidence of any significant subsequent disturbances, such as might have allowed for the establishment of additional cohorts of Douglas-fir .

Establishment of a new cohort following stand-replacement disturbance

Patterns and drivers of early Douglas-fir establishment have been a subject of scientific and management interest for over a century; despite this interest (or maybe because of it) this subject has often been a confusing and occasionally controversial topic. Also, early research focused on tree establishment and development of a forest canopy but gave no consideration to the presence and duration of early seral ecosystems now recognized as crucial for forest biodiversity and food webs (Swanson et al. 2010).

Rapid Douglas-fir regeneration with moderate to dense stocking levels was the interpretation from early 20th century observations of post-fire tree establishment in Douglas-fir forests (Isaac 1936, Munger 1940). This perspective was strongly influenced by observations following the 1902 Yacolt and 1910 Cispus fires in the southern Washington Cascades and of regenerating harvested stands in the same region (Hofmann 1924, Herring and Green 2007).

It was not until the late 1970's that researchers were surprised to discover a >200 year age range in Douglas-fir determined from stump counts (Franklin and Hemstrom 1981). Additional research in old-growth forests supported the findings of a wide age range for Douglas-fir, evidenced by stump count reconstructions indicating >150 year age ranges. (Tappeiner et al 1997, Poage and Tappeiner 2002). However, general conclusions regarding common patterns of Douglas-fir establishment and development remained confounded by conflicting study results indicating much shorter periods of (25-60 years) for Douglas-fir establishment (Yamaguchi 1986, Winter et al. 2002). Thorough investigations exist into Douglas-fir regeneration and development within the mixed-severity landscapes of the central and southern Cascade Range (Tepley 2010, Tepley et al. 2013), yet a dearth of information exists regarding the patterns of Douglas-fir regeneration following single high-severity fires especially for stands originating between 1650-1800 AD.

As described in Chapter 2 of this dissertation I addressed the topic of stand establishment by aging Douglas-fir cohorts in mature and early old-growth forests in 18 locations in western Washington and Oregon.

The general findings from this research are that rates of Douglas-fir establishment following wildfire were remarkably similar averaging ~ 60 years. Also, all sites had completed successful establishment of Douglas-fir within 100 years. I infer from the results of this work that conceptual models which outline tree establishment as a 25 to 30 year process (e.g., Franklin et al. 2002) should be revised to reflect much longer establishment durations for natural stands. There are also important inferences that can be drawn about the duration of early seral ecosystems during natural seres.

Patterns of stand development in early old-growth forests

Patterns of structural development in early old-growth forests is the subject of Chapter 3, based on measurements made in nine stands. Most previous studies of structural development have been in stands <100 or >400 years old. This early old-growth period, which approximates the vertical diversification stage, is identified as a major period of change in the current conceptual model of Douglas-fir stand development (Franklin et al. 2002) (Table 2). The early old-growth period is characterized by:

1. Significant development of old-growth characteristics particularly those related to tree size distributions;

2. Development of a vertically continuous canopy due to growth of shade-tolerant species (e.g. western hemlock, western redcedar);

3. Elongation of Douglas-fir crowns through epicormic branching;

4. Increase of decadence (e.g., bole and root decay) in individual trees;

5. Development of canopy gaps; and

6. Shifts from model-conforming to individualistic canopy architectures in the Douglas-fir trees;

However, little quantification of stand structures has been carried out in forests between 200-350 years of age. In my dissertation research stand level variables for nine early old-growth stands are quantified and compared with existing data sets from much older (>400 year) forests.

The structure of early old-growth forests sampled appears to conform well to the current conceptual model of Douglas-fir forest development (Franklin et al. (2002). The early old-growth stands appear to occupy an intermediate structural conditions based upon comparisons with older (>400 year) stands using previously constructed old-growth indices.

Future directions for structural development research in Douglas-fir forests

An overview of the results of these studies and some implications for further research (both basic and applied) are provided in Chapter 4.

LITERATURE CITED

Agee, J.K. 1993. Fire Ecology of Pacific Northwest Forests. Island Press. Washington, DC. 493pp.

Carey, A.B. 2007. AIMing for Healthy Forests: active, intentional management for multiple values. General Technical Report PNW-GTR-721, Pacific Northwest Research Station, U.S. Department of Agriculture, Forest Service, Portland, Oregon.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111: 1119–1144.

Costanza, R., d'Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., & Van den Belt, M. 1997. The value of the world's ecosystem services and natural capital. Nature. 387(6630), 253-260.

Franklin, J. F., T. A. Spies, R. Van Pelt, A. B. Carey, D. A. Thornburgh, D. R. Berg, D. B. Lindenmayer, M. E. Harmon, W. S. Keeton, D. C. Shaw, K. Bible, and J. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155:399–423.

Halpern, C. B. 1988. Early successional pathways and the resistance and resilience of forest communities. Ecology, 69(6), 1703-1715.

Halpern, C. B., & Lutz, J. A. 2013. Canopy closure exerts weak controls on understory dynamics: a 30-year study of overstory-understory interactions. Ecological Monographs, 83(2), 221-237.

Harmon, M. E., & Franklin, J. F. 1989. Tree seedlings on logs in Picea-Tsuga forests of Oregon and Washington. Ecology, 48-59.

Hemstrom, M.A., Franklin, J.F. 1982. Fire and other disturbances of the forests of Mount Rainier National Park. Quaternary Research. 18: 32-51.

Hofmann, J.V. 1924. The natural regeneration of Douglas-fir in the Pacific Northwest. Department Bulletin. 1200. Washington, DC: US Department of Agriculture. 61 p.

Impara, P.C. 1997. Spatial and temporal patterns of fire in the forests of the central Oregon Coast Range. Ph.D. dissertation, Oregon State University, Corvallis, OR.

Isaac, L. A. 1943. Reproductive habits of Douglas-fir. Charles Lathrop Pack Forestry Foundation, Washington, D.C., USA.

Kimmins, J. P. 1997. Forest ecology: a foundation for sustainable management (No. Ed. 2). Prentice-Hall Inc.

Larson, A. J., Franklin, J.F. 2005. Patterns of conifer tree regeneration following an autumn wildfire event in the western Oregon Cascade Range, USA. Forest Ecology and Management. 218, 25-36

Larson, A. J., & Franklin, J. F. 2010. The tree mortality regime in temperate old-growth coniferous forests: the role of physical damage. Canadian Journal of Forest Research, 40(11), 2091-2103.

Lindenmayer, D.B., and J.F. Franklin. 2002. Conserving Forest Biodiversity. Island Press, Washington, DC.

Lutz, J. A., Larson, A. J., Swanson, M. E., & Freund, J. A. 2012. Ecological importance of large-diameter trees in a temperate mixed-conifer forest. PloS one, 7(5), e36131.

Morrison, P. H., & Swanson, F. J. 1990. Fire history and pattern in a Cascade Range landscape. Collections.

Munger, T.T. 1930. Ecological aspects of the transition from old forests to new. Science 72: 327–332.

Munger, T.T., 1940. The cycle from Douglas-fir to hemlock. Ecology. 21, 451–459.

Perry, D. A., Oren, R., & Hart, S. C. 2008. Forest ecosystems. JHUP.

Poage, N.J., Tappeiner, J.C. 2002. Long-term patterns of diameter and basal area growth of old-growth Douglas-fir trees in western Oregon. Can. J. For. Res. 32:1232-1243.

Spies, T.A., and Franklin, J.F., 1996. The diversity and maintenance of old-growth forests. In: Szaro, R.C., Johnson, D.W. (Eds.), Biodiversity in Managed Landscapes: Theory and Practice. Oxford, New York, pp. 296–314.

Spies, T.A. 2009. Science of old growth, or a journey into wonderland. *In.* Spies and Duncan 2008. Old-growth in a new world: a Pacific Northwest icon reexamined. pp. 247-260. Springer-Verlag, Washington, D.C.

Swanson, M. E., Franklin, J. F., Beschta, R. L. Crisafulli, C. M., DellaSala, D. A., Hutto, R. L., Lindenmayer, D. B., Swanson, F. J. 2011. The Forgotten Stage of Forest Succession: Early-successional Ecosystems on Forest Sites. Front. Ecol. Environ. 9:2, 117–125. Doi: 10.1890/090157

Tappeiner, J.C., Huffman, D., Marshall, D., Spies, T.A., Bailey, J.D. 1997. Density, ages, growth rates in old-growth and young-growth forests in coastal Oregon. Can. J. For. Res. 27: 638-648.

Tepley, A.J. 2010. Age structure, developmental pathways, and fire regime characterization of Douglas-fir/western hemlock forests in the central western Cascades of Oregon. PhD. Dissertation: Oregon State University

Tepley, A. J., Swanson, F. J., & Spies, T. A. 2013. Fire-Mediated Pathways of Stand Development in Douglas-Fir/Western Hemlock Forests of the Pacific Northwest, USA. Ecology. 94: 1729-1743.

Weisberg, P.J. 1998. Fire history, fire regimes, and development of forest structure in the central Western Oregon Cascades. Ph.D. Dissertation, Oregon State University, Corvallis, OR.

Winter L.E., Brubaker L.B., Franklin JF, Miller E.A., DeWitt D.Q. 2002a. Initiation of an old-growth Douglas-fir stand in the Pacific Northwest: a reconstruction from tree-ring records. Can. J. For. Res. 32(6):1039–1056. Doi: 10.1139/x02-031

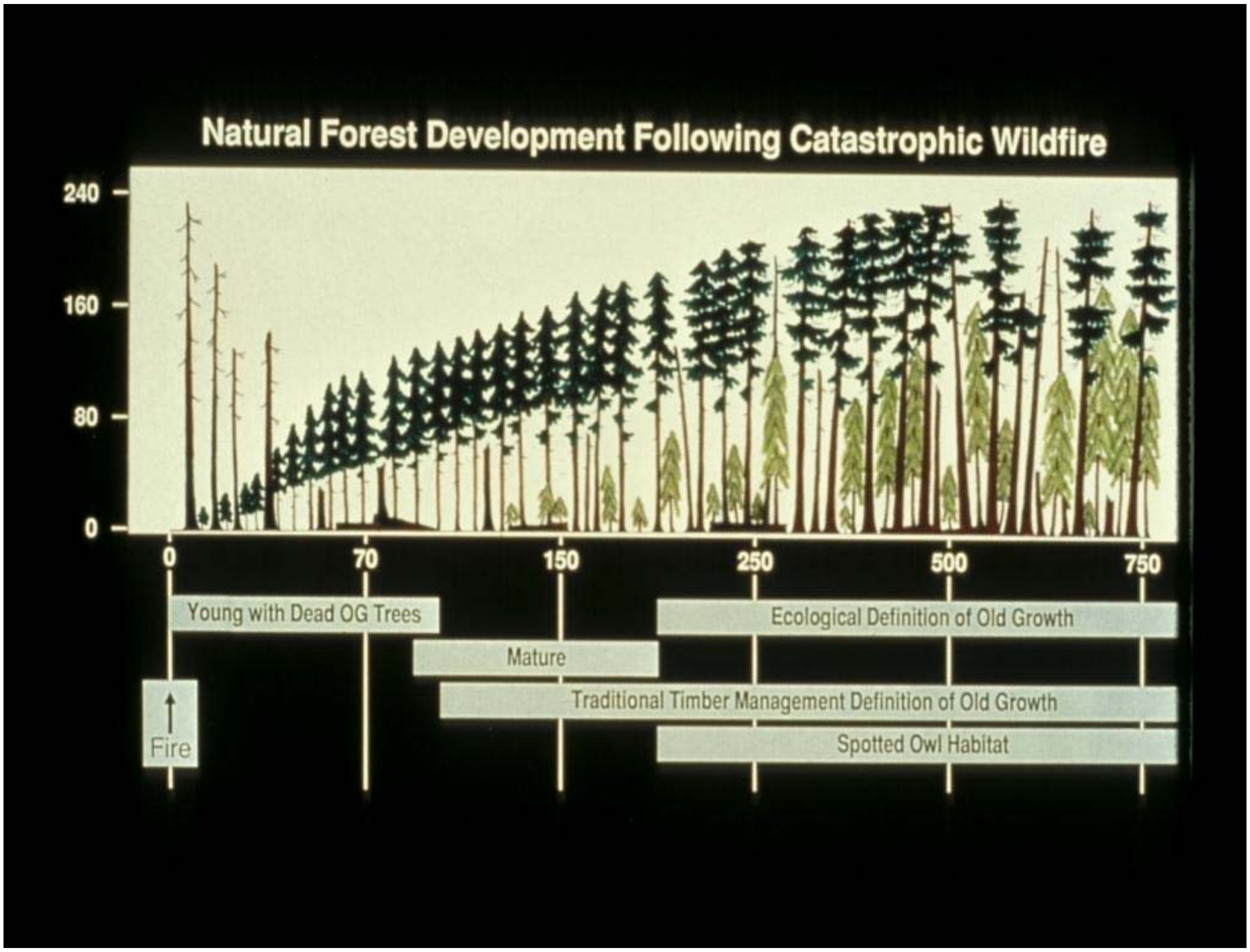
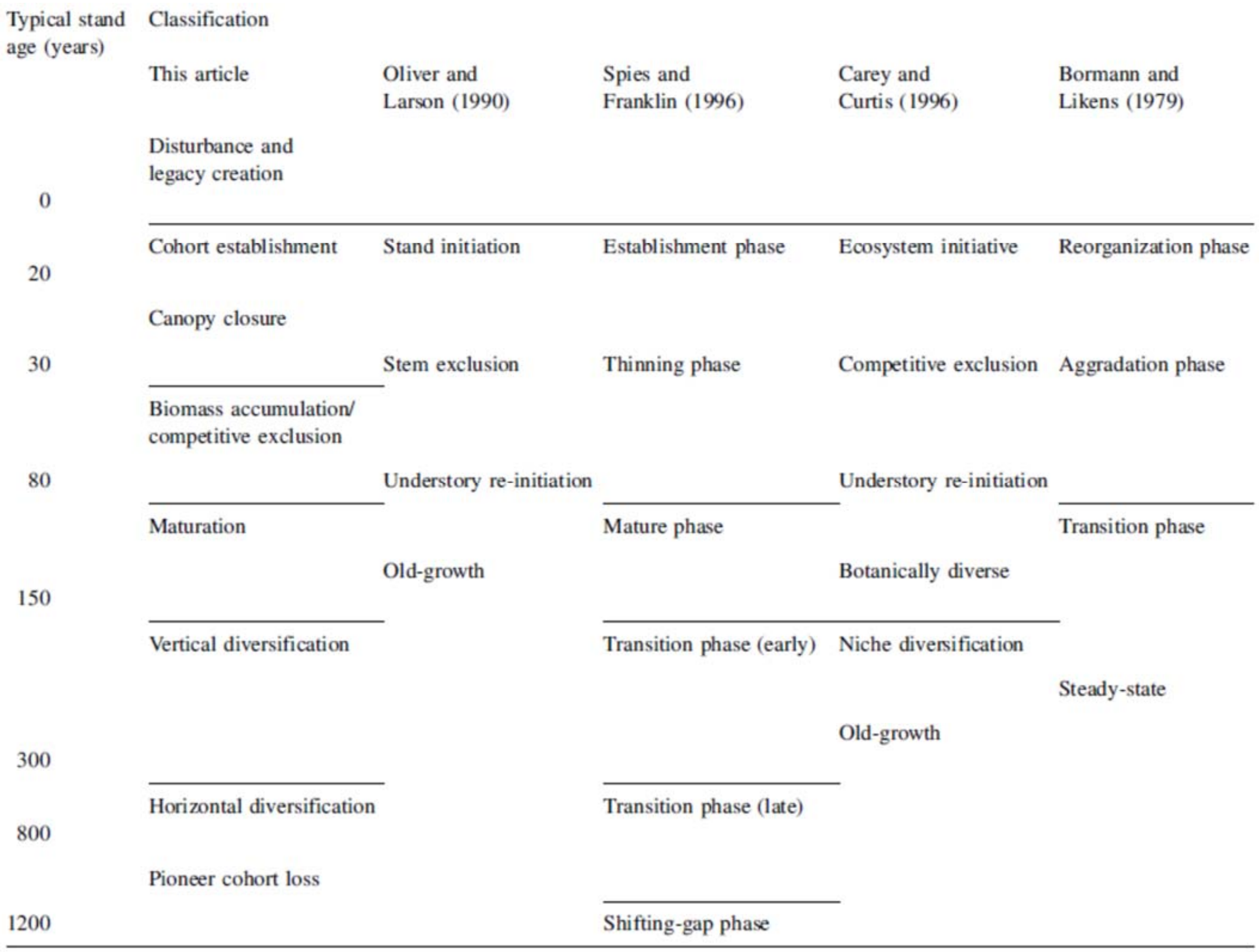


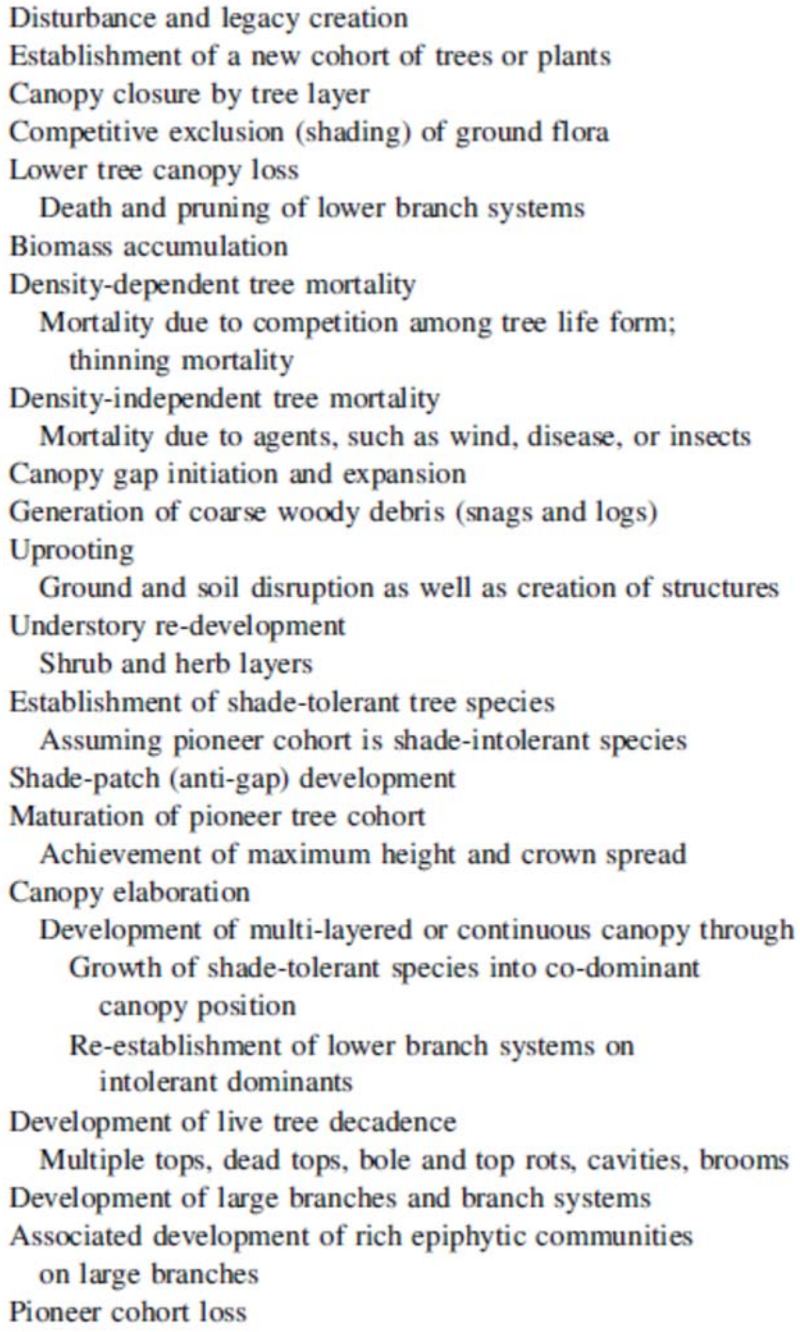
Figure 1.1. Diagram of stand structural development stages (courtesy of Jerry F. Franklin)

Table 1.1. Structural development stages from Franklin et al. (2002). Previous classification systems of developmental stages are also included.



Typical stand age (years)	Classification				
	This article	Oliver and Larson (1990)	Spies and Franklin (1996)	Carey and Curtis (1996)	Bormann and Likens (1979)
	Disturbance and legacy creation				
0					
	Cohort establishment	Stand initiation	Establishment phase	Ecosystem initiative	Reorganization phase
20					
	Canopy closure				
30		Stem exclusion	Thinning phase	Competitive exclusion	Aggradation phase
	Biomass accumulation/ competitive exclusion				
80		Understory re-initiation		Understory re-initiation	
	Maturation		Mature phase		Transition phase
		Old-growth		Botanically diverse	
150					
	Vertical diversification		Transition phase (early)	Niche diversification	
					Steady-state
				Old-growth	
300					
	Horizontal diversification		Transition phase (late)		
800					
	Pioneer cohort loss				
1200			Shifting-gap phase		

Table 1.2 List of structural processes throughout stand structural development from Franklin et al. (2002).



- Disturbance and legacy creation
- Establishment of a new cohort of trees or plants
- Canopy closure by tree layer
- Competitive exclusion (shading) of ground flora
- Lower tree canopy loss
  - Death and pruning of lower branch systems
- Biomass accumulation
- Density-dependent tree mortality
  - Mortality due to competition among tree life form; thinning mortality
- Density-independent tree mortality
  - Mortality due to agents, such as wind, disease, or insects
- Canopy gap initiation and expansion
- Generation of coarse woody debris (snags and logs)
- Uprooting
  - Ground and soil disruption as well as creation of structures
- Understory re-development
  - Shrub and herb layers
- Establishment of shade-tolerant tree species
  - Assuming pioneer cohort is shade-intolerant species
- Shade-patch (anti-gap) development
- Maturation of pioneer tree cohort
  - Achievement of maximum height and crown spread
- Canopy elaboration
  - Development of multi-layered or continuous canopy through
    - Growth of shade-tolerant species into co-dominant canopy position
    - Re-establishment of lower branch systems on intolerant dominants
- Development of live tree decadence
  - Multiple tops, dead tops, bole and top rots, cavities, brooms
- Development of large branches and branch systems
- Associated development of rich epiphytic communities on large branches
- Pioneer cohort loss

CHAPTER 2: MULTI-DECADAL ESTABLISHMENT OF SINGLE-COHORT DOUGLAS-FIR FORESTS OF WESTERN WASHINGTON AND OREGON

ABSTRACT

The rate at which trees regenerate following stand-replacing wildfire is an important but poorly understood process in the multi-century development of Douglas-fir—western hemlock forests. Temporal patterns of tree establishment in mid-aged (100- to 350-year) Douglas-fir-dominated forests have not been studied, in contrast to the abundance of work in older Douglas-fir stands (>400 years of age). To determine temporal patterns of Douglas-fir establishment following stand-replacing fire, increment cores were obtained from 1455 trees in 18 mature and early old-growth forests in western Washington and northwestern Oregon USA. Each of the stands showed continuous regeneration of Douglas-fir for many decades following initiating fire. The establishment period averaged 58 years (range of 32-99 years). These results contrast both with the view of rapid (one- to two-decade) regeneration of Douglas-fir promoted in the early forestry literature and with reports of establishment periods exceeding 100 years in older (>400 year) Douglas-fir—western hemlock stands. These results have important implications for management designed to promote the early-seral characteristics of forests for thinning to accelerate development of older forest structures.

Introduction

Temporal patterns of tree regeneration following stand-replacement disturbances strongly influence subsequent forest development (Ashton 1976, Foster et al. 1997, Cooper-Ellis et al. 1999, Franklin et al. 2002). The initial period of tree establishment following high-severity disturbance is significant because it represents a stage in forest development during which trees do not exert strong controls on other life forms. For example, the rapidity of tree establishment determines the speed with which forest dominance is re-established, and thus the potential to influence understory composition or abundance (Alaback 1982, Oliver and Larson 1996). Forest canopy closure reduces available light in the understory, moderates temperatures (Franklin et al. 2002), and regulates herb and shrub communities (Alaback 1982). Moreover, once forests undergo canopy closure intense competition (Sorrenson-Cothern et al.1993) and self-thinning mortality occur among trees (Kenkel 1988, Lutz and Halpern 2006), contemporaneous with rapid biomass accumulation (Lutz and Halpern 2006, Halpern and Lutz 2013). Patterns of post disturbance regeneration continue to be of great interest to ecologists and managers who seek to understand ecosystem development to guide forest management and conservation of biological diversity (Franklin et al. 2002, Lindenmayer and Franklin 2002).

Post-fire tree establishment in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests is a starting point for modeling changes in structure, function, and composition over multi-century developmental sequences (Franklin et al. 2002, Zenner 2005, Larson et al. 2008). Douglas-fir—western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forests in the Pacific Northwest experience large infrequent wildfires, which typically include extensive areas of stand-replacement severity (Agee 1993). Several factors can influence the establishment of Douglas-fir including the size, severity, and timing of the initiating disturbance (Tepley 2010, Tepley 2013), distance from seed sources (Donato et al. 2009), high or low seed production years (Larson and Franklin 2005), and competing vegetation (Beach and Halpern, 2001). Moreover, forests regenerating at high densities may undergo canopy closure more rapidly leading to an intense self-thinning phase while stands which gradually re-establish at lower densities may not experience canopy closure at all and may go directly into a biomass accumulation phase (Franklin et al. 2002, Lutz and Halpern 2006). Long-term studies of early succession have indicated that greater turnover of species composition occurs with increased disturbance intensity (Halpern 1988), and suppression mortality is high in young closed-canopy forests (Lutz and Halpern 2006). Thus, knowledge of the rate and density of tree establishment provides broader understanding of factors influencing compositional change and forest dynamics (e.g. competitive mortality).

Post-fire establishment of Douglas-fir is presumably influenced by many factors such, but may follow three general patterns (Figure 1). The first general pattern of establishment may follow a "dense and rapid" (e.g., 1-5 years) model. Dense and rapid tree establishment following fire can arise through a legacy of seed bearing trees or the congruence of fire with a high seed production year and ample moisture for seedling establishment (Larson and Franklin 2005). A second general pattern of establishment may follow a "protracted model." Protracted establishment could occur where seed is limiting and trees establish gradually through infilling from adjacent edges. Establishment following the "protracted model" suggests large and severe wildfire and can represent a founding population where infilling occurs because the earliest establishers mature and provide the next propagules for regeneration (c.f. Dovčiak et al. 2005). A third pattern of establishment may follow a "gradual model" representing an intermediate pattern between the "rapid and dense" and "protracted" models. Therefore, gradual establishment may reflect the combined effects of seed limitation and resource competition from early colonizing shrubs. The “gradual model” suggests large severe fire where few legacy trees remain throughout the burned area providing seed, and perhaps multiple low seed production years.

Factors contributing to alternate models of Douglas-fir establishment may be related to extrinsic and intrinsic variables within a site. Coastal Douglas-fir forests are widely distributed throughout western Washington and Oregon representing a gradient of environmental conditions. Geographic location and corresponding climate variables as well as elevation and aspect are likely extrinsic factors which could drive trends in the rate of Douglas-fir establishment. For example, sites with higher annual precipitation and lower annual temperature extremes may be more favorable for tree establishment leading to a shorter establishment duration. However, relationships among these types of environmental variables and the establishment duration are poorly understood. Intrinsic factors such as the current density and basal of Douglas-fir trees may also be important for explaining the variation of Douglas-fir establishment. For example, greater Douglas-fir density and basal area could correlate to faster establishment durations, suggesting an important relationship between current stand structure and establishment.

The rate of Douglas-fir establishment after fire is an indicator of the transition from an open canopy condition to a closed forest canopy. This is because Douglas-fir is relatively intolerant of shade, thus canopy closure can reasonably be inferred from the cessation of establishment (Isaac 1943). Therefore, duration of open forest conditions likely closely approximates the period which early seral communities persist at a location. Hence, knowledge of post-fire Douglas-fir establishment patterns is important because early successional forest habitats support a diversity of organisms and ecosystem processes not commonly found in young and mature forests (Swanson et al. 2011). Because some organisms and processes (e.g., habitat, nitrogen fixation) present in early succession may be scarce or absent in other stages of forest development, understanding the duration of open canopy will provide insight into changes in ecosystem function over time and can contribute to the basis for management.

Tree age and its relationship to tree size is suggestive of ecological processes which occur during the transition from an open canopy state to closed canopy conditions. While much research has focused on age, height, and size relationships for young planted stands of Douglas-fir (Isaac 1936, Munger1946), few data sets exist which examine these relationships for naturally regenerating Douglas-fir forests. Furthermore, few studies exist which have examined age size relationships for naturally regenerated stands early in succession. Kreuger (1960) represents one of the only studies to examine the relationships between timing of establishment and tree height. Kreuger's study concluded that when Douglas-fir established over several years the first trees to establish maintained a growth advantage from trees which established later. Trees which establish later (younger trees) smaller than trees which established earlier, it suggests that competitive influences from increased tree densities are limiting sizes. If a poor relationship between age and size exists it may suggest that the spatial arrangement of tree establishment is highly variable allowing for persistent openings which provide for similar growth opportunities even for late establishing trees. Alternatively, a poor relationship could suggest that establishment was not closely linked with a changing competitive environment, but rather a seed source limitation.

Early 20th century forest researchers proposed a model of rapid and dense Douglas-fir establishment following stand-replacement wildfire (hereafter the "traditional model"). This early view of Douglas-fir cohort establishment was strongly influenced by observations of tree establishment following the 1902 Yacolt and 1910 Cispus fires in the southern Washington

Cascades, and of regenerating harvested stands in the same region (Hofmann 1924, Herring and Green 2007). Julius Hofmann (1924), one of the earliest forest researchers investigating Douglas-fir regeneration, commented, "The main feature of interest found on the [Yacolt] burn was the good stand of young growth which almost uniformly covered the area and consisted of the same species as those which made up the burned forest." In an early synthesis paper on succession and structural development of Douglas-fir forests, Munger (1940) concluded that Douglas-fir regeneration usually occurs within a decade after the stand-initiating disturbance. Leo Isaac (1943) described Douglas-fir regeneration following logging, "When the young forest has formed a closed canopy (between 10 to 30 years of age), the herbs and shrubs are shaded out and reach their low point and remain so for several decades until the forest canopy begins to thin." The collective observations of these early forest scientists clearly pointed towards a general model of rapid, dense establishment of the initial Douglas-fir cohort following stand-replacement disturbance.

Some modern reconstructions provide evidence that supports the traditional model of rapid and dense Douglas-fir establishment. A detailed reconstruction of establishment in an old-growth stand in the southern Washington Cascades (Winter et al. 2002a) provides some of the most compelling evidence for this model, with the establishment phase completed within 21 years. The "traditional model" of rapid establishment remains well represented in the current accepted conceptual framing for Douglas-fir forest structural development: Franklin et al. (2002) describe the initial, cohort-establishment stage as lasting for ~25 years, although they do acknowledge potential for protracted establishment.

Studies of old-growth (>400 years) forests beginning in the 1970s led to the development of an alternative model in which Douglas-fir establishment is very protracted, lasting one to several centuries. Franklin and Hemstrom (1981) identified a >150 year period of Douglas-fir establishment in the central Oregon Cascades. Tappeiner et al. (1997) reconstructed establishment periods from several forests in coastal Oregon with establishment in 70% of the sites extending over >100 years (maximum of 364 years). A subsequent study by Poage and Tappeiner (2002) also reported a prolonged establishment period for Douglas-fir with a mean of 174 and a maximum of 430 years. Poage and Tappeiner (2002) further suggest that short periods of establishment (one to two decades) are anomalous and that prolonged periods are most common.

In this study I examine the duration of Douglas-fir establishment in 18 mature (100- to 200- year-old) and early old-growth (200- to-300-years-old) stands in western Washington and northwestern Oregon that regenerated naturally following single stand-replacement wildfires. Forests 200-300-years-old represents a poorly understood stage in development but are beginning to acquire older forest characteristics and thus they are named early old-growth. Forests included in this study are generally older than the regenerating burns studied by Hofmann (1924), Munger (1930) and Isaac (1943), but are significantly younger than the (>400-year-old stands analyzed by Tappeiner et al. (1997), Poage and Tappeiner (2002), and Winter et al. (2002ab). My purpose is to expand knowledge of temporal patterns of Douglas-fir regeneration following wildfires in naturally-regenerated stands that are younger than most previously studied. I pose three questions: (1) Is the length of establishment of Douglas-fir in these mature forests supportive of the "traditional model" of rapid establishment or is it more comparable to prolonged periods observed in previous studies of old-growth? Do the observed durations of establishment provide support for the general models of establishment duration provided in Figure 1? (2) How variable is the period of establishment and can it be explained by differences in local environment or current structural attributes? (3) Is there a difference in the size of Douglas-fir trees that established earlier compared with trees that established later post fire?

Methods

Study area

Douglas-fir–western hemlock forests of western Washington and northwestern Oregon are long-lived coniferous forests distributed across millions of hectares at low and middle elevations. Large, infrequent (250 to 450 years) wildfires constitute the dominant disturbance regime in the Western Hemlock zone (Agee 1993), although in some parts of the region there is increasing evidence for a more diverse fire regime (Tepley 2010) and large windstorms and volcanic eruptions can also occur (Harcombe et al. 2004, Yamaguchi 1986). Over the last millennium, large wildfires in this region have created in numerous age classes of forests dominated by Douglas-fir, western hemlock, and other conifers (Franklin and Dyrness 1988; Agee 1993, 1998, Agee and Krusemark 2001, Tepley et al. 2013). Many of these originated following a single fire event, with little evidence of subsequent disturbance of sufficient size or intensity to allow for establishment relatively shade-intolerant Douglas-fir (Isaac 1949, Herman and Lavender 1990).

Study sites

The forests sampled were distributed between 47.95 and 44.27 N latitude along the western slope of the Cascade Range except for one stand located in the eastern Olympic Mountains Washington (Table 2.1) (Figure 2.2). Forests occurred on relatively moist sites and are classified by the *Tsuga heterophylla/Polystichum munitum, Tsuga heterophylla/Polystichum munitum/Oxalis oregana*, and the *Tsuga heterophylla/Rhododendron macrophyllum/Gaultheria* *shallon* plant associations within the Western Hemlock Zone (Franklin and Dyrness 1988). One site (Huckleberry) occurred in the cooler, moister Pacific Silver Fir Zone classified under the *Abies amabilis/Vaccinium alaskaense* plant association (Franklin and Dyrness 1988). The climate is maritime with cool wet winters and warm dry summers (Table 1). Common tree associates of Douglas-fir include western hemlock, western redcedar (*Thuja plicata* Donn ex D. Don), western white pine (*Pinus monticola* (Dougl.), Pacific silver-fir (*Abies amabilis* (Dougl. ex. Loud) Dougl. ex Forbes), Pacific yew (*Taxus brevifolia* nutt.), noble fir (*Abies procera*), big-leaf maple (*Acer macrophyllum* Pursh), and Pacific dogwood (*Cornus nutallii* Aud.).

Site selection

Sample sites were of two types: 1) stands representing early, old-growth (≈200-to-300-years-old) forests sampled using multiple temporary plots; and 2) mature stands (≈100-to-200-years-old) sampled using permanent plots that had a long history of sampling (cite LTER PSP network; cite web site or key papers). Sites sampled with temporary plots (*n* = 9 sites) were established following a review of fire-history studies (Morrison and Swanson 1990, Agee 1991, Impara 1997, Sensenig 2003, Weisberg and Swanson 2003), stand age-class maps, and conversations with several ecologists familiar with the region (personal communication with Ken Bible, Rolf Gersonde, Scott Gremel, Charles Halpern, Jan Henderson, Robin Lesher, Robert Van Pelt), and extensive reconnaissance.

Eleven additional sites were selected from an established network of permanent sample plots (hereafter, PSP). Plots were selected this network based on age (100-200 years), dominance by Douglas-fir, and lack of evidence of disturbances post canopy closure. Forests originated from stand-replacing disturbances, varied in age, and were distributed over a broad latitudinal range (Table 1).

Candidate sites were carefully examined and excluded if there was evidence of post-initiating disturbance (fire or wind) that could have facilitated subsequent establishment of Douglas-fir. Fine-scale disturbances (root rot, bark beetles, or wind) that affected individual trees or small clusters of trees (creating canopy gaps) were evident in most stands and were not used criteria for rejection.

Several sites were located close enough to have regenerated after the same wildfire. Drift Creek, Osprey, Skynard Hill, and Cedar Flats lie within 10 km of each other in the central Lewis River Valley and evidently established after a single large-scale fire ca. 1800. Stands WR04, WR05, WR90, and Meditation Rock lie within 8 km of each other in the Panther Creek Division of the Wind River Experimental Forest and originated from a single wildfire ca. 1860. Although these sites may be considered pseudoreplicates (Hulbert 1984), but given the variability in fire severity and site conditions within a large wildfire it is unlikely that the two samples represent the "same" fire at a site level and understanding the variability created by single large-scale disturbances is nonetheless valuable (Turner et al. 1997, Larson and Franklin 2005).

Field procedures for temporary plots

Sampling was conducted between June and September from 2006-2010. In each stand, six 0.2 ha circular plots were established at 100 m intervals along a linear transect. Transects were initiated from a random starting point after stand shape, boundaries, and transect azimuth were determined. Within each plot all trees ≥5 cm dbh were identified by species and diameters were measured 1.37 m above the base of the tree. Douglas-fir was an abundant component of the overstory in each site indicating that Douglas-fir dominated the tree establishment phase (Table 1) Depending on Douglas-fir density in each circular plot, 6-10 live Douglas-fir were subjectively chosen for aging to represent the full range of size classes (and presumably ages).

To determine that the size distribution of aged trees was representative of the larger measured population, we used a series of Kolmagorov-Smirnov (K-S) tests; all tests confirmed that there were no significant differences in diameter distributions for all sites.

All cores were taken at breast height (1.37 m). Although cores taken closer to the ground surface may improve the accuracy of aging, they are more difficult to obtain and more likely to include butt rot. Each core was visually inspected to determine if pith was reached. If it was not and the core did not contain the majority of inner-most rings, a second core was taken; however, time and labor constraints limited any additional coring. If a suitable core was not obtained after two attempts, an alternate tree of similar diameter was sampled. Cores were placed in paper straws, labeled, and stored in a waterproof container for subsequent laboratory analysis.

Field procedures for permanent plots

Based on existing diameter data for Douglas-fir, a stratified random sample was used to select trees for aging. Diameter distributions were stratified using 15-cm diameter bins and 40-60% of individuals per diameter bin were selected for coring. Methods for obtaining increment cores the same as described for temporary plots.

Laboratory methods for aging increment cores

All increment cores were prepared using standard dendro-chronological techniques (Stokes and Smiley 1968). All cores were mounted on grooved wooden boards and sanded three times at progressively finer grit (100, 220, and 400). Cores with narrow growth rings required additional sanding at 600 and 800 grit. Annual rings were counted with a microscope (3X); cross-dating was not attempted because it was not relevant to the study objectives. While cross dating is essential for determining accurate pith dates for some species and growing conditions, I evaluated that it was not necessary for the Douglas-fir on moderately productive sites in the current research. A study by Weisberg and Swanson (2001) showed that for Douglas-fir samples, pith dates determined by careful laboratory ring counts on well prepared surfaces were very close to (mean difference of 1.24 years) pith dates determined by cross-dating the samples. To estimate the number of rings missing in cores that lacked a pith, I used a transparent template containing concentric circles that best fit the growth pattern present in the inner core (Applequist 1958). To estimate age to core height, I used height-growth curves for Douglas-fir in conjunction with a site productivity table (McArdle et al. 1961). The ring count, estimate of rings to pith, and estimate of age to core height were summed to obtain an estimated total age for each tree.

Analyses

The following summary statistics were calculated for aged Douglas-fir trees at each site: age range (including 95% confidence intervals [CI]), age range of 90% of the aged trees (including 95% CI), minimum age, maximum age (as an estimate of cohort initiation), and standard error of age, to address question 1. A frequency distribution was then created for each site; 10-year age bins were used to facilitate comparison with previous studies of Douglas-fir age structure (Klopsch 1985, Stewart 1986, Huff 1995, Tepley 2010) and to assess the pace of establishment by decade. At two sites, minimum and maximum ages differed by 82 (Meditation Rock) and 115 years (WR05); summary statistics are reported including and excluding these individuals because the trees that established later represent individuals which established in canopy gaps following forest canopy closure. Canopy gaps were visually inspected during sampling and represented areas where several Douglas-fir in early stages of decay were present.

Cumulative age distributions (as cumulative proportion of establishment) were developed to compare establishment patterns among sites (question 2). Although the total duration of tree establishment was of primary interest, the period representing 90% of individuals was also a useful metric for assessing the rapidity of conifer domination and for assessing late establishment tail of the distribution and also provides a context for assessing how the late establishers. Other studies have used various percentages of establishment to describe trends in tree establishment (Huff 1995, Tappeiner et al. 1997, Yang et al. 2005).

To quantitatively describe the shapes of the cumulative age distributions among sites, nonlinear regression was performed. Data were fit to sigmoidal models using SigmaPlot Version 11.0 (Systat Software, Chicago, Illinois, USA). Parameter estimates representing time to 50% establishment and slope (Table 2.3) were evaluated in order to describe the variation among sites as it relates to the 3 models of Douglas-fir establishment (Figure 2.1).

Pearson correlation analyses were performed to explore whether associations existed between environmental variables and duration of establishment. Correlation matrices were created for extrinsic environmental variables of latitude, elevation, aspect, mean annual precipitation, mean July precipitation, mean January precipitation, mean growing season precipitation, maximum July temperature, and minimum January temperature. Pearson correlations were also performed on some stand variables of Douglas-fir in order to explore biotic controls on establishment.

Maximum age in each stand, percent of the Douglas-fir population aged, percent Douglas-fir density, and percent Douglas-fir basal area were used as biotic correlates. Pearson correlation analyses were also performed using the parameter estimates (X0, b) derived from the sigmoid regression with the same set of environmental and stand variables in order to assess the shape of the curve of tree establishment.

Scatter plots of age and size (Figure 2.6) were generated and Mann-Whitney nonparametric tests were performed to explore whether timing of establishment had an influence on current tree size (question 3). Mann-Whitney tests were run examining the sizes (dbh in cm) with the oldest and youngest 10% of aged trees in each site in order to examine extreme values of the tail of each distribution. To further investigate whether timing of establishment was related to current tree size Mann-Whitney tests were performed for the oldest and youngest 20% of aged trees in each site.

Results

Age ranges

Duration of establishment averaged 60 years (95% CI of 50-70 years) and ranged from 32 to 99 years. Establishment periods exceeded 75 years for only three stands (Table 2.2). Seventeen percent of stands established within 40 years, 40% established within 50 years, and 83% established within 75 years. All stands achieved 90% establishment of Douglas-fir much sooner (mean of 35 years; 95% CI of 28-42 years) than full establishment. Duration of 90% establishment ranged from 19-65 years, with 67% of stands within 40 years and 83% of stands within 50 years.

Age distributions

Sites display broadly comparable cumulative age distributions regardless of the century when establishment began (Figure 2.4). Most of the variability among cumulative age distributions is found in the 12 oldest sites (Table 2.2); the greatest variability in age distributions is found in 6 sites with maximum ages between 183 and 213 years (SE 0.88-3.43). Sigmoid curves were well fit to the cumulative age distributions with r^2 values ranging from 0.94-0.99 (Figure 2.5).

Parameter estimates (X0, b) were assessed to compare the point at which each site experienced a steep increase in slope. Low values for b with corresponding low values of X0 appear to indicate rapid establishment and a shorter establishment duration. Increasing values for b with corresponding increases in X0 appear to represent a process characterized by steady and gradual establishment. The highest values for b and X0 appear to represent an establishment process characterized by slower more gradual establishment. Parameter estimates derived from the sigmoidal regressions did not yield any statistical association with either environmental or stand level variables ($\alpha = 0.05$) (Table 2.3).

Duration of establishment did not correlate with geographic location. The two shortest establishment periods (32 and 33 years at WR04 and Cedar Flats) occurred in the southern Washington Cascades and represented different wildfires. The longest establishment periods were broadly distributed over the geographic range of sites: 88, 94, and 99 years at Drift Creek, Breitenbush, and Sol Duc, respectively (Figure 2.2). In addition, the second shortest and third longest establishment periods occurred in the same river valley (several kilometers apart) presumably following the same wildfire ca. 1800 (32 years at Cedar Flats and 88 years at Drift Creek); both of these also forests represent the most productive sites (site index I; Isaac [1949]).

Pearson correlations yielded no significant statistical associations between establishment duration and elevation, latitude, aspect, maximum stand age, percent of the Douglas-fir population aged, percent Douglas-fir density, percent Douglas-fir basal area, mean annual precipitation, mean July precipitation, mean January precipitation, mean growing season precipitation, maximum July temperature, and minimum January temperature ($\alpha = 0.05$).

Timing of establishment and tree size

Timing of establishment as it relates to tree size is variable. Mann-Whitney tests comparing the mean size of the oldest and youngest 10% of the Douglas-fir population yielded significant results for 33% of sites ($\alpha=0.05$) (Table 2.4). Five out of the six sites with significantly different means are among the seven youngest forests. Mann-Whitney tests run for the oldest and youngest 20% of stands and yielded significant results for 50% of sites ($\alpha=0.05$) (Table 2.5).

Discussion

The majority of Douglas-fir forests sampled in this study established within 32 to 75 years after the initiating wildfire and always within 100 years. Duration of establishment did not differ as a function of the period during which stands established, nor did it vary with any of the environmental or stand structural variables tested. Therefore, I infer that patterns of single cohort establishment following high severity wildfire were relatively similar between 1650 and 1902, at least in the stands that I examined. Moreover, I conclude from these results that stand aspect and the regional climatic gradient covered in this study do not directly influence the pattern Douglas-fir establishment. I find it interesting that establishment periods for Douglas-fir regeneration following partial stand replacement disturbances in the central Oregon Cascades were found to be nearly as long as those observed in my study of stand replacement disturbances (Tepley 2010). These findings bolster my interpretations of a consistent range in rate of establishment and suggest that regardless of the high severity or mixed severity, cohorts of Douglas-fir in the western Cascades establish within similar envelope conditions (Figure 2.7).

The age distributions observed in this study fit well with previous theory on early development of coastal Douglas-fir in terms of the single cohort of establishment (Franklin et al.

2002). However, the duration of establishment were not as fast as suggested by the traditional model. Certainly, inferences drawn from the duration of tree regeneration –for example, as being either prolonged or attenuated—following disturbance will depend on the particular ecological process of interest. For example, an establishment period lasting 30 years may be considered short in relation to the development of decadent structural features of old forests (Franklin et al. 2002), but conversely, may be viewed as quite extended in terms of persistence of early seral habitat (Swanson et al. 2011).

To my knowledge, this study represents the only large-scale data set appropriate for the study of Douglas-fir establishment patterns from mature and early old-growth forests. Some data exist from other stands of this age. Kuiper (1994) found an age range for Douglas-fir >100 years in a ca. 200-year-old stand at Pack Forest near Mount Rainier; 70% of the trees established within 50 years. Huff (1995) documented complete Douglas-fir establishment in 75 years for a ca. 200-year-old stand in the western Olympic Mountains.

Inferences about duration of early seral ecosystems and spatial patterns by which these ecosystems transition into closed canopy forests can be drawn from my data on temporal patterns of Douglas-fir regeneration. For example, establishment periods for Douglas-fir forests in this study averaged 60 years. While it is not clear how much of the tree establishment period supports high quality early-seral conditions (Swanson et al. 2011), inferences can be drawn from the duration to estimate persistence of these conditions. One study, (Yang et al. 2005) reconstructed early succession conditions using aerial photo interpretation and a Chapman-Richards growth function and reported establishment periods of 40-50 years for the western Cascades of Oregon.

Comparisons with conceptual models of Douglas-Fir stand establishment

Douglas-fir establishment durations in this study are not well represented by any of the previously developed conceptual models. Rates of establishment observed in mature and early old-growth stands in this study contrast with the traditional model of rapid stand establishment inferred from the observations of early research foresters, such as Munger (1940), Hofmann (1924), and Isaac (1943). However, I note that their focus was actually on establishment of sufficient Douglas-fir regeneration to ultimately produce a fully-stocked stand and not on the temporal duration of tree seedling establishment or on the rate at which forest canopies closed. This may be why their accounts of successful Douglas-fir provide no indications that regeneration may continue for many decades following a stand initiating disturbance. Therefore, rates of establishment in this study provide a useful context to compare with previous theory and observations regarding Douglas-fir establishment. The conceptual model offered by Franklin et al. (2002) provides a basis on which to understand the nature of tree establishment from disturbance to canopy closure, although results presented in this study show that establishment commonly lasts into the 4th and 5th decades following wildfire.

Rates of establishment observed in this study contrast significantly with the model of plantation forestry. My results suggest that persistence of open canopy conditions for several decades is common in natural forest development. In contrast, dense and uniform plantations managed for wood production are designed to achieve immediate establishment of fully-stocked stands, with canopy closure occurring within a decade or less (Smith et al. 1997). A conceptual model is provided (Figure 2.7) to aid in the discussion of establishment durations and models of establishment.

Rates of establishment in this study also contrast with the model describing protracted, low-density establishment of Douglas-fir in older (>400 year old) forests. Douglas-fir regeneration in many older stands was interpreted as occurring over periods of greater than 100 years (Hemstrom and Franklin 1982, Tappeiner et al. 1997, Poage and Tappeiner 2002). Confidence intervals (95%) for Douglas-fir establishment are between 104-237 years (n = 10) in Tappeiner et al. (1997) and Poage and Tappeiner (2002) report 95% confidence intervals for the mean of establishment at 134-213 years (n = 27). The 95% confidence intervals for the mean of total establishment reported in this study (95% CI = 50-70 years, n = 18) clearly do not overlap with these.

A comparison of studies where Douglas-fir ages were used to reconstruct establishment duration indicates a complex suite of findings. In the 1970s scientists began their studies of Douglas-fir establishment by counting annual growth rings on cut stumps of Douglas-fir trees after the stands had been harvested. Their findings of age ranges spanning 1-2 centuries were inconsistent with the accepted wisdom of rapid Douglas-fir establishment and forest canopy closure, which puzzled them (Franklin and Hemstrom 1981). Subsequent studies of Douglas-fir ages in old-growth forests >400 years in Oregon also were interpreted as providing evidence of periods of establishment extending over 1 or more centuries (Stewart 1986, Tappeiner et al. 1997, Poage and Tappeiner 2002). Several hypotheses were proposed to explain these findings including seed source limitations after the extensive fires of the late 15th and early 16th centuries, competition from hardwood shrubs and trees, and creation of opportunities for further Douglas-fir establishment by subsequent partial stand replacement disturbances. Some investigators examined the wide early growth rings in old Douglas-fir and related them to low initial stand densities (Tappeiner 1997, Poage and Tappeiner 2002); they further hypothesized that "characteristic" old-growth forests could only arise from such circumstances. Much shorter pulses of Douglas-fir establishment were observed in two studies in Washington State, lending support for the original hypothesis of rapid forest establishment and stand closure (Yamaguchi 1986, Winter et al. 2002).

Such a diversity of study findings from old-growth forests could represent several pathways of early succession, or could be the result of several other factors which could influence conclusions regarding age ranges and establishment durations. For example, subsequent disturbance including partial, stand-replacement fires may lead to multiple cohorts and periods of establishment (Tepley et al. 2013). Tepley's (2013) meticulous study of wildfire disturbances and Douglas-fir tree ages in old-growth forests in the central Cascade Range of Oregon provides very strong evidence that at least some of the observed extended periods of Douglas-fir establishment represent multiple cohorts established after partial stand-replacement fires (Tepley et al. 2013). Another factor which could contribute to interpretations about extended periods of establishment relate to errors associated with counting rings on stumps in the field. Studies that reconstructed patterns of early development from stump counts in harvested units almost invariably involved significant errors in ring counts, which would tend to blur evidence for distinct Douglas-fir cohorts (Weisberg and Swanson 2001, Tepley 2010). When ages of cross-dated samples of old-growth Douglas-fir trees were examined in a recent study, field counts on cut stumps were conclusively found to be inaccurate and thus unsuitable for quantifying the duration of establishment (Tepley 2010).

Different study objectives and reconstruction methodology are likely causes for some of the variability in establishment durations among multiple studies. Reconstructions of forests > 500-years-old require meticulous analysis which includes crossdating (Winter et al. 2002a, Winter et al. 2002b, Tepley 2010), because evidence of disturbance and tree death and decay can be masked by many centuries of development. Small-scale disturbance events, which kill individual or small groups of canopy dominants, can eliminate structural features needed for accurate reconstructions of early tree establishment conditions (Gray and Spies 1997, Lutz and Halpern 2006) or even create entirely new cohorts. Stands which undergo gap formation created by wind, root rots, or beetles may exhibit low density recruitment of Douglas-fir. Such gap recruitment of shade-intolerant species, such as Douglas-fir, over centuries would create a complex multi-modal age structure and create confusion regarding continuous establishment. Two sites included in this study (Meditation Rock, WR05) displayed recruitment of Douglas-fir, which developed in significant canopy openings after the initial cohort had closed canopy. These trees were certified as true new recruits by field observations, measurement of the snag population (data not reported) and coring, providing evidence that Douglas-fir can successfully regenerate in forests with multiple canopy gaps. Reconstructing initial periods of establishment in younger forests – as in this study – can be more accurate reconstructions of establishment than in old-growth because: (1) extensive periods of agent-based mortality, decomposition, or gap creation have not occurred in the forest; and (2) higher quality age and ring data are more easily obtained from the smaller trees found in young and mature stages of forest development.

That said, extended (>100 year) periods of establishment can occur in Douglas-fir forests. Undoubtedly, variable rates of establishment are influenced by the extent and behavior of the initiating disturbance, presence or absence of surviving seed-bearing trees, the presence/abundance of broadleaf tree and shrub species (Franklin and Hemstrom 1981). Periods of repeated large intense wildfires might well have created areas without significant surviving Douglas-fir seed trees; such areas would initially undergo establishment of a low-density founding population, which would eventually provide a local seed source to fill in stands. Obviously, each sere will exhibit idiosyncratic patterns, which could include such a possibility but the probability would be low and most logically occur on very dry sites within the Western Hemlock zone (Means 1982, Tepley 2010), on very frosty sites within the Pacific Silver Fir zone (Franklin and Hemstrom 1981), multiple fires at short return intervals (Isaac and Meagher 1936, Huff 1995, Gray and Franklin 1997, Tepley 2010), and on subalpine sites (Franklin et al. 1988).

Establishment and among site variation

Cumulative patterns of establishment are generally similar in form, but the rate at which each stand established is variable (Figure 2.4). Establishment rate for the majority of stands supports a general model of establishment where trees gradually but consistently establish until canopy closure occurs ("Steady Establishment", Figure 2.1). The consistency with which the majority of stands follow the "steady establishment" model likely reflects a combination of availability of seed source from surviving legacy trees and competition from shrub and hardwood species (Yang et al. 2005). Some establishment rates within this data set also support alternative models. Two sites, WR05 and Cedar Flats, exhibit establishment duration and cumulative age distributions supporting a "rapid model" of tree establishment. Sites undergoing rapid and dense establishment may be the result of a canopy seed bank following the stand initiating wildfire (Larson and Franklin 2005). The "prolonged" model of establishment is also represented in this data set by the Breitenbush and Sol Duc sites, and may be the result of founding trees which become established and provide future seed source. Prolonged establishment could also occur when stands experience multiple fires within the first few decades after the stand replacement events (Gray and Franklin 1997).

Variation in among site establishment patterns is illustrated well by histograms depicting the age distributions (Figure 2.3). Several stands exhibit an initial pulse of establishment followed by a gradual slowing of establishment. Other stands follow a unimodal distribution with the peak of establishment occurring several decades after tree establishment has initiated. Two sites (Breitenbush and Drift Creek) do not exhibit any major peaks in establishment representing a slower and more gradual establishment of trees.

Establishment rates can vary even on productive sites when subjected to the same fire event. The second shortest and third longest durations for establishment occurred on productive sites several miles apart in the same river valley following the same wildfire event. Both Cedar Flats and Drift Creek are on very productive sites and Franklin et al. (2002) hypothesized that productive sites would experience canopy closure sooner than lower productivity sites. Larson et al. (2008) examined the influence of productivity on forest development and ultimately found that stands dominated by conifer species do recover from disturbances more rapidly on more productive sites. However, the differing rates of establishment at Cedar Flats and Drift Creek support the idea that relationships between productivity and stand development, including duration of tree establishment, can vary greatly. An explanation for extended periods of tree establishment could relate to the density of angiosperms that become established post fire. The Drift Creek site had six bigleaf maples (*Acer macrophyllum*) over 30cm at breast height and 15 angiosperm trees/ha. Deal et al. (2004) found that when angiosperms make up a greater proportion of the species composition the relationship between productivity and stand development is variable.

Timing of establishment and tree size

Timing of establishment was not related to tree size for the majority of stands measured in this study. However, the relationship between timing of establishment and tree size is most pronounced in many of the youngest stands. Sites which exhibit a relationship between timing of establishment and age may indicate that the first to regenerate gained a competitive advantage over trees which established later because of increasing densities and resource competition. Kreuger (1960) concluded that the first to establish did gain a competitive advantage over late establishing trees, although his analysis specifically looked at height and age relationships. Sites which do not have a relationship between timing of establishment and age could suggest that the spatial arrangement of tree establishment was aggregated, consequently leaving openings large enough where late establishing trees were not limited by competition and attained sizes similar to the initial establishers. Another possibility is that in cases when stands establish quickly the relationship between age and size is blurred (Kreuger 1960), although this is not conclusively supported by the data in this study. The fact that there is no trend with regards to timing of establishment and age provides support for other explanations besides competitive limitations.

Comparison of tree establishment in Douglas-fir with other moist temperate forests

The multi-decade period of tree establishment in these Douglas-fir forests is long compared to the post-disturbance recruitment of seral tree species in other moist temperate forests. *Eucalyptus regnans* (F. Muell) forests of Australia commonly regenerate and develop closed canopies rapidly (1-5 year) following severe wildfire; by 40 years the forest is well into a thinning phase (Ashton 1976). Forests covering the northeastern United States which are dominated by angiosperms and abundantly propagate through sprouting also exhibit rapid regeneration and canopy closure following high severity wind disturbances (Cooper-Ellis et al. 1999).

Multi-decadal tree establishment exhibited in naturally regenerating Douglas-fir forests appears to be unique among moist temperate forests of the world and therefore highlights the need for a better understanding of early stages of succession in these forests. Establishment occurring over several decades represents a continuum of structural development rather than rigid classifications of "even aged" or single-cohort stands. It also makes clear that the transition from open, early seral conditions to closed canopy forest is an extended one. Notably however, post wildfire scenarios which occur during high seed production years and where a canopy seed banks exist are most likely to create true cohorts of establishment (Larson and Franklin 2005), albeit no study has specifically examined this phenomena.

Management Implications

The Douglas-fir establishment rates in naturally regenerated forests reported in this study differ dramatically from industrial plantations. Typical plantations involve intensive site preparation activities which focus primarily on planting sites at high stocking levels in order to achieve tree dominance and canopy closure as soon as possible (Oliver and Larson 1996, Smith et al. 1997, Curtis et al. 2007). Federal forest plantations share some characteristics of industrial plantations, however there is evidence that federal plantations can have multi-decadal establishment rates (Yang et al 2005). The difference in timing of establishment between natural establishing stands and plantations has significant implications for many ecosystem values and managers seeking to mimic natural process will need to consider alternatives to dense plantations. For example, when objectives necessitate mimicking natural process, several possibilities, including reliance on natural vegetation or creating plantations that are less dense or more homogenous or both may be appropriate especially when creation of high-quality early-seral conditions is a management objective.

Early seral ecosystems develop on forested sites between a stand-replacement disturbance and re-establishment of a closed forest canopy (Swanson et al. 2011). These ecosystems typically share dominance among diverse plant life forms and include individuals and groups of trees. Animal diversity is typically high and often includes species that are restricted to early seral habitats specialists. Providing for such ecosystems is emerging as an important management goal on public lands (Franklin and Johnson 2012) but the scientific knowledge base for planning and implementing such management is limited. Specifically relevant to this study, little is known about how long such ecosystems persisted in various forest types, including those occupying the Western Hemlock Zone of the Pacific Northwest. This study provides evidence that it may not be appropriate to replant in post-wildfire landscapes where provision for early seral conditions is an objective.

Multi-decade rates of tree establishment also have implications for future processes in natural stand development. Variation in establishment rates lasting over several decades serve as an indicator of present and future carbon dynamics, especially as it relates to the sequestering of carbon in large old trees (Harmon et al. 1990). Variation in the rate of tree establishment may also have long term implications for hardwood and shrub diversity throughout stand development. For example, longer rates of tree establishment may be the result of spatially patchy tree establishment allowing for the colonization of many forest shrub species. Presence and persistence of some nitrogen fixing shrubs for many decades preceding canopy closure may provide for long term productivity. Variable rates of tree establishment may also have influences on the development of tree crown complexity. For example, dense and rapid establishment whereby trees are competing intensively by canopy closure could lead to shorter crown lengths and a longer period of development for epicormic branch structures. Variable rates of tree establishment may also drive mortality rates and causes. That is, stands establishing rapidly may undergo a more intensive self-thinning mortality phase, while stands which establish more gradually would be more influenced by density independent mortality agents in later periods of stand development.

Plantation management places a higher value on the rapid re-establishment of forest cover and generally ignores the ecological values associated with the pre-canopy closure ecosystems. Policies within the National Forest Management Act of 1976 mandate that each forest have targets and strategies to replant logged over or disturbed landscapes, yet this approach may be in total opposition to stated agency goals (e.g. restoration) and management objectives, which are aimed at mimicking natural processes. These policies and associated regulations need to be addressed in specific ways to provide National Forest managers with flexibility in order to achieve stated goals. Ultimately, nuanced policies which recognize and provide for all successional stages are needed.

LITERATURE CITED

Agee, J.K., 1991. Fire history of Douglas-Fir forests in the Pacific Northwest. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H. (Eds.), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. U.S. For. Serv. Gen. Tech. Rep. PNW- GTR-285

Agee, J.K. 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, D.C.

Agee, J.K., 1998. The landscape ecology of western forest fire regimes. Northwest Sci. 72: 24–34.

Agee, J.K., F. Krusemark. 2001. Forest fire regime of the Bull Run Watershed, Oregon. Northwest Sci. 75: (3) 292-305

Alaback, P. B. 1982. Dynamics of Understory Biomass in Sitka Spruce-Western Hemlock Forests of Southeast Alaska. Ecology, 63(6), 1932–1948.

Applequist, M. B. 1958. A simple pith locator for use with off-center increment cores. J. For. 56:141.

Ashton, D.H. 1976. The development of even aged stands of *Eucalyptus regnans* (F. Muell.) in central Victoria. Aust. J. Bot. 24: 397-414

Beach E.W., Halpern C.B. 2001. Controls on conifer regeneration in managed riparian forests: effects of seed source, substrate, and vegetation. Can. J. For. Res.; 31(3):471–482. Doi: 10.1139/cjfr-31-3-471.

Cooper-Ellis, Sarah, David R. Foster, Gary Carlton, and Ann Lezberg. 1999. Forest response to catastrophic wind: Results from an experimental hurricane. Ecology 80:2683–2696

Curtis, R.O., D.S. Debell, R.E. Miller, M. Newton, J.B. St. Claire, W.I. Stein. 2007 Silvicultural Research and the evolution for forest practices in the Douglas fir region. U.S. For. Serv. Gen. Tech. Rep. PNW-GTR-696

Daly C., Gibson W.P., Taylor G.H., Johnson G.L., Pastors P. 2002. A knowledge-based approach to the statistical mapping of climate.
Climate Research 22: 99–113.

Donato, D.C., Fontaine J.B., Campbell J.L., Robinson W.D., Kauffman J.B., Law B.E. 2009 Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath-Siskiyou Mountains. Canadian Journal of Forest Research: 39(4):823–838. Doi: 10.1139/X09-016.

Dovciak M, Frelich L.E., Reich PB. 2005. Pathways in old-field succession to white pine: Seed rain, shade, and climate effects. Ecological Monographs: 75(3):363–378.

Franklin, J.F., and Hemstrom, M.A. 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. *In* Forest succession. Edited by D.C. West, H.H. Shugart, and D.B. Botkin. Springer-Verlag, New York.

Franklin, J.F., Moir, W.H., Hemstrom, M.A., Greene, S.E., Smith, B.G., 1988. The Forest Communities of Mount Rainier National Park. USDI National Park Service Science Monograph 19.

Franklin, J.F., and C.T. Dyrness. 1988. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis, OR.

Franklin, J.F., T.A. Spies, R. F, A.B. Carey, D.A. Thornburgh, D.R. Berg, D.B. Lindenmayer, M.E. Harmon, W.S. Keeton, D.C. Shaw, K. Bible, and J. Chen. 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.

Foster DR, Aber J, Bowden R, Melillo J, Bazzaz F. 1997. Temperate forest response to catastrophic disturbance and chronic stress. BioScience 47:437–45.

Gray, A.N., and Franklin, J.F. 1997. Effects of multiple fires on the structure of southwestern Washington forests. Northwest Sci. 71(3): 174-185.

Gray, A.N., and Spies, T.A. 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. Ecology 78(8):2458-2473.

Grissino-Mayer, H.D. 2003. A manual and tutorial for the proper use of an increment borer. Tree Ring Res. 59:63-79.

Halpern, C.B. 1988. Early successional pathways and the resistance and resilience of forest communities. Ecology 69:1703-1715.

Halpern, C. B., and J. A. Lutz. 2013. Canopy closure exerts weak controls on understory dynamics: a 30-year study of overstory-understory interactions. Ecological Monographs. doi.org/10.1890/12-1696.1

Harcombe, P., Greene, S., Kramer, M., Acker, S., Spies, T., & Valentine, T. 2004. The influence of fire and windthrow dynamics on a coastal spruce–hemlock forest in Oregon, USA, based on aerial photographs spanning 40 years. For Ecol. Manage, 194: (1-3), 71–82. doi:10.1016/j.foreco.2004.02.016

Harmon, M.E., Ferrell, W.K., and Franklin, J.F. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. Science (Washington, D.C.), 247: 699–702.

Hemstrom, M.A., Franklin, J.F. 1982. Fire and other disturbances of the forests of Mount Rainier National Park. Quaternary Research. 18: 32-51.

Herman, R. K., and D. P. Lavender. 1990. *Pseudotsuga menziesii* (Mirb.) Franco. Pages 527–554 *In*. Silvics of North America. Volume 1. Conifers. U.S. Department of Agriculture, Agricultural Handbook 654.

Hofmann, J.V. 1924. The natural regeneration of Douglas-fir in the Pacific Northwest. Department Bulletin. 1200. Washington, DC: US Department of Agriculture. 61 p.

Huff, M.H. 1995 Forest Age Structure and Development Following Wildfires in the Western Olympic Mountains, Washington. Ecological Applications 5:471-483.

Hurlbert, S. H. 1984. Pseudoreplication and the Design of Ecological Field Experiments. Ecological Monographs, 54:2, 187–211.

Impara, P. C. 1997. Spatial and Temporal Patterns of Fire in the Forests of the Central Oregon Coast Range. PhD dissertation. Oregon State University, Corvallis, OR.

Isaac, L. A. 1943. Reproductive habits of Douglas-fir. Charles Lathrop Pack Forestry Foundation, Washington, D.C., USA.

Isaac. L.A. 1949. Better Douglas-fir from better seed. University of Washington Press, Seattle, Washington.

Isaac, L.A., and G.S. Meagher. 1936. Natural reproduction on the Tillamook Burn two years after the fire. Pacific Northwest Experimental Station. USDA Forest Service, Portland, OR.

Kenkel, N. C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. Ecology, 69: 1017 - 1024.

Klopsch, M.W. 1985. Structure of mature Douglas-fir stands in a western Oregon watershed and implications for interpretation of disturbance history and succession. MS Thesis, Oregon State University.

Krueger, Kenneth William.1960. The influence of time of establishment and competition on the comparative heights of second growth Douglas-fir trees. MS Thesis. Oregon State University.

Kuiper, L. C. 1994. Architectural analysis of Douglas-fir forests. PhD.Dissertation. Wageningen Agricultural University, Wageningen, Netherlands.

Larson, A.J., and J.F. Franklin. 2005. Patterns of conifer tree regeneration following an autumn wildfire event in the western Oregon Cascade Range, USA. For. Ecol. Manage. 218:25-36.

Larson, A. J., Lutz, J. A, Gersonde, R. F., Franklin, J. F., & Hietpas, F. F. 2008. Potential site productivity influences the rate of forest structural development. Ecological Applications, 18(4), 899–910.

Lindenmayer, D.B., and J.F. Franklin. 2002. Conserving Forest Biodiversity. Island Press, Washington, DC.

Lutz, J.A., and C.B. Halpern. 2006. Tree mortality during early forest development: A Long-term study of rates, causes and consequences. Ecological Monographs 76:257-75.

McArdle, R.E., Meyer, W.H., Bruce, D. 1961. The yield of Douglas-fir in the Pacific Northwest. Technical Bulletin No. 201. United States Department of Agriculture, Washington, D.C. Reprinted by Oregon State University Book Stores Inc., 1975.

Means, J.E. 1982. Developmental history of dry coniferous forests in the western Oregon Cascades. In: Means, J.E., ed. Forest succession and stand development research in the Northwest. Corvallis, OR: Forest Research Laboratory, Oregon State University: 142-158.

Minore D. 1972. Comparative autecological characteristics of northwestern tree species: a literature review. US. For. Serv. Gen Tech Rep. PNW-GTR-87.

Morrison, P., Swanson, F.J., 1990. Fire History and Pattern in a Cascade Range Landscape. U.S. For. Serv. Gen. Tech. Rep. PNW-GTR- 254.

Munger, T.T. 1930. Ecological aspects of the transition from old forests to new. Science 72: 327–332.

Munger, T.T., 1940. The cycle from Douglas-fir to hemlock. Ecology. 21, 451–459.

Pipp, A.K., C. Henderson, R.M. Callaway. 2001. Effects of forest age and forest structure on epiphytic lichen biomass and diversity in a Douglas-fir forest. Northwest Science 75:12-24.

Oliver, C.D., Larson, B.C., 1996. Forest Stand Dynamics. McGraw- Hill, New York, 520 pp.

Poage, N.J., Tappeiner, J.C. 2002. Long-term patterns of diameter and basal area growth of old-growth Douglas-fir trees in western Oregon. Can. J. For. Res. 32:1232-1243.

Sensenig, T.S. 2003. Development, fire history and current and past growth, of old-growth and young-growth forest stands in the Cascade, Siskiyou and Mid-coast Mountains of southwestern Oregon. Ph.D. dissertation. Oregon State University, Corvallis, Oregon.

Smith, D.M., B.C. Larson, M.J. Kelty, P.M.S. Ashton. 1997. The practice of Silviculture: Applied forest ecology. 9th edition. New York: John Wiley and Sons.

Sorrensen-Cothern, K.A., Ford, D.E., Sprugel, D. G. 1993. A Model of Competition Incorporating Plasticity through Modular Foliage and Crown Development. Ecological Monographs, 63(3), 277–304.

Spies, T.A., and J. F. Franklin. 1991. The structure of natural young, mature, and old-growth forests in Washington and Oregon. Pages 91-121 *in* L.F. Ruggiero, K.B. Aubry, A.B. Carey, M.H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. For. Serv. Gen. Tech. Rep. PNW-GTR-285.

Spies, T.A., and Franklin, J.F., 1996. The diversity and maintenance of old-growth forests. In: Szaro, R.C., Johnson, D.W. (Eds.), Biodiversity in Managed Landscapes: Theory and Practice. Oxford, New York, pp. 296–314.

Stewart, G.H. 1986. Population Dynamics of a Montane Conifer Forest, Western Cascade Range, Oregon, USA. Ecology 67:534-544.

Stokes, M.A., and Smiley, T.L. 1968. An introduction into tree ring dating. University of Chicago Press, Chicago, Ill.

Swanson, M. E., Franklin, J. F., Beschta, R. L. Crisafulli, C. M., DellaSala, D. A., Hutto, R. L., Lindenmayer, D. B., Swanson, F. J. 2011. The Forgotten Stage of Forest Succession: Early-successional Ecosystems on Forest Sites. Front. Ecol. Environ. 9:2, 117–125. Doi: 10.1890/090157

Tappeiner, J.C., Huffman, D., Marshall, D., Spies, T.A., Bailey, J.D. 1997. Density, ages, growth rates in old-growth and young-growth forests in coastal Oregon. Can. J. For. Res. 27: 638-648.

Tepley, A.J. 2010. Age structure, developmental pathways, and fire regime characterization of Douglas-fir/western hemlock forests in the central western Cascades of Oregon. PhD. Dissertation: Oregon State University.

Tepley, A. J., Swanson, F. J., & Spies, T. A. 2013. Fire-Mediated Pathways of Stand Development in Douglas-Fir/Western Hemlock Forests of the Pacific Northwest, USA. Ecology. 94: 1729-1743.

Van Pelt, R., J.F. Franklin. 1999. Response of understory trees to experimental gaps in old-growth Douglas-fir forests. Ecological Applications 9:504-512.

Weisberg, P.J., and Swanson, F.J. 2001. Fire Dating from tree rings in western Cascades Douglas-fir forests: An error analysis. Northwest Sci. 75: 145-156.

Weisberg, P.J., and Swanson, F.J. 2003. Regional synchroneity in fire regimes of western Oregon and Washington, USA. Forest Ecology and Management. 172: 17-28

Winter L.E., Brubaker L.B., Franklin JF, Miller E.A., DeWitt D.Q. 2002a. Initiation of an old-growth Douglas-fir stand in the Pacific Northwest: a reconstruction from tree-ring records. Can. J. For. Res. 32(6):1039–1056. Doi: 10.1139/x02-031.

Winter, L. E., Brubaker, L. B., Franklin, J. F., Miller, E. A., & DeWitt, D.Q. 2002b. Canopy disturbances over the five-century lifetime of an old-growth Douglas-fir stand in the Pacific Northwest. Can. J. For. Res. 32(6), 1057–1070. Doi: 10.1139/x02-030

Yamaguchi, D.K. 1986. The development of old-growth Douglas-fir forests northeast of Mount St. Helens, Washington, following and A.D. 1480 eruption. PhD Dissertation, University of Washington.

Yang, Z., Cohen, W. B., & Harmon, M. E. (2005). Modeling early forest succession following clear-cutting in western Oregon. Can. J. For. 35(8), 1889–1900. Doi: 10.1139/x05-132

Zenner, E.K. 2005. Development of tree size distributions in Douglas-fir forests under differing disturbance regimes. Ecological Applications 15:701-714.

Table 2.1. Site characteristics for sampled stands. Climate data from PRISM (Daly et al. 2002).

SITE	Lat.	Long.	Elevation (m)	Max Stand Age (year)	% Douglas -fir density	% Douglas-fir Basal Area	Annual Precip (mm)	July Mean Precip (mm)	Jan Mean Precip (mm)	July max Temp (C)	Jan min Temp (C)	Growing Season mean Precip (mm)
Olympic National Park, WA												
Sol Duc	47.95	-123.81	687	317	31	71	3622	60.81	483.18	20.36	-1.23	80.03
Cedar River Watershed, WA												
Huckleberry	47.31	-121.52	799	328	16	25	2584	62.44	397.27	21.05	-2.97	74.7
Mt. Rainier National Park, WA												
AX15	46.75	-121.82	1024	183	27	42	2099	44.13	317.97	22.45	-3.44	62.63
TB13	46.74	-121.84	1018	213	52	31	2004	42.58	296.31	22.28	-3.63	61.14
Ohanapecosh	46.74	-121.55	670	296	25	47	1974	34.77	305.64	23.9	-3.96	46.61
Gifford Pinchot National Forest, WA												
Cedar Flats	46.11	-122.01	400	191	2	64	2972	44.78	454.73	25.26	-1.94	64.56
Drift Creek	46.03	-122.09	324	193	54	81	2990	45.81	455.34	24.67	-1.29	65.98
Osprey	46.03	-122.08	318	190	37	83	2995	45.91	456.44	24.99	-1.14	66.11
Skynard	46.02	-122.08	379	193	31	82	3339	50.68	525.75	24.08	-1.44	71.18
WR90	45.88	-121.9	715	171	33	86	2704	27.02	450.4	23.26	-2.74	43.85
WR05	45.84	-121.87	365	177	45	88	2506	21.26	399.34	26.95	-2.08	39.72
WR04	45.83	-121.87	315	168	35	91	2508	21.12	397.46	26.83	-2.08	40.19
Meditation Rock	45.49	-121.48	823	192	87	98	1226	21.67	193.82	22.59	-4.17	21.82
Goshawk	45.80	-121.97	494	114	85	98	1081	24.66	189.97	25.30	-3.76	17.41
Mt. Hood National Forest, OR												
MH123	45.31	-121.91	605	130	46	91	2259	44.76	325.04	23.21	-2.68	63.22
Willamette National Forest, OR												
Bagby	44.94	-122.17	650	297	27	66	2123	31.10	300.92	24.18	-2.42	51.74
Breitenbush	44.79	-121.90	760	326	32	77	1997	32.72	304.3	24.72	-3.85	45.59
RS26	44.27	-122.18	990	174	39	93	2130	27.51	288.27	27.51	-1.54	46.81

Table 2.2. Summary statistics for Douglas-fir ages.

Study Area	Single Cohort Establishment Duration (years)	Years to 90% Establishment	Maximum Age (years)	Minimum Age (years)	SE	*n*	% PSME Aged
Goshawk	60	30	114	54	0.46	411	41
MH123	47	22	130	83	0.58	161	46
WR04	45	32	168	123	2.54	24	35
WR90	75	32	171	96	2.11	43	49
RS26	75	43	174	99	1.45	89	30
WR05	32	19	177	145	0.94	56	74
WR05*	147	135	177	30	5.49	65	86
AX15	44	19	183	139	0.88	82	84
Osprey	38	34	190	152	1.59	48	47
Cedar Flats	33	19	191	158	1.07	31	42
Meditation Rock	67	48	192	125	0.96	135	38
Meditation Rock**	149	48	192	43	1.28	136	38
Skynard Hill	47	33	193	146	1.37	52	67
Drift Creek West	88	51	193	105	3.43	42	40
TB13	69	25	213	144	1.56	50	45
Ohanapecosh	61	49	296	235	2.57	32	37
Bagby	48	19	297	249	1.32	42	39
Sol Duc	99	58	317	218	2.74	37	26
Breitenbush	94	65	326	232	3.19	39	30
Huckleberry	64	34	328	264	1.19	71	96
Mean Values (95% CI)* **	**60.33 +/- (10.1)** 50-70 years	**35.11 +/- (7.09)** 28-42 years	**-**	**-**	**-**	**-**	**48.38**

Note: * Includes 9 individuals that established in a canopy gap. **Includes 1 individual that established in a canopy gap.* Means and 95% CIs do not include trees establishing in gaps**

Table 2.3. Parameter estimates for sigmoidal regression on cumulative age distributions.

Site	**Model Form** f= a/(1+exp(-(x-x0)/b))	**b**	**x0**	**Adjusted R^2**	**P**
Goshawk		4.5171	44.2919	0.9772	<0.001
MH123		3.696	34.8556	0.9939	<0.001
WR04		4.0082	37.8221	0.9425	<0.002
WR90		5.9371	59.104	0.9711	<0.001
RS26		7.5568	52.1834	0.9848	<0.001
WR05		3.3077	22.3239	0.9898	<0.001
AX15		3.8452	34.2701	0.9872	<0.001
Osprey		7.66	20.6397	0.9759	<0.001
Cedar Flats		2.8945	20.147	0.9646	<0.001
Meditation Rock		5.3591	36.2826	0.9919	<0.001
Skynard Hill		5.021	31.9371	0.9507	<0.001
Drift Creek		12.699	61.1324	0.9645	<0.001
TB13		4.7072	55.9982	0.9813	<0.001
Ohanapecosh		7.5235	35.0329	0.9782	<0.001
Bagby		4.308	38.3621	0.975	<0.001
Sol Duc		7.577	65.5695	0.9791	<0.001
Breitenbush		12.6734	51.8501	0.9817	<0.001
Huckleberry		5.1052	41.3572	0.997	<0.001

Table 2.4. Results of Mann-Whitney tests comparing the means of the diameters for the oldest and youngest 10% of the Douglas-fir populations in each site. Statistically significant results are in bold.

Sites	**Maximum Age**	**Mean of oldest 10%**	**Mean of youngest 10%**	**V_val**	**P_val**
Goshawk	114	46.0	26.4	1689.5	**0.000**
MH123	130	57.4	48.8	212	0.101
WR04	168	71.7	61.8	8	0.596
WR90	171	76.0	48.2	20	**0.020**
RS26	174	59.0	44.7	71	**0.037**
WR05	177	77.4	13.1	63	**0.001**
AX15	183	51.1	37.1	123	**0.008**
Osprey	190	119.0	86.1	24	0.121
Cedar Flats	191	97.4	103.2	19	0.830
Meditation Rock	192	54.9	49.3	119	0.346
Skynard	193	119.2	93.3	38	0.081
Drift Creek	193	101.5	78.2	19	0.210
TB13	213	63.6	58.2	14	0.835
Ohanapecosh	296	79.4	82.7	7	0.885
Bagby	297	94.7	67.6	29	0.074
Sol Duc	317	111.3	75.4	15	0.270
Breitenbush	326	130.4	76.5	17	0.111
Huckleberry	328	65.8	51.1	58	**0.039**

Table 2.5. Results of Mann-Whitney tests comparing the means of the diameters for oldest and youngest 20% of the Douglas-fir populations in each site. Statistically significant results are in bold.

Sites	**Maximum Age**	**Mean of oldest 20%**	**Mean of youngest 20%**	**V_val**	**P_val**
Goshawk	114	46.5	32.2	7649	**0.000**
MH123	130	58.4	49.1	801	**0.006**
WR04	168	74.3	73.6	10	0.676
WR90	171	70.6	49.9	87	**0.027**
RS26	174	63.7	51.0	247	**0.022**
WR05	177	77.6	26.1	174	**0.000**
AX15	183	50.8	41.4	271	**0.008**
Osprey	190	110.9	90.7	79	0.098
Cedar Flats	191	97.4	99.8	26	0.862
Meditation Rock	192	63.0	55.5	534	0.076
Skynard	193	120.5	91.2	125	**0.009**
Drift Creek	193	103.5	78.6	66	0.094
TB13	213	68.3	61.2	58.5	0.833
Ohanapecosh	296	83.4	84.0	28	1.000
Bagby	297	94.2	76.2	60	0.093
Sol Duc	317	104.3	74.7	49	0.083
Breitenbush	326	125.5	77.1	62	**0.014**
Huckleberry	328	70.3	55.1	219	**0.002**

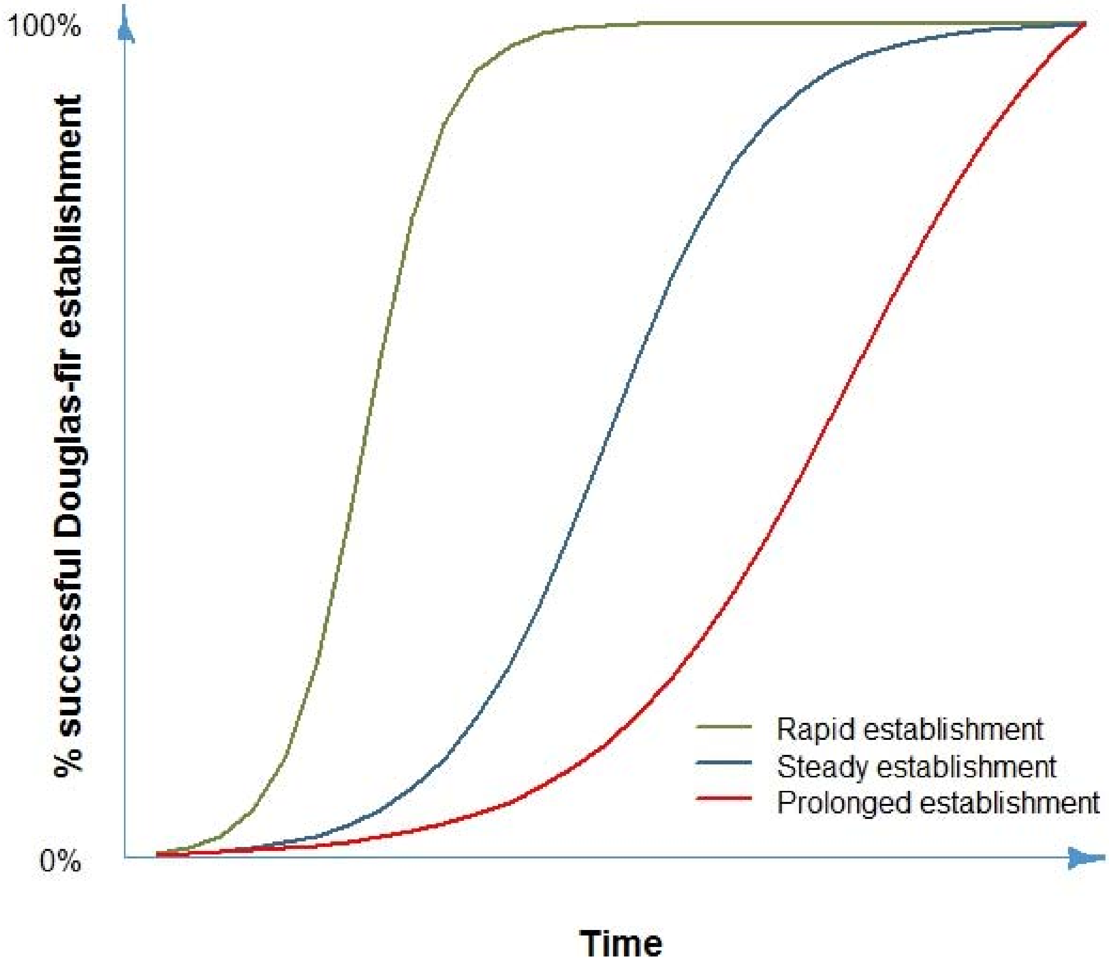


Figure 2.1. Three hypothetical curves representing alternative models of Douglas-fir establishment following high severity wildfire. The green curve represents rapid and abundant establishment during the first decade after wildfire. The red curve represents prolonged or protracted establishment. The blue curve represents an intermediate pattern of gradual, steady establishment leading to canopy closure.

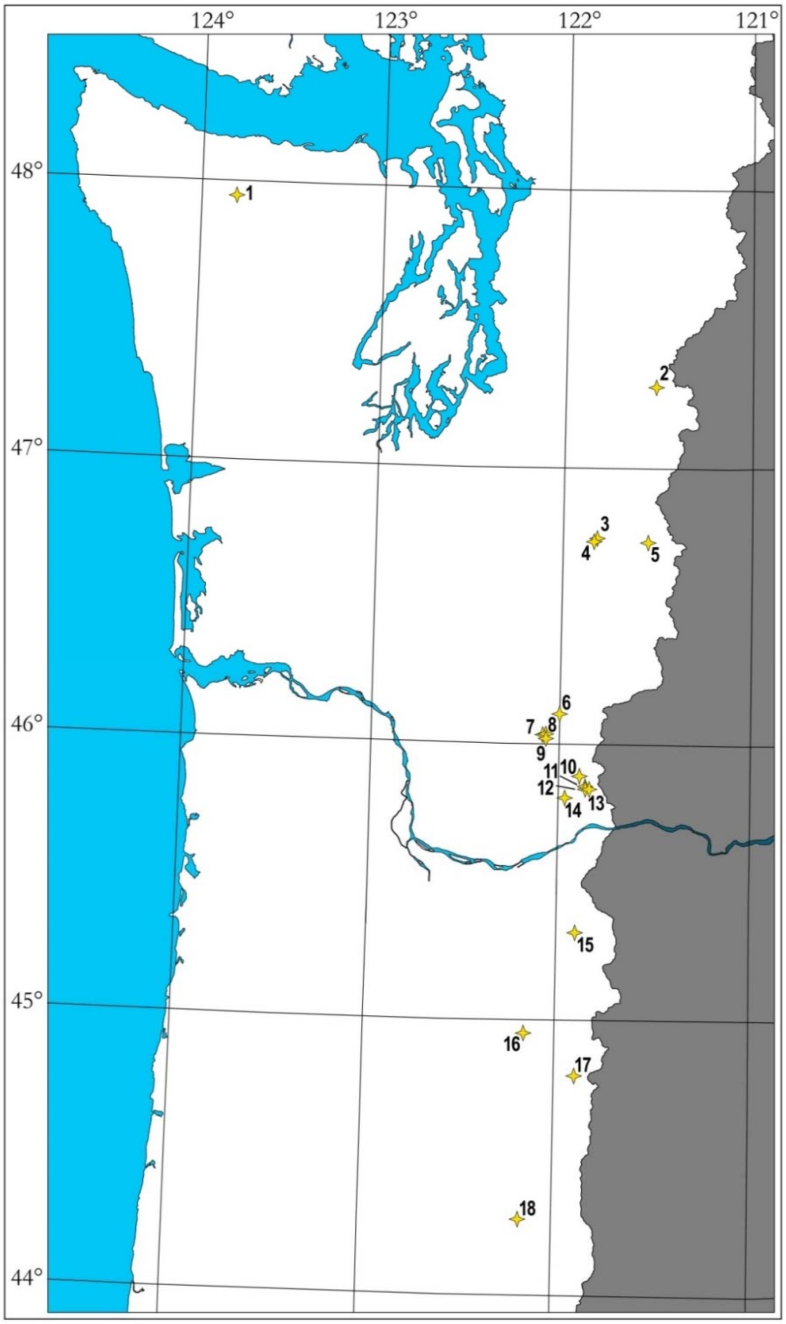


Figure 2.2 Map of Washington and Oregon with study locations marked with a yellow stars. Dark grey portion represents the crest of Cascade Mountains.

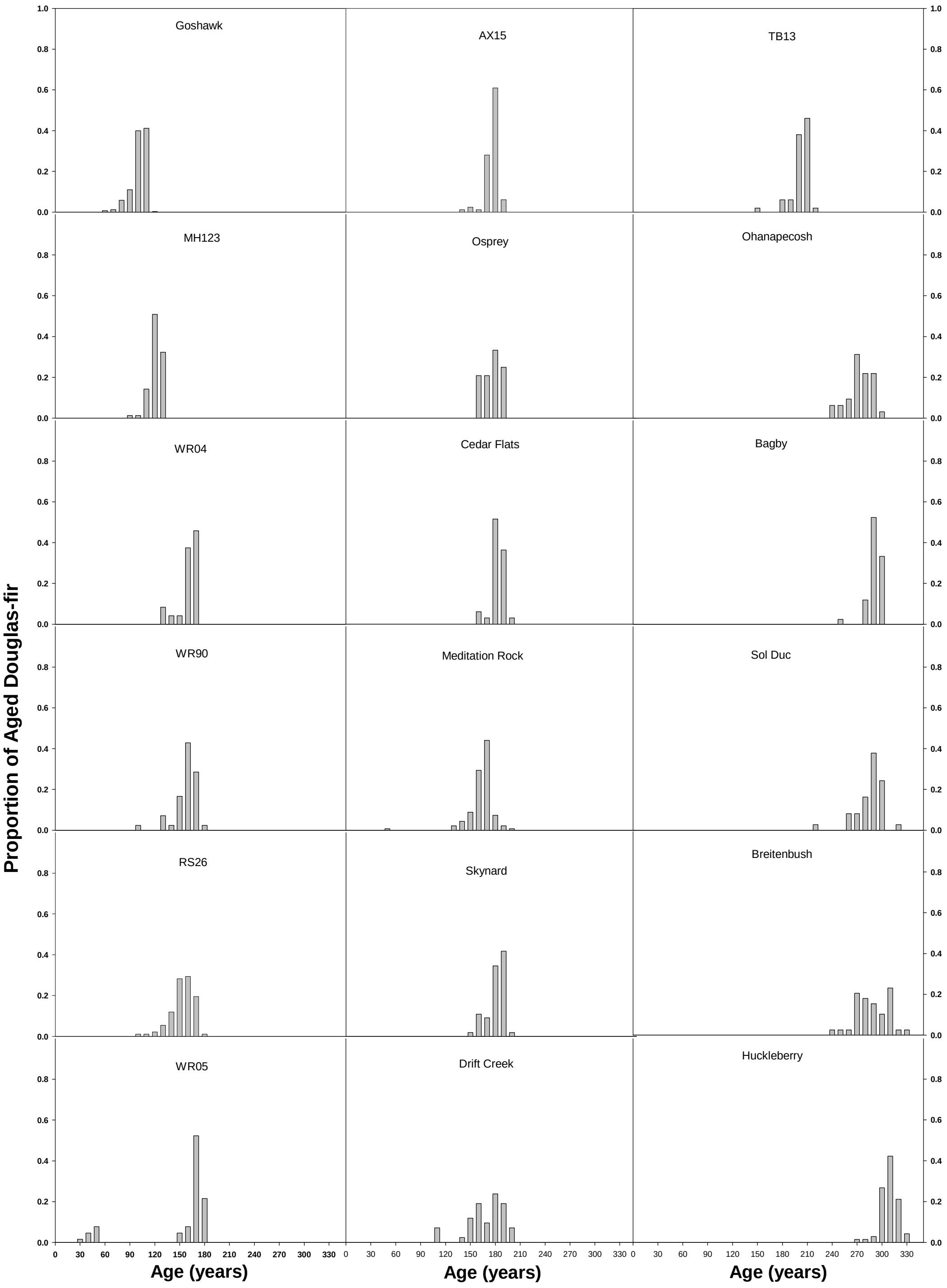


Figure 2.3. Histograms of the distribution of Douglas-fir ages in ten-year bins. Panels are arranged from youngest to oldest sites. WRO5 has nine trees that established in a canopy gap. Meditation Rock has one individual that established in a canopy gap following canopy closure.

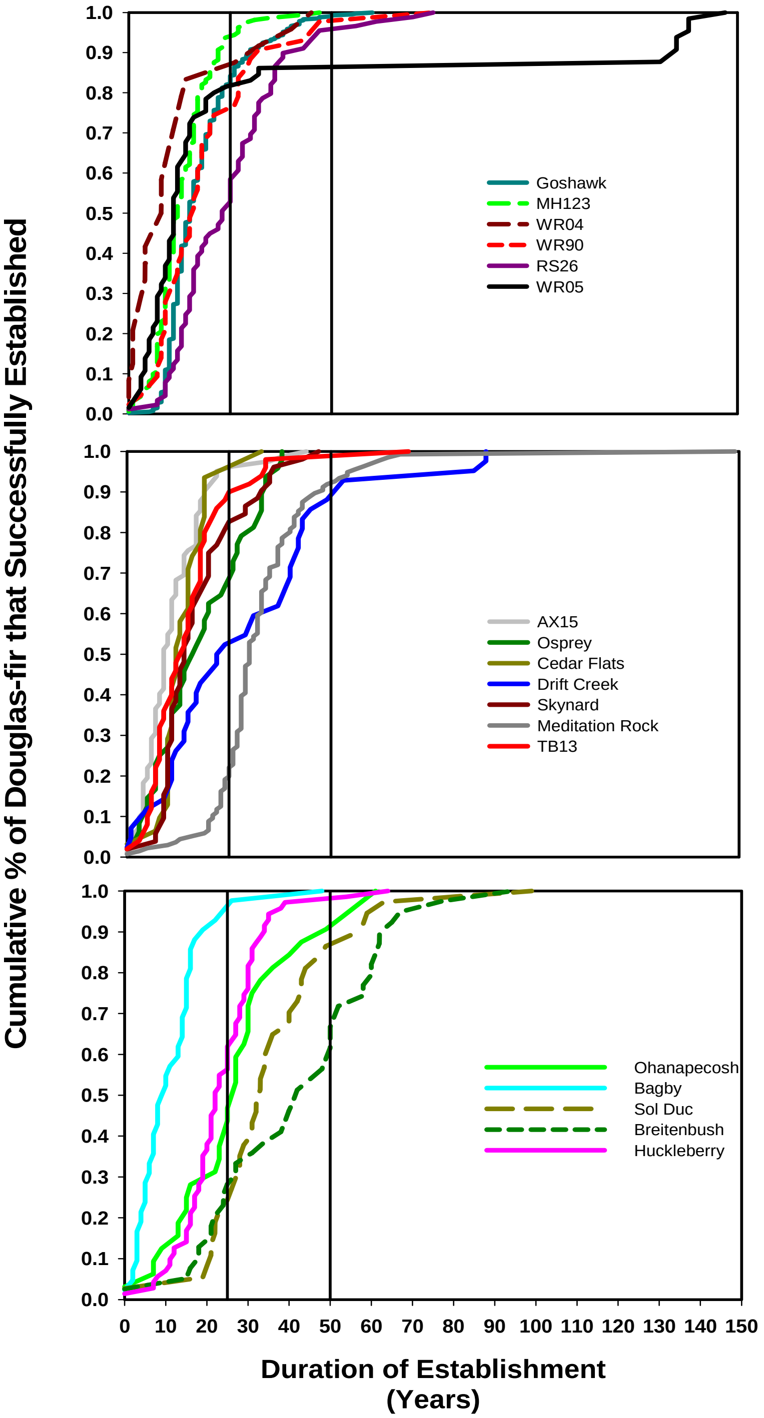


Figure 2.4. Cumulative patterns of establishment of Douglas-fir in sites of increasing age (top to bottom panels). Black vertical lines are placed at 25 years to compare with establishment rates outlined in the Franklin et al. 2002 conceptual model. Black vertical lines are also placed at 50 years to highlight establishment rates which last twice as long as or longer than suggested by the traditional model.

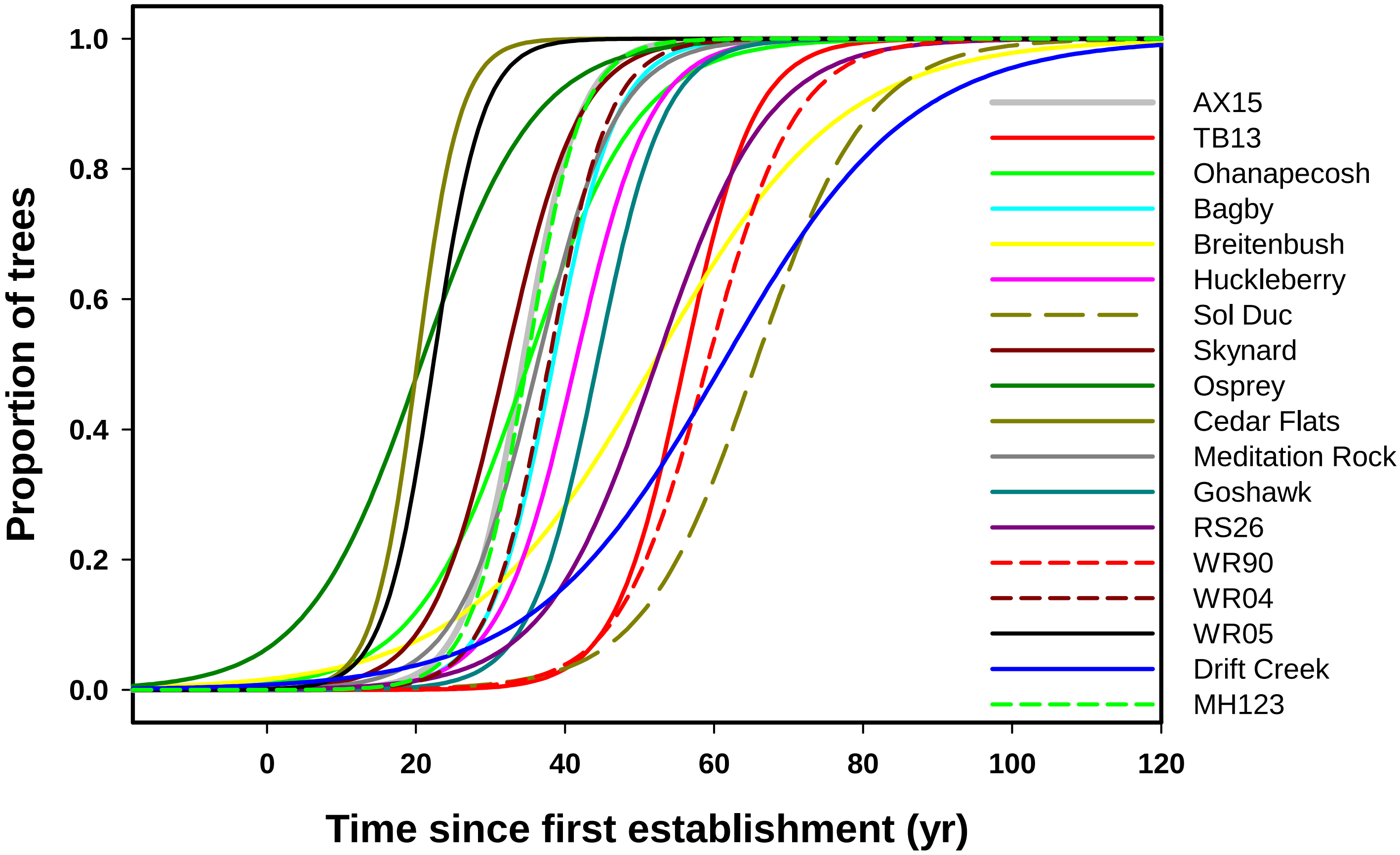


Figure 2.5. Sigmoidal regression curves fit to cumulative age distributions for each sample site.

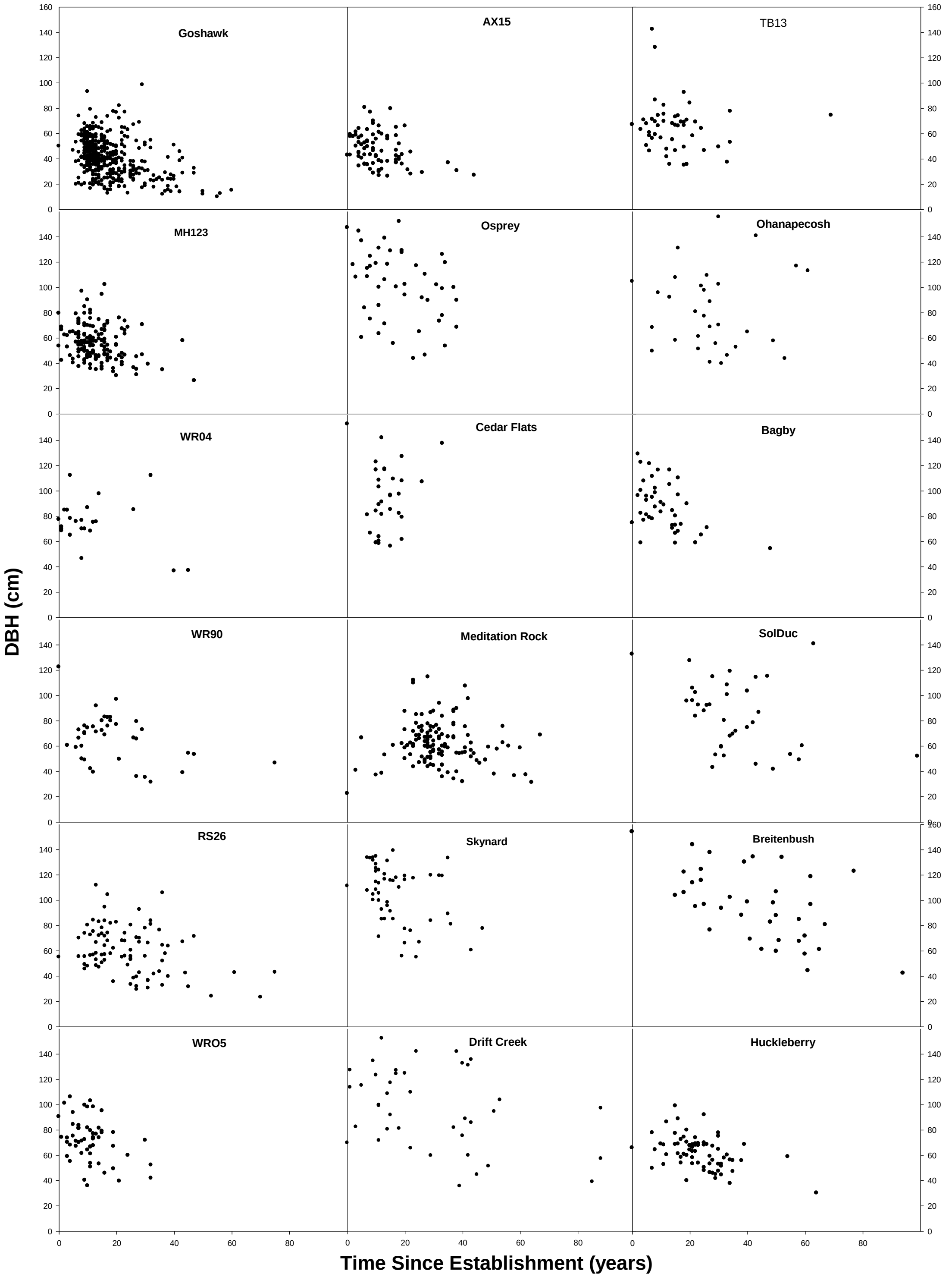


Figure 2.6. Scatter plots of Douglas-fir age and size. Ages are represented on the X axis as time (years) since the first (oldest) Douglas-fir established. Tree sizes are located on the Y axis and represent diameter at breast height (cm).

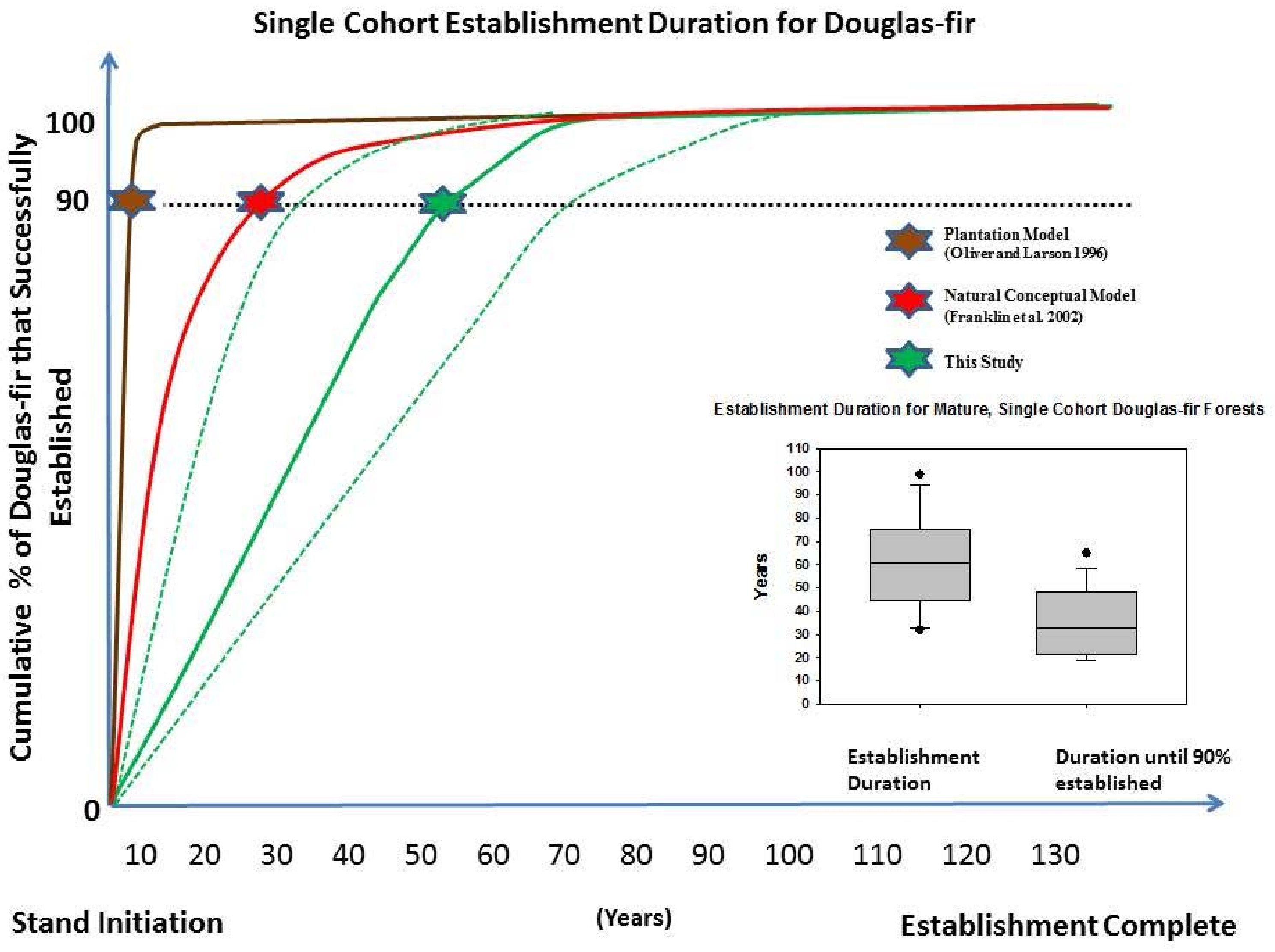

Single Cohort Establishment Duration for Douglas-fir
Cumulative % of Douglas-fir that Successfully Established
100
90
0
Plantation Model (Oliver and Larson 1996)
Natural Conceptual Model (Franklin et al. 2002)
This Study
Establishment Duration for Mature, Single Cohort Douglas-fir Forests
Years
110
100
90
80
70
60
50
40
30
20
10
0
Establishment Duration
Duration until 90% established
10
20
30
40
50
60
70
80
90
100
110
120
130
Stand Initiation
(Years)
Establishment Complete

Figure 2.7. Conceptual model of single-cohort Douglas-fir establishment following high severity wildfire. The brown line represents a plantation system with synchronous establishment and rapid canopy closure (within a decade). The red line represents a developmental pathway in which establishment extends more than two decades culminating in a closed-canopy state at 25 years as suggested by Franklin et al. (2002). The solid green line represents the establishment patterns reconstructed in this study. Dashed green lines illustrate the variation in establishment duration (minimum and maximum values). The horizontal dotted line represents the time in years at which 90% of Douglas-fir have established. The box and whisker plots illustrate the variation in the duration of establishment for all trees and 90% of trees for all sites; horizontal lines represent means lower and upper boundaries representing the 25th and 75th percentiles, respectively. Whiskers represent minimum and maximum values.

CHAPTER 3: STRUCTURAL DEVELOPMENT OF EARLY OLD-GROWTH DOUGLAS-FIR FORESTS IN THE PACIFIC NORTHWEST

ABSTRACT

Few empirical studies exist on transitions of young, structurally simple forests dominated by Douglas-fir to structurally complex older forests. Stand structure (live tree diameter and height distributions and snag and log metrics) and composition of nine "early old-growth" (200- to 350-year-old) forests are quantified and compared with those of fully developed old-growth (400- to 600-year-old) forests. All are moist-site forests dominated by Douglas-fir and western hemlock-dominated forests in which Douglas-fir had established following a single stand-replacing disturbance. Stand-level attributes are described using descriptive statistics, nonlinear regression, and old-growth indices. Variability in individual structural features was large between sites but broadly consistent with a conceptual model of Douglas-fir forest development. Diameters exhibited the reverse J-shape distributions characteristic of fully developed (>450-year-old) forests. Live tree height distributions indicate that shade tolerant species occupy lower canopy positions of the understory. Coarse woody debris was abundant in early old-growth forests considering both snags (42-140 $m^3\ ha^{-1}$) and logs (172-584 $m^3\ ha^{-1}$). Early old-growth stands scored high enough on old-growth indices to qualify as old growth but their scores were significantly lower than older forests (400-600 years-old). The structural conditions and variability of these early old-growth forests provide a closer temporal target for managers seeking to accelerate the development of structure in younger stands.

Introduction

Natural forest ecosystems characteristically subject to stand-replacement disturbances undergo repeated cycles of stand initiation and development. Structural development in these forests involve many processes, such as those associated with growth and maturation of individual trees, competitive interactions, and small-scale disturbances (Barnes et al. 1998, Kimmins 2004). Development of structurally complex older forests may require centuries, particularly in forest ecosystems that include long-lived tree species, such as those found in northwestern North America (Waring and Franklin 1979, Franklin and Dyrness 1988). Forest structural attributes that contribute to that complexity include tree population growth and dynamics, elaboration of forest canopies, and development of stocks of coarse woody debris, including snags and logs (Franklin et al. 2002).

Natural Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco.) forests in the Pacific Northwest are an outstanding example of forests in which centuries of structural development culminate in structurally complex old-growth forests (Franklin et al. 2002, Franklin and Van Pelt 2004, Van Pelt and Nadkarni 2004). Although Douglas-fir forests are extensive and include an abundance of diverse age classes, patterns of stand development are not fully understood and documented. Many aspects of existing conceptual models (e.g., Franklin et al. 2002 and Spies 2009) have had limited empirical documentation. Some developmental stages – such as the young (<100 years) forest and well-developed old-growth (>400 year) forests – have received extensive study (e.g. Franklin and Spies 1984, Spies & Franklin 1991, Huff 1995, Tappeiner et al 1997, Van Pelt and Nadkarni 2004, Lutz and Halpern 2006, Larson et al. 2008, Halpern and Lutz 2013).

Structure and developmental processes in the mature and early old-growth stages of development (i.e., the period from 100 to 350 years) are relatively poorly documented despite its importance. For example, this is the period during which there are profound shifts in canopy architecture from the top-loaded, single-layered canopy of young forests to a bottom-loaded and essentially continuous canopy characteristic of older forests. Chronic small-and intermediate scale disturbances that create gaps and provide for growth of shade-tolerant sub-dominant trees is hypothesized as one of the processes that is responsible for the change in canopy architecture (Franklin et. al 2002, Tepley et al. 2013); however, observations of conditions and processes in these developmental stages are limited.

Structural and compositional conditions in natural, intermediate-aged (200- to 350-year-old) Douglas-fir-dominated forests are the subject of this paper. This study is based on an examination of above-ground attributes of nine forest stands that originated ca. 1650 to 1800 AD in western Washington and Oregon and a comparison of their characteristics with both younger and older Douglas-fir-dominated forests. Four general questions are addressed: (1) What are the structural dimensions of early old-growth forests, including the variability between stands; (2) Are these structural features consistent with the conceptual models that have been developed for Douglas-fir forests (e.g., Franklin et al. 2002), (3) How do early old-growth stands score on the structural indices that have been developed and in comparison with young-mature forests and well-developed (>400-year-old) old-growth forests; and (4) Will the Douglas-fir population densities in the early old-growth stand be similar to the densities of existing older (>400-year-old) Douglas-fir stands?

Methods

Study Area

A total of nine early old-growth stands were sampled during this study. Eight of nine sampled stands are distributed along the western slope of the Cascade Range between 47.95 and 44.27 N latitude and at elevations of 300 to 1000 m. The remaining stand is located in the eastern Olympic Mountains, Washington (Table 3.1) (Figure 3.1). Eight stands occupy moist to relatively dry sites representative of the Western Hemlock Zone (Franklin and Dyrness 1988) (Table 3.1). One (Huckleberry) is located in the cooler, moister Pacific Silver Fir Zone (Franklin and Dyrness 1988).

These sites have a maritime climate characterized by cool wet winters and warm dry summers (Table 3.1). Annual precipitation ranges from 1500 mm to 3000 mm with the majority occurring during the months of October through April; conditions in the Pacific Silver Fir zone are somewhat cooler and moister and include a significant winter snowpack accumulation.

Douglas-fir is an important shade-intolerant, pioneer tree species in the Western Hemlock and Pacific Silver Fir zones (Franklin and Dyrness 1988). It can grow to very large dimensions, develop complex canopies (Van Pelt and Sillett 2008) and live for 700 to 1000+ years. Common tree associates of Douglas-fir include western hemlock, western redcedar (*Thuja plicata* Donn ex D. Don), western white pine (*Pinus monticola* (Dougl.), Pacific silver-fir (*Abies amabilis* (Dougl. ex. Loud) Dougl. ex Forbes), Pacific yew (*Taxus brevifolia* nutt.), noble fir (*Abies procera*), big-leaf maple (*Acer macrophyllum* Pursh), and Pacific dogwood (*Cornus nutallii* Aud.). Plant associations vary by site and are summarized in Table 1 (Franklin and Dyrness, 1988). Soils range from sandy loams to clay loams and great soil groups include Haplorthods, Xerumbrepts, and Vitrandepts.

Wildfire is the principal agent of disturbance. Historically, stand-replacement events occurred relatively infrequently (every 200 to 400 years) (Hemstrom and Franklin 1982, Agee 1993) although partial stand-replacement events are also characteristic (Tepley et al. 2013), particularly in more southerly latitudes. Smaller-scale disturbances include wind, pathogens, and insects, which are important in creating and sustaining structural complexity in older stages of forest development (Franklin et al. 2002).

Site selection

The principal criterion for site selection was presence of Douglas-fir-dominated stands ~200 to 350 years of age which established after a single wildfire event. Forests of this age are not widely distributed in the Douglas-fir region but, rather, are concentrated in a few locations, such as the Clackamas and Breitenbush River drainages in the northern Oregon Cascade Range, in the Lewis River and Ohanapecosh River drainages of the Washington Cascade Range, and in eastern portions of the Washington's Olympic Peninsula. Candidate stands were located following reviews of fire-history studies (Morrison and Swanson 1990, Agee 1991, Impara 1997, Sensenig 2003, Weisberg and Swanson 2003), stand age-class maps (US Forest Service), conversations with forest ecologists familiar with the region (personal communications with Ken Bible, Rolf Gersonde, Scott Gremel, Jan Henderson, James Lutz, Robin Lesher, and Robert Van Pelt), and extensive reconnaissance and preliminary aging of stands.

I selected nine stands that had evidence of a single initiating wildfire event and no evidence of subsequent post-establishment disturbances, such as fire scars, charcoal, very high or low levels of CWD, or uniform sizes and heights of shade-tolerant tree species. Presence of smaller-scale, low-severity disturbance attributable to agents such as the Douglas-fir bark beetles (*Dendroctonus pseudotsugae)* or fungi (e.g. *Phaeolus schweinitzii*)) was deemed acceptable.

The youngest age class of forest sampled was about 200 years in age but stands of this age were uncommon, which made it impossible to replicate sampling in this age class over a broad geographic range. The four suitable stands that were located were all in the Lewis River drainage in southwestern Washington and probably originated from a single extensive wildfire event. Hence, these four stands could be viewed as "pseudo-replication" (Hurlbert 1984), at least of the initiating fire event. However, the sampled stands were broadly dispersed over the available forest of this age class to provide some measure of structural variability in this age class.

Field Methods

Sites were selected after extensive ground reconnaissance (see Freund et al. in review), which included aging dominant Douglas-fir trees at each location. At each site, six 0.2-ha fixed-radius plots were established at 100 m spacing along transects initiated from a random starting location. Transects were established >50 m from any road, river, or previously disturbed area. Slope was measured at plot center using an Impulse Laser 200 (Laser Technology Inc.). Within each plot all trees ≥ 5 cm dbh (diameter breast height) were identified by species and measured for dbh. Tree heights were estimated for a sample of each species within each plot (n = 6-10 trees per species). Three measurements were taken on each tree: total height, height to primary branches, and height to epicormic branches. All seedlings < 5 cm dbh within 1 meter of transect lines were identified by species and measured for height. Snags ≥ 10 cm and ≥ 1.37 m were identified by species and measured for diameter and height and classified by decay class (Cline et al 1980). Volume of logs on the forest floor (≥ 10 cm) was determined using a line intercept method (Harmon and Sexton 1996); 606 m of line intercept were sampled in each stand.

Analyses

Summary statistics (question 1) for stand-level attributes of each early old-growth stand were calculated for live trees and coarse woody debris. Live tree summary statistics by species included: (1) mean, minimum, and maximum dbh, (2) standard error of dbh, (3) basal area, and (4) density. Mean height, mean crown length, and mean epicormic height and corresponding standard deviations were calculated for Douglas-fir, western hemlock, and western redcedar. Snag data were summarized by calculating stand-level statistics for total snag density, large snag (>50 cm) density, basal area, mean height, and standard deviation of height. Snags were also characterized by calculating density, volume, mean height, and standard deviation of mean height by decay class. Similarly, logs were characterized by calculating stand level values for mean piece diameter, volume, density, and large log (> 50 cm) density. Volume of logs was also calculated by decay class. Seedling data were summarized by calculating density and height statistics (mean, range, and standard deviation).

Principal component analyses (PCA) were used to explore structural variability among early old-growth sites. PCAs were computed for a 9 x 17 covariance matrix of study sites (n = 9) and stand-level variables (n = 17) utilizing the R statistical package (R Core Development Team). Prior to analysis variables were standardized by their maxima and then by site totals. Variables were: total basal area, Douglas-fir basal area, western hemlock basal area, Douglas-fir tree density, shade-tolerant tree density, standard deviation of dbh, density of snags >50 cm dbh, mean live tree diameter, log volume, snag volume, density of trees >100 cm dbh, Douglas-fir age range, standard deviation of Douglas-fir age range, mean Douglas-fir crown depth, standard deviation of Douglas-fir crown depth, and standard deviation of western hemlock heights.

Data from the early old-growth stands were compared with the qualitative descriptions provided in the Franklin et al. (2002) conceptual model of Douglas-fir stand development (question 2) to assess the degree of fit. Focal points of these comparisons were whether the early old-growth stands were (1) developing old-growth tree-size distributions, (2) reinitiating a shade tolerant understory, (3) experiencing elongation of the Douglas-fir crown through epicormic branching, and (4) accumulating high levels of coarse woody debris. Histograms displaying the size distributions for all species in 15 cm bins were created. Cumulative diameter distributions were used as a basis for comparing the size distributions with known distributions of older stands. Two parameter exponential decay curves were fit to the cumulative diameter distributions to assess variability among live-tree populations except for one site (Huckleberry) which was fit with a 3 parameter sigmoid curve. Goodness of fit was assessed using r^2 values obtained from each fit curve using SigmaPlot version 11.0, from Systat Software Inc, San Jose, California USA (Appendix I). Histograms displaying tree height distributions separated into 5 m bins were created and line plots of the crown length distribution were overlaid onto total height histograms. Histograms displaying the coarse woody debris size distributions separated into 15 cm bins were created.

Two indices of old-growth characteristics were computed to address the question of whether the structure of early old-growth forests is comparable to that in older (>400-year-old) stands (question 3). The first index (Iog) was developed by Acker et al. (1998) and utilizes four variables: 1) standard deviation of diameter at breast height, 2) density of large diameter trees >100 cm (dbh), 3) mean tree dbh, and 4) total tree density. Thorough descriptions of the index are provided elsewhere (Acker et al. 1998, Larson et al. 2008).

The Old Growth Habitat Index (OGHI) was the second index utilized. This index incorporates both live and dead components of forests (Franklin et al. 2005). OGHI utilizes five variables that are scored between 0 and 100 based on large trees per hectare (> 100 cm), large snags per hectare (> 50 cm dbh and 15 m tall), volume of downed woody debris, diameter diversity within each stand, and stand age. Total scores can be calculated in three forms of the OGHI. The "standard" OGHI is calculated from the average of the five element scores, the "modified" OGHI excludes stand age, and the "weighted" OGHI is scored using a relative Spearman rank correlation coefficients of each structural element and stand age.

Structural differences between early and older (>400 year) old-growth stands was done by calculating OGHI Index scores for stands and comparing their scores. The mature and older stands were from an independent data set created in an earlier study (Spies and Franklin 1991) and ranged in age from 42- to 900-years-old. The range of element scores from early old-growth were graphed in boxplots along with those of a subset of the Spies and Franklin (1991) plots. The subset of Spies and Franklin (1991) plots were selected to represent younger stands (42-140 years-old) and stands of the most common age class of old-growth forest in the region (400-600 years-old). One-way ANOVA and post hoc Holm-Sidak multiple comparisons were used to test for significant differences ($\alpha = 0.05$) among age classes. The two groups of stands used from the Spies and Franklin (1991) data set include 27 young-mature stands (42-140 years), and 15 old-growth stands (400-600 years). In addition, the means, ranges, and 95% confidence intervals of values for several structural elements of early old-growth were tabulated and compared with values for old-growth from Spies and Franklin (1991).

A comparison of OGHI element scores between high and low productivity early old-growth sites was made using Mann-Whitney tests to compare the highest productivity sites with the lower productivity sites. Site index was determined using height growth curves (McArdle and Meyer 1971).

Projected Douglas-fir densities were calculated for the early old-growth stands to see what their densities would be when they reached ages in excess of 400 years – i.e., to compare projected densities with those in existing older (>400-year-old) stands (question 4). This was done by using current Douglas-fir densities to project future densities using a mortality equation of the form:

$$\text{Projected density} = N_1 * (1- m_1)^t$$

where N_1 is the current Douglas-fir density, m_1 is annual mortality rate, and t is the number of years. Populations were projected for 300 years into the future in 25 year increments. Three rates of annual mortality (0.28%, 0.5%, and 0.9%) were used in these projections based on known rates of mortality of Douglas-fir in old-growth forests (Spies et al. 1990, Franklin and Debell 1988, Bible 2001). Projections were also made using a 1.1% annual mortality rate to represent a scenario in which mortality rates increased as a consequence of climate change (van Mantgem et al. 2009). Projected densities of early old-growth stands were compared with current densities of Douglas-fir in 450-600 year-old Douglas-fir forests (Spies and Franklin 1991, Lutz et al. 2013 in review) using Mann-Whitney rank sum tests.

Results

Live tree size structure

Cumulative diameter distributions generally follow a reverse J-shape (Appendix I) with a strong fit to a 2-parameter exponential-decay curve (r^2=0.96-0.99). Only the oldest stand (Huckleberry) was better fit to a 3-parameter sigmoid curve (r^2 =0.99).

The highest tree densities were generally in the smaller ($\leq$45 cm) diameter classes and were composed primarily of shade-tolerant species, particularly mostly western hemlock (Figure 3.2). Douglas-fir dominated the largest diameter classes, except at Huckleberry, and had a unimodal size distribution. Western hemlock was abundant and at least present throughout the diameter sizes at most sites (Figure 3.2). Western redcedar was primarily limited to smaller diameter classes (<60 cm) except at three sites (Cedar Flats, Ohanapecosh, Huckleberry) where it was present throughout the diameter distribution (Figure 3.2).

Total tree density (stems >5 cm dbh) varied greatly among sites, ranging from 162 to 464 trees/ha with a mean of 302 trees/ha (Appendix II). Density of Douglas-fir ranged from 62 to 118 trees/ha with a mean of 85 trees/ha. Density of western redcedar was also highly variable with a range of range of 0 to 78 trees/ha and a mean of 18 trees/ha; western redcedar was either absent or scarce in four stands.

Total basal area varied greatly among sites, ranging from 68.6 to 121 m^2 ha^{-1} (mean of 89.6 m^2 ha^{-1}) (Table 3.2). Douglas-fir dominated the basal area at all sites, except Huckleberry, with western hemlock and western redcedar of secondary importance (Table 3.2).

Mean tree diameter of stands ranged from 40.7 to 60.8 cm with a range in stand deviations of 19.9 to 43.7 (Table 3.2). Mean diameters of Douglas-fir in stands ranged from 62 to 101 cm dbh. Western hemlock mean diameters range from 21.5 to 45.9 cm dbh. When western redcedar was present in the stand its mean diameters are larger and more variable (range 30 to 70 cm) than those of western hemlock.

Douglas-fir was the tallest tree species at all sites (maximum height of 70-80 m; Figure 3.3). Generally, there was a distinct trough or separation in the stands between the distribution of

Douglas-fir heights and those of western hemlock and western redcedar (Figure 3.3), with some overlap in heights of Douglas-fir and western hemlock. Mean height of Douglas-firs ranged from 52.7 to 66.1 m (SD = 7.5 to15 m); western hemlock mean heights were 23 to 34 m (SD = 7.7-18.37) (Table 3.3).

Crown lengths varied among species with the shade-tolerants exhibiting the longest crowns; western hemlock crown lengths ranged from 0.3 to 49.5 m (mean = 16.7 and SD = 11.8) and those of western redcedar from 1.35-51.6 m (mean = 18.8 and SD = 1.1). The shorter crowns of the Douglas-fir ranged from 9.4 to 27.6 m (mean = 22.9 m and SD = 5.5) (Table 3.3).

Epicormic branches were present on Douglas-fir at all sites and were usually located near the base of the primary live crown. Mean heights of epicormic branches ranged from 18 to 25.7 m (Table 3.3).

Snags and logs

Snags were abundant at all sites but snag volumes varied greatly (Table 3.4) (Figure 3.4). Mean snag densities ranged from 34 to 112 snags/ ha (mean = 76 and SD 26). Snag volumes ranged from 42.6 to 140.2 m^3 ha^{-1} (mean = 81.8 and SD = 13.5) (Table 3.4). Most snags were 15 to 60 cm in diameter (Figure 3.4), but all sites (except Huckleberry) had at least a few large snags (>100 cm dbh).

Log densities and volumes varied greatly among sampled stands (Table 3.5). Most logs were small to medium in size with mean diameters ranging from 28 to 42 cm. Five sites had close to or greater than 100 logs per hectare and all sites had at least some large logs (>50 cm). The two youngest sites sampled had the highest density of large logs and the three oldest sites the lowest density of large logs. Coarse woody debris exhibited moderate volumes in decay class one followed by peaks in decay classes two and three (Table 3.5). Volume of CWD for decay classes one and five were almost identical.

Important elements of early old-growth structure

Four primary contributors to variation in structure along Axis 1 in a principal components analysis of sites and stand-level variables exist. These four variables were 1) basal area of western hemlock, 2) density of shade-tolerant trees, 3) log volume, and 4) density of large trees (> 100 cm dbh) (Table 3.6). Elements correlated with Axis 2 of the analysis were volume of snags and logs and, to a lesser extent, basal area of Douglas-fir and duration of Douglas-fir establishment.

Old-growth Indices

All sites scored values of 100% using the Iog old-growth index developed by Acker et al. (1998) except for Huckleberry (Table 3.7). Similarly, all sites except Huckleberry had values comparable to old-growth (albeit at the lower end of the old-growth range) using the OGHI index developed by Franklin et al. 2005 (Table 3.8; Figures 3.5 and 3.6). The scores were similar for all of the early old-growth forests with all three variants of the OGHI, with the standard OGHI providing the highest index scores.

Comparison of Early Old-growth with Younger and Older stands

The structure of early old-growth forests is different from independent data sets of younger and older forests (Spies and Franklin 1991), although some structural similarities exist. Element scores of the OGHI for early old-growth differed significantly ($\alpha = 0.05$) from scores of younger and older stands of Spies and Franklin (1991) (Table 3.10). However, there is overlap between means and 95% confidence intervals for some structural variables (Table 3.9). Notably, the mean values for tree density and for stand basal area were not comparable (Table 3.9). Post-hoc Holms-Sidak multiple comparison tests indicated significant differences among all age classes (Table 3.11). Comparisons of early old-growth sites with forests of similar age (Franklin et al. 2005) did not result in statistically different scores (Table 3.10). Element scores from the four most productive sites (Site Index I) were generally higher than element scores from lower productivity sites but the differences were not significant ($\alpha = 0.05$ and $p = 0.299$).

Projections of future Douglas-fir densities

Projected future densities of Douglas-firs are variable and depend upon the annual mortality rate that is used (Figure 3.7). When the 0.28% annual mortality rate is used the Douglas-fir population densities 200 and 300 years in the future due not differ significantly from those in existing older (>400 year) Douglas-fir—western hemlock stands (Table 3.12). When the 0.5% annual mortality rate is used projected Douglas-fir population densities in the early old-growth are comparable to those in existing older (>400 year) stands for 200 years but a statistical difference (lower densities in the projected early old-growth stands) at 300 years. Projections of Douglas-fir population densities in the early old-growth Douglas-fir stands are significantly lower than those in existing older (>400 year) stands (Table 3.13) when either the 0.9% or 1.1% rates of mortality are used (Table 3.12)(Figure 3.7).

Discussion

The structure of early old-growth forests represents an intermediate level of development between younger and older forests. This intermediate structural space is evidenced by the tree size distributions, species height distributions, and volumes of snags and logs. Early old-growth forests vary in the level of structural complexity, which is consistent with the patterns of variability found in other age classes. Early old-growth structural variation was primarily related to the density and basal area of Douglas-fir, density of shade-tolerant trees, and volumes of coarse woody debris. Composite measures of forest structure computed from one old-growth index (OGHI) provides strong evidence for structural differences from younger and older forests and bolsters support for model descriptions of this stage of forest development. Additionally, based on current mortality rates, Douglas-fir densities in the early old-growth stands are projected either to be similar or slightly lower than Douglas-fir densities in current well developed (>400-year-old) old-growth forests. However, an increase in annual mortality rates, such as might be associated with climate change, could result in significantly lower future Douglas-fir densities in the early old-growth stands.

The conceptual model advanced by Franklin et al. (2002) on Douglas-fir forest structural development is largely based on empirical data and analyses of young, early mature, and well-developed (>400 year) old-growth forests. Stages of structural development following a single high severity disturbance are characterized using space (e.g. stands of a particular age) for time substitutions. Space for time or chronosequence approaches have many limitations (e.g. Pickett 1989) but can be very useful when sequential data on the full developmental sequence are not available (Spies and Franklin 1991). A complicating issue is that the model characterizations of old-growth structure are largely based on stands that originated ca. 1500 AD (Spies and Duncan 2010). These forests are one to two centuries older than the early old-growth stands in this study and may represent idiosyncratic stand developmental trajectories. For example, many of the old-growth stands used to construct the current conceptual model may have experienced one or more additional disturbances severe enough to regenerate new cohorts of Douglas-fir (Van Pelt 2007, Tepley et al. 2013). Intermediate disturbances may also influence development of structure by reducing densities of other tree species, consuming coarse woody debris, and changing canopy morphology. Hence, it is important to examine this conceptual model using early old-growth stands which developed in the absence of moderate severity intermediate disturbances.

The structure of early old-growth forests in this study is consistent with the conceptual model developed by Franklin et al. (2002)—with some exceptions. In the model old-growth characteristics are predicted to begin developing during the early old-growth period. Data on diameter distributions in the early old-growth stands, which show a shift to greater density of shade-tolerant species, are consistent with the conceptual model. Reverse-J or negative exponential tree size distributions have been used to characterize old-growth forests (Franklin and Spies 1984, Zenner 2005). Early old-growth tree size distributions had good fits with exponential decay curves, providing further support for descriptions related to the significant development of old-growth structure. The height distributions are evidence for the development of a continuous canopy from the ground to the tops of the tallest trees. Douglas-fir are the tallest trees with western hemlock and western redcedar filling in the lower and mid canopy positions. Observed levels of CWD in early old-growth forests are also consistent with conceptual model characterization of snag and log accumulation during this period.

Structural variability among early old-growth stands relates primarily to four variables: basal area of western hemlock, density of shade-tolerant trees, large-diameter trees, and volume of logs. Surprisingly, the standard deviation of dbh was not related to stand age and was not identified as a strong contributor to the explained variation in the principal components analysis; this variable has been identified as a defining structural variable in other analyses of old-growth forest structure (Spies and Franklin 1991, Acker et al. 1998, Van Pelt and Nadkarni 2004).

Rather, structural variation among early old-growth stands may reflect differences in site productivity or stand history. For example, the standard deviation of dbh was higher in my early old-growth stands (mean= 36.4, 95% CI= 5.3) compared with the old-growth (>400 year) data set, which is probably due to differences in shade-tolerant tree densities among these age classes.

Many structural attributes of early old-growth stands differ from those reported by Spies and Franklin (1991) for older (>400 year) old-growth stands. For example, mean tree densities are considerably lower in the early old-growth even though mean Douglas-fir densities are greater (Table 9). The density of large trees (>100cm dbh) and total stand basal area are also higher in the early old-growth forests sampled in this study.

Old-growth indices

All but one of the early old-growth stands sampled in this study qualify as "old growth" using the index developed by Acker et al. (1998). They also qualified as old-growth based on the Old Growth Habitat Index used in Franklin et al (2005) the exception being Huckleberry (Table 7); this was true regardless of which of the three separate variants of the OGHI that were used in the calculation (Standard, Modified, Weighted). Scores from all three variants of the OGHI place the early old-growth forests between both mature and older stands (Figure 7). Furthermore, the OGHI scores for early old-growth forests are statistically different from OGHI scores for the older (400-600 years-old) and younger (42-140 years-old) stands that were used for the comparison; early old-growth stands have lower median values and little overlap with 50% of the scores for older stands (Figure 8).

Coarse-filter indices have great utility for classifying forest structure in a management context, yet vary in their ability to discriminate among stands in relation to old-growth structure.

The OGHI index appeared to do best in structurally distinguishing the different categories of stands (i.e., mature, early old-growth, and old-growth). All of the early old-growth sites had values similar to, but slightly lower than, those of older stands (except Huckleberry), despite their simpler disturbance histories (single vs. multiple disturbance events). This provides further support for the hypothesis that structural complexity can arise through multiple developmental pathways from a variety of disturbance and establishment histories (Franklin et al. 2002, Franklin et al. 2005).

Projected Future Densities of Douglas-fir

Projections of future Douglas-fir population densities are similar among the early old-growth stands and generally result in similar or lower Douglas-fir densities than in present-day well-developed (>400 year) old-growth forests, depending upon the mortality rate used in the calculations.

Using the lowest rates of mortality (0.28% or 0.5%/year) projected Douglas-fir densities in early old-growth stands 200 years in the future are similar to densities of current well-developed (>400 year) old-growth stands. Hence, these stands would have what is considered to be a characteristic and critical old-growth structure in the form of large and old Douglas-fir trees. These results are also inconsistent with the proposition advanced by some scientists that dense younger forests cannot develop old-growth characteristics without thinning (Tappeiner 2009). Stands originating from a single disturbance from ca.1650-1800 did establish in less than 100 years (Freund et al. In review) and generate Douglas-fir densities which are projected to be comparable to those in existing old-growth forests.

Using higher rates of mortality (0.9 and 1.1% annually) alter the projections of Douglas-fir densities in the early old-growth stands sampled in this study. Future densities of Douglas-fir are significantly lower than densities in existing well-developed (>400 year) stands with these higher rates (Table 12, Table 13). Van Mantgem et al. (2009) identified a general increase in mortality rates in older forests in their (van Mantgem et al. 2009). If the annual tree mortality rate were to increase from 0.9% to 1.1% per annum, Douglas-fir densities could decline by 80% when these forests reach 500 years of age. Future declines in Douglas-fir densities as a result of climate change may have impacts on wildlife habitat (Wilsey et al. 2013).

Influence of Site Productivity on Forest Development

It has been proposed that rates of stand development increase with site productivity on both theoretical (Franklin et al. 2002) and empirical bases (Larson et al. 2008, Gray et al. 2009). This study provides further evidence regarding this hypothesis. In this study the higher-productivity sites (those rated as Douglas-fir Site Class I based on McArdle and Myer 1961) generally had higher element scores using the OGHI index, despite the fact that these higher productivity sites are all from the younger (~200 year) cohort of stands.

Limitations of the data

The small sample size (9 stands) is the primary limitation of this data set. It was difficult to find stands of the desired age range that were also well-distributed geographically. The clustering of the 200-year-old forest stands and high-productivity sites in the Lewis River valley was an additional limitation. The historical distribution of fires in this region and the extensive logging of natural stands over the last 150 years both contribute to these limitations (Marlon et al. 2012). Thus, in this study I have captured only a limited amount of the variability in structural development that is associated with early old-growth forests.

Several other factors may have contributed to variability in structure. Although sites were selected based on age, many other variables, such as site productivity, severity of initiating disturbance, and limitations of seed source, may have contributed to variation in structural development. Some forest structural elements, such as large snags, have high variability and, hence, can be difficult to actually estimate based on small plots.

Improving Indices of Stand Development

Indices that combine multiple structural parameters can be useful as surrogates for ecological function (e.g., as wildlife habitat; Gray et al. 2009). However, most indices that are currently available use a few easily measured variables. Current indices could be enhanced with the inclusion of additional variables known to be associated with stand aging, such as additional measures of crown complexity and decadence (Spies and Franklin 1991, Van Pelt and Sillett 2008, Carey 2007). For example, the complexity of tree crowns has been documented as increasing with forest age (Van Pelt and Nadkarni 2004, Van Pelt and Sillett 2008). One or more measures of crown complexity associated with epicormic branch systems and decadent features (broken tops, reiterations, and size of limb systems) could be a useful metric as well as having a direct relationship with niche diversification (Carey et al. 1999, Carey 2009). A further possibility would be to rate dominant Douglas-firs as to whether the crowns still retain a model-conforming appearance (as defined by Van Pelt and Sillett 2008) or exhibit individualist crown forms (e.g., dead, broken, and reiterated tops) characteristic of many older (>400 year) trees.

I did not systematically sample crown form in this study because I only became aware that the vast majority of the crowns in the early old-growth Douglas-fir trees were still model-conforming (*sensu* Van Pelt and Sillett 2008) – i.e., free of extensive breakage with limited decadence and exhibiting whorl branch formation and distinct (but short) leaders. I did not expect this because of the high levels of decadence (top breakage and dead wood) and lack of apical dominance that is characteristic of Douglas-fir trees in stands that are only 1 to 2 centuries older than those that were sampled (Spies and Franklin 1991, Van Pelt and Sillett 2008). Two possible explanations for the contrast between the Douglas-fir crown conditions in the early old-growth stands that I sampled and the older (>400 year) old-growth stands are (1) high levels of crown decadence only develop after 350 years or (2) canopies of existing older (>400 year) trees experienced one or more widespread and severe disturbance event(s) that generated high levels of canopy decadence.

Some other easily measured aspects of decadence might also be considered for inclusion in old-growth indices. Examples include abundance of western-hemlock dwarf mistletoe (*Arceuthobium tsugense* subsp. *tsugense*) in western hemlock and abundance of Douglas-fir trees that have collapsed as a result of velvet top fungus (*Phaeolus schweinitzii*). Mistletoe-generated brooms are important structural features for a variety of animals and are largely a feature of old-growth forests. Velvet top fungus is a slow-developing rot that decays the heartwood at the butt (root crown and lower bole), eventually resulting in mechanical failure (breakage) and death. It is the most important single cause of death of old-growth Douglas-fir trees (Bible 2001) and affects many other species. Onset of mortality due to velvet top fungus first becomes apparent during the transition from mature to old forests (Franklin et al. 2002), thus making it a potential useful indicator of old-growth development. Although there was no systematic collection of data on occurrence of velvet-top-related mortality in this study, I would include it in any future study of stand development.

Management Implications

Conservation and restoration of structurally complex forest stands is emphasized in federal land management objectives within the Douglas-fir region (Franklin and Spies 1991, USDA and USDI 1994, Carey 2003, Larson et al. 2008). The structural data on early old-growth forests from this study provides forest managers with additional natural reference points for management. Common approaches to accelerating old-growth structures in young stands include: (1) increasing growth of live trees and the abundance of large trees; (2) increasing canopy complexity, including the number and size of epicormic branch structures; and (3) accelerating development of vertically-continuous canopies. The goal of such treatments generally is to improve habitat conditions for late-successional wildlife (Carey 2003, 2007).

Structural data from these early old-growth forests provide “intermediate” targets for managers, especially appropriate target densities and sizes for Douglas-fir trees as forests enter the “old-growth” stage. Managers seeking to manipulate dense, younger stands may find the range of variation among shade-tolerant trees and dead wood as useful guides for thinning, planting shade-tolerant species (western hemlock, western redcedar, Pacific yew), and managing for snags. In fact, one possible inference that could be made from this study is that many single-cohort mature and early old-growth forests are probably on trajectories that will produce suitable structural complexity and do not require active management. As the conservation of forest biodiversity remains of paramount importance to society and land management agencies it is imperative that management incorporate the variability found throughout the forest sere. Baseline data on natural forest stands, such as I present here, provide the scientific basis in managing for ecological values.

Conclusions

Structural analyses of forests early in development of old-growth attributes fill a significant gap in the knowledge base regarding Douglas-fir stand development. Structural conditions observed in the nine early old-growth forests sampled provides empirical support for the conceptual model of Douglas-fir stand development provided by Franklin et al. (2002). Appropriately, structural attributes of these early old-growth are intermediate between mature and well-developed (>400 year) old-growth forests but the early old-growth stands have many structural attributes characteristic of old-growth forests (e.g. tree size distributions, vertically continuous canopies, and large volumes of CWD).This study enhances the understanding of multiple developmental pathways because the structural conditions in these early old-growth stands have developed following a single initiating disturbance whereas many older stands have developed following multiple disturbances. The structural future of these early old-growth forests are stands similar to current older (>400 year) forests in terms of Douglas-fir tree densities unless there is an increase in mortality rates.

LITERATURE CITED

Acker, S.A., T.E. Sabin, L.M. Ganio, and W.A. McKee. 1998. Development of old-growth structure and timber volume growth trends in maturing Douglas-fir stands. Forest Ecology and Management 104:265-280.

Agee, J.K., 1991. Fire history of Douglas-Fir forests in the Pacific Northwest. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H. (Eds.), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. U.S. For. Serv. Gen. Tech. Rep. PNW- GTR-285

Agee, J.K. 1993. Fire Ecology of Pacific Northwest Forests. Island Press. Washington, DC. 493pp.

Agee, J.K. 1998. The landscape ecology of western forest fire regimes. Northwest Science 72:24-34

Agee, J.K., F. Krusemark. Forest fire regime of the Bull Run Watershed, Oregon. 2001. Northwest Science 75 :(3) 292-305.

Allen, G.S., and Owens, J.N. 1972. The life history of Douglas-fir. Environment Canada, Forestry Service.

Barnes, B. V., D. R. Zak, S. R. Denton, and S. H. Spurr. Forest ecology. 4th edition. 774 p. New York, NY: John Wiley & Sons.

Bible, K. J. 2001. Long-term patterns of Douglas-fir and western hemlock mortality in the western Cascade Mountains of Washington and Oregon. PhD. Dissertation. University of Washington, Seattle, Washington, USA.

Carey, A.B., M.L. Johnson. 1995. Small mammals in managed young, mature, and old-growth forests. Ecological Applications. 5: (2) 336-352.

Carey, A.B. 2003. Biocomplexity and restoration of biodiversity in temperate coniferous forest: inducing spatial heterogeneity with variable density thinning. Forestry. 76, 127-136.

Carey, A.B. 2007. Aiming for Healthy Forests: active, intentional management for multiple values. General Technical Report PNW-GTR-721, Pacific Northwest Research Station, U.S. Department of Agriculture, Forest Service, Portland, Oregon.

Carey, A.B. 2009. Maintaining biodiversity in managed forests. *In.* Spies and Duncan 2008. Old-growth in a new world: a Pacific Northwest icon reexamined. pp. 247-260. Springer-Verlag, Washington, D.C.

Cline, S. P., A. B. Berg, and H. M. Wight. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. Journal of Wildlife Management 44:773-786.

Gray, A.N., Monleaon, Vicente J., Spies, T.A. 2009. Characteristics of remnant old-growth forests in the northern Coast Range of Oregon and comparison to surrounding landscapes. Gen. Tech. Rep. PNW-GTR-790. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 45 p.

Foster, D.R., Orwig, D.A., McLachlan, J.S., 1996. Ecological and conservation insights from reconstructive studies of temperate old-growth forests. Trends Ecol. Evol. 11, 419–424.

Franklin, J.F. and Waring, R.H. 1980. Distinctive features of the northwestern coniferous forest: development, structure, and function. In 40th Annual Biological Colloquium, 1979, Proceedings. Oregon State University Press, Corvallis, OR. pp.59-85.

Franklin, J.F. and Hemstrom, M.A. 1981. Aspects of Succession in Coniferous Forests of the Pacific Northwest. *In*: Shugart, H.H. & Botkin, D.B. (Eds) Forest Succession: Concepts and Application, pp. 212-229. Springer-Verlag, New York, NY.

Franklin, J. F., and T. A. Spies. 1984. Characteristics of old growth stands. Pages 328–334 *in* New forests for a changing world. Proceedings of the 1983 SAF National Convention Society of American Foresters, Bethesda, Maryland, USA.

Franklin, J.F., and C.T. Dyrness. 1988. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis, OR.

Franklin, J.F., T.A. Spies, R. F, A.B. Carey, D.A. Thornburgh, D.R. Berg, D.B. Lindenmayer, M.E. Harmon, W.S. Keeton, D.C. Shaw, K. Bible, and J. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155:399-423.

Franklin, J.F. 2009. Conserving old-growth forests and attributes: reservation, restoration, and resilience. *In.* Spies and Duncan 2008. Old-growth in a new world: a Pacific Northwest icon reexamined. pp. 247-260. Springer-Verlag, Washington, D.C.

Freund, J.A. 2013. Multi-decadal establishment of single-cohort Douglas-fir forests of western Washington and Oregon. Canadian Journal of Forest Research. *In Review*

Halpern, C. B., and J. A. Lutz. 2013. Canopy closure exerts weak controls on understory dynamics: a 30-year study of overstory-understory interactions. Ecological Monographs. doi.org/10.1890/12-1696.1

Harmon M E and Sexton J 1996 Guidelines for measurements of woody detritus in forest ecosystems *US LTER Publication No.20* US LTER Network Office, University of Washington, Seattle, WA

Hemstrom, M.A., Franklin, J.F. 1982. Fire and other disturbances of the forests of Mount Rainier National Park. Quaternary Research. 18: 32-51.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs. 54: 187-212.

Huff, M.H. 1995. Forest Age Structure and Development Following Wildfires in the Western Olympic Mountains, Washington. Ecological Applications 5:471-483

Isaac, L.A. 1940. Vegetative succession following logging in the Douglas-fir region with special reference to fire. Journal of Forestry 38: 716-21.

Isaac, L.A. 1949. Better Douglas-fir forests from better seed. University of Washington Press, Seattle, Washington. 64 p.

Keeton, W.S. and J.F. Franklin. 2005. Do remnant old-growth trees accelerate rates of succession in mature Douglas-fir forests? Ecological Monographs 75:103-118.

Kimmins, J. P. 2004. Forest ecology. 3rd edition. 611 p. Upper Saddle River, NJ: Prentice Hall.

Larson, A. J., Franklin, J.F. 2005. Patterns of conifer tree regeneration following an autumn wildfire event in the western Oregon Cascade Range, USA. Forest Ecology and Management. 218, 25-36

Larson, A. J., Lutz, J. A, Gersonde, R. F., Franklin, J. F., & Hietpas, F. F. 2008. Potential site productivity influences the rate of forest structural development. Ecological Applications, 18(4), 899–910.

Larson, A.J., Churchill, D.C., 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. Forest Ecology and Management. 267, 74–92.

Lindenmayer, David. 2009. Forest pattern and ecological process. 308 p. Collingwood, Australia: CSIRO Publishing.

Lutz, J.A., and C.B. Halpern. 2006. Tree mortality during early forest development: a long-term study of rates, causes and consequences. Ecological Monographs. 76, 257-75.

Lutz, J.A., Larson, A.J., Swanson, M.E., Freund, J.A., 2012. Ecological importance of large-diameter trees in a temperate mixed-conifer forest. PLoS ONE 7, e36131.

Lutz, J.A., Larson, A.J., Freund, J.A., Swanson, M.E., Bible, K.J. 2013. The importance of large-diameter trees to forest structural heterogeneity. PLoS ONE, In review.

Marlon, Jennifer R., Patrick J. Bartlein, Daniel G. Gavin, Colin J. Long, R. Scott Anderson, Christy E. Briles, Kendrick J. Brown, Daniele Colombaroli, Douglas J. Hallett, Mitchell J. Power, Elizabeth A. Scharf, and Megan K. Walsh. 2012. Long term perspective on wildfires in the western USA. Proc. Nat. Acad. Sci. (on line at www.pnas.org/cgi/doi/10.1073/pnas.1112839109).

McArdle, R.E., W.H. Meyer, D. Bruce. 1961. The yield of Douglas-fir in the Pacific Northwest. Technical Bulletin No. 201. United States Department of Agriculture, Washington, D.C. Reprinted by Oregon State University Book Stores Inc, 1975.

Minore D. 1972. Comparative autecological characteristics of northwestern tree species: a literature review. USDA Forest Service Pacific Northwest Forest and Range Experiment Station General Technical Report PNW 87.

Oliver, C.D., Larson, B.C., 1996. Forest Stand Dynamics. McGraw- Hill, New York, 520 pp.

Pabst, R. 2005. Methodology for developing the old-growth index. Appendix 1. In: Franklin, J.F.; Spies, T.; Van Pelt, R. Definition and inventory of old-growth forests on DNR-managed state lands. Olympia, WA: Washington State Department of Natural Resources.

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. Canadian Journal of Forest Research. 32, 1232-1243.

R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Spies, T.A., Franklin, J.F., Thomas, T.B., 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69, 1689–1702.

Spies, T. A., Franklin, J. F., & Klopsch, M. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. Canadian Journal of Forest Research, 20(5), 649-658.

Spies, T.A., Franklin, J.F. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H. (Eds.), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. USDA Forest Service General Technical Report PNW-GTR-285, pp. 91–110.

Spies, T.A., Franklin, J.F., 1996. The diversity and maintenance of old-growth forests. In: Szaro, R.C., Johnson, D.W. (Eds.), Biodiversity in Managed Landscapes: Theory and Practice. Oxford, New York, pp. 296–314.

Spies, T.A. 2009. Science of old growth, or a journey into wonderland. *In.* Spies and Duncan 2008. Old-growth in a new world: a Pacific Northwest icon reexamined. pp. 247-260. Springer-Verlag, Washington, D.C.

Stewart, G.H. 1986. Population Dynamics of a Montane Conifer Forest, Western Cascade Range, Oregon, USA. Ecology 67:534-544.

Tappeiner, J.C. 2009. Managing young stands to develop old-growth characteristics. In. Spies and Duncan 2008. Old-growth in a new world: a Pacific Northwest icon reexamined. pp. 247-260. Springer-Verlag, Washington, D.C.

Tepley, A. J., Swanson, F. J., & Spies, T. A. 2013. Fire-Mediated Pathways of Stand Development in Douglas-Fir/Western Hemlock Forests of the Pacific Northwest, USA. Ecology. 94: 1729-1743.

Turner, M.G., Romme, W.H., Gardner, R.H., Hargrove, W.W. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs. 67: 411-433.

USDA and USDI. 1994. Record of decision on management of the habitat for late successional and old-growth forest related species within the range of the northern spotted owl (Northwest Forest Plan). U.S. Department of Agriculture and U.S. Department of the Interior, Portland, Oregon, USA.

van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule´ , P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the western United States. Science 323, 521–524.

Van Pelt, R. 2007. Identifying Mature and Old Forests in Western Washington. Washington State Department of Natural Resources, Olympia, WA. 104 p.

Van Pelt, R., J.F. Franklin. 1999. Response of understory trees to experimental gaps in old-growth Douglas-fir forests. Ecological Applications. 9, 504-512.

Van Pelt, R., N.M. Nadkarni. 2004 Development of canopy structure in *Pseudotsuga menziesii* forests in the southern Washington Cascades. Forest Science. 50(3) 326-341.

Van Pelt, R., S.C. Sillett 2008. Crown development of coastal *Pseudotsuga menziesii* including a conceptual model for tall conifers. Ecological Monographs. 78: 283-311.

Waring, R. H., & Franklin, J. F. 1979. Evergreen coniferous forests of the Pacific Northwest. Science, 204, 1380-1386.

Winter, L.E, L.B. Brubaker, J.F. Franklin, E.A. Miller, and D.Q. Dewitt. 2002. Initiation of an old-growth Douglas-fir stand in the Pacific Northwest a reconstruction from tree ring records. Canadian Journal of Forest Research 32:1039-1056.

Yamaguchi, D.K. 1986. The development of old-growth Douglas-fir forests northeast of Mount St. Helens, Washington, following and A.D. 1480 eruption. PhD Dissertation, University of Washington.

Zenner, E.K. 2005. Development of tree size distributions in Douglas-fir forests under differing disturbance regimes. Ecological Applications 15:701-714.

Table 3.1. Site characteristics for the nine early old-growth stands.

Site	**Lat.**	**Long.**	**Elev. (m)**	**Aspect**	**Plant Association**	**Precipitation (mm)**				**Temperature C°**	
						Annual	**July Mean**	**Jan Mean**	**Growing Season**	**July max**	**Jan min**
Olympic National Park, WA											
Sol Duc	47.95	-123.81	687	S	TSHE/POMU/OXOR	3622.9	60.81	483.18	80.03	20.36	-1.23
Cedar River Watershed, WA											
Huckleberry	47.31	-121.52	799	NE	ABAM/VAAL	2584.53	62.44	397.27	74.7	21.05	-2.97
Mt. Rainier National Park, WA											
Ohanapecosh	46.74	-121.55	670	SW	TSHE/ACCI/ACTR	1974.74	34.77	305.64	46.61	23.9	-3.96
Gifford Pinchot National Forest, WA											
Cedar Flats	46.11	-122.01	400	NE	TSHE/POMU/OXOR	2972.54	44.78	454.73	64.56	25.26	-1.94
Drift Creek	46.03	-122.09	324	SE	TSHE/POMU/OXOR	2990.7	45.81	455.34	65.98	24.67	-1.29
Osprey	46.03	-122.08	318	W	TSHE/POMU/OXOR	2995.22	45.91	456.44	66.11	24.99	-1.14
Skynard	46.02	-122.08	379	W	TSHE/POMU/OXOR	3339.54	50.68	525.75	71.18	24.08	-1.44
Willamette National Forest, OR											
Bagby	44.94	-122.17	650	E	TSHE/RHMA/BENE	2123.28	31.1	300.92	51.74	24.18	-2.42
Breitenbush	44.79	-121.09	760	W	TSHE/RHMA/BENE	1997.92	32.72	304.3	45.59	24.72	-3.85

Note: Plant associations from Franklin and Dyrness 1988. Precipitation and temperature data obtained from PRISM database. Growing season calculated from June through September.

Table 3.2. Live tree structure variables for primary tree species ≥ 5 cm dbh.

		Max Age	Basal Area	Trees /	Tree DBH (cm)			SE
Site	**Species**	**(years)**	**($m^2 ha^{-1}$)**	**ha**	**Mean**	**Min**	**Max**	**(DBH)**
Osprey	Douglas-fir	190	65.3	85	93.6	23.3	168.6	3.29
	western hemlock		9.6	114	28.0	5.2	83.1	1.46
	western redcedar		0.0	0	n/a	n/a	n/a	n/a
	Other species		3.8	30	35.6	7.0	85.7	3.39
	Totals		**78.7**	**230**				
Cedar Flats	Douglas-fir	191	50	61	98.3	33.8	166.1	2.94
	western hemlock		10.5	173	21.5	5.0	90.1	1.22
	western redcedar		16.5	44	51.9	6.7	207.2	6.13
	Other species		1.3	29	16.8	5.1	116.5	3.27
	Totals		**78.3**	**310**				
Drift Creek	Douglas-fir	193	67.4	86	91.9	16.4	176.9	3.74
	western hemlock		10.4	52	40.2	5.3	120.4	3.84
	western redcedar		2.9	5	71.0	26.9	127.4	14.91
	Other species		3.0	16	34.7	5.9	120.2	7.26
	Totals		**83.7**	**161**				
Skynard	Douglas-fir	193	56.1	65	101.4	19.7	163.8	3.02
	western hemlock		9.2	108	29.1	5.2	66.3	1.33
	western redcedar		0.4	5	30.3	14	47.5	5.72
	Other species		2.9	29	30.8	6.8	80.1	2.94
	Totals		**68.6**	**207**				
Ohanapecosh	Douglas-fir	296	40.7	71	81.44	35.1	155.6	2.67
	western hemlock		22.2	142	34.98	5.1	104.9	2.01
	western redcedar		21.9	60	61.27	7.2	133.3	3.58
	Other species		0.9	9	20.53	5.0	115.3	9.57
	Total		**85.9**	**287**				
Bagby	Douglas-fir	297	57.5	92	87.56	54.2	129.1	1.52
	western hemlock		18.6	213	25.83	5.0	97.9	1.32
	western redcedar		10.8	34	59.22	6.5	117.7	3.97
	Other species		0.49	8	19.78	5.7	66.8	6.33
	Total		**87.4**	**347**				
Sol Duc	Douglas-fir	317	85.6	117	90.97	31.8	198	2.68
	western hemlock		35.2	255	30.92	5.0	121.9	1.62
	western redcedar		0.00	0.00	n/a	n/a	n/a	n/a
	Other species		0.00	0.00	n/a	n/a	n/a	n/a
	Total		**120.9**	**373**				
Breitenbush	Douglas-fir	326	84.5	107	95.68	35.2	166.4	2.58
	western hemlock		22.1	195	32.74	5.0	102.2	1.27
	western redcedar		3.0	15	40.66	9.7	117.0	6.38
	Other species		0.5	20	15.01	5.0	58.1	2.58
	Total		**110.2**	**338**				

Huckleberry	Douglas-fir	328	23.24	74	61.94	30.0	98.9	1.49
	western hemlock		54.74	287	45.93	6.4	96.2	1.06
	western redcedar		13.56	78	42.71	9.0	112.5	19.86
	Other species		0.78	25	14.02	5.0	63.7	14.4
	Total		**92.32**	**464**				

Note: Other species includes pacific silver fir, grand fir, pacific yew, bigleaf maple, pacific dogwood, black cottonwood.

Table 3.3. Height characteristics for the live trees ≥ 5 cm dbh

Site	Species	Mean Height (m)	(SD)	Mean Crown Length (m)	(SD)	Mean Epicormic Height (m)	(SD)
Osprey							
	Douglas-fir	62.5	13.0	16.2	15.4	22.5	7.4
	western hemlock	23.7	11.9	4.2	9.2	n/a	n/a
	western redcedar	n/a	n/a	n/a	n/a	n/a	n/a
Cedar Flats							
	Douglas-fir	60.1	7.5	27.6	7.9	21.5	6.8
	western hemlock	17.5	12.4	10.3	8.9	n/a	n/a
	western redcedar	28.56	15.2	19.9	12.4	n/a	n/a
Drift Creek							
	Douglas-fir	54.5	15.3	17.6	16.6	18.0	6.5
	western hemlock	29.1	15.4	5.2	11.0	n/a	n/a
	western redcedar	34.8	22.1	23.3	21.4	n/a	n/a
Skynard							
	Douglas-fir	66.1	11.1	25.6	12.8	25.7	5.6
	western hemlock	21.5	12.4	7.9	10.4	n/a	n/a
	western redcedar	22.7	11.0	8.4	10.8	n/a	n/a
Ohanapecosh							
	Douglas-fir	52.7	12.3	18.6	7.4	19.9	12.0
	western hemlock	34.2	17.4	21.8	11.3	n/a	n/a
	western redcedar	40.3	11.9	23.2	10.6	n/a	n/a
Bagby							
	Douglas-fir	60.5	7.7	12.4	14.0	25.3	7.0
	western hemlock	28.2	7.7	18.4	13.9	n/a	n/a
	western redcedar	32.1	11.9	18.4	8.9	n/a	n/a
Breitenbush							
	Douglas-fir	55.4	11.5	22.4	10.0	19	8.3
	western hemlock	26.9	14.6	19.7	12.7	n/a	n/a
	western redcedar	28.0	8.4	21.1	8.8	n/a	n/a
Sol Duc							
	Douglas-fir	55.3	9.4	17.8	8.0	24.9	5.9
	western hemlock	31.4	18.37	21.3	15.2	n/a	n/a
	western redcedar	n/a	n/a	n/a	n/a	n/a	n/a
Huckleberry							
	Douglas-fir	37.3	5.9	12.9	9.3	21.8	4.3
	western hemlock	33.6	11.0	15.7	5.5	n/a	n/a
	western redcedar	30.0	10.1	14	8.4	n/a	n/a

Table 3.4. Characteristics of snags ≥ 10 cm dbh and ≥ 1.37 m in height.

Site	Snags/ha	Snags/ha, (>50 cm dbh)	Snag BA (m^2 ha^{-1})	Snag volume (m^3 ha^{-1})	Snag height, mean (m)	Snag height, SD (m)
Osprey	74	32	20.7	140.2	12.7	13.6
Cedar Flats	60	25	17.6	66.5	7.7	7.3
Drift Creek	34	20	13.6	42.6	9.3	9.6
Skynard	92	18	14.8	46.3	6.5	7.8
Ohanapecosh	89	30	21.5	129.7	10.5	11.4
Bagby	112	37	20.1	86.4	8.6	8.9
Sol Duc	85	30	16.9	95.7	12.5	1.2
Breitenbush	39	15	8.2	46.9	10.0	12.9

Table 3.5. Characteristics of coarse wood ≥ 10 cm at intercept diameter.

					Volume (m^3 ha^{-1}) of logs by decay class				
Site	**Mean diameter (cm)**	**Volume (m^3 ha^{-1})**	**Logs /ha**	**Logs/ha (>50 cm dbh)**	**1**	**2**	**3**	**4**	**5**
Osprey	35.9	356.7	20	24	66.0	104.0	70.6	94.0	22.1
Cedar Flats	42.4	584.3	99	27	5.7	379.0	96.6	88.4	14.4
Drift Creek	38.6	236.0	61	13	15.0	144.0	51.5	17.9	6.9
Skynard	30.1	280.9	117	12	1.3	4.1	99.4	75.6	165.4
Ohanapecosh	36.1	240.5	78	14	39.2	28.8	69.6	19.3	22.9
Bagby	34.6	294.1	108	13	33.9	28.2	129.4	40.3	4.9
Sol Duc	25.0	186.1	98	4	12.4	44.0	78.1	13.6	6.9
Breitenbush	34.3	172.3	57	9	64.3	29.4	37.1	5.5	2.3
Huckleberry	28.1	182.3	100	3	20.4	35.3	68.7	11.0	7.1
Total					258.2	797.9	700.9	365.8	252.8

Table 3.6. Principal components analysis of the nine sites and their 17 structural variables.

Variable	**PC1**	**PC2**
Total basal area	0.173	-0.051
Basal area of Douglas-fir	-0.155	**-0.303**
Basal area of western hemlock	**0.548**	0.104
Basal area of western redcedar	0.022	-0.133
Density of Douglas-fir	0.104	-0.154
Density of shade-tolerant tree species	**0.406**	**0.387**
Standard deviation of dbh (all species)	-0.205	-0.072
Density of snags >50 cm dbh	-0.072	0.282
Mean dbh of live trees	0.010	-0.139
Volume of logs	**-0.353**	**0.413**
Volume of snags	-0.210	**0.438**
Density of trees >100 cm dbh	**-0.360**	-0.283
Age range of Douglas-fir	0.201	**-0.374**
SD of Douglas-fir ages	0.054	-0.013
Mean Douglas-fir crown depth	-0.269	0.027
SD of Douglas-fir crown depth	0.050	-0.109
SD of western hemlock height	0.056	-0.017

Note: Tree density for all stems ≥ 5 cm dbh. Values represent loadings. Cumulative proportion of variance explained by the first two principal components = 62%.

Table 3.7. Element scores and ranking of the nine sites using the Iog index of old-growth (Acker et al. 1998).

SITE	Max age (yr)	Iog_SD_DBH	Iog_TPH_>100 cm	Iog_Mean_DBH	Iog_TPH_>5 cm	Iog
Osprey	190	25	25	25	25	**100**
Cedar Flats	191	25	25	25	25	**100**
Drift Creek	193	25	25	25	25	**100**
Skynard	193	25	25	25	25	**100**
Ohanapecosh	296	25	25	25	25	**100**
Bagby	297	25	25	25	25	**100**
Sol Duc	317	25	25	25	25	**100**
Breitenbush	326	25	25	25	25	**100**
Huckleberry	328	9	6	25	24	**65**

Table 3.8. Element scores and ranking of the nine sites using the Old Growth Habitat Index (Franklin et al. 2005).

Site	Oldest Canopy Dominant	Big tree score	Large Snag score	Log Volume score	DDI	Age Score	Standard OGHI	Modified OGHI	Weigted OGHI
Osprey	190	83.9	82.9	76.6	51.7	76.0	74.2	73.8	71.5
Cedar Flats	191	85.3	60.4	86.6	50.3	76.4	71.8	70.6	70.5
Drift Creek	192	86.1	41.7	65.7	42.0	76.8	62.4	58.8	60.8
Skynard	193	83.9	41.7	70.7	45.2	77.2	63.7	60.3	62.3
Ohanapecosh	296	75.3	60.4	71.5	37.2	87.6	66.4	61.1	59.8
Bagby	297	61.8	82.9	72.2	38.4	87.7	68.6	63.8	59.3
Sol Duc	317	96.1	79.1	56.7	37.8	89.3	71.8	67.4	65.8
Breitenbush	326	89.7	50.0	58.6	64.4	90.0	70.5	65.6	68.9
Huckleberry	328	3.1	60.4	56.3	23.9	90.2	46.8	35.9	29.7
								Average	
		73.9	62.1	68.3	43.5	83.5	66.2	61.9	61.0

Table 3.9. Means and 95% confidence intervals for 8 structural variables from early old-growth and old-growth stands. Old-growth data come from Spies and Franklin 1991.

Variable	Early Old-growth (This Study)		Spies and Franklin (1991)		Overlap
Tree density (trees/ha)	302	(231-373)	448	(394-511)	No
Mean Douglas-fir density (trees/ha)	84	(70-90)	63	(49-79)	Yes
Shade tolerant density (trees/ha)	171	(113-229)	270	(199-353)	Yes
Density of Large trees (> 100 cm) dbh	34	(22-45)	19	(16-23)	Yes
Mean basal area (m^2 ha^{-1})	90	(77-102)	69	(64-74)	No
Standard deviation of dbh (cm)	36	(31-42)	32	(30-34)	Yes
Snag volume (m^3 ha^{-1})	78	(183-464)	159	(128-199)	Yes
Log volume (m^3 ha^{-1})	281	(136-377)	266	(219-324)	Yes

Table 3.10. ANOVA results for structural element scores of multiple age classes of forest using the OGHI method.

Group Name	N	Mean	Standard Deviation	SEM
Early old-growth (this study)	9	66.9	9.3	3.2
400-600 (Spies and Franklin 1991)	16	80.3	7.2	1.8
40-150 (Spies and Franklin 1991)	27	37.3	8.0	1.5
200-300 (Spies and Franklin 1991)	9	64.0	11.8	4.1

Source of Variation	DF	SS	MS	F	P
Age class	3	19403.19	6467.73	86.795	<0.001
Residual error	53	3949.395	74.517		
Total	56	23352.59			

Table 3.11 Holms-Sidak multiple comparison procedure for ANOVAs of age class structural element scores.

Comparison	**Diff of Means**	**t**	**Unadjusted P**	**Critical Level**
Early old-growth (this study) vs. 40-150 years	29.647	8.495	**<0.001**	0.01
Early old-growth (this study)vs. 400-600 years	13.341	3.53	**<0.001**	0.025
Early old-growth (this study) vs. 190-320 years	2.889	0.669	0.506	0.05

Note: Comparisons are made with data from Spies and Franklin 1991. Significant results are in bold. Comparisons made using values calculated for the standard variant of the OGHI.

Table 3.12. Projections of early old-growth Douglas-fir density at 100, 200, and 300 years in the future.

	Current Douglas-fir Density	**Projected Douglas-fir Density**											
		100 years				**200 years**				**300 years**			
Annual Mortality Rate		**0.28%**	**0.50%**	**0.90%**	**1.10%**	**0.28%**	**0.50%**	**0.90%**	**1.10%**	**0.28%**	**0.50%**	**0.90%**	**1.10%**
Osprey	85	64	51	34	28	49	31	14	9	37	19	6	3
Cedar Flats	62	47	38	25	21	35	23	10	7	27	14	4	2
Drift Creek	87	66	53	35	29	50	32	14	10	38	19	6	3
Skynard	65	49	39	26	22	37	24	11	7	28	14	4	2
Ohanapecosh	72	54	44	29	24	41	26	12	8	31	16	5	3
Bagby	93	70	56	38	31	53	34	15	10	40	21	6	3
Sol Duc	118	89	71	48	39	67	43	19	13	51	26	8	4
Breitenbush	108	82	65	44	36	62	40	18	12	47	24	7	4
Huckleberry	74	56	45	30	24	42	27	12	8	32	16	5	3
Mean (CI)		64 ± 11	51 ± 8	34 ± 5	28 ± 4	48 ± 8	31 ± 5	13 ± 2	9 ± 1	37 ± 6	18 ± 3	5 ± 1	3 ± 0.5
Sig. Different from Old-growth density		**P= 0.008**	P=0.142	P=0.593	P=0.205	P=0.282	P=0.385	**P=0.005**	**P=< 0.001**	P=0.481	**P=0.019**	**P=< 0.001**	**P=< 0.001**

Note: Mortality rates from Spies et al. 1990, Debell and Franklin 1987, and Bible 2001. Highest mortality rate represents potential increase in annual mortality (van Mantgem et al. 2009). Bold p values indicate significant difference.

Table 3.13. Douglas-fir density from 13 old-growth forests. Douglas-fir density data come from Spies and Franklin 1991 and the Wind River Forest Dynamics Plot.

Area	**Stand**	**Age**	**PSME/density**
2_25	25	450	44.02
2_27	27	450	44.90
2_30	30	450	84.93
2_98	98	450	32.37
3_16	16	500	60.31
3_17	17	500	43.28
3_2	2	500	30.00
3_32	32	600	62.49
4_1	1	500	20.01
4_3	3	500	10.01
Wind River	WFDP	500	21.90
4_18	18	550	50.79
3_3	3	600	11.09
Mean density (95% CI)			**39.7 (± 13.19)**

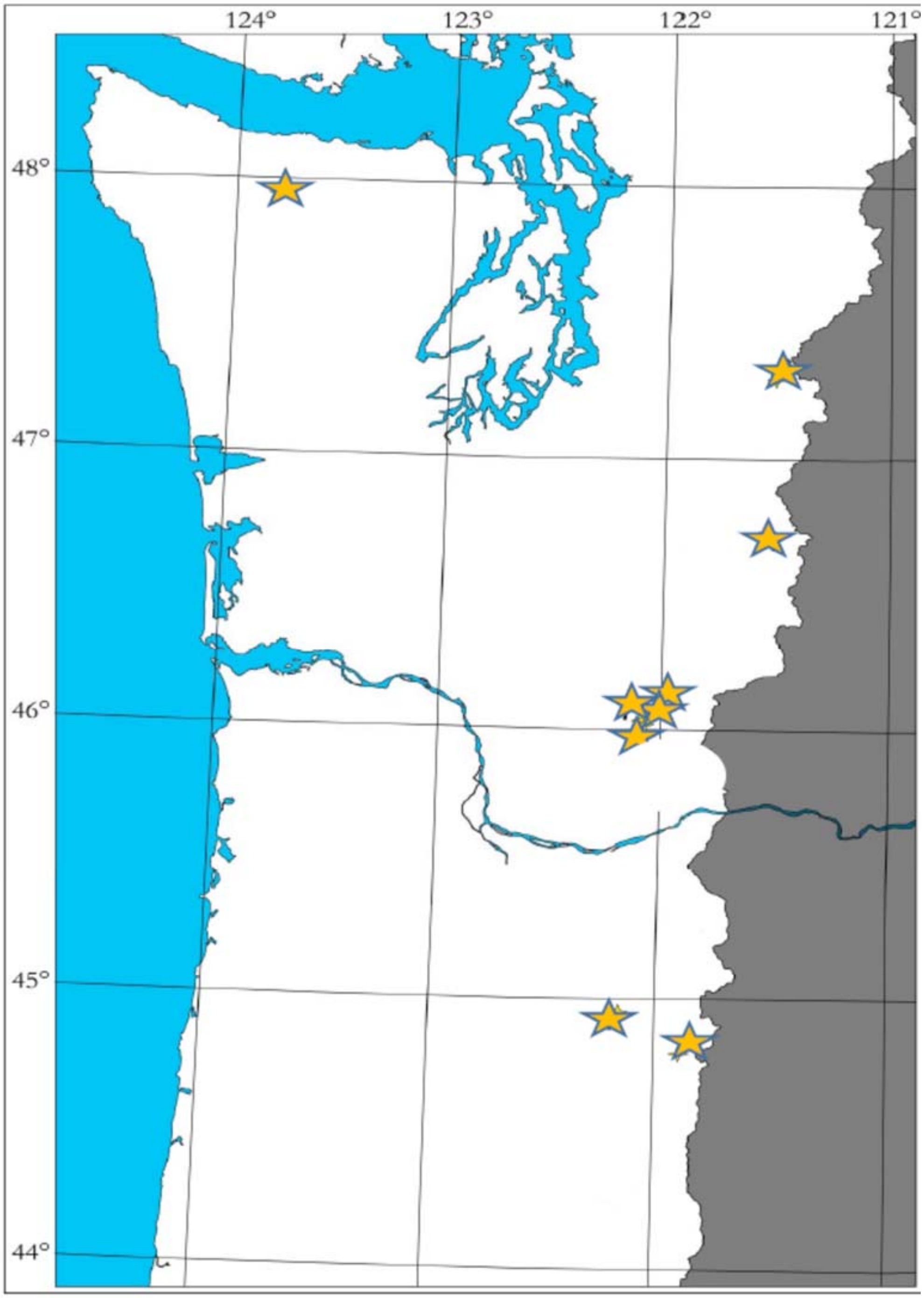


Figure 3.1. Map of western Washington and Oregon. Gold stars indicate early old-growth study sites. Dark grey region indicates the crest of the Cascade Mountains.

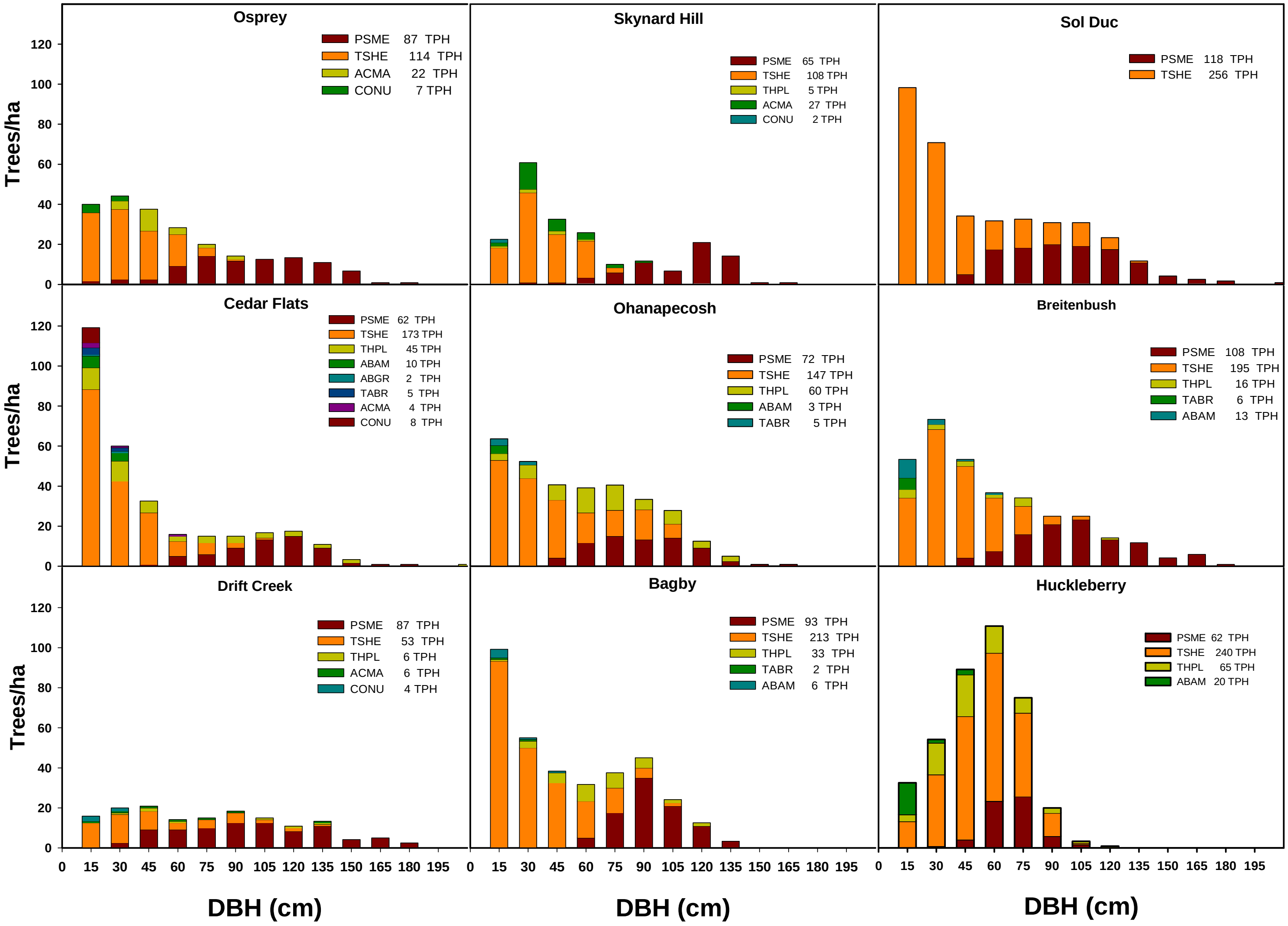


Figure 3.2. Species' diameter distributions among study sites separated into 15 cm bins for live trees ≥ 5 cm dbh.

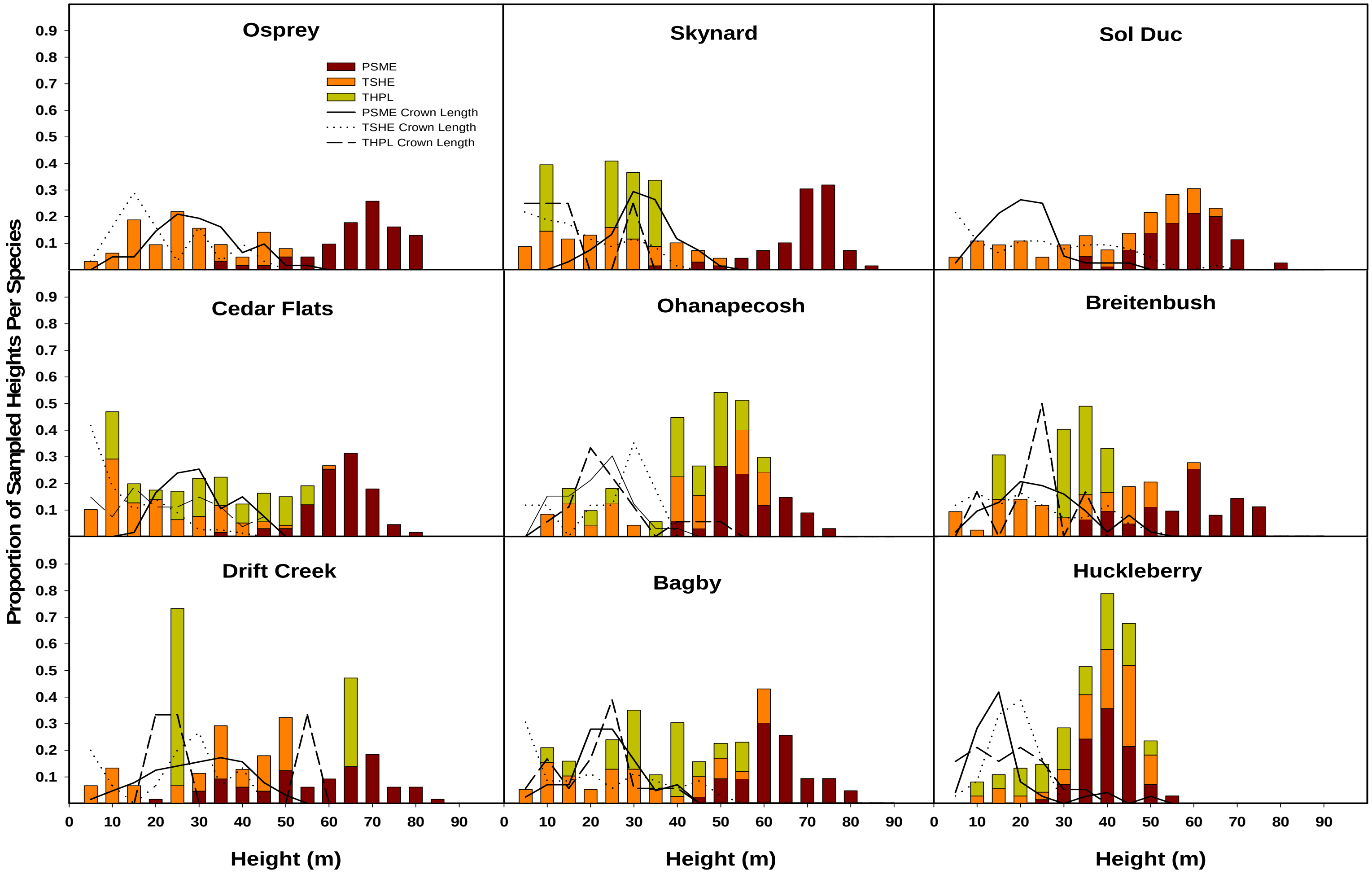


Figure 3.3. Height distributions of Douglas-fir, western hemlock, and western redcedar. Red bars represent the distribution of Douglas-fir heights. Orange bars represent distribution of western hemlock heights. Green bars represent distribution of western redcedar heights. Lines indicate distributions of crown lengths for each of the three species.

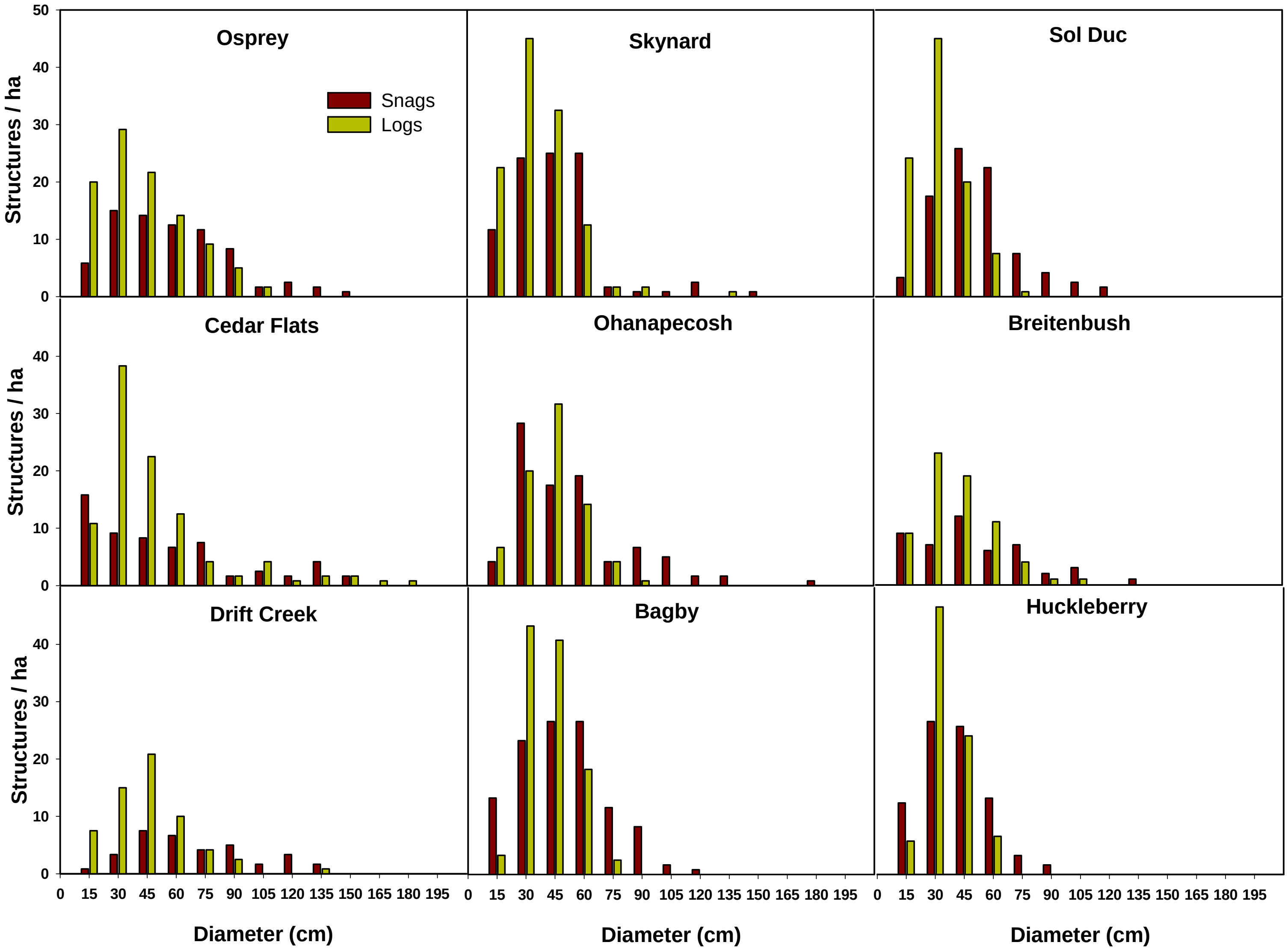


Figure 3.4. Snag and log size distributions in 15cm bins for each sample site. Black bars indicate the size distribution of the snags. Grey bars indicate the size distribution of the logs.

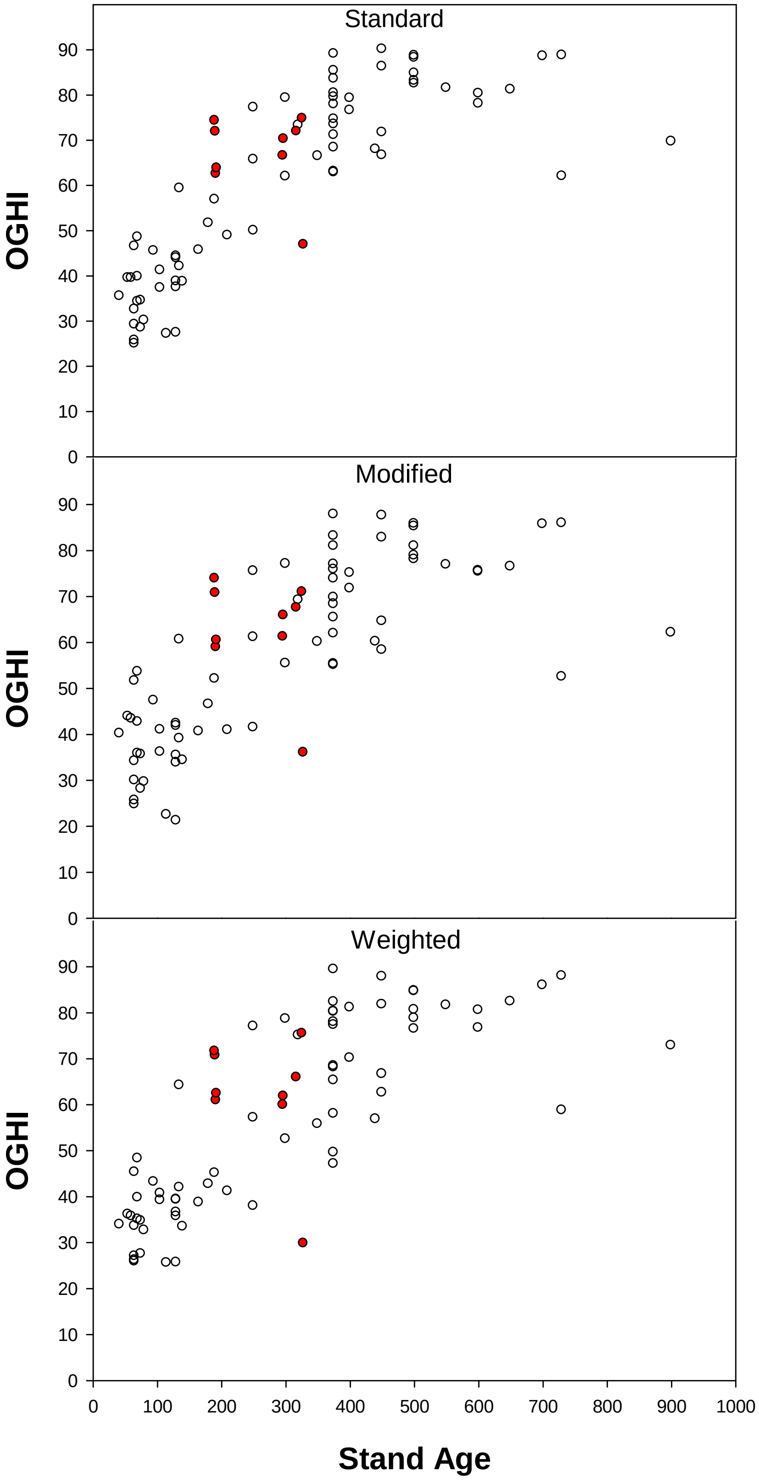


Figure 3.5 Stand age versus index score using the standard, modified, and weighted Old Growth Habitat Index (OGHI). Open circles represent data from Spies and Franklin (1991) and filled red circles represent early old-growth sites from this study.

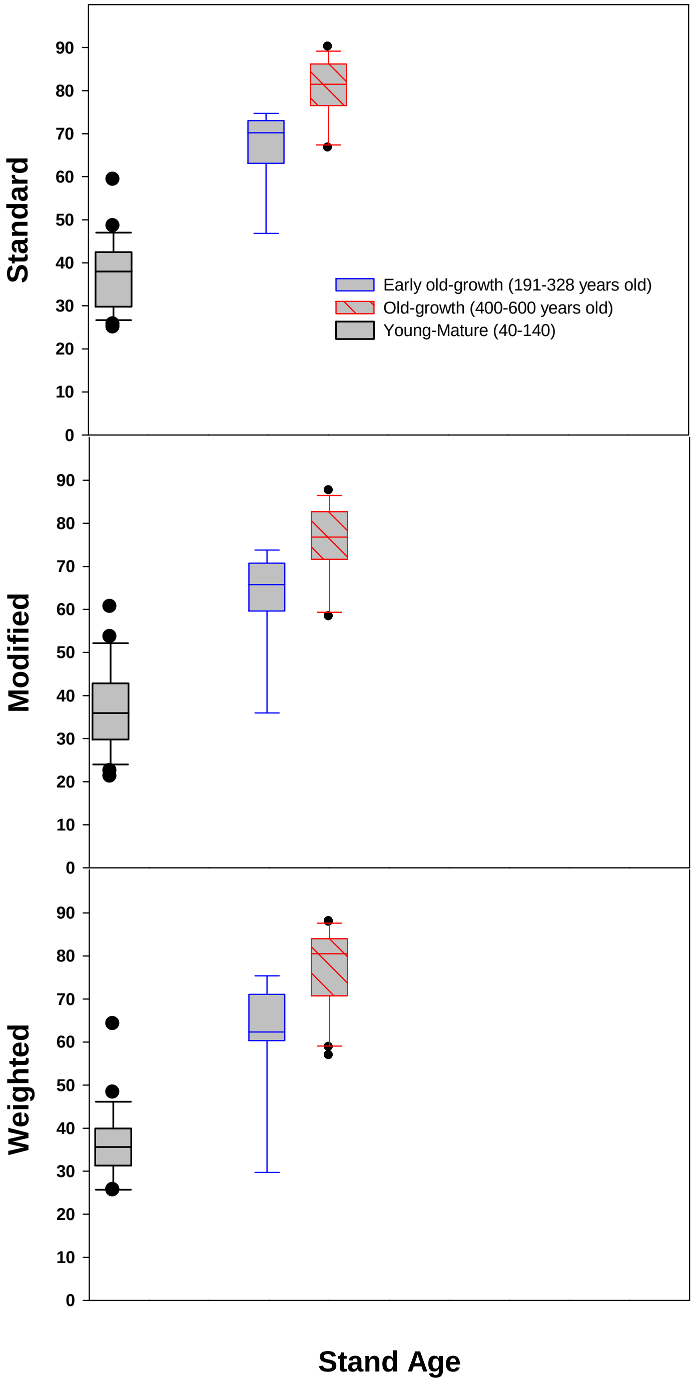


Figure 3.6. Box plots of the range of standard, modified, and weighted OGHI scores for early old-growth sites and stands from Franklin et al. 2005. Young-mature stands are between 40-140 years old and old-growth stands are between 400-600 years old.

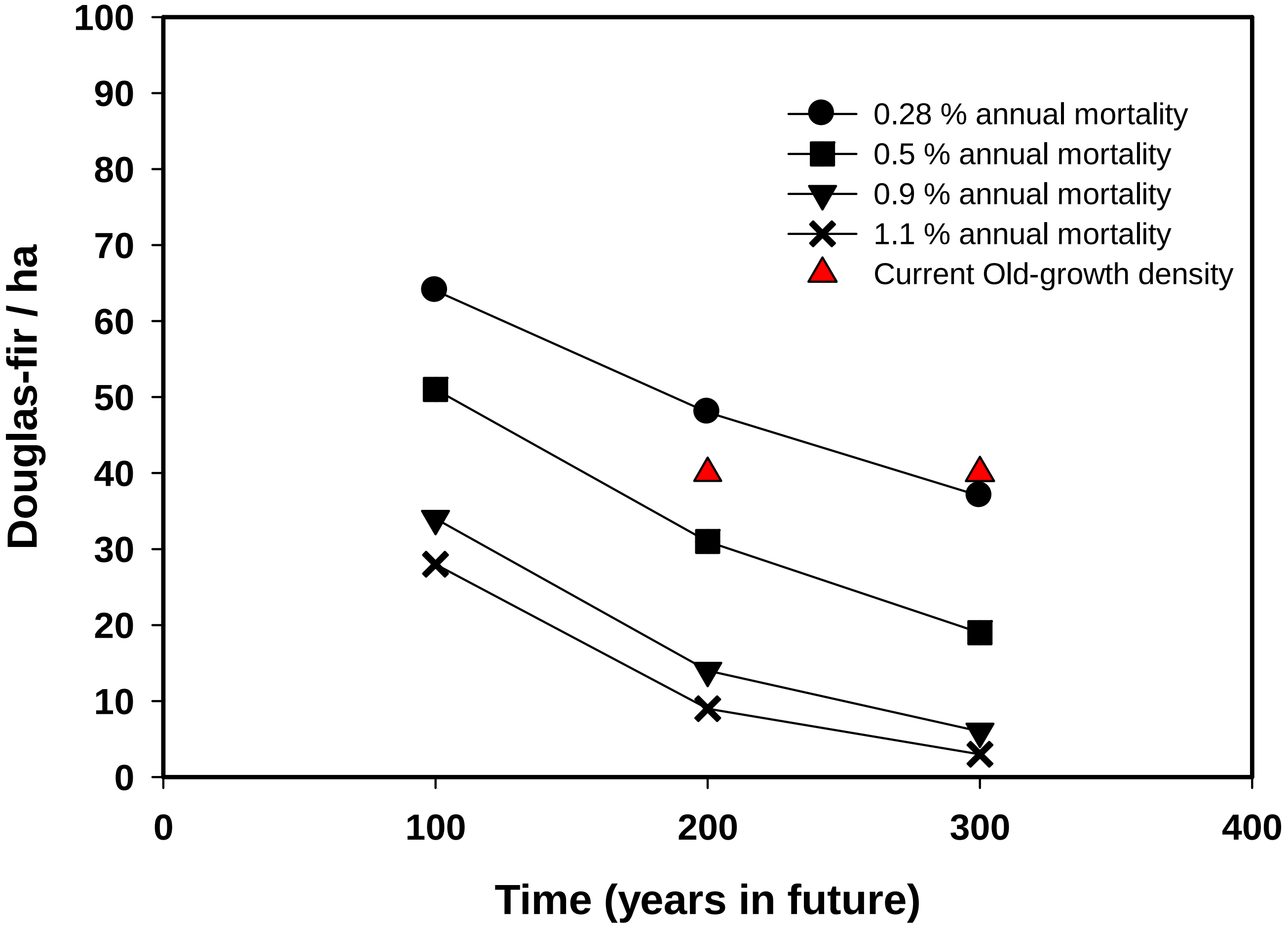


Figure 3.7. Projected Douglas-fir densities for 9 early old-growth sites. Lines represent Douglas-fir densities at 100, 200, 300 years in the future based on 4 rates of annual mortality. The 0.28% annual mortality is used from Spies et al. 1990. The 0.5%-0.9% annual mortality rates are based on Bible 2001. The 1.1% annual mortality rate was subjectively selected to represent a potential future increase in mortality rates (van Mantgem et al. 2009). Red triangles represent the mean density of 13 old-growth forests.

CHAPTER 4: CONCLUSIONS

Tree establishment and stand structural development are and will remain focal areas for research on succession in long-lived forest ecosystems. My dissertation research provides valuable and significant new information on aspects of two important but inadequately understood stages of the Douglas-fir sere. The rates of post-disturbance tree regeneration and canopy closure following wildfire elucidated in this study are directly linked and are important aspects of the sere because of early seral ecosystems and structural development in the young closed-canopy forest. Similarly, the structural analysis of early old-growth forests enhances the conceptual understanding of the Douglas-fir sere, including the important transition from the more simply structured mature to the complex old forest. Inferences can also be drawn about the probable nature of future old-growth forests and about the importance of young stand management.

Findings from both elements of the dissertation also highlight some useful lines for further research on the Douglas-fir sere.

Patterns of tree establishment

Rates of tree establishment appear to be remarkably similar in Douglas-fir-dominated forests, exhibiting a consistent and extended period between the initiating disturbance and tree canopy closure. The developmental pattern is clearly one that is always multi-decadal in duration, although the precise details vary with essentially each forest sampled in this study. This variability involves relatively slight differences in the tails and slope of the age distribution. This multi-decadal pattern of establishment in single cohort stands is nearly identical with what was observed in an investigation of Douglas-fir regeneration following multiple, mixed-severity fires (Tepley et al. 2013). These observations suggest that there is a, model of Douglas-fir establishment that is largely independent of the dominant disturbance regime. An important inference is that the multi-decadal period of establishment allows for a significant period during which the diverse-plant-life-form early seral ecosystem can develop and mature on disturbed sites. There are probably no other moist temperate forests ecosystems in the world that incorporate such an extended early seral period before tree canopy closure is re-established.

The observations and conventional wisdom of the early 20th century scientists are generally not supported by results from this study, although – in their defense – it must be acknowledged that they were not focused on the duration of tree establishment or rate of development of closed canopies. Their interests were in determining whether there was sufficient regeneration to eventually produce a fully stocked forest. The concept of greatly extended periods of tree establishment (greater than 100 to 150 years) (Tappeiner et al. 1997, Poage and Tappeiner 2002) is also not supported by results reported in this dissertation. Rather I infer from the study reported here that very long periods (>150 year) of Douglas-fir establishment must be the exception rather than the rule. It is probable that the wide age ranges reconstructed from old growth forests were either the result of multiple disturbances (as documented by Tepley et al. (2013) or occurred on sites with severe environmental conditions.

Future research on tree establishment

Rapidity of tree establishment following large wildfires influences both the longevity of the early seral forest ecosystems and processes that contribute to structural development. Retrospective studies of establishment provide a wealth of information about tree establishment but cannot capture the full sequence of tree establishment and many of the processes that influence establishment (e.g. legacy structure, climate, seed source). Much work is still needed to investigate tree establishment in the immediate post wildfire landscape. Long-term studies that focus on the density and rate of Douglas-fir establishment starting with the first growing season following wildfire will be important for understanding fire effects, relationships between seedling establishment and mortality, and factors influencing seed source, shrub competition, and herbivory.

Since the rate of tree establishment relates to the duration of early seral conditions, another important area for future research are long-term studies of compositional changes that occur from disturbance through canopy closure. Early successional studies exist (Halpern 1988, Halpern 1989, Halpern and Lutz 2013) but they are not replicated widely throughout the Douglas-fir region. Wide variability in composition and dynamics of early seral ecosystems might be expected related to such variables as the habitat type (as defined by plant associations), pre-disturbance forest conditions, and disturbance severity. Further, there have not yet been any studies covering the dynamics of the entire early seral/tree establishment sequence from the initiated wildfire (natural disturbance) to canopy closure. Such studies could provide frameworks for other important studies, such as investigations of trophic dynamics and competitive interactions between plant species.

Spatial patterns of tree canopy closure and its suppression of early seral ecosystems is another important developmental aspect of the early Douglas-fir sere that is sorely in need of investigation. Such studies could provide badly needed knowledge regarding factors influences species diversity and compositional change as the sere becomes tree dominated.

Intermediate stand development: maturation to old-growth

Structural patterns in the early old-growth stands sampled in this dissertation research support the conceptual model of forest development developed by Franklin et al. (2002). Scores computed using old-growth indices for the early old-growth stands fill in the structural space between younger and older stands sampled in other studies (Spies and Franklin 1991).

Furthermore, the structural variability measured in the early old-growth period is consistent with what others (Franklin and Spies 1984, Spies and Franklin 1991) have found in old growth forests. Variables which characterize early old-growth stands are the sizes and densities of the Douglas-fir trees, basal area and density of shade tolerant trees, and volume of coarse woody debris. Standing and downed woody debris volumes are high and highlight the rapid rebuilding of woody detritus stocks during the early old-growth stage.

Future research on stand development

The conceptual framework provided by Franklin et al. (2002) has helped to stimulate a large body of subsequent research on the structural development of Douglas-fir forests. The dissertation research reported here adds information on two important phases of the Douglas-fir sere; tree establishment and the transition period from mature to old-growth.

Future research on the Douglas-fir sere could focus on revision of the conceptual model of Douglas-fir development. Elements that require updating include the much more comprehensive information that is available on early seral ecosystems, tree regeneration, and canopy closure on: tree establishment (Larson and Franklin 2005, Tepley et al. 2013, Freund et al. 2013 in review), mortality (Lutz and Halpern 2006), early seral conditions (Swanson et al. 2010), importance of legacies (Keeton and Franklin 2004), development of structural complexity (Van Pelt and Nadkarni 2004, Van Pelt and Franklin 2004, Van Pelt and Sillett 2008), multiple developmental pathways (Zenner 2005, Spies 2009), importance of large diameter trees (Lutz et al. 2013 In review), development of epicormic structures (Ishii and Ford 2001), and influences of productivity (Larson et al. 2008).

There are many important topics for additional research on the Douglas-fir sere including patterns of structural development in stands moving from the young to the mature stage of development (100-200 yr.). Additional work is also needed on mature stands that have experienced multiple burns, although some research of this type has been conducted in areas of the 1902 Yacolt fire (Gray and Franklin 1997).

A better understanding of influence of site productivity on stand development is needed. More rapid development of stands on sites of higher productivity has been hypothesized for Douglas-fir forests (Franklin et al. 2002) along with proposals that stands on very low productivity sites tend to undergo stagnation. Some recent work in young forests has provided evidence that development does occur faster on more productive sites (Larson et al. 2008) and this is also supported by the results of the early old-growth forests.

Future work is needed to examine the crown architecture of early old-growth forest stands and begin identifying the mechanisms that subsequently lead to development of the complex and highly idiosyncratic canopies of older Douglas-fir trees. Although crown characteristics were not directly measured in this study, I observed that the majority of Douglas-fir crowns in early old-growth stands were relatively model-conforming (*sensu* Van Pelt and Sillett 2008). I infer from those observations that – if this is consistent in all early old-growth stands -- processes leading to the complex, decadent crown features characteristic of older (>400 year) existing forests must occur relatively late in succession – after the early old-growth stage to more fully characterize complex crown development and understand the mechanisms which direct this development during this phase.

Because complex crown structures only begin to develop during early-old growth, future work is needed to determine how growth is allocated and how that growth may affect long-term biomass accumulation. Sillett et al. (2010) found increasing wood production in a large conifer species (*Sequoia sempervirens*). This previous work leads to questions about whether other large and old conifers also exhibit increasing wood production. For example, do early old-growth Douglas-fir trees exhibit increasing wood production due to their epicormic branch structures and reiterated tops?

The research conducted for this dissertation has served to revise the understanding of both duration of Douglas-fir establishment and the structural conditions which exist in Douglas-fir forests at 200-350 years old. Future work can be directly based on the data sets presented here to provide a comprehensive understanding of the full Douglas-fir sere.

LITERATURE CITED

Franklin, J.F., T.A. Spies, R. F, A.B. Carey, D.A. Thornburgh, D.R. Berg, D.B. Lindenmayer, M.E. Harmon, W.S. Keeton, D.C. Shaw, K. Bible, and J. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155:399-423.

Franklin, J. F., & Van Pelt, R. 2004. Spatial aspects of structural complexity in old-growth forests. Journal of Forestry, 102(3), 22-28.

Freund, J.A. 2013. Multi-decadal establishment of single-cohort Douglas-fir forests of western Washington and Oregon. Canadian Journal of Forest Research. *In Review*

Gray, A.N., Franklin, J.F. 1997. Effects of multiple fires on the structure of southwestern Washington forests. Northwest Sci. 71, 174–185.

Halpern, C.B. 1988. Early successional pathways and the resistance and resilience of forest communities. Ecology 69:1703-1715

Halpern, C. B., and J.A. Lutz. 2013. Canopy closure exerts weak controls on understory dynamics: a 30-year study of overstory-understory interactions. Ecological Monographs. doi.org/10.1890/12-1696.1

Ishii, H., & Ford, E. D. 2001. The role of epicormic shoot production in maintaining foliage in old *Pseudotsuga menziesii* (Douglas-fir) trees. Canadian Journal of Botany, 79(3), 251-264.

Keeton, W.S. and J.F. Franklin. 2004. Fire-related landform associations of remnant old-growth trees in the southern Washington Cascade Range. Canadian Journal of Forest Research 34:2371-2381.

Larson, A.J., Churchill, D., 2008. Spatial patterns of overstory trees in late successional conifer forests. Canadian Journal of Forest Research 38, 2814–2825.

Larson, A. J., Lutz, J. A, Gersonde, R. F., Franklin, J. F., & Hietpas, F. F. 2008. Potential site productivity influences the rate of forest structural development. Ecological Applications, 18(4), 899–910.

Larson, A.J., Churchill, D.C., 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. Forest Ecology and Management 267, 74–92.

Lutz, J.A., and C.B. Halpern. 2006. Tree mortality during early forest development: a long-term study of rates, causes and consequences. Ecological Monographs. 76, 257-75.

Lutz, J.A., Larson, A.J., Freund, J.A., Swanson, M.E., Bible, K.J. 2013. The importance of large-diameter trees to forest structural heterogeneity. PLoS ONE, In review.

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. Canadian Journal of Forest Research. 32, 1232-1243.

Sillett, S. C., Van Pelt, R., Koch, G. W., Ambrose, A. R., Carroll, A. L., Antoine, M. E., & Mifsud, B. M. 2010. Increasing wood production through old age in tall trees. Forest Ecology and Management, 259(5), 976-994.

Spies, T.A., Franklin, J.F., Thomas, T.B., 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69, 1689–1702.

Spies, T.A. 2009. Science of old growth, or a journey into wonderland. *In.* Spies and Duncan 2008. Old-growth in a new world: a Pacific Northwest icon reexamined. pp. 247-260. Springer-Verlag, Washington, D.C.

Swanson, M. E., Franklin, J. F., Beschta, R. L., Crisafulli, C. M., DellaSala, D. A., Hutto, R. L., & Swanson, F. J. 2010. The forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment, 9(2), 117-125.

Tappeiner, J.C., Huffman, D., Marshall, D., Spies, T.A., Bailey, J.D. 1997. Density, ages, growth rates in old-growth and young-growth forests in coastal Oregon. Can. J. For. Res. 27: 638-648.

Tepley, A. J., Swanson, F. J., & Spies, T. A. 2013. Fire-Mediated Pathways of Stand Development in Douglas-Fir/Western Hemlock Forests of the Pacific Northwest, USA. Ecology. 94: 1729-1743.

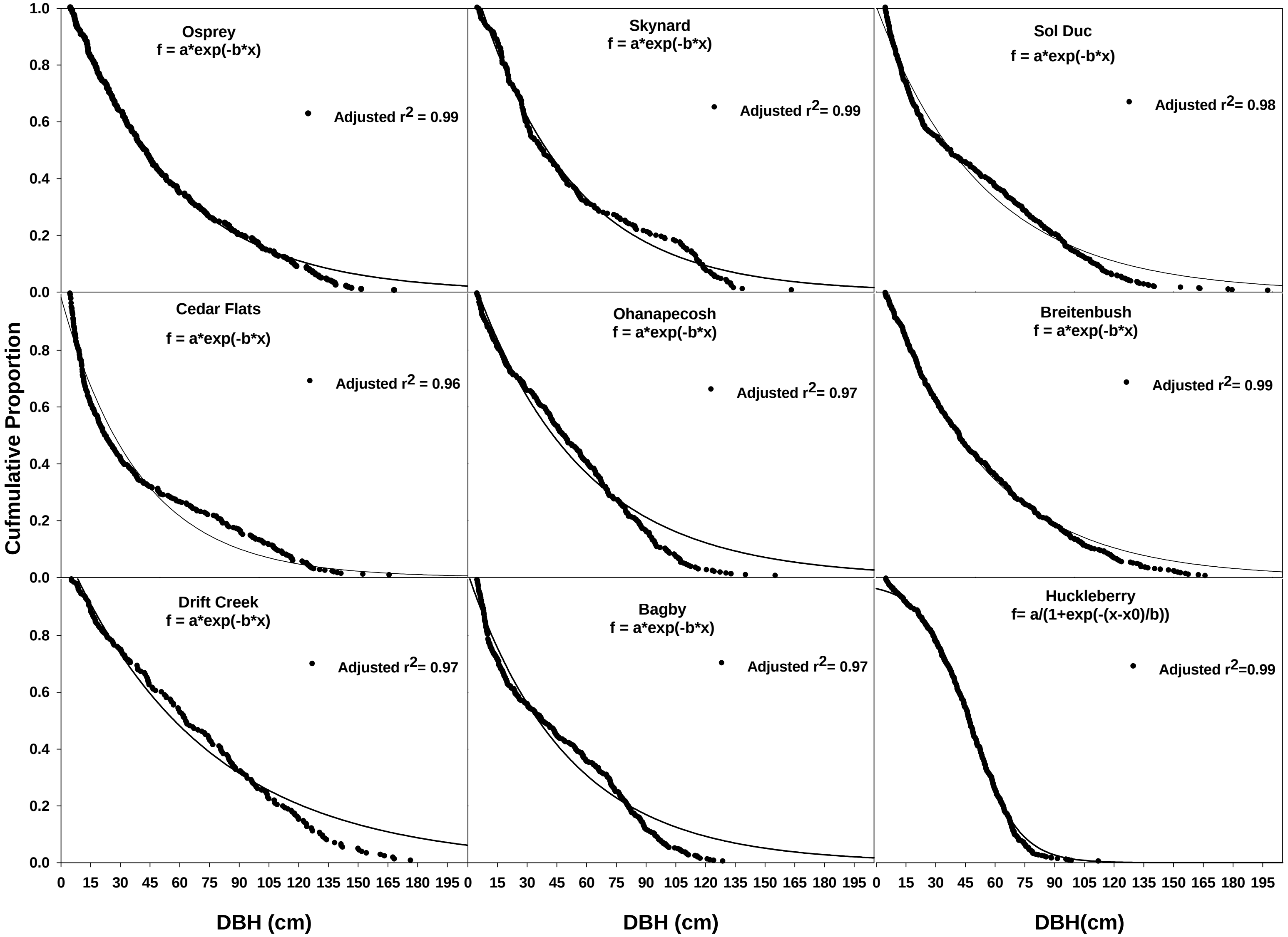
Yamaguchi, D.K. 1986. The development of old-growth Douglas-fir forests northeast of Mount St. Helens, Washington, following and A.D. 1480 eruption. PhD Dissertation, University of Washington.

Van Pelt, R., N.M. Nadkarni 2004. Development of canopy structure in *Pseudotsuga menziesii* forests in the southern Washington Cascades. Forest Science. 50(3) 326-341.

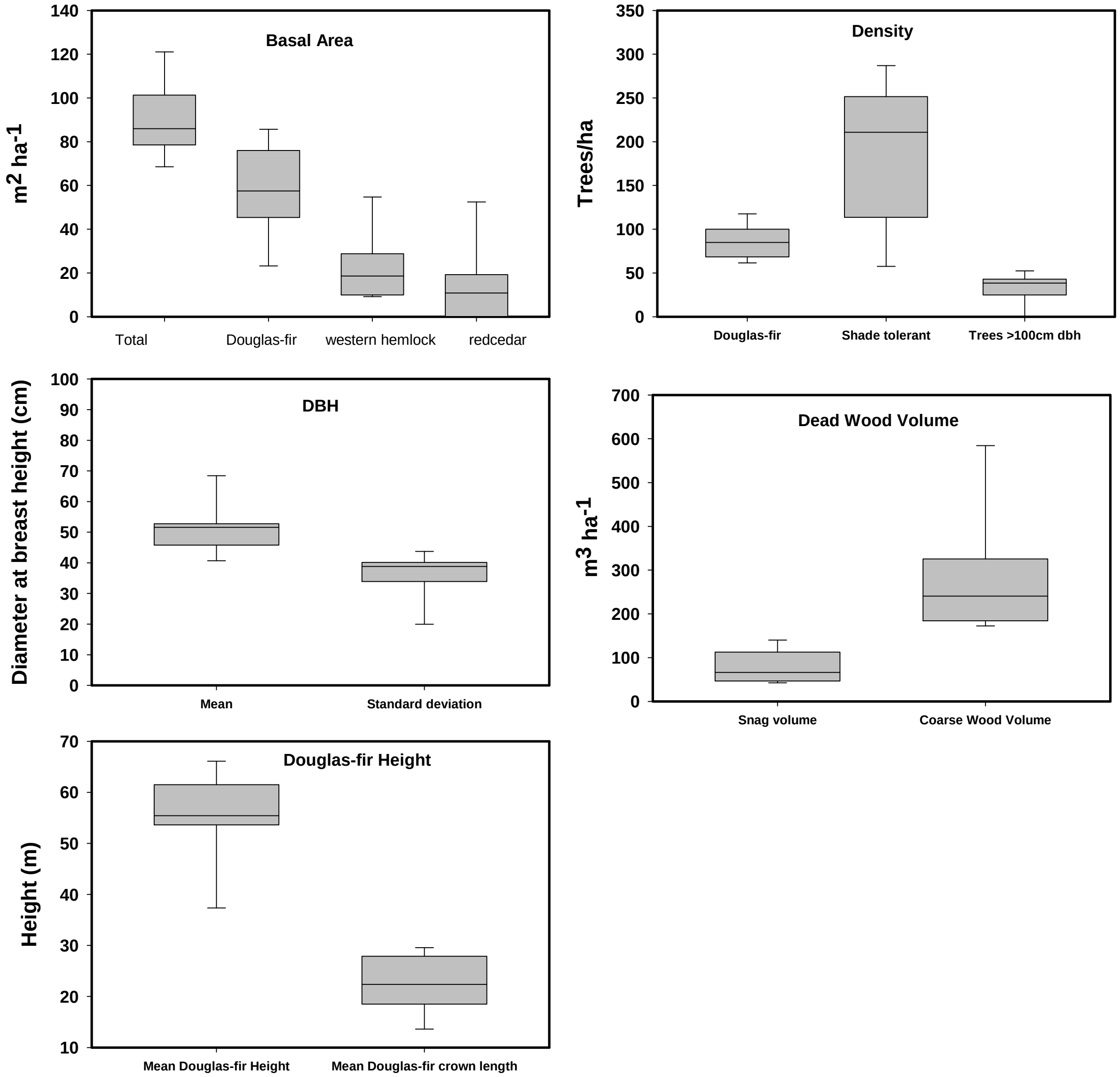
Van Pelt, R., S.C. Sillett 2008. Crown development of coastal *Pseudotsuga menziesii* including a conceptual model for tall conifers. Ecological Monographs. 78: 283-311.

Winter L.E., Brubaker L.B., Franklin JF, Miller E.A., DeWitt D.Q. 2002. Initiation of an old-growth Douglas-fir stand in the Pacific Northwest: a reconstruction from tree-ring records. Can. J. For. Res. 32(6):1039–1056. Doi: 10.1139/x02-031.

Zenner, E. K. 2005. Development of tree size distributions in Douglas-fir forests under differing disturbance regimes. Ecological Applications 15:701–714.



Appendix I. Curve fits for cumulative diameter distributions at each early old-growth site. All distributions were best fit with 2 parameter exponential decay curves with the exception of one site (Huckleberry).



Appendix II. Box plots of structural variables for early old-growth stands.

Appendix III. Characteristics of seedlings ≤ 5 cm dbh.

		Height (cm)		
Site	**Seedlings/ha**	**Mean**	**Range**	**SD**
Osprey	19	49	10-110	32.93
Cedar Flats	18	70	15-230	53.39
Drift Creek	21	44	10-120	32.13
Skynard	7	17	10-30	7.56
Ohanapecosh	1045	15	5-200	22.35
Bagby	714	19	5-140	20.88
Sol Duc	240	16	5-200	23.05
Breitenbush	190	25	5-140	27.06
Huckleberry	294	43	5-300	50.65