A Quantitative Succession Model for Nine Montana Forest Communities

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ABSTRACT / A quantitative succession model was developed both to meet resource management needs in Montana's Lewis and Clark National Forest and to develop a modeling methodology. It builds upon previous concepts and incudes three new features: quantitative prediction of all tree species and seedlings; quantitative predictions of important understory species; and successional pathways determined by fire intensity and scorch height. The method is described and demonstrated for selected Montana habitat (community) types. It is also available in managerial guidelines and has been programmed as a new module in the FORPLAN simulator. Weaknesses of this and other models are discussed. Conclusions relate succession modeling to resource management needs.

Recent studies of postfire plant succession have developed qualitative models of species replacement patterns. Several of these models consider the effects of fire periodicity, the species' adaptive traits, and their life-history characteristics. For example, Noble and Slatyer (1977) developed a model that described realistically postfire succession patterns observed in New South Wales (Australia) based on the interfire periodicity and the component species' characteristics. That model has been further refined and elaborated for the Australian situation (Noble and Slatyer 1978, 1980). Cattelino et al. (1979; Kessell 1979a) successfully modified and applied that model to forest overstory species for several western Montana communities. Yet despite continued study of species' adaptive characteristics (see, for example, Lyon and Stickney 1976; Lyon 1971, 1976; Gill 1977, 1980), the modeling scheme of Cattelino et al. demonstrated the several weaknesses inherent in many of these recent succession models.

First, the Cattelino model predicted presence or absence of species at various stages of fire recovery, but could not predict quantitative changes in species composition. Second, it ignored the role of fire intensity by assuming that all fires were of sufficient intensity to destroy most of the forest canopy. Third, it was unable to predict the succession of understory species (shrubs, grasses, and forbs). And fourth, it did not take into account the probabilistic nature of seed dispersal from adjacent, undisturbed communities.

KEY WORDS: Plant succession, Fire effects modeling, Montana, Lewis and Clark National Forest, Rocky Mountains, Coniferous forests, Fire frequency, Fire intensity

We present here a more refined succession model, which rectifies the first three problems. This model produces quantitative predictions of the succession of both overstory and understory species and also includes the effects of fire intensity. The fourth problem of probabilistic seed dispersal patterns is not yet fully solved; however, we have developed a preliminary model for selected Montana forest communities which is described elsewhere (Potter et al. manuscript).

Purposes of the Study

In addition to addressing the noted deficiencies of previous models, this study had two other major purposes. First, it was conducted to improve plant succession modeling capabilities provided by ***FORPLAN*** as implemented on the Lewis and Clark National Forest in Montana. ***FORPLAN*** is a computer-based Forest Planning Language and Simulator (Potter et al. 1979) which is being used by managers of that forest to integrate fire management into land management planning (Lotan 1979). This forest's communities are described by the Montana habitat type community classification system of Pfister et al. (1977). Thus, ***FORPLAN*** is also based on this system, which includes quantitative data on each type's mature community composition, but cannot systematically provide such information for postfire seral stands. Thus the ability to predict vegetation changes following fire, and thereby to infer fuel and animal habitat changes, is very desirable for fire management planning (Franklin 1979; Lotan 1979; Kessell 1979b).

The second major purpose of this study was to provide guidelines on how to develop succession models to meet local forest management needs. These guidelines

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Table 1. Seven habitat types from the Lewis and Clark National Forest modeled during this study

Code name	Habitat type
PSME/SYAL (includes AGSP, CARU, and SYAL phases)	*Pseudotsuga menziesii/Symphoricarpos albus* (includes *Agropyron spicatum, Calamagrostis rubescens*, and *Symphoricarpos albus* phases)
PSME/VAGL, VAGL	*Pseudotsuga menziesii/Vaccinium globulare, Vaccinium globulare* phase
ABLA/LIBO (includes LIBO, XETE, and VASC phases)	*Abies lasiocarpa/Linnaea borealis* (includes *Linnaea borealis, Xerophyllum tenax*, and *Vaccinium scoparium* phases)
ABLA/VAGL	*Abies lasiocarpa/Vaccinium globulare*
ABLA/VASC (includes CARU, VASC, and THOC phases)	*Abies lasiocarpa/Vaccinium scoparium* (includes *Calamagrostis rubescens, Vaccinium scoparium*, and *Thalictrum occidentale* phases)
ABLA-PIAL/VASC	*Abies lasiocarpa–Pinus albicaulis/Vaccinium scoparium*
PIAL-ABLA	*Pinus albicaulis–Abies lasiocarpa*

[a] Two additional types from western Montana which do not occur on this forest were also modeled (see text).

(Kessell and Fischer 1980) were written for forest managers rather than for researchers, and they describe specifically how to develop different levels of succession modeling resolution using existing and/or readily obtainable data.

Consequently, although the results reported herein describe a general modeling approach, the choice of study areas as well as the community stratification system were dictated by the above considerations. Furthermore, since the model was developed for forest-level land management planning, approaches that require stand prognosis using tree-by-tree simulation (such as the JABOWA model of Botkin et al. 1972) were not considered. These constraints dictated that we build a model compatible with existing USDA Forest Service data bases, stratification systems, and planning procedures.

Study Methodology

In consultation with forest managers, seven common habitat types (Pfister et al. 1977) were chosen for study on the Lewis and Clark National Forest (Table 1). Replicate samples were taken during June 1979 from four age classes of each type: less than 50 years, 50–100 years, 100–150 years, and greater than 150 years since major disturbance. For each sample, we recorded site characteristics, fire history, habitat type, relative density of overstory trees (those at least 1.4 m in height) by species, absolute cover of tree regeneration (seedlings) by species, total canopy cover, absolute cover of all understory vascular plants by species, total shrub cover, and total grass and forb cover. These data were analyzed in conjunction with the data of Pfister et al. (1977 and personal communication) and Stephen Arno (unpublished) collected for the same habitat types on that forest. In addition, they were augmented by data from Glacier National Park (Kessell 1979a) for the two subalpine habitat types of *Abies lasiocarpa–Pinus albicaulis/Vaccinium scoparium* (ABLA-PIAL/VASC) and *Pinus albicaulis–Abies lasiocarpa* (PIAL–ABLA). Tables of species composition, stratified by habitat type and disturbance history, were then developed from this consolidated data base.

An additional pair of closely related and intergrading habitat types, *Pseudotsuga menziesii/Vaccinium globulare* (PSME/VAGL) and *Abies lasiocarpa/Xerophyllum tenax* (ABLA/XETE), which occur in western Montana, were also included for modeling because of the excellent data base available from Arno (unpublished).

Development of the Model

The dual concepts of successional pathways and of species-replacement sequences predicated upon fire periodicity and species attributes, as developed by Noble and Slatyer (1977) and applied in Montana by Cattelino et al. (1979), provide the basic framework of our model. Application and modification of this methodology to provide new capabilities are described below.

Successional Pathways and Model States

Although succession is usually conceptualized as a process of continuously changing species patterns and community characteristics, it is convenient to view the community as making transitions from one "state" to another (Clements 1916). Thus, one divides the con-

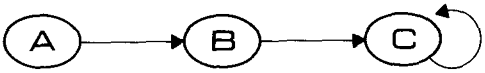

Figure 1. A very simple model of succession showing transitions of the community from state to state in the absence of further disturbance.

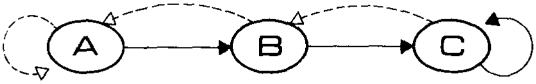

Figure 2. An extension of the Fig. 1 model which shows transitions both without further disturbance (solid arrows) and those caused by additional disturbances (broken arrows).

tinuum into a suitable number of states, based upon available information and the resolution required (Kessell 1979a, b). Figure 1 shows a very simple model of this process. A postdisturbance community of intolerant pioneer species (State A) gives way to a midseral community of both tolerant and intolerant species (State B), and is eventually replaced by a sustaining community of tolerant "climax" species (State C). The sustaining nature of State C is indicated by the closed arrow; State C does not make a transition to a new state in the absence of further disturbance. A more detailed model might include numerous states, which reflect changes in species importance as well as species replacements.

Such an approach models adequately community changes following an initial disturbance, but it does not represent the effects of additional perturbations. We might therefore extend this initial modeling effort to take into account the results of subsequent disturbances (Fig. 2). In this and all subsequent models illustrated, transitions that occur without disturbance are indicated by solid arrows (as in Fig. 1), whereas those transitions resulting from additional disturbances are shown by broken arrows. In the model depicted in Fig. 2 a disturbance of State A retains the community as State A, a disturbance of State B causes a transition back to State A, and a disturbance of State C causes a transition back to State B. Transitions without disturbance are as described in Fig. 1.

One might next expand this sort of representation by considering different transitions to be a function of the type and/or intensity of disturbance. For example, Fig. 3 shows different pathways which might be followed subsequent to a "mild" or "severe" disturbance. In this example, the response of State C is a function of disturbance intensity; a severe disturbance causes a transition to State A but a mild disturbance causes a transition to State B.

Further modification might include different responses and thus transitions for different structural and/or taxonomic units of the community. For example, different pathways might be followed by overstory trees, understory plants, and mammals.

The level of information and resolution provided for each state can be determined by the modeler, predicated upon both available data and managerial requirements. For some applications, characterization of State C as "mature spruce forest" might be adequate. Another user might require that State C correspond to a detailed quantitative list of vascular plants, vertebrate populations, and flammable fuels present.

Transition Ages and Species Characteristics

Application of this approach to specific communities requires that the times at which nondisturbance transitions occur and the critical events that trigger different transitions be determined from actual field observations. Furthermore, the determination of ages at which certain transitions occur (such as loss of a species from the community) require certain information on the adaptive and life-history characteristics of the component species. Let us now consider how these might be determined and modeled.

Returning to our simple example, suppose field studies show that the seral community is replaced by the mixed community about 25 years postdisturbance and that the "climax" community is reached about 200 years postdisturbance. Let us also assume that a "mild disturbance" is a fire with scorch height[1] of less than 10 m, and a "severe disturbance" is a fire with scorch height of 10 m or more. Figure 4 shows how we calibrate our general model (from Fig. 3) to these local observations. We may next describe species composition of each state as determined from field samples of communities represented by each state, as shown in Table 2. Thus, our field observations not only allow us to determine which transitions occur (e.g., that burning State C causes a transition to A or B, depending on scorch height), but also to determine the ages of natural transitions and to describe the community composition represented by each state.

An important part of this process is determining the critical ages in the life histories of the species. This

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[1] Scorch height is the height above the ground at which living foliage will be killed by the fire (Van Wagner 1973).

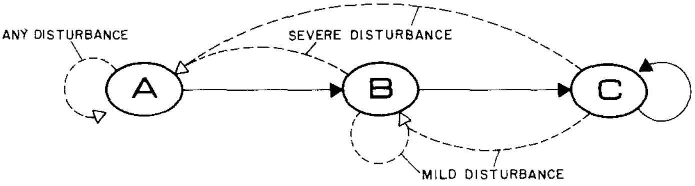

Figure 3. A further elaboration of the Fig. 2 model showing state transitions as a function of disturbance intensity.

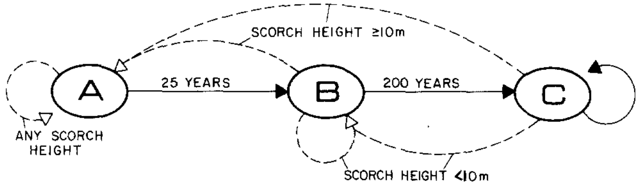

Figure 4. Application of the Fig. 3 model to a specific community allows inclusion of transition ages and the critical scorch heights which determine alternative transitions. Hypothetical species composition for each state is given in Table 2.

Figure 5. A portion of a succession model showing loss of an intolerant species (aspen) at age 130 years. State D and previous states include aspen, but State E and subsequent states do not.

process is a simplified application of the "vital attributes" and life-history information presented by Noble and Slatyer (1977, 1978, 1980) and Cattelino et al. (1979). For example, once a tolerant species becomes established in the community, it will remain there at least until a further disturbance. However, if we define an intolerant species as one that will eventually fail to reproduce in a sufficiently old community, it is eventually lost in the absence of further disturbance. An example is aspen (*Populus tremuloides*) modeled by Cattelino et al. (1979). This species is intolerant; it becomes established immediately after a fire, but lives for only 130 years. A transition in the model is required at age 130 years as shown in Fig. 5; State D includes aspen, but State E and subsequent states do not. Thus the life spans of intolerant species determine some of the transition ages required by the model.

To illustrate further the role of critical ages, consider a species that is unable to disperse into a stand or to reproduce vegetatively, and therefore must regenerate from stored seeds (stored either on living individuals or in the soil). If this species is also intolerant, it will not only eventually be lost from the stand (as was aspen), but it will also be unable to establish after a disturbance if its seeds are no longer viable. Thus a sufficiently long interdisturbance period will cause its permanent loss from the community. This situation is shown in Fig. 6 using the intolerant serotinous lodgepole pine (*Pinus contorta*) example from Cattelino et al. (1979). States F and G include lodgepole pine; its loss is indicated by the

Table 2. Hypothetical species composition of successional states A, B, and C (see Figures 1–4 and the text)

Species	States[a]		
	A	B	C
Intolerant 1	35	10	0
Intolerant 2	20	0	0
Intolerant 3	10	5	0
Intolerant 4	15	5	0
Intolerant 5	10	0	0
Tolerant 1	0	3	20
Tolerant 2	1	25	30
Tolerant 3	1	20	25
Tolerant 4	0	1	10

[a] Absolute ground cover, in percentage.

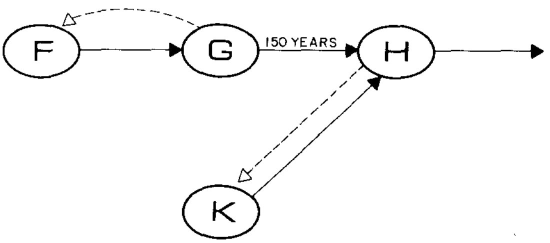

Figure 6. A portion of a succession model showing permanent loss of a stored seed reproducing intolerant species (lodgepole pine). The species is lost from the community at age 150 years in the transition from State G to State H. Disturbance of State H causes a transition to State K in which the pine is unable to reestablish. In this model, it is not possible to return to State G from State H or subsequent states.

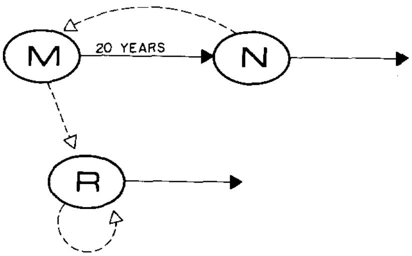

Figure 7. A portion of a succession model showing permanent loss of a stored seed reproducing species (again lodgepole pine) caused by disturbing a young stand. The species requires 20 years to produce seeds, and thus a severe disturbance to State M causes a transition to State R and the pine's permanent loss from the community.

transition to State H at 150 years. But disturbance of State H causes a transition to State K, which includes no lodgepole pine. It is not possible to return to States F or G once State H has been reached, due to the loss of the pine's seed source. This same process also occurs with vegetative intolerant species but not with dispersal-intolerant species.

Serotinous lodgepole pine, as a stored seed species, serves to illustrate another critical age situation. If a stand which includes this species is disturbed, it vigorously regenerates from its stored seeds. But this process uses the existing seed source and new seeds will not be available for approximately 20 years until the regenerating pine individuals reach maturity and produce seeds. If the stand is again disturbed during this 20-year period, no seeds are available and the species can be permanently lost from the community. Figure 7 shows this process; burning State M which includes lodgepole pine causes a transition to State R during the first 20 years postfire, and again serotinous lodgepole pine is lost from the community.

The succession of lodgepole pine is often complicated by the fact that it functions as both a stored seed species and a dispersal species in many communities. Cattelino et al. (1979) attempted to include this situation, and the observation that the species reproduces less successfully when regenerating only from dispersed seeds, in their model. For the purposes of the above illustration, we have assumed that lodgepole pine reproduces only from seeds stored in serotinous cones. The presentation of the model of the Montana forest communities will further consider this problem.

Other Considerations

In addition to state changes that show the loss or addition of a species to the community, it may be desirable to model state changes that reflect changes in species importance. The number of states recognized will depend upon data availability, the rate of species importance changes, and the intended use of the model.

For example, consider a simple forest which includes three tree species: subalpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta*). For purposes of illustration, we shall assume the following: Subalpine fir regenerates from dispersed seeds and is tolerant; therefore, once established in the postfire community, it remains there indefinitely. Douglas-fir in this community is also a seed dispersal type but is considered to be intolerant; it ultimately will fail to reproduce under the subalpine fir and Douglas-fir canopy, and given a sufficient interfire period, will be lost from the community. Lodgepole is also intolerant and is assumed to regenerate only from seeds stored in serotinous cones. It requires 20 years to reach maturity and lives for about 220 years.

We can use the above data to produce the model shown in Fig. 8. State A includes all three species, but a second disturbance of State A causes a transition to State J and the permanent loss of lodgepole pine. If State A is

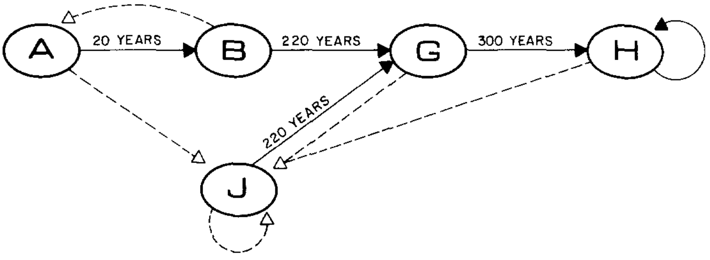

Figure 8. A model of a simple forest community which includes subalpine fir, Douglas-fir, and lodgepole pine. Transitions show where species may be lost from or added to the community. See text for further explanation.

undisturbed for 20 years, a transition is made to State B. State B includes all three species; a disturbance returns the community to State A. If the community endures 220 years without a disturbance, it reaches State G; lodgepole pine is lost and the community consists of subalpine fir and Douglas-fir. A disturbance now will result in a transition to State J; lodgepole pine has been permanently lost from the community. If the community endures 300 years without a disturbance, it reaches State H, Douglas-fir is lost from the present community, and the forest is pure subalpine fir. Because it is a dispersal species, Douglas-fir will reestablish after the next disturbance and resulting transition to State J, but lodgepole pine will not. Finally, State J represents the loss of lodgepole pine but retension of subalpine fir and Douglas-fir. After 220 years of no disturbance, it makes the transition to State G. If State J is disturbed during the first 220 years, it remains as State J.

This model, as shown in Fig. 8, accounts for all possible combinations of transitions that can occur under different disturbance regimes. It does not account for changes in species importance during succession; transitions occur only when a species actually is, or potentially could be, lost from the community. Yet we know that between the ages of 20 and 220 years (State B), there is a gradual reduction in both lodgepole pine and Douglas-fir and an increase in subalpine fir. Similarly, there is a gradual reduction in Douglas-fir and increase in subalpine fir in State J as it ages from 0 to 220 years postdisturbance.

We can account for these changes by expanding the model as shown in Fig. 9. Extra states have been added at 50-year intervals to reflect the quantitative changes in species composition. For example, where the first model (Fig. 8) had a single State B between age 20 and age 220, the new model (Fig. 9) shows five states occurring during this time span (B, C, D, E, and F). Similarly, the single State J in Fig. 8 has been replaced by States J, K, L, M, and N. The choice of a time interval between transitions is influenced by several factors, as noted above; we found 50 years convenient for this example.

The Model of Montana Forest Communities

The nine habitat types that we modeled include a maximum of six tree species and 25 important understory species. The trees include subalpine fir (*Abies lasiocarpa*), spruce (*Picea* hybrid complex), Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), whitebark pine (*Pinus albicaulis*), and ponderosa pine (*Pinus ponderosa*); but not all species occur in any one habitat type.

Each tree species except lodgepole pine regenerates from dispersed seeds. As discussed previously, lodgepole pine regenerates primarily from seeds stored in serotinous cones. Therefore it can be lost from the community under certain fire periodicities. As noted by Cattelino et al. (1979), lodgepole pine in some communities will reproduce poorly from dispersed seeds if a stored seed source is not available. However, for the present study, we assumed that this effect is neither widespread nor important in our study area.

Ponderosa pine is an intolerant species in all nine habitat types but its longevity ranges from 200 to 350 years as a function of the habitat type. The remaining four species may be either tolerant or intolerant depending upon the habitat type; their longevity is also a function of the habitat type.

Although we originally anticipated that each habitat type would require an individual succession model, we

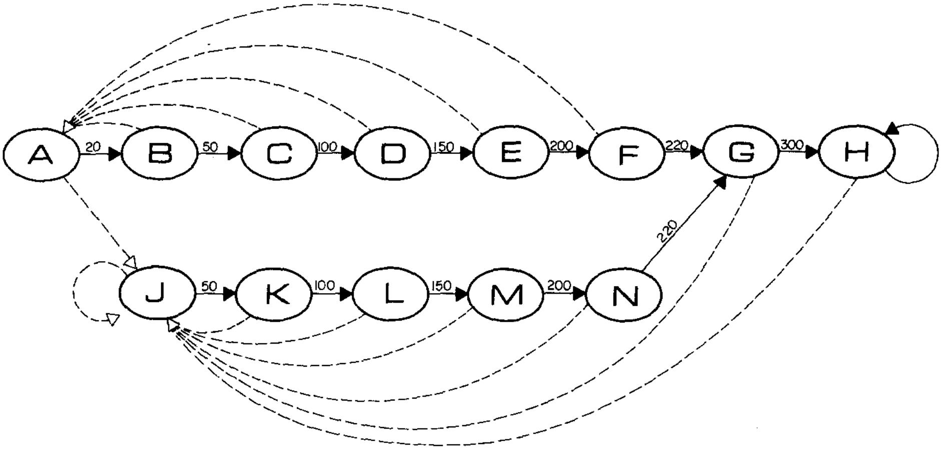

Figure 9. A more refined version of Fig. 8 includes additional states and more closely approximates observed changes in species composition. See text for further explanation.

were able to develop a general model of states and transitions that fits the data from all nine habitat types. Thus while the species composition of any given state is a function of the habitat type, the states, transitions, and ages proved to be independent of habitat type.

The general model for overstory species succession is shown in Fig. 10. It includes a number of features illustrated by the examples of the last section. Thirteen staes are included in the model. States 1–6 represent succession with seral lodgepole pine. States 10–13 represent succession in the absence of seral lodgepole pine. States 7–9 show late succession and climax development beyond the longevity of lodgepole pine. Solid directed lines show transitions which occur without further disturbance; the age in years at which each transition occurs is indicated. Broken lines show transitions after disturbance.

Note that most states show two possible transitions after a disturbance; the choice of transition is a function of scorch height. Based on field observations and studies in adjacent areas (Kessell 1979a), we estimated that fires that kill over half the overstory are usually "severe fires," which cause major transitions. Those that kill less than half the overstory are usually "mild fires," which cause little or no change in overstory species composition. An exception is the fire scorch height required to cause a transition from State 1 to State 10 and thus the removal of young lodgepole pine; here the critical value is one that kills the entire lodgepole pine population.

Because the critical scorch heights are dependent upon the heights of canopy trees and the distribution of canopy foliage, they can be modeled as functions of habitat type and stand age. These critical scorch heights were determined by field sampling representative habitat types as part of a more general study relating canopy mortality to fuel loadings and the weather conditions which exist during a fire (Kessell and Keane manuscript). The critical values, shown as variables on the Fig. 10 model, are given in Table 3 as a function of habitat type.

The critical ages for transitions in the model were determined from life-history information: the transition from State 1 to State 2 at age 20 years (the time required for lodgepole pine to reach maturity and produce seeds); the transitions from State 6 to State 7, and from State 13 to State 7, at age 220 years (the average longevity of lodgepole pine); the transition from State 7 to State 8 at 300 years (the longevity of intolerant spruce in one of the habitat types); the transition from State 8 to State 9 at 350 years (the longevity of intolerant whitebark pine, ponderosa pine, and spruce in various habitat types); and the steady-state condition at 350 years (State 9) where further directed variation is not observed and the communities are considered as "climax." Additional states and transition ages have been added at 50-year

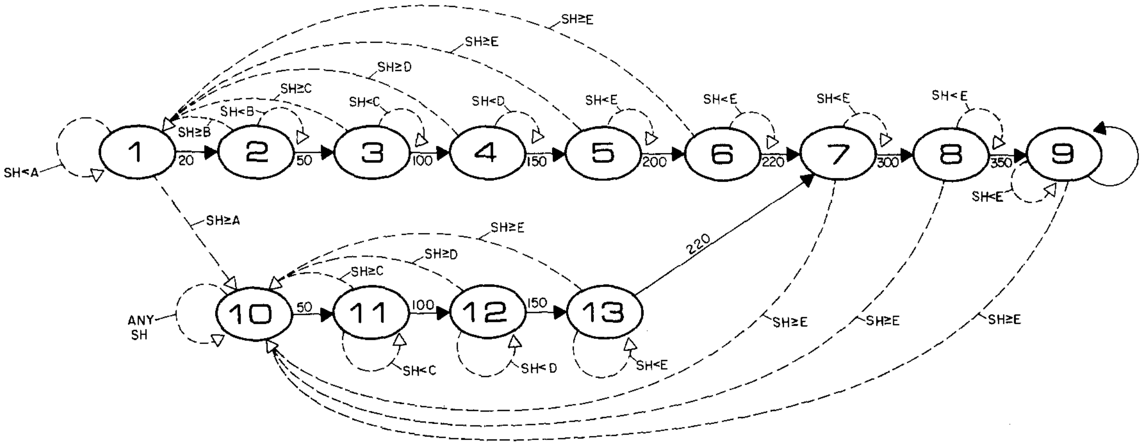

Figure 10. The full succession model for overstory species of the nine Montana habitat types. Transitions in the absence of further disturbances are determined by stand ages (years) shown on the solid arrows. Transitions due to further disturbance are a function of stand age and fire scorch height. The critical scorch height variables are given in Table 3. The species composition of each state for two habitat types, PSME/SYAL and ABLA/VAGL, is given in Tables 4 and 5, respectively.

Table 3. Critical scorch height values for the seven Lewis and Clark National Forest habitat types determined by Kessell and Keane manuscript[a]

Habitat type	Critical scorch height values (m)				
	A	B	C	D	E
PSME/SYAL	1.8	5.5	6.1	6.1	12.2
PSME/VAGL	2.1	6.4	9.1	10.4	10.4
ABLA/LIBO	3.1	6.4	12.5	13.1	13.7
ABLA/VAGL	2.1	6.4	9.1	10.4	10.4
ABLA/VASC	2.1	6.4	9.1	10.4	10.4
ABLA-PIAL/VASC	2.1	6.4	9.1	10.4	10.4
PIAL-ABLA	2.1	6.4	9.1	10.4	10.4

[a] These values determine the successional pathways followed in the Montana models (Fig. 10 and 11). Full names of the habitat types are given in Table 1.

increments to reflect quantitative changes in species composition.

Use of the model in Fig. 10 requires the development of a matrix for each habitat type, in which species composition is recorded as a function of the state. The upper portion of Table 4 shows this matrix for the PSME/SYAL (*Pseudotsuga menziesii/Symphoricarpos albus*) habitat type. During the first 50 years postfire (States 1 and 2 or State 10), trees are present as seedlings only; the regeneration includes lodgepole pine, ponderosa pine, and Douglas-fir in States 1 and 2, while lodgepole pine is absent in State 10. Succession with lodgepole (States 1–9) shows an early predominance of Douglas-fir (States 3 and 4), with the species eventually becoming the sole dominant (State 9). Lodgepole pine slowly declines through succession, and drops out of the community after 220 years. Ponderosa pine lives much longer, but also drops out at age 350 years.

Succession without lodgepole pine (States 10–13 and 7–9) shows an increase in ponderosa pine and Douglas-fir abundance through State 13, and then convergence with the other successional pathway after 220 years. Also note that there are virtually no seedlings present after 150 years postfire on either successional pathway.

The effects of additional disturbances, shown by the broken lines in Fig. 10, are predicted as a function of the present state of the community and scorch height. Scorch height can be calculated (Van Wagner 1973) from fire intensity (Byram 1959) using inputs describing the fuels and the meteorological conditions under which they burn (Rothermel 1972; reviewed by Kessell et al. 1978). For several habitat types on the Lewis and Clark National Forest, these relationships have been determined as a function of season, weather percentiles, and wind velocity (Kessell and Keane manuscript) by using field canopy data and the FORPLAN simulator (Potter et al. 1979).

For example, a severe fire in State 5 (scorch height of

Table 4. Matrix relating species composition to successional states for the PSME/SYAL (*Pseudotsuga menziesii/ Symphoricarpos albus*) habitat type[a]

	Succession model states												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Trees ≥ 1.4 m tall							*Overstory Species*						
Pinus contorta (Lodgepole pine)			3	2	1								
Pinus ponderosa (Ponderosa pine)			2	2	2	2	1	1			3	3	2
Pseudotsuga menziesii (Douglas-fir)			4	4	5	5	5	6	6		4	4	5
Tree seedlings (<1.4 m tall)													
Pinus contorta (Lodgepole pine)	1	1											
Pinus ponderosa (Ponderosa pine)	1	1								1			
Pseudotsuga menziesii (Douglas-fir)	1	1	1	1						1	1	1	
Total canopy cover			4	4	4	4	4	4	4		4	4	4
Shrubs and subshrubs							*Understory Species*						
Juniperis communis			2	1							2	1	
Potentilla fruticosa				1	1	1	1	1	1			1	1
Ribes spp.	2	2											
Rosa spp.			1	2	2	2	2	2	2		1	2	2
Shepherdia canadensis			2	1	1	1	1	1	1		2	1	1
Spiraea betulifolia			2	2	2	2	2	2	2		2	2	2
Symphoricarpos albus	1	1	2	2	2	2	2	2	2	1	2	2	2
Berberis repens			1	1	1	1	1	1	1		1	1	1
Total shrub cover	2	2	4	4	4	4	4	4	4	2	4	4	4
Forbs and grasses													
Calamagrostis rubescens	1	1	3	1	1	1	1	1	1	1	3	1	1
Carex geyeri	2	2	3							2	3		
Festuca scabrella	1	1	1		1					1	1		1
Gramineae	1	1		1	1					1		1	1
Arnica spp.			2		1	1	1	1	1		2		1
Astragalus spp.			1	1	1	1	1	1	1		1	1	1
Fragaria spp.	2	2	1		1	1	1	1	1	2	1		1
Total forb and grass cover	5	5	3	2	1	1	1	1	1	5	3	2	1

[a] The successional state numbers correspond to the model shown in Fig. 10 and 11. Importance values are expressed on a seven point scale where: blank = <1%; 1 = 1–5%; 2 = 6–25%; 3 = 26–50%; 4 = 51–75%; 5 = 76–95%; 6 = >95%. Importance values for trees at least 1.4 m tall are relative density; all other importance values are absolute cover. The "Gramineae" entry includes all grasses not previously listed by species.

12.2 m or more; Table 3) causes a transition to State 1, but a mild fire (scorch height of less than 12.2 m) retains the community in State 5. An additional severe disturbance to State 1 (scorch height at least 1.8 m) causes a transition to State 10 and the loss of lodgepole pine. A severe disturbance to States 7, 8, or 9 (scorch height at least 12.2 m) also causes a transition to State 10 and the loss of lodgepole pine.

Use of the Fig. 10 model for another habitat type requires only an additional matrix; an example for the ABLA/VAGL (*Abies lasiocarpa/Vaccinium globulare*) habitat type is shown as Table 5. Note the addition of three species not occurring in the PSME/SYAL type (subalpine fir, spruce, and whitebark pine), the absence of ponderosa pine in this type, and the intolerant status of Douglas-fir which is the sole climax dominant in the

Table 5. Matrix relating species composition to successional states for the ABLA/VAGL (*Abies lasiocarpa*/*Vaccinium globulare*) habitat type[a]

	Succession model states												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Trees ≥ 1.4 m tall						*Overstory Species*							
Abies lasiocarpa (Subalpine fir)			1	3	4	5	5	5	6		2	4	4
Picea (Spruce hybrid complex)			1										
Pinus albicaulis (Whitebark pine)					1	1	1	1					1
Pinus contorta (Lodgepole pine)	5	5	5	4	3	1							
Pseudotsuga menziesii (Douglas-fir)	2	2	2	2	2	1	1			6	4	2	2
Tree seedlings (<1.4 m tall)													
Abies lasiocarpa (Subalpine fir)	2	2	2	2	2	2	2	2	2	2	2	2	2
Pinus albicaulis (Whitebark pine)					1	1							
Pinus contorta (Lodgepole pine)	3	3											
Total Canopy Cover	2	2	4	4	4	3	3	3	3	4	4	3	3
Shrubs and subshrubs						*Understory Species*							
Alnus sinuata	1	1								1			
Juniperis communis			1	1							1	1	
Lonicera utahensis	1	1								1			
Rosa spp.	1	1								1			
Spiraea betulifolia	1	1	1	1	1	1	1	1	1	1	1	1	1
Symphoricarpos albus				1								1	
Vaccinium globulare	1	1	2	2	2	2	2	2	2	1	2	2	2
Berberis repens			1								1		
Total Shrub Cover	3	3	3	4	4	4	4	4	4	3	3	4	4
Forbs and grasses													
Calamagrostis rubescens	4	4	3	3	1	1	1	1	1	4	3	3	1
Carex geyeri	2	2	1	1	1	1	1	1	1	2	1	1	1
Festuca scabrella	1	1								1			
Gramineae	1	1								1			
Antennaria racemosa			1								1		
Arnica spp.	2	2	2	2	2	2	2	2	2	2	2	2	2
Chimaphila umbellata					1								1
Epilobium angustifolium	1	1								1			
Valeriana sitchensis					1								
Total forb and grass cover	4	4	4	3	2	2	2	2	2	4	4	3	2

[a] See Footnote *a* to Table 4 for an explanation of values.

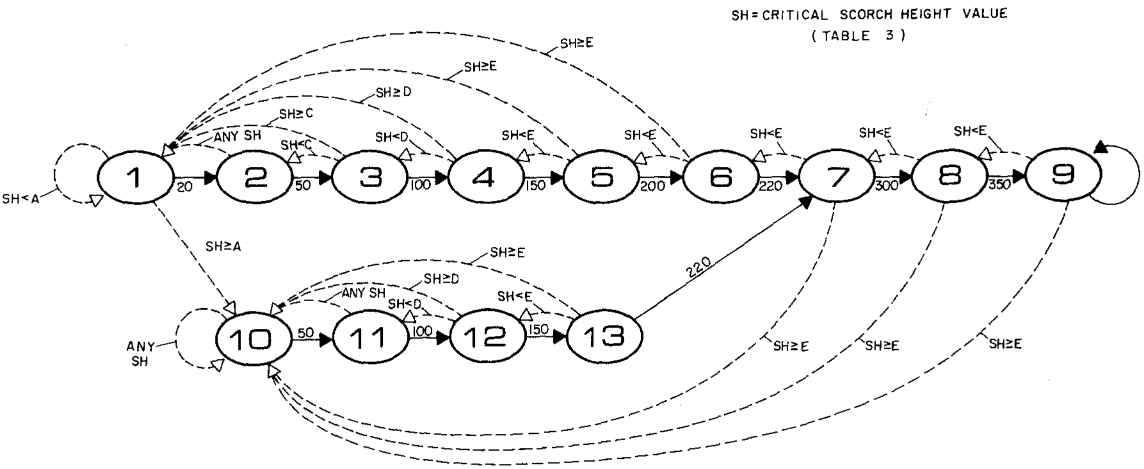

Figure 11. The full succession model for understory species of the nine Montana habitat types. The model is very similar to the overstory model of Fig. 10 except that mild fires usually cause the understory to retrogress one state. Species composition of each state for two habitat types is given in Tables 4 and 5.

PSME/SYAL type. The use of the model to predict succession is identical to its use for the PSME/SYAL type with the exception that different critical values of scorch height are presented in Table 3.

A very similar model of understory succession was developed and is shown as Fig. 11. The only difference between this model and the overstory model of Fig. 10 is that a mild fire usually causes a transition of the understory to the preceeding state (e.g., a mild fire in State 5 causes a transition to State 4), whereas a mild fire does not cause the overstory to change states (Fig. 10). The understory model is also used in conjunction with the matrices in Tables 4 and 5 (lower portions are understory data) to predict changes in understory for the PSME/SYAL and ABLA/VAGL types, respectively.

Using the PSME/SYAL habitat type as an example (Table 4), a mild fire (scorch height less than 6.1 m) in State 4 causes a transition to State 3. Table 4 shows the results are: an increase in *Juniperis communis*, *Shepherdia canadensis*, and *Calamagristis rubescens*; a decline in *Rosa* spp; the addition of *Carex geyeri*, *Festuca scabrella*, *Arnica* spp., and *Frageria* spp.; and the loss of *Potentilla fruticosa*. A severe fire in this community would cause a transition to State 1 and a much greater effect on the understory vegetation (see Table 4).

Similar results were obtained using matrices developed for the other habitat types; those results are available in Kessell and Fischer (1980).

Discussion

The model presented here is a straightforward elaboration of previous models and concepts yet it offers several capabilities not previously available. Its inclusion of quantitative predictions by assigning importance values to every species within each model state and its use of scorch height to determine successional pathways provide a comprehensive view of plant succession at the habitat-type level. The model was easily programmed as a new module for the *FORPLAN* simulator (Potter et al. 1979), and its simple construction should allow managers in other areas to build similar models from their own data.

Yet the development of this model also demonstrated a number of areas where our data are weak and our understanding is incomplete. For example, despite recent success in building a seed-dispersal and seedling-survival model for the same geographical area (Potter et al. manuscript), we are still unable to determine precisely which species will disperse into a disturbed stand and establish successfully. Obviously, if one of the major species in our model does not establish after a disturbance, disparities will exist between the real situation and the successional predictions of the model.

Another assumption of our model is that tree mortality can be predicted solely from scorch-height information. Yet we do not fully understand the relationship between foliage mortality and tree mortality, nor the relationship between intensity and duration of foliage heating and foliage mortality (Van Wagner 1968, 1973). We have also been forced by lack of data to assume that cambial mortality is not a significant factor in these communities.

We had originally hoped to develop the understory succession model from life history and adaptive information on the understory species themselves. Yet we found, as did Cattelino et al. (1979), that sufficient information simply is not available for these shrub, grass, and forb species. Instead, we were required to develop the understory model by fitting empirical field data to a slightly modified version of the overstory model.

Our model also shows a clear distinction between successional pathways with and without lodgepole pine. Yet several, and perhaps many, western Montana forest communities contain lodgepole pine populations which include both serotinous individuals and open cone (seed dispersal) individuals. This situation could potentially allow a continuum of successional responses intermediate to those shown on our two major pathways. Additionally, a fire in State 1 with an intermediate scorch height could kill some but not all of the lodgepole pine population and again produce responses intermediate to those predicted by the model. Our desire to keep the model simple, and to construct it from readily available information, has thus required that we oversimplify the real world situation.

Other limitations are imposed by our decision to model at the habitat-type resolution level. Some of these types include rather heterogeneous communities that can vary significantly from the modal type. Within-type variation in elevation, aspect, topography, slope steepness, and substrate can cause responses in species composition, growth rates, life-history characteristics, and successional processes. Yet the use of more refined units, such as individual habitat type phases (a subdivision of a habitat type—Pfister et al. 1977) or stratification of the communities on environmental gradients (Kessell 1979a, 1979b), would have required a narrower study of less value for forest management.

Invariably, compromises must be reached in studies of this sort. We hope that we have achieved a model which is both sufficiently comprehensive to meet managerial needs and sufficiently simple to be applied successfully to existing data bases.

Succession Modeling and Land Management

The model described here was specifically developed to help integrate fire management considerations into land management planning. With its present data base, it is intended for immediate use in the Lewis and Clark National Forest; it is also intended to demonstrate a methodology that can be used by managers in other areas. Let us conclude by considering this topic of succession modeling a bit further.

Management planning, and the resulting management actions, affect the biotic community in varying ways (Franklin 1979; Egging and Barney 1979; Lotan 1979). Our need to understand the changes which result from these actions, and therefore to maximize desired results while minimizing undesirable effects, is imperative. Plant succession models are therefore important tools for a land manager, who will use them not only to estimate effects on the vegetation but also to infer other related effects on wildlife, fire hazard, water quality, and recreation (Kessell 1979b; Kessell et al. 1980).

Tools such as succession models are developed for a variety of specific applications and resolution levels; some must be very broad and general, others require the prediction of very specific details. For example, for fire management planning at a national forest level, the habitat-type group models presented by Davis et al. (1980) are appropriate. The user obtains a succinct presentation of the general patterns without getting lost in unnecessary detail. At the other end of the spectrum, certain forestry applications benefit greatly from detailed stand-prognosis models (Stage 1973), which use tree-by-tree simulation. Application of these concepts to succession modeling has been successfully demonstrated by Botkin et al. (1972).

The various approaches to modeling succession can be judged only in terms of how well they solve the problems at hand; a variety of methods and resolution levels not only offers a range of tools to meet diverse needs, but more importantly allows a diversity of ideas from which we all ultimately benefit. We do not pretend that the model presented here is the only way to model succession, or even the best way; rather, we found it to be an appropriate way to meet the goals of this study.

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