Aging in Pacific Northwest forests: a selection of recent research

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Summary This paper provides an overview of the work reported at a symposium on age-related changes in the structure and function of forests in the United States Pacific Northwest. Some of the work presented at this meeting is reported in the peer-reviewed papers comprising this journal issue. Age-related changes in leaf structure, CO_2 assimilation rate, stable carbon isotope ratio, nitrogen concentration and stomatal limitation were demonstrated at many organizational scales. At larger scales, age-related changes were reported in canopy structure and light profile, stand productivity, tree mortality and respiration. These data raise new questions about the potential interaction among the structural and functional changes in aging forests, and indicate many avenues for future research concerning tree growth and ecosystem functioning.

Keywords: aboveground net productivity, canopy, carbon isotope, chronosequence, Douglas-fir, ecosystem, eddy covariance, old-growth.

The articles in this special issue developed from papers presented at a symposium that focused on age-related changes in the structure and function of forests in the United States Pacific Northwest, which took place at Oregon State University, Corvallis, OR on October 19, 2000. These papers are only a sample of the information shared at the symposium. A complete list of presenters, titles and abstracts is available on the web (http://www.fsl.orst.edu/~bond/age-symposium_files/ INDEX.htm), and we refer to some of the unpublished contributions below. The symposium, in turn, included only a sample of the current research on changing structure and function of aging trees and forests in the Pacific Northwest. Nevertheless, the papers in this issue represent a wealth of new information about tree and forest aging on scales ranging from cells to ecosystems.

Our goal was to focus on physiological studies, and to include a selection of ecosystem-scale studies that are important in interpreting the intimate linkage between aging processes in trees and age-related changes in the forest ecosystem. For this reason, some papers in this collection focus more on ecosystems than on the trees within ecosystems, and there are no papers that deal with structural complexity and biodiversity in aging forests—an area that has received much attention. Studies of aging forests have a long history in the Pacific Northwest. In 1969, a group of Oregon State University and Forest Service scientists met to debate the focus of their participation in the Coniferous Forest Biome project of the United States International Biological Program (IBP). The main question was whether this new ecosystem research effort would focus on the second-growth forest stands or the old-growth forests of the northwestern Pacific Coast. The issue was eventually resolved in favor of work on the structure and function of natural, old-growth *Pseudotsuga menziesii* (Mirb.) Franco-*Tsuga heterophylla* (Raf.) Sarg. (Douglas-fir-western hemlock) forests and associated stream ecosystems at the H.J. Andrews Experimental Forest on the western slopes of the Oregon Cascade Range. Thus began the first ecosystem-oriented research on old-growth forests.

It quickly became clear that these old-growth coniferous forests contrasted greatly with young, and especially managed, forests in both structure and function (Franklin et al. 1981). Organic accumulations were immense and included a large quantity of dead wood in the form of snags, logs and other debris. Canopies were deep and multi-layered-continuous, in fact-and provided habitat for a broad array of organisms, including nitrogen-fixing foliose lichens. Structural complexity-the richness of individual structures and spatial patterns-was extremely high. It became clear that the complex structures, in turn, create unique habitat for wildlife and are essential in maintaining biological diversity (Spies and Franklin 1988, Hansen et al. 1991). This understanding has generated entirely new approaches to forest management, with the goal of recreating these complex structures in managed forests (McComb et al. 1991, Franklin 1992, Cole 1996, Spies and Franklin 1996). Whether forests that are managed to mimic the structural characteristics of old-growth also maintain other functional characteristics, such as hydrological processes, nutrient cycling or carbon sequestration, remains to be determined and is an impetus for current research.

Research in the Pacific Northwest continues to push the boundaries of our knowledge about the changes that occur in individual trees as well as whole ecosystems as they age. This research has been funded by organizations like the National Science Foundation, USDA Forest Service Pacific Northwest Station and the U.S. Department of Energy. It has been stimulated by immense public interest and acrimonious policy debates, such as those leading to the Northwest Forest Plan for land management of federal forests and the 1997 Kyoto Accord to address anthropogenic influences on increased CO_2 in the atmosphere.

Major research facilities, such as the H.J. Andrews Experimental Forest and the Wind River Canopy Crane Research Facility (WRCCRF, Carson, WA), have been critical in facilitating and focusing research on forest aging in the Pacific Northwest. The WRCCRF (http://depts.washington.edu/ wrccrf/) is relatively new, established in 1994 as a cooperative scientific endeavor among the University of Washington College of Forest Resources, Seattle, WA, the USFS Pacific Northwest Research Station, Portland, OR and the Gifford Pinchot National Forest, Vancouver, WA. The 87-m crane was constructed in 1995 in an old-growth mixed conifer stand, allowing unprecedented access to the canopies of old-growth coniferous trees. Like most forests in the western United States, the forest surrounding the canopy crane contains a patchwork of age classes resulting both from natural disturbances (usually stand-replacing fires) and land management activities (see Figure 1 in Chen et al. 2002). Several papers in this issue (Apple et al. 2002, Chen et al. 2002, Fessenden and Ehleringer 2002, Klopatek 2002, Parker et al. 2002, Phillips et al. 2002, Thomas and Winner 2002, Waring and McDowell 2002) report on studies in and around the WRCCRF. These studies, together with many other recent studies at this site, are contributing to a deeper understanding of the ecosystem. For example, the importance of non-growth-season photosynthesis in coniferous forests of the Pacific Northwest has been known for many years, but there is now evidence that light is an important limitation to carbon assimilation during the dull winter days (W.E. Winner, Oregon State University and S.C. Thomas, University of Toronto, Canada, personal communication). Also, although it is well known that mature Douglas-fir are capable of developing epicormic branches, it is now apparent that epicormic branching can reestablish deep canopies in large, old trees long after canopy closure results in self-pruning of lower branches. It appears that as much as 90% of the foliage on old-growth trees may be produced on epicormic branches and twigs (Ishii and Ford 2001).

Another important stimulus to recent research has been the advent of new research tools. Several studies reported in this issue (Chen et al. 2002, Fessenden and Ehleringer 2002, Irvine et al. 2002, Phillips et al. 2002) were possible because of new approaches to measuring tree and forest function. These include eddy covariance techniques, improved instruments for measuring sapflow in stems and gas exchange in leaves, stems and soils, and new approaches for measuring isotope discrimination on the ecosystem scale. New techniques and tools are also enhancing studies of forest structure. Parker et al. (2002) used small balloons to obtain detailed, three-dimensional views of the changing light environment in maturing conifer forests. Thomas and Winner (2000) adapted the line-intercept technique to determine with great precision total leaf area index, as well as the contributions of different species to this total, in a complex old-growth forest. Lidar (see Lefsky and Parker, symposium abstracts) offers a powerful way to map the three-dimensional structure of complex forests through remote sensing. Finally, new developments in database management (Van Pelt et al., symposium abstracts) and data analysis (Thomas and Winner 2002) are having a big impact on the sharing and analysis of data resulting from studies of complex forests.

Many of the studies reported in this issue rely on comparative measurements at a few sites in different aged forests. This substitution of "space-for-time" is full of potential pitfalls. Site conditions and history are never identical in different locations, and these differences can easily be misinterpreted as change due to age or time (Yanai et al. 2000). Unfortunately, the intensity of most physiological studies precludes extensive replication, and the life span of most forests relative to forest researchers precludes continuous measurements over the life of a forest. One solution is to remeasure sites within a chronosequence over many years (Yanai et al. 2000), and to look for correspondence between changes over time within sites and among sites of different ages at any point in time. Acker et al. (2002) successfully employed this approach. Another solution is to employ a "nested" experimental approach, with intensive measurements designed to test specific hypotheses at a few locations, complemented by extensive replication of simple measurements or modeling over larger scales of space and time. In a sense, all of the papers in this journal issue represent this approach in an ad hoc way. Better communication among researchers in planning and implementing experiments is needed to improve the complementarity of such studies in the future.

The papers in this issue reveal age-related changes in structure and function of forest trees in the Pacific Northwest at many organizational scales, and when we examine the results as a group they suggest common themes as well as many new questions. Apple et al. (2002) investigated structural change at the leaf scale and found larger vascular cylinders, smaller resin canals, a lower proportion of non-photosynthetic relative to photosynthetic tissue, and a much higher proportion of lignin-containing structures known as astrosclerids in needles of old Douglas-fir trees compared with same-age foliage of younger trees. At present, we can only speculate as to whether these changes result from ontogenetic causes or from differences in conditions during leaf development (for example, as a result of the hydrostatic gradient).

Thomas and Winner (2002) made direct measurements of gas exchange of Douglas-fir at Wind River and found that net CO_2 assimilation (*A*, expressed on a leaf area basis) was greater for old trees compared with saplings. In contrast, Bauerle et al. (1999) found no significant difference in gas exchange (again on a leaf area basis) of a different set of old and young Douglas-fir trees at the same site. Carbon isotope measurements in top-of-canopy foliage of Douglas-fir at Wind River provide a different perspective (Bauerle et al. 1999, Fessenden and Ehleringer 2002, N.G. McDowell, Oregon State University, unpublished observations). Fessenden and Ehleringer (2002) concluded that the isotope data, in conjunction with measurements of leaf nitrogen (Klopatek 2002) and

photosynthetic capacity (N.G. McDowell, personal communication), indicate that time-averaged stomatal limitation to photosynthesis increases with tree age. Similar changes in isotope discrimination with tree age have been reported for Pinus ponderosa Dougl. ex Laws. (Yoder et al. 1994), P. aristata Engelm. (Schoettle 1994), Quercus garryanna Dougl. (N. Phillips et al., Boston University, Boston, MA, unpublished observations) and Nothofagus solandrii (Hook.f.) Ørst. (D. Whitehead, Manaaki Whenua Landcare Research, Canterbury, N.Z. and M.G. Ryan, Rocky Mountain Experiment Station, Fort Collins, CO, personal communication). The isotope data reflect assimilation-weighted discrimination against ¹³C (i.e., the time-average ratio between CO₂ internal to the leaf and at the leaf surface) that occurred during the time that leaf carbon was fixed. These data may differ from measurements obtained with gas analyzers during the times of day and weeks during the year when maximum photosynthesis occurs, as in the studies of Bauerle (1999) and Thomas and Winner (2002). For example, Yoder et al. (1994), who compared old with young-mature ponderosa pine trees, reported that maximum A and stomatal conductance (g_s) were similar, although time-averaged A and g_s as well as C isotope discrimination were lower in old trees than in young trees.

Moving to larger scales of organization, canopy structure and growth change significantly as trees grow older. New leaf development is primarily at canopy tops in young conifers (Sprugel et al., symposium abstracts). Similarly, profiles of canopy structure measured with Lidar (Lefsky and Parker, symposium abstracts) and light profiles in canopies (Parker et al. 2002) show that canopies of young conifer forests are "top heavy," and gradients of light extinction are steep. In older forests, the development of new foliage is distributed more evenly and light penetrates more deeply through the crowns. These observations raise questions about structure-function relationships: is the change in foliage production a function of tree size and age, with light gradients changing as a consequence, or do light gradients in older forests cause the shift in patterns of foliage development? Possibly the cause and effect relationship occurs in both directions. The changes in canopy structure with age are also likely to affect patterns of throughfall and interception. The chronosequence studies being conducted by Van Pelt et al. (symposium abstracts) should provide more insights into these processes.

It has often been noted that aboveground net productivity (ANPP) decreases as forest stands grow older (e.g., Gower et al. 1996, Ryan et al. 1997, Janisch and Harmon 2002, Waring and McDowell 2002). Acker et al. (2002) showed that increases in mortality are of a similar magnitude to decreases in ANPP in aging Douglas-fir forests in western Oregon, so mortality and ANPP each accounted for about half of the decreased accumulation of bole biomass with age. The cause of reduced ANPP in aging forest stands remains enigmatic. Phillips et al. (2002) found some evidence for hydraulic limitations (Ryan and Yoder 1997), but other measurements were inconclusive. On the other hand, Latham and Tappeiner (2002) report significant increases in radial growth in old-growth Douglas-fir and ponderosa pine following thinning, indicating

that old trees of these species are not inherently "decadent."

Changes in carbon sequestration with age do not necessarily occur in parallel with changes in ANPP. Soil respiration was much higher in young stands than in old stands in the chronosequence at Wind River (Klopatek 2002), probably because of the large stores of carbon in soil and woody debris from previous stands at the sites. Eddy covariance measurements of ecosystem gas exchange also indicated much higher respiratory losses of carbon in younger forests than in older forests (Chen et al. 2002). Model results and allometric measurements in a chronosequence of 37 stands suggest that net ecosystem productivity shifts from negative to positive at Wind River when forests are 20–30 years old (Janisch and Harmon 2002). At this age, growth efficiency (biomass accumulation per unit leaf area) of trees is near its peak, and more than double that of old-growth trees (N.G. McDowell, personal communication).

The articles in this journal issue suggest many potential interactions among the structural and functional changes in aging forests. For example, carbon isotope measurements at Wind River indicate that water-use efficiency of overstory trees increases substantially with age (Fessenden and Ehleringer 2002); eddy-covariance measurements, on the other hand, suggest the opposite trend for whole-ecosystem water-use efficiency (Chen et al. 2002). It is likely that greater soil respiration in the youngest stand accounts for much of this discrepancy; the discrepancy also raises additional questions. Do changes in forest structure, which result in deeper penetration of light into the canopy of old-growth forests, have an impact on water use by lower canopy strata and understory vegetation? How do changes in vertical light gradients in aging stands affect gross primary production? Does the abundance of heavily lignified astrosclerids in needles of old-growth trees affect rates of litter decomposition (and potentially nutrient availability) or the palatability of foliage to herbivores? Our hope is that these articles will raise many more questions for readers and thereby help stimulate and focus future research.

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