

FOREST SUCCESSION RESEARCH IN THE
PACIFIC NORTHWEST: AN OVERVIEW

by

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ABSTRACT--Papers from this symposium volume illustrate several important trends in successional research. These include: development of a quantitative data base from age structure analyses and stand reconstructions, stratification of successional research by habitat types, recognition of multiple successional pathways on a given site, increased attention to disturbances at all scales of frequency and intensity, and development of computer models which synthesize existing information and provide predictions of successional rates and directions. Important topics in successional research that are poorly represented in this symposium include chronosequence studies and use of stand structure analyses and permanent sample plots. Key needs in future successional research include: establishment and use of permanent sample plots and transects, spatial and temporal patterns of tree mortality, roles of coarse woody debris, models of early successional stages, and manipulative experiments to test specific hypotheses. A general successional paradigm is offered based upon the life histories of available species, environmental conditions, and disturbance patterns, including stochastic elements in each of these components. The general formulation can be applied operationally by utilizing models such as JABOWA and FORET.

KEYWORDS--stochastic processes, plant succession, age-structure analysis, stand-structure analysis, wildfire, natural disturbance, permanent sample plots, tree mortality, coarse woody debris, forest succession models.

Papers in this symposium illustrate very well the active state of forest succession research, activities that cover theory, field studies, and development of simulation models. In this paper I will try to synthesize some of the more important trends and concepts that have been presented, indicate some of the current research missing from the symposium, and outline some remaining research needs. I will conclude with my current views on a successional paradigm and the importance of models in successional research.

TRENDS

Several important trends are apparent in today's presentations. First and foremost is the move away from inference and anecdotal accounts of succession toward a quantitative data base. Much of this information is being gathered in age structure analyses and stand reconstructions. Surprisingly, these analyses are providing some important new insights into forest types that we thought we knew very well. Examples are the papers on coast redwood (*Sequoia sempervirens*) by Veirs (1982), the paper on Douglas-fir (*Pseudotsuga menziesii*) by Means (1982), and the one on eastside mixed-conifer forests by Larson (1982b) (see also Larson 1982a).

Another obvious trend is the stratification of successional information by sites or environmental types. This is apparent in Thornburgh's (1982) presentation on the mixed evergreen forest of the Siskiyou Mountains and Arno's (1982) presentation on secondary succession on four forest sites in Montana as well as the papers by Henderson (1982), Pfister (1982),

Stage and Ferguson (1982), and Zamora (1982). Obviously, habitat types are a common basis for stratification.

Successional research is beginning to concern itself more with the forest understory as well as with the age- and size-structures of the trees. Papers by Zamora (1982) from the northern Rocky Mountains and by Alaback (1982) for coastal Alaska forests illustrate this attention. Understory development has, of course, important implications for livestock and for wildlife, especially ungulates.

Many papers recognize the possibility of multiple successional pathways on the same site. I suspect that this is not a new concept, but at least it is having a rebirth of recognition. Scientists no longer think in terms of one possible sequence for a given site. The existing vegetation, disturbance type and intensity, and other factors play a major part in determining the particular successional track. These concepts are very clearly seen in the papers by Arno (1982), Thornburgh (1982), Smith (1982), and Larson (1982b).

Disturbances on all scales are now recognized as important in viewing successional phenomena. These occur in many forms including wildfires which may burn only portions of stands, leaving a variety of age classes as reported by Means (1982), or as larger fires which allow the escape of only a few large, fire-resistant individuals and lead to generation of younger stands. The natural fire regime on the northern California coast results in an all-aged coast redwood component and a Douglas-fir component of several distinct age classes (Veirs 1982). Catastrophic windstorm, insect epidemics, disease (see, e.g., Cook 1982), and floods (including mudflows) often generate successional patterns that contrast sharply with those developed following wildfire. Tree species represented in the understory, such as western hemlock (*Tsuga heterophylla*) on the west side and grand fir (*Abies grandis*) on the east side, have an advantage following windthrow but generally will be heavily impacted by even the lightest of wildfires.

Disturbance frequency can be as important a variable as disturbance intensity as pointed out by Martin (1982) in the case of wildfire. An excellent example of how disturbance frequency determines the successional pathway is provided by Kessell (1981). Mixed forests of quaking aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), ponderosa pine (*Pinus ponderosa*), Douglas-fir, spruce (*Picea glauca* x *engelmannii*), and western larch (*Larix occidentalis*) develop on a site type in Glacier National Park under normal fire frequencies. Aspen or lodgepole pine or both can be eliminated from the site and the amount of western larch drastically increased by varying frequency of disturbance.

Computer models are increasingly a major element of current successional research efforts as pointed out by West et al. (1982). This is probably the most important single trend of any identified here, perhaps because it involves more than simply more sophisticated natural history research. Computer models are allowing us to synthesize information, develop and test hypotheses, and provide predictions about successional directions and rates. Pfister (1982) indicates clearly some ways these models can be designed to meet managers' needs. The diversity of such modeling

efforts is indicated by this symposium which includes papers on long-term stand simulations (Hemstrom and Adams 1982), regeneration modeling (Stage and Ferguson 1982), and landscape-level simulations (Reed 1982).

I am in strong agreement with comments made by Smith (1982) and by Oliver (1982) in this symposium. It is important that we avoid semantic arguments and, as a generality, simply define our terms when we use them. The semantic difficulties that arise can be illustrated by the concepts of pioneer and climax species which are often equated with tolerant and intolerant species. Depending on the circumstances (and the definitions) a very intolerant tree species, such as ponderosa pine, can not only be the pioneer but also the climax species for the site. Successional roles vary from situation to situation and are not a physiological characteristic of a tree.

A second admonishment is to maintain an open mind. There seems to be a tendency to look for one ruling doctrine, such as a singular cause for succession. In fact there are many causes and many aspects to successional phenomena. There are many winning strategies for organisms, many ways in which they can make a living; and patterns of vegetation development reflect these infinite possibilities. The caution against simple (single) mindedness is a most critical one for ecological researchers. Examples of potential traps include the arguments about the relative importance of initial and relay floristics in succession (McIntosh 1980) and generalizations about r- and k-selected species (Harper 1977). In the first case it is intuitively obvious that either strategy can dominate in a given situation and that many, and perhaps most, forest seres will be a mixture of both. The desire to generalize about genetic selection for species adapted to open (early succession) and competitive (late succession) environments has led to concepts of r- and k-selected species that certainly don't hold up well in the case of tree species. Large seeds, for example, are not associated primarily with late successional species as is predicted by the generalization nor are pioneer trees necessarily characterized by small seeds.

UNDERREPRESENTED TOPICS

A symposium of this type cannot review all important successional information and research in a region as large as the Pacific Northwest. And some important studies are, of course, simply not yet underway. In reviewing these poorly represented topics we can begin with the several research methods outlined by Oliver (1982). These include the use of chronosequences, inferences from stand structure, permanent sample plots, and reconstructions of stand history, including age structure analyses.

Size structure analyses have received little discussion in this symposium especially considering how heavily they have been used in the past. Inferences from size class analyses have provided us with most of our knowledge on the successional status of various tree species in various environments. Certainly size-structure analyses have been misused. Interpretations have often assumed a close relation between size and age, a relationship frequently disproved. Gross misconceptions can arise as illustrated by Oliver and Stephens (1977).

Nevertheless, useful ecological inferences do not necessarily depend upon high age-size correlations. When abundant, vigorous seedlings, saplings, and poles of grand fir are encountered under an overstory of ponderosa pine, age data would probably add little ammunition to a prediction of eventual replacement of pine by fir. Many studies show us how useful size-structure analyses can be. We don't want to forget this valuable tool or discount it in the face of more sophisticated techniques.

One notable absence from all the papers was the use of permanent sample plots to develop successional information. I'll have more to say about this later.

Several of the most important forest types in the Pacific Northwest are poorly represented in this symposium. Henderson (1982) reported the only work on Douglas-fir-western hemlock forests typical of much of western Oregon and Washington. Substantial research has been completed or is in progress on these forests and is producing important new information. Wierman and Oliver (1979) have looked at developmental patterns in young mixed stands. Age structure analyses of old-growth forests (Franklin and Hemstrom 1981) have led to the surprising discovery of a wide age range in dominant Douglas-firs. The age range appears to vary with episode; e.g., they are wider in forests burned 400 to 500 years ago than in those burned approximately 250 years ago. Numerous explanations for the age ranges are under study. Agee et al. (1981) are using a chronosequence of stands in the Olympic Mountains to examine post-wildfire succession in plants and animals with the 1978 Hoh Fire as the zero point. The lack of rehabilitation and salvage logging at this site makes it exceptionally valuable for research. Hemstrom (1979) examined the fire history of temperate and subalpine forests at Mount Rainier National Park as well as the flammability of various habitat types (Hemstrom 1980). Swanson (personal communication) and Henderson (personal communication) are doing similar studies in the central Oregon Cascade Range and on the Olympic Peninsula, respectively. Probably the most important post-logging successional research is associated with long-term plots established by Dyrness (1973) at the H. J. Andrews Experimental Forest in the western Oregon Cascade Range; more about these later. Despite all of this activity, much remains to be learned about these very important Douglas-fir-western hemlock forests.

Similarly, little has been presented at this symposium on current successional research in other important forest types: subalpine true fir-hemlock (Pacific Silver Fir Zone); coastal Sitka spruce (*Picea sitchensis*)-western hemlock (Sitka Spruce Zone); and red alder (*Alnus rubra*). Many studies of the Douglas-fir-western hemlock forests also cover subalpine types (e.g., Hemstrom 1979 and Agee et al. 1981). Henderson's (1982) report to this symposium includes a Pacific silver fir habitat type. In addition to Henderson two other Forest Service area ecologists (Hemstrom and Brockway, personal communication) are concentrating much of their work in the Pacific Silver Fir Zone. Substantial successional research at the University of Washington is concentrated in this zone as exemplified by Oliver et al. (1979). Alaback's (1982) research focuses on Sitka spruce-western hemlock forests in Alaska. These forests are also under study on the alluvial terraces of the western Olympic Peninsula (e.g., McKee, LaRoi,

and Franklin 1980) following up on Fonda's (1974) pioneering research. The importance of rotting logs in regeneration of the dominant tree species is apparent in these superhumid forests. These forests also illustrate how a species, Sitka spruce in this case, can alter its ecological role on different sites within a vegetation zone. It is generally a seral species in forests of the coastal zone but appears to be a climax component on alluvial habitats. Red alder stands are receiving research attention despite the lack of reports in this symposium. Stubblefield and Oliver's (1978) study of mixed alder-conifer stand development is an example.

NEEDS FOR RESEARCH ON FOREST SUCCESSION

Many important research needs exist in the area of forest succession. My candidate for the most important is the establishment and use of permanent plots and transects. A very few permanent sample plots exist in the Pacific Northwest. The oldest plots in old-growth forest are those established as recently as 1947 on the Thornton T. Munger Research Natural Area in the southern Washington Cascades. Another major set of relevant permanent sample plots are the mensurational plots established in relatively young stands by the USDA Forest Service during the early decades of this century (Williamson 1963). Most of these plots have since been lost to logging, road construction, and other activities but the existing plots are proving to be valuable in various ecological research projects. An example is Sollins' (1982) use of the plots in studying rates of mortality in natural stands.

A program in the establishment, maintenance, and use of permanent sample plots has been established at Oregon State University, part of which is funded by the National Science Foundation under the Long-Term Ecological Research Program. One large set of plots archived under this program was established to study successional development following logging of Douglas-fir-western hemlock forests. This set includes more than 200 plots established prior to logging (Dyrness 1973) and measured at frequent intervals now extending over 18 years following logging. Another set of permanent plots are the reference stands established over a broad array of forest age classes and environmental conditions. Locations include H. J. Andrews Experimental Forest, Mt. Rainier, and Olympic National Parks, and many Research Natural Areas. Reference stands are typically areas of a hectare or more that are gridded for mapping and measurement of live trees, snags, and logs (see, e.g. Hawk et al. 1978 and Franklin 1980). These reference stands and systematically spaced 0.1 hectare plots, designed for systematic sampling of entire tracts, are being established over a variety of habitats within the H. J. Andrews Experimental Forest as well as in Research Natural Areas representing a variety of forest types from Sitka spruce to ponderosa pine.

Many other plot series in the Pacific Northwest can be utilized in ecological studies although the focus is typically on mensurational, silvicultural, or timber inventory objectives rather than ecological objectives. Examples include plots established as part of the cooperative levels-of-growing-stock (LOGS) study, fertilization plots established by University of Washington scientists and cooperators, plots established in young conifer stands at the Black Rock

Forest by Oregon State University, forest growth plots established by State and industrial landowners, such as the Washington Department of Natural Resources and Weyerhaeuser Company, and inventory plots of the USDA Forest Service on private and National Forest lands. This wealth of forest plots should not obscure the need for establishment of ecologically oriented successional plots because forest growth plots typically lack key information even when they are in the right vegetation types or locales; ecologists do need to be aware of this resource, however.

Many more sample plots are needed to provide definitive successional data sets. We can build all of the "quick-and-dirty" or "slow-and-precise" successional models, and make all of the short-term studies we want; but the only real proof of our predictions is to observe the actual development of forest stands over time.

Mortality is another critical area for successional research. Efforts to develop successional simulation models make very clear our limited understanding of how mortality really occurs in forest stands. It would seem that, after many decades of research, foresters would have a good understanding of mortality but this is not the case. When does mortality occur singularly and when episodically? How does mortality relate to stages in stand development. To particular tree species? What are the direct agents of mortality? What proportion of the dead trees are standing and down? Graham (1981) has recently made a contribution to this topic with her analysis of probabilities regarding toppling versus standing death of trees in intact stands and with some surprises; larger trees are less likely than small trees to die as windthrows. Nevertheless, research efforts so far are a fraction of what is needed. These questions are central to our understanding of successional dynamics in northwestern forest stands.

Successional roles and temporal patterns of coarse woody debris are another research need. This was alluded to in the discussion of standing dead and down trees. We need to be able to track dead organic material as well as the live components since coarse woody debris is important for seedbed, in nutrient cycling, as wildlife habitat, and for stream functioning (see Franklin et al. 1981). Consequently, successional models will have to simulate dead organic matter as well as live in order to answer many ecological and management questions. Again, Graham (1981) has made a significant contribution by developing a model of woody debris in a Douglas-fir--western hemlock sere at the H. J. Andrews Experimental Forest in the central Oregon Cascade Range. Sollins' (1982) study of input rates for coarse woody debris is a pioneering effort that makes use of several sets of permanent sample plots.

Models of early successional stages designed to simulate stands from bare ground to maturity and senescence are another important research need. The biological and environmental complexity involved with such models is a major problem. The combined size and complexity of both regeneration and stand models suggest that they will have to be handled separately in simulations designed to track forests for one or more centuries. Furthermore, the large number of factors involved in early succession and tree regeneration and their widely varying importance from location to

location will probably require development of rather specific models. In effect, a highly predictive general model of early succession is not likely.

Finally, many more descriptive and experimental studies are needed. These include stand reconstructions, study of chronosequences, and manipulative experiments designed to isolate individual factors. We need to know more about successional processes in natural stands, on typical sites, with various species mixtures, and after various types and intensities of management actions and natural disturbances. Simply getting the basic information on a few of the most common situations is a very large job. We need to know what is really out there, how it is behaving, and why.

A SUCCESSIONAL PARADIGM

I would like to conclude with some comments on a successional paradigm and the importance of models in successional research. Any general theory of succession has to accommodate a very broad array of phenomena. The variables include time scale, organisms, environments, disturbance types and regimes, and dominant successional processes. Experience shows that successional theory developed solely from study of one ecosystem is almost invariably going to be a special case, inapplicable in detail, to another ecosystem.

Several successional features are common to a broad array of ecosystems. These observations are not original but perhaps need reiteration. One feature is that at the finest scale of resolution, the number of potential seres on a site is infinite, and any one sere is unique and unreproducible. Succession is perhaps the outstanding case of "you can't go home again" because the circumstances surrounding the original sere can never be exactly reproduced. Nevertheless, because of varying probabilities for different types of seres, repeating or general successional patterns can be defined for the ecosystems on many sites. Another commonality is that all mechanisms of succession (competition, facilitation, tolerance, inhibition) are operative but widely varying in importance in different seres. Similarly, both initial and relay floristics are appropriate to the description of particular successional sequences in many forest situations; seres are typically combined consequences of both initial and relay floristics.

A key question is: Can we make a general statement that encompasses the diversity of phenomena and incorporates information from the various subfields of ecology appropriate to succession (i.e., population biology, autecology, and synecology). I propose the following as an attempt at a general formulation. In this formulation:

$$\text{ecosystem change (succession)} = f \left(\begin{array}{l} \text{available species} \\ \text{life histories,} \end{array} \begin{array}{l} \text{environment (including disturbance),} \\ \end{array} \begin{array}{l} \text{stochastic elements} \end{array} \right)$$

This formulation implies an infinite array of possible outcomes, as well as paths, with some having much higher probabilities than others. Life history attributes of the available species include their reproductive behavior, physiological responses to environment (such as light and temperature conditions), growth habits, and timing and causes of mortality; i.e.

autecological and population aspects of the species. Environment includes such basic elements as moisture, temperature, nutrient, and mechanical (e.g., snow and soil mass movement) regimes. Disturbances can be recognized as a separate element, if they are insufficiently highlighted by inclusion in the environmental term. The disturbances can vary in type, frequency, and extent and can be either catastrophic or chronic, episodic or regular. Some disturbances, such as disease, may be dealt with as part of the species' life histories. The stochastic elements recognize that we are dealing with probabilities and not absolutes. We could, in fact, view seres as gigantic crap games, albeit games with loaded dice. Stochastic elements are, of course, parts of the life history and environment (including disturbance) terms. They include annual variations in climate and seed availability. We are reminded of those highly infrequent combinations of a good seed crop and favorable summer moisture conditions that allow ponderosa pine to become established in parts of the Southwestern United States. But some stochastic elements are distinct from the other terms of the formulation (e.g., the timing of a volcanic eruption) and inclusion of a specific stochastic term highlights the importance of chance elements in successional developments.

This construct appears to be the most succinct general statement that we can make about succession. Merits of the construct as developed in model form include its ability to incorporate: feedback mechanisms (e.g. plants to environment); periodic disturbances of appropriate type, frequency and intensity; an infinite number of seres; an array of ecosystems; site degradation or retrogression; all the successional mechanisms; and autogenic and allogenic influences.

The proposed successional formula is so general that it could well bring despair to ecologists. Fortunately, the formulation is the conceptual basis for an array of successional models, particularly the JABOWA-FORET model family, that shows it is possible to use the construct in both basic and applied research. Such models incorporate the three basic elements of the formula--autecological characteristics of the species, the environment of the site, and stochastic elements, such as in the birth of new trees and selection of trees for death. Collective or emergent properties of communities or ecosystems (e.g., productivity or leaf area) can be calculated or predicted on the basis of species demography, satisfying both the ecosystem and population biologist. Models can be collapsed or simplified for specific purposes (e.g., functional groups instead of species). Testable hypotheses can be developed and theory explored. For example, the importance of various successional processes can be compared in different ecosystems. General successional patterns associated with particular life history--environment combinations can be explored, e.g., tolerant and intolerant species pairs on mesic forest sites or desert shrubs in an arroyo. The role of absent species (unfilled niches) and alternative "winning" ecosystem or species strategies for the same environment can be explored. Simulations from such models can be used to define a concept, such as climax, in different ecosystems.

Models based on the successional formulation also integrate existing knowledge of ecosystem characteristics and behavior. A major benefit is

identification of critical gaps in knowledge, particularly when the model fails to simulate real-world behaviors.

The predictions of models based on the successional formulation are of special value in applied ecology. The individualistic nature of each sere is recognized and preserved. Yet, general patterns and variations can be identified along with their probabilities.

One peripheral advantage of providing outputs with varying probabilities is that we begin getting land managers, politicians, and the general public thinking in such terms. A major problem in land management, and one that results in excessive costs, is the tendency to think in terms of and seek absolute goals, such as establishment of tree regeneration. This can result in a manager spending hundreds of dollars per acre to artificially regenerate a forest stand even when there is a high probability of natural regeneration.

In summary, a general statement about succession that encompasses the variability encountered in nature is possible, but its generality greatly reduces its usefulness. Simulation models can provide the mechanism for applying the general construct to real-world situations as well as in theoretical explorations of successional processes.

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