

Managing Forest Ecosystems

Patrick J. Baker
David R. Larsen
Alark Saxena *Editors*

Forests as Complex Social and Ecological Systems

A Festschrift for Chadwick D. Oliver



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Managing Forest Ecosystems

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Patrick J. Baker • David R. Larsen • Alark Saxena
Editors

Forests as Complex Social and Ecological Systems

A Festschrift for Chadwick D. Oliver

Editors

Patrick J. Baker
School of Ecosystem and Forest Sciences
University of Melbourne
Melbourne, Victoria, Australia

David R. Larsen
Forestry
University of Missouri
Columbia, Missouri, USA

Alark Saxena
School of Forestry
Northern Arizona University
Flagstaff, Arizona, USA

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Foreword

I am honored to offer these introductory comments to this Festschrift honoring my long-time friend and colleague, Chad Oliver.

Chad and I first met when he was a Fulbright Senior Lecturer at Middle East Technical University, Ankara, Turkey, in 1982 and I was on the Faculty of Forestry, İstanbul University. We were both Associate Professors of Silviculture at that time. He gave a seminar at the Faculty of Forestry, İstanbul University, that I volunteered to translate simultaneously (Oliver 1983). In talking with Chad to prepare for the talk and during subsequent meetings, it was clear that we shared similar perspectives on forests and forestry. Thus began a long collaboration and friendship.

Both Chad and I come from rural backgrounds and have a fondness for nature and forests. We both were fascinated by fundamental research, but also wanted to solve practical forestry problems. Chad first worked with development of mixed species stands because that is where he felt knowledge was needed; I spent most of my scientific career studying the silviculture of Turkish red pine (*Pinus brutia* Ten.) and Lebanon cedar (*Cedrus libani* A. Rich) because that is where I felt knowledge was needed (Boydak and Calikoglu 2008; Boydak et al. 2006). We both expanded our research into other aspects of silviculture and forest ecology over time as we saw opportunities to learn.

Chad is well known for his original research, teaching, and leadership in collaborative, interdisciplinary research. Importantly, Chad's research included forests from a wide range of countries in many parts of the world (Oliver 1992b). In addition to his academic reputation, Chad is also well known for his discussions with students, colleagues, and friends in the middle of the woods and mid-career short courses for forestry professionals. He has also advised government leaders, academicians, and public and private professional foresters, including the United States Congress and various foreign governments.

Chad and I have collaborated and published together (Boydak et al. 1995, 1998; Oliver et al. 1999). We have had many trips to forests together. We enjoyed many good times together—from ocean fishing off the Olympic Peninsula to feasting on a traditional Turkish dinner in an Alpine meadow. I call him Chad Gardaş; he calls

me Melih Gardaş. Gardaş means brother in the Elazığ dialect of Turkish, which is spoken where I was born.

Chad's interest in forestry came initially from his father. His real breakthrough came when he asked Professor David Smith if he could study for a PhD under him. Professor Smith was the Morris K. Jessup Professor of Silviculture, Yale University, at the time and author of *The Practice of Silviculture* (Smith 1962). Chad had admired the way Professor Smith thought—and Chad wanted to learn how to think the same way. He was also attracted to Professor Smith when Chad was lamenting that other professors were advising him to specialize to get a PhD. Chad remembers Professor Smith answer: "There's a need for generalists." Chad owes three important characteristics of his work to Professor Smith:

The first is Professor Smith's emphasis on starting with practical, silvicultural problems and digging into—and changing—the theory as needed. This has since been described as Pasteur's quadrant (Stokes 1997). In the context of forest stand dynamics, Chad and Bruce Larson were focused on applied problems related to the management of complex systems, but their research contributed to the shift in ecological theory, as applied to forests, from a steady-state perspective to one focused on system dynamics influenced by stochastic events.

Second, Professor Smith also contributed the concept of stratified, even-aged, mixed species forests. Before Chad arrived, Professor Smith already had developed the concept of stratified, even-aged mixtures when listening to a tropical ecologist talk about them, then noticing similar patterns while visiting a mixed stand in New England. Chad's thesis proceeded to document them and uncover some of their subtleties (Oliver 1975, 1978). I had the privilege of meeting Professor Smith while giving a seminar at Yale in 1987; Bruce Larson hosted me here when I was a Fulbright Fellow at the University of Washington with Chad.

Third, because of Professor Smith's influence, much of Chad's professional work has approached forests from the perspective of what we now call complex adaptive systems. The way of thinking that Chad learned from Professor Smith was sometimes referred to as mechanistic. One looks at the behaviors of the interactions of individual elements in a system. Various emergent patterns and properties can emerge from the initial, the spatial, and temporal distributions of elements of the system and their environment. This way of thinking emerged as a discipline in the 1970s and 1980s in response to situations that were too complicated to be explained by simple systems (Weaver 1948; Botkin and Sobel 1975; Waldrop 1992).

As far as I am aware, neither Chad nor Professor Smith knew that their approach to thinking about forests aligned with the concept of complex adaptive systems when they were working together in the early 1970s. However, over the years, through collaborations with his students, including David Larsen, Alark Saxena, and others, and his wife Fatma, an engineer, Chad came to embrace the core concepts of this way of thinking.

When I was on sabbatical at the University of Washington in 1986–1987, I read an early draft of what was to become Chad and Bruce's forest stand dynamics book. I was not aware of the names "forest stand dynamics" or "complex adaptive

systems” at the time. The complex adaptive systems perspective can be found in three major aspects of Chad’s works.

1. For stand dynamics, the individual actors are the individual plants of different species. Each species has characteristic ways that it can behave. However, there are emergent behaviors that groups manifest due to the environmental conditions (e.g., soil, weather) and the structure of the local neighborhood (i.e., position, size, age, species of the surrounding individuals), which collectively defined the stand’s initial conditions. Depending on the initial conditions, different patterns will emerge—stratification, overcrowding, fire, or insect susceptibility—not as a predefined natural law but as the result of the interactions of the individuals. The emergent properties change over time with growth and death. In some cases, these patterns change dramatically when threshold conditions are reached—a susceptible stand burns, blows over, or is consumed by an insect outbreak. When looking at the behaviors of the individual actors, distinguishing between natural and human-managed stands does not really help understand what is going to occur.
2. Chad began looking at forest landscapes as complex adaptive systems when he was asked to advise forest managers on the Olympic Peninsula in Washington State. Each stand was managed well, but the effect across the landscape was creating problems. By shifting the perspective from individual trees as actors within a stand to individual stands as actors within a landscape, it was easier to study and understand the interactions and emergent properties of the landscape. However, modelling this landscape behavior required such large datasets and complex interacting models that new computer modelling tools and techniques needed to be developed. Jim McCarter and many of Chad’s students contributed to this effort over the better part of two decades (Oliver 1992; McCarter et al. 1998; Oliver et al. 1998, 2004, 2009, 2012; Marzluff et al. 2001; Han et al. 2012).
3. Finally, Chad applied the concept of complex adaptive systems in his recent book, co-authored with Fatma: *Global Resources and the Environment* (Oliver and Oliver 2018). Here, Chad and Fatma took an even broader view of resource use and treated countries (or country groups) as the individual actors to explore how their conditions and behaviors have led to emergent patterns in global resource use.

These ideas have permeated Chad’s work and, as Professor Smith influenced Chad’s thinking, these ideas have, directly and indirectly, influenced the work of many of Chad’s students and colleagues.

I would like to close by recalling two Turkish expressions to describe Chad:

“He has made many firsts” and

“He will be remembered as one who left a nice echo in the cupola.”

I wish Chad Gardaş, Fatma, and their family happiness in the next phase of their lives.

Professor of Silviculture, Işık University, Şile, Turkey
melih.boydak@isikun.edu.tr

Melih Boydak

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Preface

The papers in this Festschrift were presented at a symposium held at the Yale School of the Environment on 11 October 2019 to mark the occasion of Chadwick D. Oliver's retirement as Pinchot Professor of Forestry and Environmental Studies from Yale University. This book is presented as a collection of current research and thinking on the subject of forests as complex systems and an opportunity to recognise Professor Oliver's sweeping contributions in this area.

Over the past century, there have been two countervailing trends in forest ecology and management in the USA. Early ecological studies proposed that many plant communities were relatively ordered systems that developed after disturbance in predictable ways through the process of succession towards a fixed endpoint, the climax stage. The work of Frederick Clements from the early 1900s is most closely associated with this school of thought, but many ecologists working on plant communities and forests through the 1970s (and beyond) broadly adhered to this view. In contrast, in the early 1900s, foresters were grappling with a resource once thought limitless that was being rapidly depleted by logging, land clearance, and a rash of devastating fires and windstorms across the country. They found a system that was unregulated, unpredictable, and seemingly unmanageable. Over the course of the twentieth century, ecologists increasingly came to appreciate the heterogeneity and complexity inherent in natural ecosystems. A growing appreciation for the influence of natural disturbances, the importance of unique events, and the role of chance in determining the how individuals and populations responded to disturbances—these all became core tenets of the ecological canon by the beginning of the twenty-first century. In contrast, foresters and forest scientists worked feverishly to bring order to complex and unruly systems. Genetically improved planting stock, enormous machinery to ensure uniform site preparation over large areas, and efficient fertilisation protocols to maintain uniform early growth—these all became part of the forest management toolkit by the end of the twentieth century.

Between the 1950s and 1970s, these trends passed each other like two ships in the night. Ecologists were beginning to realise that their ordered systems could develop along a variety of pathways and that disturbances were endemic to natural systems. Foresters were developing the tools and technologies to create more homogeneous

trees in more homogeneous stands at greater spatial scales. Consequently, this was a period of explosive progress in understanding how forest stands changed over time and how management could use this knowledge to improve productivity. However, it was also a period of emerging conflict as advances in engineering and machinery facilitated harvesting of forests at scales and rates that were previously unimaginable. It was during this period that many of the core ideas of forest stand dynamics began to emerge independently from forest scientists around the world. At Yale, Professor David M. Smith and his students were working on understanding how mixed-species stands developed. The forests of New England provided a useful system for exploring these patterns because they had enough tree species to highlight the variability within stand development, but not so many species that this complexity was overwhelming.

A critical breakthrough during this period was the recognition that there are emergent patterns of stand development in these complex systems after stand-replacing disturbances. Professor Oliver showed that key processes amongst driving individual interactions (e.g., competition for resources) drove observed stand-level patterns in forest structure—and that these emergent patterns were consistent across vastly different forests (i.e., oak-hardwood forests in Connecticut, Douglas fir forests in the Pacific Northwest). This then provided a bridge between the different trajectories of thought amongst ecologists and foresters. By treating forests as complex systems, a system could be characterised by heterogeneity and stochasticity at one scale but generate consistent patterns at the next higher scale. This allowed for both the ordered or structured understanding of forests of the early ecologists and the experience of forest managers, as well as the more recent appreciation of stochasticity in forest dynamics.

Over the past two decades, there has been considerable discussion about forests as complex adaptive systems. Theoretical efforts have been advanced to conceptualize forests beyond natural systems as more integrated human and natural systems that respond (learn and adapt) to changes in their environment. Advances in computing techniques (modelling paradigms), remote sensing, social survey methods, and data collection and processing have enabled more detailed characterisations of complex dynamics of these adaptive systems across a wider range of spatial and temporal scales and at higher resolutions than ever before. Making sense of these data, however, requires conceptual frameworks that are robust to the complexities of the human and natural systems, and the dynamics within and across human and natural systems, particularly in the context of global change. The chapters in this book explore human and natural systems and their dynamics through the lens of complex adaptive systems. Each chapter offers new insights into how these systems can be managed to enhance their sustainability to ensure that they provide a diversity of ecological and social values well into the future. Together they offer new insights into conceptualizing and operationalizing the forests as complex adaptive systems and finding solutions to challenges that forest landscapes face and how we as society may best address them.

This book is divided into three parts. Part I presents a series of chapters on complex forest stand dynamics; Part II explores forests as complex ecological

systems; and Part III considers forests as complex social systems. In the first chapter in Part I, Bruce Larson and Mariano Amoroso revisit the concept of growing space and propose a more robust version that better accounts for stand dynamics in complex forests. Bob Deal then describes several stand reconstruction studies that explore the potential for partial cutting of the overstory and including red alder to meet various stand management objectives. Dave Larsen uses stocking diagrams to consider the development of uneven-aged oak forests in the Missouri Ozarks and describes several distinct patterns of uneven-aged stand development. This is followed by a chapter by Patrick Baker, Craig Nitschke, and Raphael Trouvé that explores how the underlying stand dynamics of tall eucalypt forests in South-Eastern Australia create a conservation challenge for a critically endangered arboreal marsupial. John Kershaw, Ting-Ru Yang, and Yung-Han Hsu then examine a range of quantitative indices describing stand structure and test them using airborne LiDAR scans for forests in New Brunswick, Canada, and explore various ways that LiDAR can be used to map structural complexity across landscapes. The final chapter in Part I is a review by Chad Oliver and Bruce Larson of the genesis and history of forest stand dynamics—the ideas and the book.

Part II starts with Pil Sun Park's review of the interactions between climate and forest disturbance regimes in Korea and the consequences for forest dynamics. Morris Johnson, Maureen Kennedy, and Sarah Harrison then discuss the dynamics of fuel loads in forests of the Pacific Northwest after stand-replacing disturbances and the implications for post-wildfire forest management strategies to manage fuel loads in a warming climate. Jim McCarter then explores how we can use various types of visual representations to understand forests and forest dynamics at various scales. The part closes with a chapter by Jeremy Wilson and Patrick Baker on the challenges of landscape management given the enormous momentum of forested landscapes created by their accumulated and accumulating biomass.

Part III begins with a chapter by Xuemei Han, Limin Feng, and Jianping Ge that focuses on the challenges of developing forest management plans for Amur tiger conservation in landscapes with potentially conflicting management objectives that are driven by local and global social issues. Glenn Galloway then discusses forest-based development in the context of complex social-ecological systems, highlighting the challenges that they present, and lessons that have been learned by treating these as complex systems. Gerardo Segura Warnholtz continues with this theme to look back on how community-based forest management has evolved over the past half century and the challenges (and opportunities) that exist in the coming decades. We close this part with a chapter by Alark Saxena and Burak Gunerlap that provides a novel approach to operationalize integration and analysis of human and natural dynamics to explore how conservation policy impacts forest-dependent communities and how those policies might be modified to generate more effective outcomes for both conservation and rural livelihoods.

Finally, we have followed in the tradition initiated by Matt Kelty, Bruce Larson, and Chad Oliver in the *Festschrift* that they coordinated for Dave Smith by inviting Professor Oliver to offer some thoughts on forests as complex systems and the impact of forest stand dynamics.

This collection of papers is presented in recognition of Professor Chadwick D. Oliver's contributions to forest ecology and management. It is also done with a profound appreciation for his good humour, his kind wisdom, and the endless source of ideas and stories that he has so generously shared with his students, collaborators, and colleagues over the course of his career.

Melbourne, VIC, Australia
Columbia, MO, USA
Flagstaff, AZ, USA

Patrick J. Baker
David R. Larsen
Alark Saxena

Profile of Chadwick Dearing Oliver



Chad Oliver held the position of Pinchot Professor of Forestry and Environment Studies and Director of the Global Institute of Sustainable Forestry at Yale University from 2002 until his retirement in 2020. Prior to that he was Professor of Silviculture and Forest Ecology at the University of Washington from 1975 until 2001. Professor Oliver earned a BS in forestry (with Honours) from the University of the South in 1968. He then moved to the Yale School of Forestry to take his MFS in 1970 and his PhD in 1975. His doctoral work was supervised by Prof David

M Smith, the Morris K Jesup Professor of Silviculture at Yale, and focused on the development patterns of mixed-species, even-aged stands in central New England. In the last year of his PhD, Prof Oliver taught plant ecology at Harvard University. He held a Fulbright Fellowship to Germany and Turkey in 1982–83. Prof Oliver was awarded an Honorary Doctorate of Sciences from his alma mater, the University of the South in 2002. He was named a Fellow of the Society of American Foresters in 2008 and received the IUFRO Host Country Scientific Award in 2014.

Over the course of his career, Prof Oliver has had a profound influence on the science and practice of forest ecology and management. The son of a forester, Prof Oliver has always been keenly attuned to the needs of field foresters and the problems that they confront in trying to balance diverse and sometimes competing interests. In many ways his career has focused on advancing theoretical understanding to solve practical challenges in forestry and forest science. He encouraged this type of thinking in his teaching of hundreds of undergraduate and graduate students and through the short courses for forest management professionals that he and Prof Bruce Larson taught for 32 years. With his graduate students he extended his forest reconstruction studies to different parts of North America, and subsequently, to other parts of the world. In the 1990s, he and his students pioneered research and software development addressing the challenge of incorporating stand dynamics into landscape-scale management planning for multiple values. Professor Oliver has contributed to a wide range of State and Federal government advisory panels and task forces. He also influenced forest science more broadly as an associate editor for *Forest Science*, *Canadian Journal of Forest Research*, *Journal of Forestry*, *New Forests*, and the *Journal of Sustainable Forestry*.

The publication in 1990 of *Forest Stand Dynamics* (with Bruce Larson) cemented Prof Oliver's reputation as one of the leading forest scientists of his generation. The book was updated in 1996 and remains the most highly cited text in forest science. *Forest Stand Dynamics* synthesised a vast body of literature on forests, forest ecology, and forest management. It brought together more than a century of forest science research to provide a coherent framework for understanding how individual tree growth and competition for resources drive emergent, and globally consistent, patterns in stand development. The forest stand dynamics approach is now the standard framework for thinking about stand development patterns around the world.

Contents

Part I Complex Forest Stand Dynamics

1 How the Concepts of Traditional Stand Dynamics Might Be Used for More Complex Stands	3
Bruce C. Larson and Mariano M. Amoroso	
2 Assessment and Dynamics of Complex Forest Structure and Understory Plant Diversity to Develop Sustainable Forest Management Options in Alaska	13
Robert L. Deal	
3 A Long-Term Record of Uneven-Aged Management in a Mixed Oak-Hickory-Pine Forest in Missouri, USA	41
David R. Larsen	
4 Quantifying and Mapping Stand Structural Complexity Using Airborne LiDAR Scanning	67
John A. Kershaw, Ting-Ru Yang, and Yung-Han Hsu	
5 Forest Stand Dynamics Drive a Conservation Conundrum for the Critically Endangered Leadbeater’s Possum	93
Patrick J. Baker, Craig R. Nitschke, Raphael Trouvé, and Andrew P. Robinson	
6 The Nexus of Events That Led to Forest Stand Dynamics	115
Chadwick D. Oliver and Bruce C. Larson	

Part II Forests as Complex Ecological Systems

7 Effects of Climate and Rehabilitation on Forests and Forest Disturbances in Korea	137
Pil Sun Park	

8	Understanding Woody Fuel Dynamics Following Stand-Replacing Wildfires	155
	Morris C. Johnson, Maureen C. Kennedy, and Sarah C. Harrison	
9	Understanding Forestry Through Pictures – A Journey of Graphics, Pictures, Visualizations, and Graphics	189
	James B. McCarter	
10	The Momentum of Forested Landscapes and the Implications for Forest Management	211
	Jeremy S. Wilson and Patrick J. Baker	
 Part III Forests as Complex Social Systems		
11	Tiger in the Woods, Elephant in the Room: Designing a Forest Management Plan for Amur Tiger (<i>Panthera tigris altaica</i>) Conservation	223
	Xuemei Han, Limin Feng, and Jianping Ge	
12	Forests as Complex Systems: Implications for Forest-Based Development Initiatives	253
	Glenn Galloway	
13	Forest Management by Local Communities: Evolution and Current Trends Since the 1970s	275
	Gerardo Segura Warnholtz	
14	Understanding the Dynamics Between Forest Landscapes and Rural Livelihoods: A Case Study from Central India	295
	Alark Saxena and Burak Güneralp	
 Part IV Concluding Remarks		
15	Forest Stand Dynamics, Complex Adaptive Systems, and the Future	323
	Chadwick Dearing Oliver	

Part I
Complex Forest Stand Dynamics

Chapter 1

How the Concepts of Traditional Stand Dynamics Might Be Used for More Complex Stands



Bruce C. Larson and Mariano M. Amoroso

Abstract The concept of growing space represents the integration of all growth factors (e.g., light, water, nutrients and physical space) required for trees to establish and grow. It is based on the notion that at any time growth can be restricted by any number of different factors, and it is often impossible to discern exactly what the specific limiting factor is. Over time, the concept has been a powerful heuristic framework for understanding competition as a driver of the development of even-age stands, but it also helped the understanding of stand dynamics after partial disturbances. Because the concept of ‘growing space’ was so simplistic, concerns arose over its limitations for stands with more complex structures, such as mixed species. We propose here an expanded concept of growing space in order to explain more complex situations and include some illustrative examples, which may include niche differentiation and facilitation. Our expansion adds categories of growing space (*used*, *controlled-unused*, and *inaccessible*) which sum to total growing space. This expansion of the traditional concept of growing space may be useful to help frame current discussions on how stand development models based primarily on competition can be modified to include other ecological processes such as facilitation.

Keywords Growing space · Controlled unused · Inaccessible · Mixed species · Woodlands

B. C. Larson

Forest Resources Management Department, Faculty of Forestry, University of British Columbia, Vancouver, Canada

M. M. Amoroso (✉)

Instituto de Investigaciones en Recursos Naturales, Agroecología y Desarrollo Rural (IRNAD), Universidad Nacional de Río Negro, Viedma, Argentina

Instituto de Investigaciones en Recursos Naturales, Agroecología y Desarrollo Rural (IRNAD), Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina

e-mail: mamoroso@unrn.edu.ar

1.1 Introduction

In *Forest Stand Dynamics* Oliver and Larson (1990, 1996) put forward the concept of growing space as the integration of all factors (e.g., light, water, nutrients and physical space) required for tree growth. This was a departure from the commonly accepted idea of growing space only being the physical space occupied by the crown of a tree. The Oliver and Larson concept recognized that at any point in time, any number of different factors can restrict growth, and it is often impossible to discern exactly what the specific limiting factor is. In fact, the concept of multiple interacting limiting factors is the usual case (Nijland et al. 2008). Oliver and Larson's concept was based on the notion of total growing space (the integration of all growth factors at a certain time and place) could be divided into occupied growing space (those amounts of growth factors actually being used) and available growing space (those amounts of growth factors that were available for growth and expansion of existing trees or regeneration of new trees). Explaining competition in this way made clearer the concept of dominance and suppression (through reallocation of occupied growing space) and the lack of regeneration during the stem exclusion phase (insufficient available growing space). Because 'growing space' was such a simplistic concept, serious doubts arose over its relevance to complex stands; it seemed to not fit.

Oliver and Larson (Chap. 6 in this book) describe the history of how Oliver developed the actual term and the rationale for its use. However, the term took on much more significance as the ideas of forest stand dynamics gained acceptance over time among foresters. Growing space could be seen as both the link and the means of differentiation between the stages of development of a forest stand. It became an important tool in the explanation of concepts, such as stand density management diagrams (Drew and Flewelling 1979). The fact that stands developed differently depending on whether growth resources were limited explained much of the observed tree growth patterns.

Disturbances are defined as events making growing space available. Disturbances, however, can also preferentially directly reduce a species competitive ability (e.g., some species are more susceptible to wind crown breakage). Tree growth and establishment (regeneration) were the processes by which available growing space became occupied. Competition between trees for growing space was then seen as a driver of stand development (Oliver 1981; Oliver and Larson 1996). In the immediate aftermath of a stand-replacing disturbance (i.e. the *stand initiation* stage), all or most of the total amount of growing space on a site becomes available allowing many trees, herbs, grasses, and other plants to regenerate and grow. This stage lasts until plants occupy all the available growing space. During the *stem exclusion* stage, during which growing space is fully occupied and taken by trees, it is redistributed among trees as differentiation occurs and some trees start growing faster and get bigger. The initial cohort is eventually not vigorous enough to use and occupy all growing space resulting in some density-dependent mortality which releases growing space allowing the establishment and development of an

understory, creating the *understory reinitiation stage*. In a hypothetical continued stand development pattern in absence of disturbances, growing space will continue to be made available as trees grow, decline, and die.

In many cases, tree death and the release of growing space clearly results from discrete disturbance events such as fires, avalanches, landslides, windthrows. We feel that the definition of disturbance, as an event that releases growing space, should not just focus on specific, discrete nature of the events (*sensu*) (White and Pickett (1985)). There are disturbance types when growing space is released more frequently (even within the growing season) making it more difficult to differentiate discrete events and rather becomes more continuous. Growing space can be then released gradually. This would be, for example, the case of forest declines where trees would decline and lose vigour over time before death (Amoroso and Larson 2010; Amoroso et al. 2012). From a disturbance point of view, while individual tree death in declining forests can be considered as a discrete event or disturbance, overall overstory vigour loss and mortality could be viewed as a chronic disturbance (Amoroso and Larson 2010). It is essential to concentrate on processes of how growing space gets released. Even when the disturbance events that lead to the release of growing space are discrete (e.g., a windstorm), they can be considered as a single occurrence or a periodic event. Repeating periodic events which partially release growing space can lead to development of multi-cohort stands (Amoroso and Larson 2010). This type of complex stands can usually be thought of as stands that have had a complex series of growing space release events.

As well as changes in available growing space resulting from disturbances, there are fluctuations in total growing space. This is not different from the fluctuating niche ideas described by Chase (2011). There are regular fluctuations in total growing space, such as seasons. Annual death of seedlings after the onset of summer drought is well documented (e.g., Keyes et al. 2007) which can be considered an example of total growing space reduction. Likewise, episodic mortality from drought (e.g., Suarez et al. 2004) could be considered a disturbance causing reduction in *total* growing space resulting in mortality rather than mortality leading to an increase in *available* growing space. There are also long-term temporal fluctuations in growth factors that can lead to increases in available growing space. Long-term precipitation variations, along with disturbance regime changes, have led to tree establishment at the regional scale in different ecosystems (Villalba and Veblen 1997; Morales et al. 2005; Swetnam and Brown 2011). Higher rainfall can lead to seedling establishment and then, as they grow larger, they are able to access deeper water leading to a long term increase in accessible growing space. While the concept of growing space was rapidly accepted by forest ecologists and silviculturists around the globe (e.g., Goebel and Hix 1997; Folli et al. 2003; O'Hara and Gersonde 2004; Fei and Steiner 2009; Amoroso and Larson 2010), as these examples show that there is a need for a more nuanced view of growing space and its application to understanding stand dynamics.

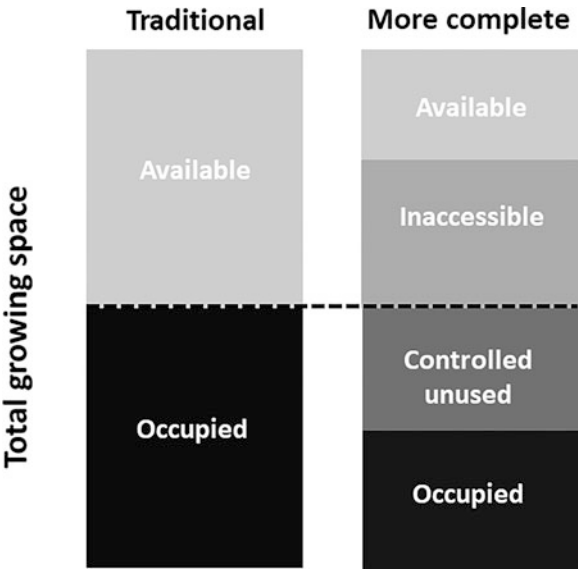
1.2 Rethinking the Growing Space Concept for More Complex Stands

Although mixed species stands were included in *Forest Stand Dynamics* (Oliver and Larson 1990, 1996), competition for growing space was considered similar to single species stands. Over time, questions arose about issues such as enhanced productivity of mixed species stands and competition in savannahs where belowground competition from non-tree species may be more important. The concept of growing space as originally proposed appeared inadequate and some proposed dropping the idea in these more complex situations.

Here we propose an expanded concept of growing space that is better suited to more complex stand dynamics and that can account for observed patterns such as resource partitioning situations (niche differentiation) and facilitation (Fig. 1.1). This expansion separates total growing space into four categories (instead of two). We keep the idea of *available* growing space which consists of growth factors that are available for the expansion of existing plants and regeneration but give recognition that some of the growth factors may be *inaccessible* to some or all trees in the stand. The former category of occupied growing space is now also divided into two categories: *used* and *controlled-unused*.

The category of *used* is similar in concept to the old terminology of occupied growing space. This consists of the growth factors that are being assimilated and used by trees on the site. It is, however, unlikely even in a single cohort, single species stand, in the stem exclusion stage that all factors are being consumed; not every species has the same needs. An obvious example of this is that there

Fig. 1.1 Original versus proposed new conceptualization of growing space. Growth resources above the dashed line can be used by a tree if the conditions are appropriate. Resources below the dashed line can only be used if another tree dies and releases the resources



is sufficient light for shade tolerant plants beneath the closed canopy of a shade intolerant species. There are other examples where one species may require a greater amount of a particular soil nutrient than another species. If all factors were being used, stand growth would approach optimal NPP; however, forests seldom approach even 50% (Farnum et al. 1983). This means that growth factors are not being used even if there is no regeneration taking advantage of their availability. Some of the growth factors fall into the category of *controlled-unused*. An obvious example of this is light which is either absorbed as heat or reflected back to the atmosphere, but not used in photosynthesis. This would vary over the course of the day. For example, when stomates close during mid-day moisture stress, more light would be ‘wasted by the canopy trees’, but unavailable to other trees. Much smaller trees and regeneration might actually be able to use this light because they may be able to keep their stomates open in the cooler understory environment, but the light does not reach them. Another example would be crown interception of precipitation. In closed canopy situations much precipitation is evaporated back into the atmosphere without being used by the canopy trees.

Perhaps the most interesting category for thinking about resource availability in more complex stand development situations is *inaccessible* growing space. This category represents growth factors, often below-ground, that are available, but some trees are unable to access. Kelty (1992) speculated that mixed species stands might out-produce monocultures in certain conditions. Two of these conditions were niche differentiation and facilitation. In 2006 he elaborated on this with specific examples and explained potential higher productivity of mixed species stands by pointing out that species with complementary characteristics have interspecific competition that is much lower than intraspecific. Niche differentiation of shallow and deep rooted species is an obvious example that would apply to mixed species stands (including those with tree and non-tree life forms, such as in savannahs). Facilitation contributes to stand development when one tree makes a growth factor available to other trees even if the first tree is not completely using the factor. Kelty (2006) described the well studied example of nitrogen fixing species growing with non-fixing trees. Simard and collaborators (1997) detailed how trees can share nutrients such as nitrogen if they share mycorrhizal connections. She and others expanded this concept by showing that large trees accessing deeper water sources can make the water available to smaller trees of the same species through mycorrhizal connections (Teste et al. 2009).

1.3 How Does the ‘New’ Growing Space Concept Lead Us into Understanding Complex Stands

1.3.1 Example 1: Mixed Species Stands

Differences in photosynthetic efficiency of foliage, height growth patterns, tree form, phenology, and root structure, have all been suggested as possible mechanisms that could lead to a mixed species stand having overall productivity greater than a monoculture of the component species (Kelty 1992). However, this is likely to occur only if the supply of the resource for which competition is reduced is limiting the productivity in the pure stands (Kelty 1992). Differences in shade tolerance among species in mixed stands may lead to less interspecific than intraspecific light competition as a stratified canopy would, in theory, maximize the use of light because of increased light interception and light-use efficiency (Kelty 1992; Kelty and Cameron 1995), leading to greater total productivity than in pure stands (Smith et al. 1997). By capturing light at different intensities and locations within the canopy, a stratified canopy composed of shade-tolerant species growing underneath a shade-intolerant species would collectively intercept more photosynthetically functional light than a pure stand of the most shade-intolerant species and would maximize the use of it (Kelty 1989; Garber and Maguire 2004; Amoroso and Turnblom 2006; Pretzsch and Schütze 2009). In other words, light at low intensity is available in single-species stands but it is not being used. Similarly, until a stratified canopy develops in mixed species stands, light would only be intercepted and used in a single layer where species will compete for the same light quantity and quality within the same layer of foliage; yet, there would be light that will still go through the canopy without being intercepted and used for photosynthesis. This is an example of *controlled unused* growing space. Once a stratified canopy develops, the more shade intolerant species intercepts and uses most of the incident radiation but that of less intensity would now be used by the foliage of the most shade tolerant species growing underneath. Similarly, stronger spatial separation of the roots of the different species in mixed stands likely contributes to a higher partitioning of nutrient uptake within the soil profile, which would lead to higher aboveground total stand biomass compared to pure stands (Mekontchou et al. 2020).

1.3.2 Example 2: Woodlands

Arid and semi-arid climates sustain open forests and woodlands worldwide. On a given site there may be some resources for growth that are not accessible to trees or plants because the architecture or growth patterns of the plants are not appropriate. Below-ground resources, such as water and nutrients, represent good examples of *inaccessible* growing space. Niche differentiation of the root system of trees (e.g., shallow- vs. deep-rooted species) would allow a more complete exploration

and use of the inaccessible growing space (Kalliokoski et al. 2008; Rewald and Leuschner 2009; Mekontchou et al. 2020). As the stand develops resources that were initially inaccessible may be accessed by species that form deep tap roots. Savannas and woodlands present complex groundwater systems, where water and nutrient availability may vary temporally and spatially. Thus, the ability of trees and other plants to access these resources may depend on both root architecture and temporal patterns of resource availability.

Shallow groundwater can sustain the productivity of arid ecosystems at much higher levels than would be expected solely from local rainfall (Eamus et al. 2006; Jackson et al. 2009). Furthermore, shallow aquifers are usually sustained by local or distant recharge sources, thus making its availability complex in space and time. Recent findings in *Prosopis flexuosa* woodlands have shown tree species in this environment have a high degree of phenotypic plasticity in their root systems when growing in different landscape units, with different access to the water table and under different soil environments (Guevara et al. 2010). For example, valley trees have extensive and horizontal surface roots that spread several meters away from the tree, whereas dune trees have a lower number of surface roots that grow tortuously and sink vertically from the tree base, as well as a more branched taproot (Guevara et al. 2010). These differences in root architecture and growth patterns allow differential water exploration and uptake (Guevara et al. 2010; Giordano et al. 2011). Valley trees utilize larger and more stable (superficial) water reservoirs than dune trees, resulting in increased radial growth rates (Giordano et al. 2011). The ability of *P. flexuosa* to respond to unpredictable rainfall pulses appears as an important adaptation to ensure ecosystem functioning (Debandi et al. 2020). In summary, *Prosopis* trees in woodlands have a different capacity to access and use available growing space, than trees growing in valleys with a superficial root system. Underground water is mostly not accessible, for trees growing in upper landscape positions (dunes) superficial and sporadic rainfall water would not be accessible for them. The same water that might be available to some trees is not available to others.

1.4 Final Remarks

The concept of total growing space divided into available and occupied has been a powerful tool for understanding competition as a driver of the four stages of even-age stand development after a stand-replacing disturbance. Furthermore, it also shaped our understanding of overall stand dynamics after partial disturbances, particularly cohort establishment. However, for more complex patterns of stand development with multiple species, positive interactions, and belowground competition, the utility of the original growing space concept had limitations. Here we argue that a simple expansion of the original concept is a powerful tool to explore these stands. This expansion is especially helpful to frame current debates such as how other ecological processes such as facilitation can fit into our competition-based models. At some time in the future the concept of growing space may be replaced,

but for the moment, competition for growing space is still an excellent heuristic framework for understanding development of the more complex stands.

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Chapter 2

Assessment and Dynamics of Complex Forest Structure and Understory Plant Diversity to Develop Sustainable Forest Management Options in Alaska



Robert L. Deal

Abstract This paper synthesizes information on management options in older forests that have never been actively managed, and in younger even-aged forests in Alaska and their associated effects on biodiversity and sustainable forest management. Partial cutting was evaluated in older spruce-hemlock stands that were harvested 12–96 years ago in southeast Alaska. Cutting occurred without a planned silvicultural system with little consideration for spruce regeneration, stand growth or the maintenance of stand structures found in old-growth forests. Stand structural diversity and plant diversity and abundance were all much greater in partially cut stands than in young even-aged stands developing after clearcutting. These results indicate that uneven-age silvicultural systems using partial cutting could alleviate some of the problems associated with conventional even-aged stands developing after clearcutting and increase stand structural diversity and enhance sustainable forest management in the region. Forty-year-old mixed red alder conifer stands were evaluated to assess stand structure and understory plant diversity and abundance. These red alder-conifer stands contained more heterogeneous structures than pure conifer stands that typically develop in even-aged forests following clearcutting. Altering the composition of even-aged young-growth forests with the inclusion of red alder greatly improved habitat for deer and other wildlife, and thereby offsets some of the negative consequences of typical even-aged management. Well planned even-aged silvicultural systems that include a mixture of red alder-conifer compositions could provide trees for timber production and also provide multiple forest ecosystem services including songbirds, fish and aquatic resources that are often compromised in pure conifer young-growth forests in the region.

Keywords Alternative silviculture · Red alder · Riparian habitat · Sitka spruce · Uneven-aged stands

R. L. Deal (✉)

USDA Forest Service, Pacific Northwest Research Station, Portland, OR, USA

2.1 Introduction

Disturbance is a major force in stand development that defines the structure and function of forests (Bormann and Likens 1979; Oliver and Larson 1990; Attiwell 1994). Over the past 70 years the role of disturbance on the structure and composition of plant communities has been increasingly recognised and documented (Whittaker 1953; Egler 1954; Pickett and White 1985; White 1979; Halpern 1989; Anglestam 1998). In forestry, there is an increasing focus on providing multiple ecosystem services for social and economic sustainability while maintaining ecological integrity through sustainable forest management. Such strategies include developing older forest characteristics, enhancing biodiversity in younger forests, retaining aquatic ecosystem integrity, water quality and wildlife habitat, and forestry products that people rely on for their livelihoods (Franklin 1989; Larsen 1995; Deal et al. 2017). Forest management strategies that create more complex forests may also provide a broader range of ecosystem services than plantation forestry. This is particularly relevant for regions where plantations were traditionally managed for simple species composition but now need to consider a broader range of natural resources beyond simply timber production (Notaro et al. 2008; Deal et al. 2014; Grilli et al. 2016). Many managed forest plantations intentionally contain single species compositions, often even-aged conifer stands that are managed on relatively short rotations with a focus on wood production (Davis and Johnson 1987; Fox et al. 2007). There are some advantages to short-rotation, single-species compositions including better understanding of stand dynamics of individual species, ability to produce uniform wood on relatively short rotations, and greater certainty of forest growth and wood production (Evans and Turnbull 2004; Boyer 1990). However, there are a number of tradeoffs in single-species stands that are primarily managed for wood production. These typically uniform conifer plantations have simple tree height and diameter distributions and forest structures that often lead to reduced plant diversity and abundance, compromised wildlife and aquatic habitat and lower aesthetic values (Hanley 1993; Deal 2007; Notaro et al. 2008). Therefore, reconciling the economic benefits of wood production with tradeoffs in biodiversity and other ecosystem services is needed to inform management decisions for sustainable forest management.

In the Sitka spruce (*Picea sitchensis* (Bong.) Carr.) -western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forests of Alaska, trees naturally establish after timber harvest, but even-aged silvicultural systems such as clearcutting have been predominantly used since the beginning of large-scale timber operations in the early 1950s (Harris and Farr 1974; McClellan et al. 2000). Forest development following stand-replacing disturbances is different than typical forest development following natural small-scale disturbances. Post-harvest conifer regeneration is frequently abundant ($>10,000$ trees ha^{-1}) with the development of a dense new cohort of western hemlock and Sitka spruce trees. The forest canopy typically closes in 20–30 years followed by a dense, long-lasting stage of stem exclusion that can persist for 100 years or longer (Alaback 1982, 1984; Deal et al. 1991). These dense