MODELING SHRUB SUCCESSION FOLLOWING

CLEARCUTTING AND BROADCAST BURNING

Penelope Morgan and L. F. Neuenschwander

ABSTRACT: This conceptual model of early seral shrub succession following clearcutting and broadcast burning synthesizes ideas from previous research and modeling approaches into a simple diagrammatic model of the critical successional influences and processes. Illustrative examples are drawn from observations of successional development following high-and low-severity burns on the *Thuja plicata/Clintonia uniflora* habitat type in northern Idaho.

INTRODUCTION

The general trend in the study of succession following fire is from natural history descriptions to quantitative models that yield predictions of community development. The study of shrub succession in northern Idaho is a typical example.

Early seral shrub development following fire in the moist cedar-hemlock forests of northern Idaho was described by Leiberg (1900) and has since been studied in detail by Mueggler (1965), Lyon and Stickney (1976), and others. Shrubs rapidly invade burned areas and may dominate a site for many years (Mueggler 1965). Large-scale fires in the early 1900's created many shrubfields that provided abundant browse for big game. This prompted many studies, particularly of the shrub species important for big game forage. Early descriptions of succession following fire were general, seldom quantitative, often limited to one or two species, and usually poorly documented. Information useful in drawing a cohesive understanding of the factors affecting shrub succession is therefore often scattered, unpublished, incomplete, or otherwise unavailable.

Existing models that predict change in forest understory communities are often unsatisfactory to meet more than the specific needs for which they were developed. The goal of this report is to review some of these models and their limitations and to present a general conceptual model for early shrub succession.

Development of our model draws heavily on the previous work of Lyon and Stickney (1976), the existing literature, and our documentation of shrub succession following clearcutting and broadcast burning. We have been studying shrub succession following clearcutting and burning of dense coniferous forests on the *Thuja plicata/Clintonia uniflora* habitat type (Cooper and others 1983) in northern Idaho. Here, early seral communities are often dominated by shrubs that establish themselves immediately following fire. Native forbs and grasses do not have the potential to dominate the site and the forb/grass stage of succession is short lived. Forbs are common, and grasses are uncommon in this habitat type. More than 30 different shrub species grow on the habitat type, many of which are critical to timber and wildlife resource management.

We are building a simulation model based on the conceptual model presented here. The simulation model will predict regeneration, establishment, and subsequent changes in species composition in the early seral shrub communities that develop following high- and low-severity burns.

Ecological impact of fire on understory vegetation depends on burn severity. Severity is a function of the total fuel consumed by fire, a reflection of both total heat produced and duration of heating of the soil surface. We evaluated burn severity using visual criteria based on litter and duff consumption, evidence of mineral soil alteration due to heating, and size and depth of char on large woody fuels remaining after the burn. These criteria are similar to those developed for depth of char (Ryan and Noste, in press) and depth of burn (Rowe 1983). Burn severity may be unrelated to fire intensity. Fire intensity refers to maximum above-ground heat pulse and principally depends on consumption of fine fuels. In contrast, the degree of soil heating depends on consumption of duff and large woody fuels. Burn severity affects response of understory species and cambial damage to tree boles and roots more than fire intensity does.

PREVIOUS MODELS

Most existing forest successional models include only trees. If understory vegetation is considered, it is only by general growth form (Shugart and West 1980). The model of Bartos and other (1983) is a good example. Understory development affects aspen and conifer succession in

---

Paper presented at the Symposium on Fire's Effects on Wildlife Habitat, Missoula, Mont., March 21, 1984.

Penelope Morgan is Doctoral Fellow and Leon F. Neuenschwander is Associate Professor, Department of Forest Resources, University of Idaho, Moscow.

this model; however, all understory species are grouped into shrub and herb components. More detailed descriptions of understory successional dynamics are needed in many disciplines. These descriptions should include changes in community structure, species composition, and growth rates of important understory species (Pfister 1982).

The stand prognosis model (Stage 1973; Wykoff and others 1982) predicts forest vegetation development following stand disturbance. It applies primarily to trees, but one can predict percent canopy cover, biomass, and height of some important understory shrub and grass species. The predictions are based on regression equations developed by Irwin and Peek (1979). Extensions to the model are being developed to predict total shrub cover, probability of establishment, percent canopy cover, and height of 42 shrub species (Laursen 1984). The regression equations were developed from empirical data collected in various forest habitat types and stand ages under different site conditions, tree stand densities, and types of disturbance (Stage 1973; Wykoff and others 1982). The regression approach is fairly easy to use as it does not require inclusion of mechanistic relationships, but it is data intensive. Predictions may have limited reliability for stand conditions, areas, or treatments other than those included in the original data base. The stand prognosis model does not consider the influences of severity of fire disturbance or existing understory vegetation on successional development.

The forest habitat type classification system provides a common means of stratifying the physical environment and is, therefore, a logical framework for studying secondary succession (Arno 1982). The secondary succession classification systems being developed by Arno and Simmerman (1982) and Steele (Steele and Geier-Hayes 1982) are diagrammatic models of tree and understory succession on selected habitat types in Montana and Idaho. Both approaches allow for different pathways of successional development depending on the nature of disturbance and initial stand conditions. However, neither is quantitative and neither identifies causal factors of observed successional patterns.

Recent descriptions of succession emphasize the influence of initial stand and site conditions, nature of disturbance, and life history characteristics of individual species as determinants of the multiple pathways of succession following disturbance. These include models based on the vital attribute concept of Noble and Slatyer (1980), and the JABOWA model (Botkin and others 1972) and its derivatives.

Vital attributes are those life history characteristics of a species that determine disturbance response. They include means of arrival and persistence, establishment, and timing of critical life stages (Noble and Slatyer 1980). The approach provides a conceptual framework for predicting response of individual species to disturbance based on general ecological and morphological characteristics. These characteristics are known for many understory species for which more detailed autecological data are unavailable. Local applications have been to trees only, including models of tree succession following fire in Glacier National Park (Cattelino and others 1979) and some forest communities in Montana (Kessell and Potter 1980). Multiple pathways of succession depend on vegetation existing before disturbance and the fire return interval. These and other vital attribute models (Noble and Slatyer 1980; Noble 1981) are diagrammatic, but the approach need not be limited to nonquantitative applications. Kessel and Potter (1980) provided general predictions of abundance for common understory species.

JABOWA and its derivatives are forest gap regeneration models (Shugart and West 1980). Predictions of regeneration, establishment and changing species composition of trees through time are stochastic. Life history characteristics of individual species determine successional development. Despite simplistic representations of growth and competition, the models have been successfully adapted to many forest ecosystems and a variety of disturbances (Shugart and others 1981). This illustrates the importance of recognizing the influence of disturbance, existing vegetation, and individual species characteristics on the major processes of regeneration and establishment. The models do not include understory species or effect of severity of disturbance.

The BRIND model (Shugart and Noble 1981) predicts successional dynamics following fire in Australian forests. It is derived from JABOWA but differs by including fire intensity effects on tree regeneration and mortality. Fire kills trees directly by scorching crowns or increasing susceptibility to other sources of tree mortality in the model. Germination of tree seeds is enhanced or stimulated by fire depending on fire intensity. This model thus recognizes that not all fires have the same ecological impact on ecosystems. Although fire intensity and severity both affect fire damage of trees, severity would be a better indicator of seed germination effects and some of the tree mortality factors. Species characteristics are important in the model, but the vital attribute approach is not specifically incorporated in the BRIND model.

Two particularly useful conceptual models applicable to shrub succession are those of MacMahon (1980, 1981), developed as a general model of succession, and Lyon and Stickney (1976), developed to describe succession following northern Rocky Mountain wildfires. Both emphasize the importance of on- and off-site propagule sources; the processes of survival, dissemination, and establishment; and the importance of individual species characteristics as determinants of the pattern of successional development.

The variety of modeling approaches reflects recognition of need for predictions of early succession following forest disturbance (Pfister 1982; Franklin 1982), yet few theories have been advanced to describe the causes of early successional patterns (Zamora 1982). Modeling of early succession in forests has been largely avoided due to its apparent complexity. Large numbers of species are involved, autecological data for even the most important species are often lacking, and species exhibit a wide array of life-cycle strategies (Zamora 1982). Few models of understory succession exist, as there is a belief that once communities reach the forest stage, the sequence of successional events becomes more predictable.

Early succession is neither too complex nor too variable to defy prediction. Previous research and modeling attempts have identified critical successional influences and useful approaches to handling them in a modeling context. Identifying critical life history characteristics of successional species (Gill 1977, 1981; Naveh 1975; Noble and Slatyer 1980; Rowe 1983); stratifying environments by habitat type (Arno 1982; Arno and Simmerman 1982; Stage 1973); and describing differential species response to burn severity (Rowe 1983) provide means to reduce variability and allow prediction. Availability of these ideas has greatly simplified our conceptual development to one of synthesis. We have combined the best characteristics of previous research and modeling approaches into a simple conceptual model of shrub succession following clearcutting and burning.

CONCEPTUAL MODEL

Our model of early succession (fig. 1) is briefly outlined in an overall description of the linkage of major successional processes and influences. More detailed treatment of successional processes included in the model follows in subsequent sections. A separate section is dedicated to the role of chance and our incorporation of stochastic and deterministic approaches into the conceptual model.

Those propagules (seeds, buds, rootstocks, and others) that survive disturbance on-site or are disseminated from off-site sources give rise to the initial flora. The initial flora includes those species available for colonizing the site following disturbance. The likelihood that the initial flora includes a particular species depends on environmental conditions (e), existing vegetation (v), and chance (c). Through the process of ecesis (Clements 1916), some of the initial flora establish and grow to form the vegetation in the first year after disturbance(s). Individuals may establish whenever suitable conditions for ecesis occur in the years following disturbance; however, establishment is limited to the first year following clearcutting and fall broadcast burning on the *Thuja plicata/Clintonia uniflora* habitat type. The process of ecesis is strongly influenced by burn severity (b), life history characteristics of individual species (l), and chance (c). Change in vegetation from the first year (S_1) to subsequent years (S_N) is the result of growth and the biotic interactions that affect growth. Growth and biotic interactions are affected by chance (c) and the life history characteristics of the successional species (l).

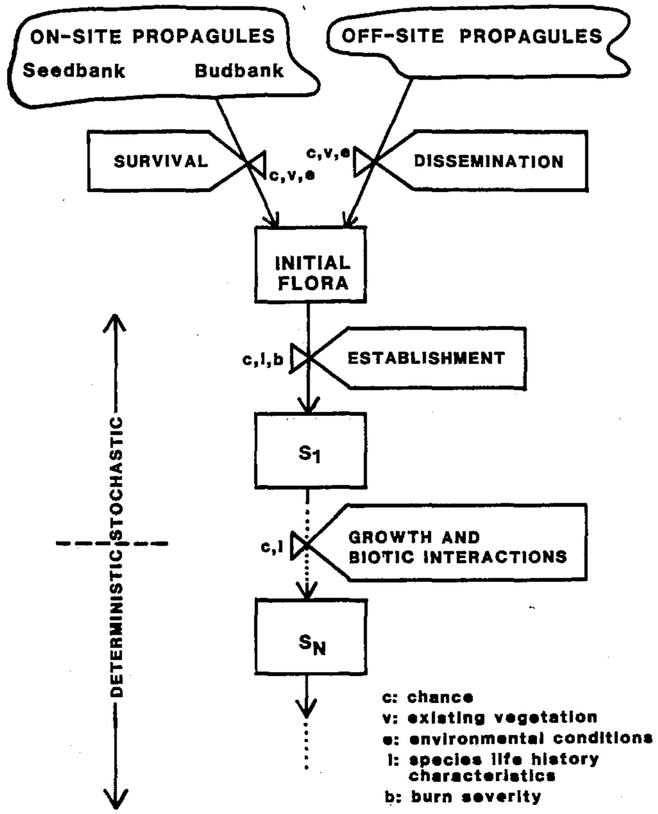

Figure 1.—Conceptual model of shrub succession following clearcutting and broadcast burning. The initial flora includes those species available for postburn colonization. It consists of those propagules surviving the burn on-site and those disseminated from nearby off-site areas. Species composition of the initial flora depends on chance (c), the vegetation existing before disturbance (v), and environmental conditions (e). Some of the initial flora establish to form the first year shrub community (S_1). The establishment process is affected by chance (c), life history characteristics of individual species (l), and burn severity (b). After establishment, changes in shrub communities to those of subsequent years S_N are the result of growth and biotic interactions. These processes are strongly influenced by chance and the life history characteristics of individual species.

The major postburn successional influences identified in the conceptual model are environmental conditions (e), existing vegetation (v), burn severity (b), life history characteristics of species (l), and chance (c). Environmental effects include physical site conditions such as soil conditions, elevation, slope, aspect, and forest habitat type. Tree canopy closure and seed bank and live shrub species composition of the forest vegetation existing before clearcutting may strongly influence successional development. Life history characteristics of species that affect disturbance response include possible reproductive modes, intrinsic growth rates, longevity, and shade tolerance. Burn severity affects the potential contribution of various reproductive modes to postburn regeneration, establishment and growth of species. Chance plays an important role in all early successional processes.

We incorporate the effect of chance on succession through stochastic modeling in addition to deterministic approaches. Shrub community dynamics in the first few postburn years are modeled stochastically. These include the processes of determination of the initial flora, establishment, early growth, and biotic interactions. Subsequent changes in shrub communities are represented deterministically.

On-site Propagule Sources

Understory vegetation is usually top killed by fire; therefore, most understory vegetation is adapted to regenerate after fire. Sources of regeneration are of two general types: on- and off-site (Lyon and Stickney 1976), which have also been called residuals and migrants (Clements 1916; MacMahon 1980, 1981). On-site sources may be dormant buds on surviving plants parts (the "bud bank") or dormant seeds stored on site in duff and surface soil (the "seed bank") (Roberts 1981).

The above ground parts of understory plants are usually partially or totally consumed and the cambial tissue killed or damaged by fire; however, the root system and subsurface plant parts may survive even intense fires. Understory vegetation commonly resprouts from previously dormant buds on rhizomes, root crowns, bulbs, corms, and other plant parts (Gill 1981; Heinselman 1981). Postburn sprouting is widespread in ecosystems worldwide (Keeley 1981). Postburn shrub growth from sprouts is often abundant and vigorous, particularly for low shrubs such as *Rosa, Symphoricarpos,* and *Spiraea* (Lyon and Stickney 1976). Root crown sprouting has been called the most important fire survival adaptation for northern Rocky Mountain shrub species (Lyon and Stickney 1976). It is particularly important for tall shrubs such as *Acer, Salix, Alnus,* and others (Lyon and Stickney 1976). Severe or deep burns, those that consume organic layers and heat the soil surface for some time, result in reduced sprouting response (Flinn and Wien 1977; Ohmann and Grigal 1979; Rowe 1983). This is likely due to direct lethal heating of the plant tissues but may also be due to changes in the postburn microenvironment such as soil water and temperature regimes or nutrient availability (Heinselman 1981). Generally, on-site seedling or sprout regeneration occurs even on severe burns (Heinselman 1981).

Seed banks may contribute significantly to postburn regeneration (Archibold 1979; Roberts 1981; and others). Seeds may lie dormant on site for many years, often through an entire successional cycle. For instance, many *Ceanothus* species apparently produce abundant seed beginning shortly after establishment. These accumulate in the soil until dormancy is broken, often by heat from fire (Gratkowski 1973). Postburn seedling regeneration from seed bank sources may be very abundant. We found that eight of 12 common and abundant shrub species on the *Thuja plicata/Clintonia uniflora* habitat type relied on seed banks for postburn regeneration (Morgan and Neuenschwander, in preparation). Live fruiting shrubs of these mostly shade-intolerant early successional species were not present in the undisturbed forests, nor is off-site dispersal likely (Morgan and Neuenschwander, in preparation). Thus, the majority of seeds in the duff and soil seed bank must have been produced on-site in a previous shrub stage.

Some seeds are specifically adapted to lie dormant until stimulated to germinate by heat from fire or the changed postfire environment. Germination of *Ceanothus* species is stimulated by heat scarification (Gratkowski 1973). *Ribes* (Quick 1956) and other species appear similar in their germination response to fire. Seeds of other species that lack specific adaptations for heat tolerance may survive fire by chance. The seedbed created by fire is seldom uniform. Even severe fires often leave small islands of unburned or only partially consumed duff. Seedling composition on such microsites is often different from that on more severely burned microsites. Regeneration from seed banks may be enhanced by moderately severe fires (Heinselman 1981).

The on- and off-site propagules sources that predominate on a given site affect successional dynamics. On-site sources are immediately available and postburn response may be rapid as is the case when sprouting is abundant and vigorous. Off-site sources may be but are most often not as quickly available and abundant postburn.

Off-site Propagule Sources

Propagules may be disseminated from areas adjacent to burns by wind, animal, bird, or water vectors. Usually the propagules are small airborne seeds or fruits (Lyon and Stickney 1976). The importance of off-site sources to a particular species varies with availability of suitable vectors and proximity of flowering source plants in unburned areas within or at the edge of burns. These factors are highly subject to topography and chance. Therefore, the postburn abundance of vegetation with off-site origins may be highly unpredictable (Lyon and Stickney 1976).

Species vary greatly in their adaptations to dispersal. Occasionally, off-site sources enable species to be very abundant postburn, as is often true with *Epilobium* species. Generally, however, off-site sources lead to infrequent and continuous establishment through time (Lyon and Stickney 1976). Shrubs that have seed adapted for wind dispersal (such as *Salix, Acer, Betula,* and *Alnus* species) also rely heavily on sprouting for postburn regeneration.

Initial Flora

The on- and off-site propagule sources determine the initial flora, those species available for postburn establishment (Lyon and Stickney 1976). The composition of the initial flora is strongly influenced by environment, existing vegetation, and chance. The environmental conditions of the site influence successional pathways (Zamora 1982) by limiting the species potentially present on-site and in adjacent areas that might provide off-site sources of propagules. On-site sources are particularly affected by the vegetation existing before disturbance. Sprouting potential is a function of age and vitality of shrubs (Naveh 1975; Gill 1981). Thus, post-burn sprouting depends on the presence of vigorous shrubs in the undisturbed understory. Many of the species important in early seral shrub communities are shade intolerant and unable to exist under the closed canopy of the undisturbed forest. Such species will sprout if they are present in the stand before disturbance, but many rely on dormant seed stored on-site in duff and soil seedbanks. Stand history may affect seedbank composition. On-site propagule sources will be nonexistent if the time since on-site seed production exceeds seed longevity.

Many shrub species regenerate from more than one propagule source on a given site. *Salix scouleriana* may establish post-burn from root crown sprouts or from wind-blown seed (Lyon and Stickney 1976). *Rubus parviflorus* may sprout from rhizomes and regenerate from seed stored on-site in the seedbank. Establishment probabilities and early growth rates of seedlings and sprouts of the same species often differ greatly, hence it is useful to treat the reproductive modes of the same species as separate entities in the model until they become difficult to differentiate in the field. Seedlings and sprouts of the same species are probably sufficiently similar to be treated as equivalents in the model after the first few post-burn growing seasons.

Establishment

The species present in the first post-burn growing season will depend on the initial flora, but not all initial flora will survive and regenerate after fire. It is unlikely that establishment success will be proportionate to the abundance of propagules in the initial flora.

Successful establishment depends on the kind and severity of disturbance, mode of reproduction, and other factors, including weather, microsite conditions, and herbivory. Burn severity affects the overall postburn abundance of shrub seedlings and sprouts. Both rhizomatous and root crown sprouts are more abundant on low-severity than on high-severity burns. Burn severity reflects the potential damage to seeds and plant organs in the duff and soil (Flinn and Wien 1977). It also strongly affects the postburn microenvironment. Thus, burn severity may strongly influence the likelihood of establishment from both seed and sprout propagules.

In the simplest case, establishment is limited to immediately following fire. Virtually all important early successional species establish in the first postburn year (Lyon and Stickney 1976; Gomez-Pompa and Vazquez-Yanes 1981; Zamora 1982). No significant additional establishment of either shrub seedlings or sprouts occurred after the first growing season on the fall broadcast burns we observed. Immediate establishment of shrubs is similarly probable for productive sites where establishment is primarily from on-site sources. Factors affecting regeneration are particularly important influences on successional pattern when establishment is immediate and characteristics of the species that do establish may strongly affect the pattern of successional development for many years. For instance, the apparent forb, shrub, and tree "stages" of succession are the result, not of successive establishment and replacement, but of differential growth rates of species that establish simultaneously (Lyon and Stickney 1976).

Growth and Biotic Interactions

Shrub community dynamics subsequent to establishment are the result of survival and differential growth of individuals (Lyon and Stickney 1976). It is useful to treat growth and establishment as separate processes even if they occur simultaneously, which accommodates the site poor for establishment but favorable to growth (Stage and Ferguson 1982).

In our conceptual model, growth is expressed as net growth, including mortality. Biotic interactions include competition, interference, and any other influences of one organism upon another that contribute to differential growth and size potential. Growth and biotic interactions encompass all processes, including the innate characteristics of individual shrub species, which determine apparent dominance over time (Lyon and Stickney 1976).

The mechanisms of growth and biotic interactions are difficult to quantify. Growth is a function of intrinsic growth rate, competition, mode of reproduction, physical site characteristics, weather, time, and other factors. Chance plays a major role, contributing to the spatial and temporal variability of these effects. Early growth is especially subject to a variety of factors. A few of these can be identified and quantified. Others may best be treated as chance influences. In a model, this is accomplished through use of stochastic functions. Growth and biotic interactions may be adequately represented by simple stochastic equations as in JABOWA (Botkin and others 1972) and the many models derived from it (Shugart and others 1981).

Role of Chance

Chance plays an important role in succession (Franklin 1982). It affects every successional process, whether that effect is identified and quantified in the model or not. The role of chance can be represented in simulation models by random and probabilistic components. Models that incorporate such effects are stochastic. Predictions of stochastic models are not single, absolute numbers; instead, they consist of a range of numbers with associated probabilities that express the likelihood that a particular outcome will occur. Inclusion of a separate stochastic element in a model stresses the important influence of chance on successional pattern (Franklin 1982). Models are simplifications. The effort to build an accurate model forces an elucidation of the most critical processes and controlling influences of succession. Many less important effects must be excluded. Stochastic elements may be used in simulation models to represent the influence of some of these excluded effects. Thus, stochastic functions may be used in simulation models to represent both natural variation due to chance and variability due to other influences on successional processes than those included in the model.

Deterministic models are usually simpler and less expensive to execute than stochastic models. Stochastic predictions more realistically represent natural variability in postburn succession.

We believe that a combination of stochastic and deterministic approaches provides flexibility and accuracy in a less expensive model. Stochastic functions can be used to represent processes that are strongly influenced by chance and by many factors that are difficult to identify and quantify, namely determination of initial flora, establishment, early growth, and biotic interactions. Shrub community dynamics following establishment and early growth are less subject to the vagaries of chance. A deterministic model may adequately represent successional development after the first few postburn years.

LIMITATIONS

The conceptual model presented here and the examples used to demonstrate it draw heavily on our experience with postburn shrub succession in northern Idaho. We hope that this model is generally applicable to postburn succession; however, differences in detail are likely. For instance, seed banks are probably not as significant as contributors to postburn regeneration of understory vegetation in some other habitat types. Johnson (1975) found evidence for lesser importance of seed banks in northern ecosystems. Relative contribution of on- and off-site sources may also be strongly influenced by fire regimes (Keeley 1981). Establishment may extend through many years elsewhere, especially if off-site sources predominate. This could strongly affect successional dynamics. In such situations, the relative importance of the successional processes and influences may differ from the one we described.

Much data may be required to obtain the knowledge of the on- and off-site propagule sources needed to apply this model. This is a serious limitation unless indicators of disturbance response can be easily identified. Seed morphology may be indicative of the likelihood of long-lived dormancy in seedbanks, the potential importance of seedbanks may be predictable by habitat type, and rooting habit may offer clues to sprouting potential. Ideally, adaptive characteristics of species could be simply identifed from such general morphological and ecological characteristics.

The conceptual approach is untested. Pilot simulation model development suggests that the modeling approach has promise. Once complete, the simulation model will be tested against field observations of shrub succession on the *Thuja plicata/Clintonia uniflora* habitat type. Results should reflect whether the conceptual approach is appropriate.

CONCLUSIONS

The complexity of early seral succession can be unraveled when casual factors are identified. We have outlined a conceptual model of shrub succession following clearcutting and broadcast burning. The model incorporates the critical influences and processes determining successional development. Environmental conditions, existing vegetation, life history characteristics of species available for colonization, kind and severity of disturbance, and chance are identified as important influences on successional patterns. The critical successional processes are determination of the initial flora, establishment, growth, and biotic interactions. Many of these influences and processes have been previously identified as important determinants of successional patterns. Here they are synthesized into a simple conceptual model of shrub succession following fire.

Development of our conceptual model draws heavily on the conceptual models presented by MacMahon (1980, 1981) and Lyon and Stickney (1976), existing literature, and previous successional modeling approaches. The best attributes of many separate approaches are combined in the conceptual model. The resulting integration differs substantially from any of the parts. We recognize the role of chance in successional development. Chance is most influential in the first few postburn years, and we represent early successional processes stochastically. Deterministic equations are adequate representations of community dynamics subsequent to establishment and early growth, when changes in the community are less subject to the vagaries of chance. This time-dependent linkage of stochastic and deterministic equations in a single successional model is unique. The conceptual model provides a valuable synthesis of ideas valuable in developing an understanding of the course of early seral shrub succession following clearcutting and burning.

Forest successional models have been used to integrate existing knowledge, explore theories, test specific hypotheses, and stimulate critical thinking about the causes and consequences of successional dynamics (Shugart and West 1980; Franklin 1982). We hope that the conceptual model presented here will stimulate similar critical thinking about succession of forest understory species.

REFERENCES

Archibold, O. W. Buried viable propagules as a factor in postfire regeneration in northern Saskatchewan. Canadian Journal of Botany. 57: 54-58; 1979.

Arno, S. F.; Simmerman, D. G. Forest succession on four habitat types in western Montana. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; [in press].

Bartos, D. L.; Ward, F. R.; Innis, G. S. Aspen succession in the Intermountain West: a deterministic model. General Technical Report INT-153. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1983. 60 p.

Botkin, D. B.; Janak, J. F.; Wallis, J. R. Some ecological consequences of a computer model of forest growth. Ecology. 60: 849-872; 1972.

Cattelino, P. U.; Noble, I. R.; Slatyer, R. O.; Kessell, S. R. Predicting the multiple pathways of succession. Journal of Environmental Management. 3: 41-50; 1979.

Clements, F. E. Plant succession: an analysis of the development of vegetation. Publication 242. Washington, DC: Carnegie Institute; 1916. 512 p.

Cooper, S.; Nieman, K.; Steele, R. Forest habitat types of northern Idaho. Missoula, MT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1983. 210 p. Review draft.

Flinn, M. A.; Wien, R. W. Depth of underground plant organs and theoretical survival during fire. Canadian Journal of Botany. 55: 2550-2554; 1977.

Franklin, J. F. Forest succession research in the northwest: an overview. In: Means, J. E., ed. Forest succession and stand development research in the Northwest: symposium proceedings. Corvallis, OR: Oregon State University; 1982: 164-170.

Gill, A. M. Plant traits adaptive of fires in Mediterranean land ecosystems. In: Mooney, H. A.; Conrad, C. E., eds. Environmental consequences of fire and fuel management in Mediterranean ecosystems. General Technical Report. WO-3, Washington, DC: U.S. Department of Agriculture, Forest Service; 1977: 17-26.

Gomez-Pompa, A.; Vazquez-Yanes, C. Successional studies of a rain forest in Mexico. In: West, D. C.; Shugart, H. H.; Botkin, D. B., eds. Forest succession: Concepts and application. New York: Springer-Verlag; 1981: 246-266.

Gratkowski, H. Pregermination treatments for redstem ceanothus seeds. Research Paper. PNW-156. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1973. 10 p.

Heinselman, M. L. Fire and succession in the conifer forests of North America. In: West, D. C.; Shugart, H. H.; Botkin, D. B., eds. Forest succession: concepts and application. New York: Springer-Verlag; 1981: 374-405.

Irwin, L. L.; Peek, J. M. Shrub production and biomass trends following fire and logging treatments within the cedar-hemlock zone of northern Idaho. Forest Science; 25: 415-426; 1979.

Johnson, E. A. Buried seed populations in the subarctic forests of Great Slave Lake, Northwest Territories. Canadian Journal of Botany. 53: 2933-2941; 1975.

Keeley, J. E. Reproductive cycles and fire regimes. In: Fire regimes and ecosystem properties. General Technical Report WO-26. Washington, DC: U.S. Department of Agriculture, Forest Service; 1981: 231-277.

Kessel, S. R.; Potter, M. W. A quantitative model of nine Montana forest communities. Environmental Management. 4: 227-240; 1980.

Laursen, S. B. Personal communication. Moscow, ID: University of Idaho. Forest Resources Department; 1984.

Leiberg, J. B. The Bitterroot Forest Reserve. In: 20th annual report, Part V: Forest reserves. Washington, DC: U.S. Department of the Interior, Geological Survey; 1900: 317-340.

Lyon, L. J.; Stickney, P. F. Early vegetal succession following large Northern Rocky Mountain wildfires. Tall Timbers Fire Ecology Conference. 14: 355-376; 1976.

MacMahon, J. A. Ecosystems over time: succession and other types of change. In: Waring, R., ed. Forests: Fresh perspectives from ecosystem analyses. Corvallis, OR: Oregon State University; 1980: 27-58.

MacMahon, J. A. Successional processes: comparisons among biomes with special reference to probable roles of and influences of animals. In: West, D. C.; Shugart, H. H.; Botkin, D. B., eds. Forest succession: Concepts and application. New York: Springer-Verlag; 1981: 277-304.

Morgan, P.; Neuenschwander, L. F. Seedbank contribution to shrub regeneration following clearcutting and burning. [in preparation].

Mueggler, W. F. Ecology of seral shrub communities in the cedar-hemlock zone of northern Idaho. Ecological Monographs. 35:165-185; 1965.

Naveh, Z. The evolutionary significance of fire in the Mediterranean region. Vegetatio. 29: 199-208; 1975.

Noble, I. R. Predicting successional change. In: Fire regimes and ecosystem properties. General Technical Report WO-26. Washington, DC: U.S. Department of Agriculture, Forest Service; 1981: 278-300.

Noble, I. R.; Slatyer, R. O. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio. 43: 5-21; 1980.

Ohmann, L. F.; Grigal, D. F. Early revegetation and nutrient dynamics following the 1971 Little Sioux fire in northeastern Minnesota. Forest Science Monographs. 21; 1979; 80 p.

Pfister, R. D. Designing successional models to meet management needs. In: Means, J. E., ed. Forest succession and stand development research in the Northwest: symposium proceedings. Corvallis, OR: Oregon State University; 1982: 44-53.

Quick, C. R. Viable seeds from duff and soil of sugar pine forests. Forest Science. 2: 36-42; 1956.

Roberts, H. A. Seedbanks in soils. Applied Biology. 6: 1-45; 1981.

Rowe, J. S. Concepts of fire effects on plant individuals and species. In: Wien, R. W.; MacLean, W. A., eds. The role of fire in northern circumpolar ecosystems. New York. Wiley; 1983: 135-154.

Ryan, K. C.; Noste, N. Evaluating prescribed fire. In: Wilderness fire symposium: proceedings. Odgen, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; [in press].

Shugart, H. H.; Noble, I. R. A computer model of succession and fire response of the high altitude *Eucalyptus* forests of the Brindabella Range, Australia Capital Territory. Australian Journal of Ecology. 6:129-141; 1981.

Shugart, H. H.; West, D. C. Forest succession models. BioScience. 30: 308-313; 1980.

Shugart, H. H.; West, D. C.; Emanuel, W. R. Patterns and dynamics of forests: an application of simulation models. In: West, D. C.; Shugart, H. H; Botkin, D. B., eds. Forest succession: concepts and application. New York: Springer-Verlag; 1981: 274-94.

Stage, A. R. Prognosis model for stand development. Research Paper INT-137. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1973. 32 p.

Stage, A. R.; Ferguson, D. E. Regeneration modeling as a component of forest succession simulation. In: Means, J. E., ed. Forest succession and stand development research in the Northwest: symposium proceedings. Corvallis, OR: Oregon State University; 1982: 24-30.

Steele, R.; Geier-Hayes, K. The grand-fir/blue huckleberry habitat type: succession and management. Boise, ID: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station Laboratory; 1982. 57 p.

Wykoff, W. R.; Crookston, N. L.; Stage, A. R. User's guide to the stand prognosis model. Gen. Tech. Rep. INT-133. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1982. 112 p.

Zamora, B. A. Understory development in forest succession: an example from the Inland Northwest. In: Means, J. E., ed. Forest succession and stand development research in the Northwest symposium proceedings. Corvallis, OR: Oregon State University; 1982: 63-69.