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The Niche and Forest Growth

K. L. Reed and S. G. Clark

INTRODUCTION

In the preceding chapters the reader was introduced to the concept of ecological indexes. Hawk et al. (Chapter 2) showed that these indexes are useful for ordinating plant communities along moisture and temperature gradients, and Emmingham (Chapter 3) discussed their relation to productivity.

The strong correlation of community ordinations with measured environment supports the idea that the environment can in turn be predicted from community ordination, once the relation has been established. For example, in Waring et al. (1972), the distribution of certain trees, shrubs, and forbs was found to be constrained to certain ranges of two moisture indexes and a heat index as measured on numerous plots in southern Oregon. These sensitive species were termed "indicator species." Other plots were selected, and their environment was predicted from the presence of indicator species. Subsequently, the environment was measured on those plots and was found to agree very well with the predicted environment. Reed (1980) discussed this subject from a niche theoretic perspective.

In practice, once an area has been mapped as to community type, the communities can be selectively monitored with respect to environment, and the whole mapped region can be assigned environmental values. The environmental variables can then be used as inputs to models such as the photosynthesis simulator of Emmingham and Waring (1977). They reported that productivity of four forest stands in Oregon was strongly correlated with simulated yearly net photosynthesis. Reed and Waring (1974) demonstrated that height of conifers was strongly related to the heat index and a ratio of simulated seasonal transpiration to potential water loss.

This approach provides a ready means of integrating the disciplines of plant physiology and biometeorology with plant ecology (Reed and Waring 1974; Zobel et al. 1976; Emmingham and Waring 1977; Reed 1980), with implications for prediction of productivity. Further, the ordination of measured environment provides an opportunity to apply Hutchinson's (1957) niche theory to real-world situations. By imposing certain constraints on classical niche

definitions, it is possible to propose research for investigation of concepts that have eluded definitive experiments for years, such as competition, succession, adaptive strategies, and the classical concept of niche. Given a working definition of the niche, forest models can be developed based upon ecological and physical principles.

In this chapter we: (1) discuss niche theory and its relation to ecological indexes, illustrated by examples of hypothetical niches for ponderosa pine, western red cedar, and Douglas-fir in the western United States; (2) show how the niche concept can be related to succession; and (3) discuss a model that integrates the concepts of ecological indexing and environmental quantification, niche theory, and succession. This model is a forest stand growth simulator called SUCSIM (SUCcession SIMulator).

DEVELOPMENT OF NICHE THEORY

Niche theory goes back to Grinnell (1917), who noted that the California thrasher (*Toxostoma redivivum*) was very restricted in its range, being found almost exclusively in the chaparral association, which in turn was limited by elevation (temperature) and moisture. He suggested that these factors define the niche of the species; however, not until Hutchinson (1957) formalized the concept could mathematical analysis be applied. Hutchinson proposed that environment be expressed as linear coordinates of an abstract space, called "environment space" or "E-space." Each environmental variable forms one dimension of the space. Since there are many possible variables, E is an n -dimensional space.

It is difficult to visualize n -dimensional space, but it is easily expressed mathematically. For a simple illustration, consider two environmental variables that represent, say, moisture and temperature. The two variables, then, form a plane or "2-space." Any point in the plane can be referenced by the simple Cartesian notation $P(x,y)$. Addition of a third dimension produces a space like a box; a point is referenced by the coordinates $P(x,y,z)$. Likewise, if there are four dimensions the space is called a "hyperspace" and a point in that space is simply $P(w,x,y,z)$.

Hutchinson suggested that with respect to a single variable an upper and lower limit could be found beyond which a given organism cannot survive. Similarly, survival limits can be established with respect to other environmental variables. In 2-space, these limits give four points, $P(x_1,y_1)$, $P(x_1,y_2)$, $P(x_2,y_1)$, and $P(x_2,y_2)$, that delimit the environmental coordinates within which the species can survive (Figure 4.1a). Those basic limits reflect survival without competition—the *fundamental niche*. Hutchinson suggested that competition with other species restricts the niche. This restricted region in E-space is the *realized niche* (shaded area in Figure 4.1a). In three dimensions, the niche will have a three-dimensional shape (Figure 4.1b).

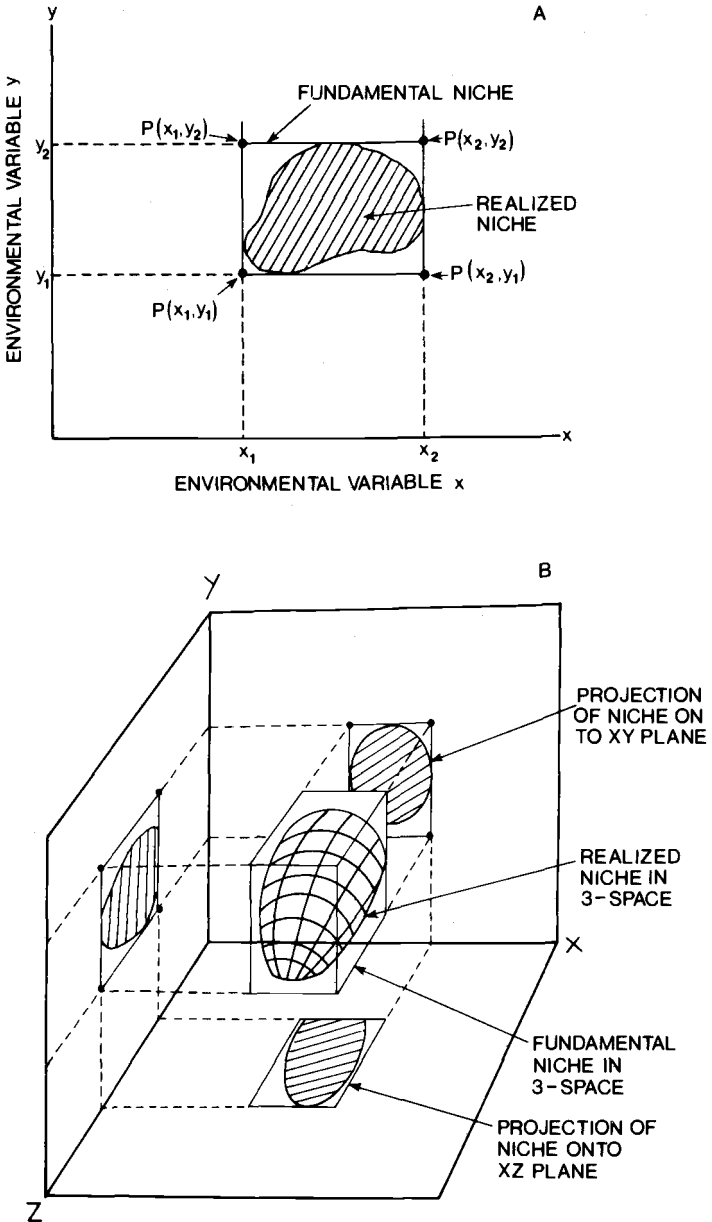


FIGURE 4.1 Fundamental and realized niches of a species expressed as survival relative to two and three environmental variables (after Hutchinson 1957). (a) 2-dimensional projection of E-space; (b) 3-dimensional projection of E-space with 2-dimensional projections of the niche onto the appropriate planes.

As this concept, formalized by Hutchinson, was elaborated and expanded by numerous researchers (see Whittaker and Levin 1975), much confusing terminology appeared, and attempts to relate the concept of niche to real-world situations were disappointing (Green 1971; Whittaker et al. 1973). Much of the difficulty has resulted from imprecise distinctions between site characteristics and environment. Some of the quantities that are conveniently measured are not truly sensed by the organism of interest, so attempts to quantify responses to those quantities are correlative at best, and useless at worst.

Because organisms and communities of organisms are systems, it is germane to examine some systems concepts here. In a systems context, environment is described as that which is external to the system but interacting with the system and evoking a response (Bertalanffy 1969; Klir 1969). Environment can be quantified as a set of inputs to the system causing certain behavior in response to those inputs. The responses are quantified as outputs. A central tenet of this perspective is that environment must be sensed by the system; if it is not, there can be no response.

Mason and Langenheim (1957) attempted to apply some semantic concepts to the definition of environment and also concluded that environment must be expressed in terms of the sensing organism. Quantities important to one system may be irrelevant to another. For example, degree of ocean salinity is important to sea organisms and may be included in their environmental specifications, but it is meaningless to a Rocky Mountain pine tree.

Factors commonly measured by foresters and ecologists, such as elevation, slope, and aspect, are not "environment," but instead are correlated with environment. These indirect measures of environment have been useful in ecology and forestry, but, because of their relative nature, they lack predictive power except in the specific locale wherein the data were taken. For example, mountain hemlock, *Tsuga mertensiana*, grows at elevations of 1300 to 1700 m in northern Washington and 1700 to 2000 m in southern Oregon (Franklin and Dyrness 1973). Direct measurement of light, temperature, and moisture status throughout the hemlock zone would probably yield a range of values that would be more consistent from north to south. Therefore a growth model of mountain hemlock based on elevation would be applicable only in a specific locale, but a model based on measured environment should be more general in its applicability.

Green (1971) agreed that proper definition of environment is critical but noted that there exists no generally accepted methodology of measurement and interpretation of environment in forest ecosystems. The approach reported by Waring (1969), Waring et al. (1972), Reed and Waring (1974), Emmingham and Waring (1977), Reed (1980), and Emmingham (Chapter 3) was a central effort of the Coniferous Forest Biome and is consistent with the concepts discussed above: (1) environment must be organism specific; (2) it must be sensed by the organism; and (3) it must evoke a response from the organism. These environmental variables can be used to form axes of an n -dimensional Hutchinsonian

environment space. Given such an environmental coordinate system, it is possible to define mathematically a set of responses to environment (Maguire 1973). These responses can be interpreted as a realization of the species' *niche*. Delimitation of the niche by use of our growth model is illustrated in Figure 4.2. We are analyzing data to check these functions at the time of this writing.

Figure 4.2 shows two 2-dimensional projections of E ; the contours describe hypothetical niches for three forest species (ponderosa pine, western red cedar, and Douglas-fir) simulated by our growth model. The environmental variables are displayed on the lower and left axes; the species response (simulated) is expressed as height after 50 years on the right axis. Three sites are represented at points e_1 , e_2 , and e_3 . Remember that these points are defined as $P(x,y,z)$ in 3-space, but in our projections $P(x,y,z)$ is illustrated as $P(x,y)$ and $P(x,z)$. The environmental variables used in Figure 4.2 are those discussed in Chapter 3 and by Reed and Waring (1974). One of the axes is the temperature-growth index (TGI), which reflects the influence of air and soil temperature on growth, and the units of which are optimum temperature days (OTD) (Cleary and Waring 1969; Waring 1969). The axis that reflects moisture supply and demand is the transpiration ratio of Reed and Waring (1974). This is a ratio of potential transpiration on a site to "actual" transpiration computed from on-site environmental data. Potential transpiration is the total amount of water that would be lost if there were no stomatal control (an assessment of atmospheric water demand). The transpiration model includes the effect of stomatal closure, which is a function of plant water stress. When the ratio is equal to 1, that site has all the water needed. There is a species-specific lower limit below which that species does not occur; so far as we know, all species will grow where the ratio is 1 if other factors permit. Waring et al. (1972) present numerous examples of species limits to the transpiration ratio. The third axis is simply light expressed as a fraction of full sun.

The trajectory shown for e_1 at time t_1 to e_{1,t_3} represents changes in environment on a site over a period of years. In Figure 4.2a, the site becomes cooler and wetter as the stand develops. Also, note that the trajectory crosses the niche boundary of Douglas-fir. If other factors (not illustrated) permit, Douglas-fir could become established on the site. Thus a community of ponderosa pine and Douglas-fir would be expected at e_{1,t_3} . Also, both species would be expected to grow more than 30 m in 50 years; however, Figure 4.2b shows that the same site at time t_3 would be too dark for good growth. Growth for Douglas-fir at time t_3 would be much better than that of ponderosa pine. From Figure 4.2b alone it might be expected that western red cedar would occur in the community, but from Figure 4.2a we see that it would be too hot.

THE NICHE AND SUCCESSION

A community is possible only on sites where the environmental loci are within the niche volumes of each species; that is, $e(\theta) \in N_c$, where θ is the set of

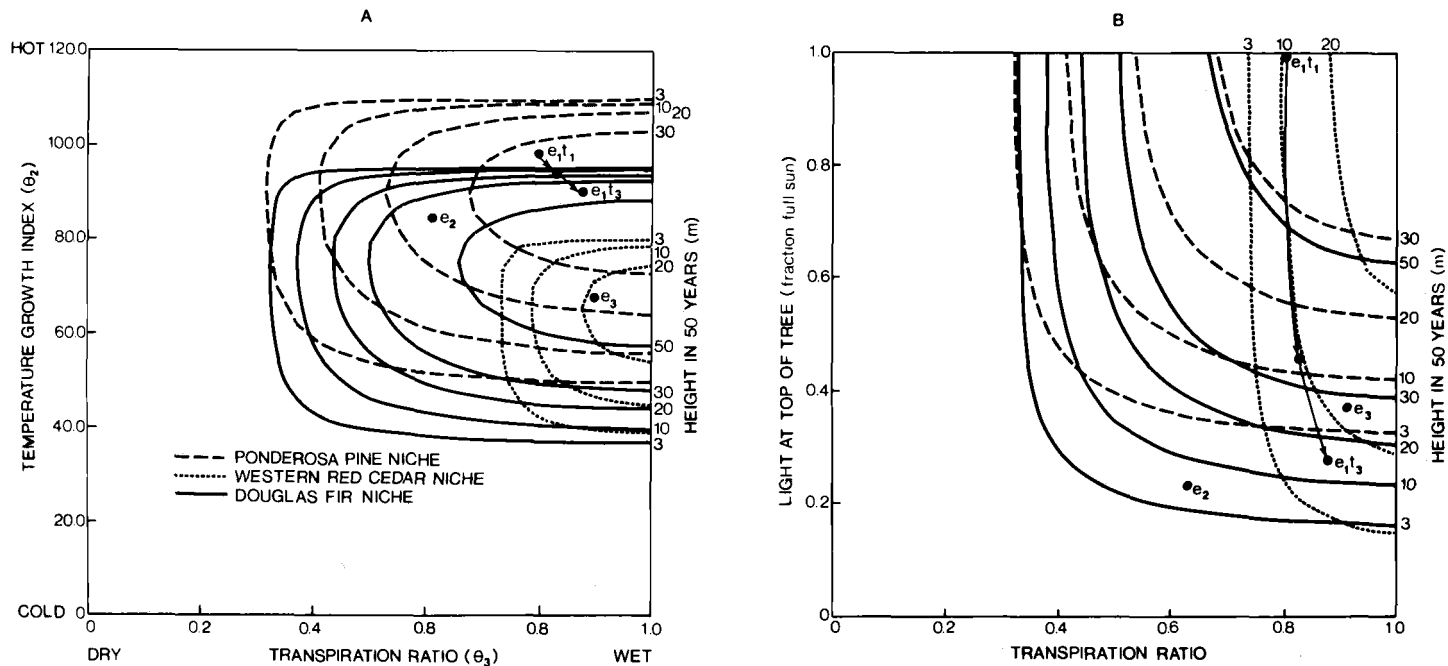


FIGURE 4.2 Postulated niches of three coniferous species defined in terms of height growth. The points e_{1,t_1} and e_{1,t_3} represent environment on a site at different times; e_2 and e_3 are environmental conditions on other sites measured at one time only. (a) niches relative to temperature and moisture; (b) the same niches relative to light and moisture.

environmental variables and N_c is the set of niche volumes of the C species composing the community (Reed 1980). Some factors such as fire, although important for establishment of a species, cannot be conveniently defined along a continuous ordinate. These factors could be called "trigger variables," and can be modeled.

As the site's environment changes, its representation, $e(\theta)$, moves through E-space; as it crosses a niche boundary, a new community is possible. This could be termed a potential community, or $e(\theta) \in N_p$, where N_p is the set of niche hypervolumes that *could* be realized on the site. Given an appropriate trigger, the new species can invade, and N_p becomes equal to N_c if all possible species invade. The *realized* community is defined as N_c . In nature, plant succession can result from environmental changes on a site over time; prediction of the environmental changes could allow prediction of succession. Human activities that result in environmental change can strongly influence forest community structure and succession.

The above theory provides a foundation for the work discussed in Hawk et al. (Chapter 2) and Emmingham (Chapter 3). Because a community can exist only where the site locus e is an element of all the niches N_c , then the converse is also true: The location of e in E-space can be defined as the intersection of the set of niches comprising the community (Reed 1980). If the niches of the major species are known, the environmental coordinates of a particular site can be determined by simply extrapolating from the point of intersection to the ordinates, as did Waring et al. (1972).

A practical application of this theory to land management is possible. If the land were mapped according to vegetation, habitat types, or other plant ordination systems, then the environment or selected community types could be measured and the habitat types could be characterized in terms of their environmental ranges. Land management practices could be based on knowledge of management impact on environment, hence community type and productivity. Models could be developed that use environment as input and more directly and accurately predict ecosystem response to environmental change. Such a model is discussed below.

THE FOREST GROWTH MODEL (SUCSIM)

The work discussed above defines environment space and can delimit community and niche. The time-trajectories of a site reference locus through E-space, and the resulting community response, can be simulated by a forest growth model. To this end, a forest growth and SUCcession SIMulator (SUCSIM) based on the above theory was developed (Reed and Clark 1978). Tree growth is expressed as a function of environment, leaf biomass, and tree size. This growth function can be used to illustrate niche as in Figure 4.2. Natural establishment of the forest is simulated according to niche and trigger variables,

and mortality is predicted as a function of slow growth and other trigger variables. These ideas, while expressed differently, do not differ greatly from most forest and tree simulation models (for example, Botkin et al. 1972; Fries 1974; Botkin 1977).

A principal disadvantage of most forest growth models is that they require individual trees to be grown on small plots. This causes two serious problems: (1) the population must be limited to avoid reaching computer time and size limits; and (2) extrapolation from the small plot to more useful units (for example, quantities per hectare) can be difficult. For example, if the simulation plot size is 0.1 ha, each tree on the plot represents 10 trees/ha; it is impossible to "kill" fewer than 10 trees/ha. Consequently, to simulate reality, numerous runs with random mortality functions must be made and averaged. This can be prohibitively expensive.

The problem is avoided in SUCSIM, which is so structured that the plot size can be large. Simulation of a forest requires that the forest be divided into discrete plots. The only criterion for determining plot size is the requirement that environment be relatively homogeneous across the plot. Because the plot size can be specified at 1 ha or greater, conversion to useful units is easy and only one run is required for simulations.

Plots of variable size are simulated easily and efficiently in SUCSIM by growing *cohorts* of trees rather than individuals. A cohort is defined as an *object* with a set of attributes including species (with an associated set of specific parameters for the growth function, and so on), population, height, diameter, leaf biomass, and age. In SUCSIM these attributes are more precisely defined as, for example, "height of trees in cohort i ." This can be considered to be the mean height of the trees in the i th cohort. One species of a given age, height, diameter, and the like is defined as a *cohort*. This does not imply that there is only one cohort per species; there can be n different cohorts of species j , each having one or more differences among their attributes. Table 4.1 shows a partial cohort list from a typical SUCSIM run (1-ha plot, 102 years).

The algorithm is simplified and run-time is greatly reduced by use of cohorts. At each step, the program calls each subroutine (GROW, BROWSE [optional], LITTER, DEATH, and so on) once for each cohort. Certain plot attributes, such as light at each level of the stand and fraction of the plot covered by leaves, are computed after the cohort attributes are updated. The seeding subroutine (SEED) decides which species to establish, depending on environment. If the environmental coordinates of the stand are within the niche of a given species, that species can be established. The number of seedlings varies with environment and the number of other species to be established. Once SEED has decided which and how many species with an initial height of 3 cm to seed, the system computes the other cohort attributes.

→ At present there are two ways for trees to die: slow growth and random mortality. As the canopy closes, certain cohorts receive less light and their growth slows. When diameter growth is reduced below a certain species-

TABLE 4.1 *List of selected cohort attributes from a typical SUCSIM run at year 102 (good Douglas-fir/hemlock site).*

Cohort number ^a	Species	Population (stems/ha)	Age (yr)	Height (m)	DBH (cm)	Leaf biomass (kg)	Diameter increment ^b (cm)	Height increment (cm)	New leaf biomass ^c (kg)	Litterfall (kg)
1	Douglas-fir	367	102	33.3	66.6	40.7	0.26	11.5	2.1	2.1
3	Western hemlock	527	102	22.4	38.9	16.2	0.15	7.15	0.72	0.72
7 ^d	Western hemlock	2	92	0.68	0	0.033	0.0015	0.083	0.0002	0.0002
14	Western hemlock	1	92	0.65	0	0.021	0.00089	0.051	0.0001	0.0001
Plot total		958				190 ^e m ² /ha	23.5 t/ha		1.15 t/ha	1.15 t/ha

^aNot all cohorts are given here. Cohort identities are retained and not reused. Cohort 6, for example, has died out.

^bDiameter increment is at the base of the tree.

^cNew leaf biomass and litterfall reach an equilibrium depending on light and growth rates.

^dCohort 7, seeded in at year 8, was browsed at some time, creating cohort 14. Both cohorts are doomed.

^eBasal area of the two dominant cohorts.

specific critical level, a fraction of the cohort is killed. The number of trees killed is given as a function of growth rate. Subroutine DEATH reduces the population of the cohort accordingly. When the population is zero, the system's memory management removes that cohort from the program's allocated core.

The dynamic core allocation keeps the operating space requirements as small as possible. A typical 100-year run requires fewer than 40,000 words (60 bits per word) of central memory of the CDC computer at the University of Washington, and usually runs in less than 5 seconds. Several 500-year runs were tried; run-time ranged from 35 to 40 seconds. Very simple runs (such as the stocking level runs discussed below) required slightly more than 1 second of central processing unit time per 100 years. The system maintains its own files, allows direct access to any function or parameter at any given time, and can be run interactively or batched with equal ease. The syntax is simple and easily learned. The program development required a large effort, and the models themselves are still at a primitive stage.

The program uses the environmental variable TGI as the heat input variable (see Emmingham, Chapter 3); moisture is given by the ratio of seasonal transpiration to potential transpiration (Reed and Waring 1974); and the third variable is light. Complete model documentation is presented in Reed and Clark (1979). Three-dimensional representations of the niche of two species with respect to SUCSIM environment are shown in Figure 4.3.

Space allows only two examples of SUCSIM runs. The simulated effects of different environments on mixed Douglas-fir/ponderosa pine stands after establishment are illustrated in Figure 4.4a to f. Stand development is simulated under two climatic regimes, warm and dry versus warm and wet, conditions that approximate two sites in the Mt. Adams area of Washington. In each case, 500 Douglas-fir and ponderosa pine were seeded (3 cm tall) on a 1-ha plot. The plot was browsed at irregular intervals and no management activity was simulated. In an effort to emphasize the differential effects of environment on establishment of the two species, seed years were restricted to nine-year intervals with no off-year seeding. One of the principal differences between the two species is an assumption that Douglas-fir cannot seed into an area exposed to direct sunlight, while ponderosa pine may. This assumption is based on unpublished observations by K. L. Reed in the Mt. Adams area.

In Figure 4.4a, the population on both plots rapidly declined during the first eight years with a large influx of pine seedling at year 9, but no additional Douglas-fir was added because the light level at the forest floor was excessive. Ultimately, by the third seed year (year 27), Douglas-fir and other species (not illustrated) became established on the dry site, but the wet site was by then fully stocked and too dark at the forest floor for pine and Douglas-fir. The light climate can be inferred from the total leaf biomass curves in Figure 4.4b. Also, because we have set a greater potential for browse of pine, more pine was killed

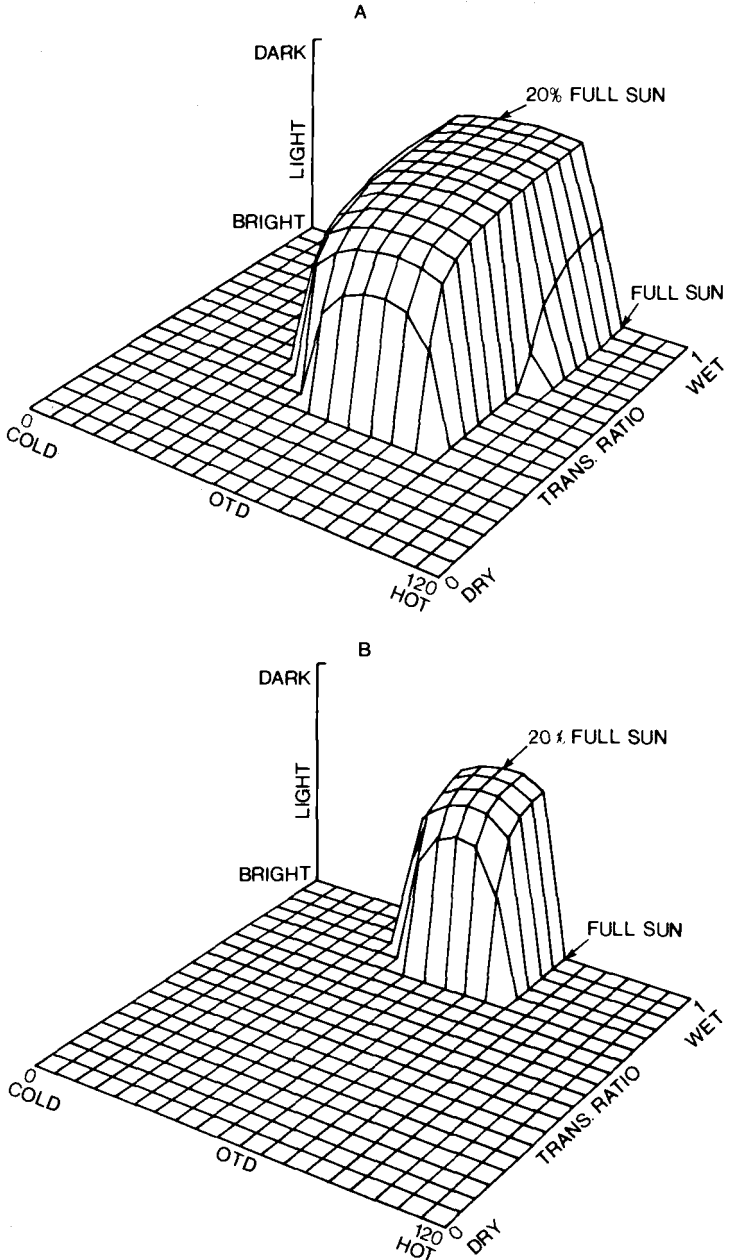


FIGURE 4.3 Three-dimensional representations of the niches of two species. (a) Douglas-fir niche defined by a minimum height growth of 10 m in 50 years; (b) western red cedar niche defined by the same criteria.

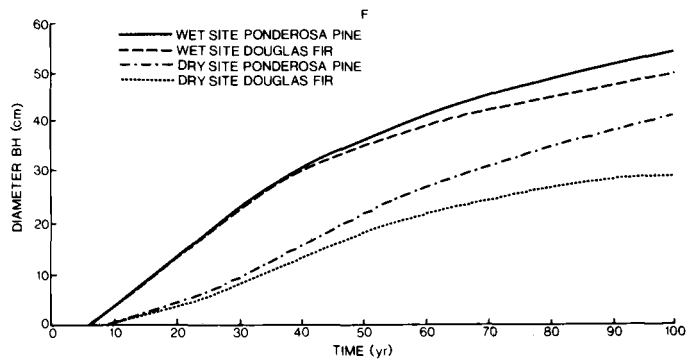
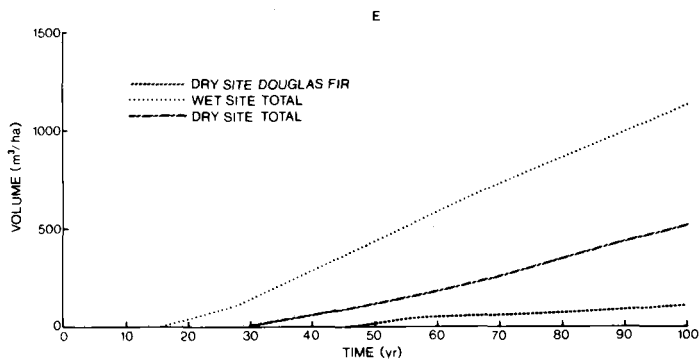
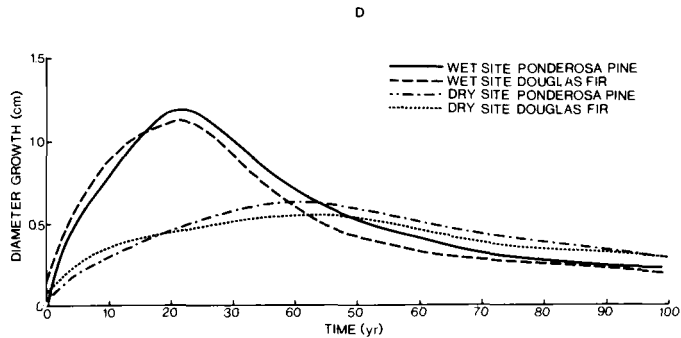
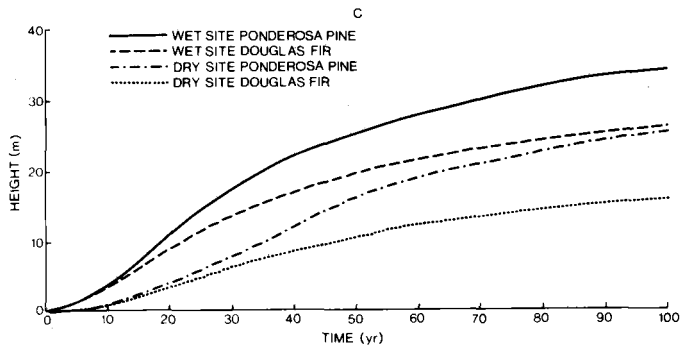
by browse than was Douglas-fir (Figure 4.4a, years 1 to 9). Browse losses are heavier on dry sites because slower growing trees are more susceptible, given an equivalent population of hungry animals with the same browse preference.

A seeming paradox in Figure 4.4b is evident. In spite of the fact that Douglas-fir makes up only about 17 percent of the "stand" on the wet site at year 50, approximately half the leaf biomass is Douglas-fir. This seeming paradox is explainable by the fact that Figure 4.4a shows the total population of the "stand"; most of the subsequent pine cohorts are small and suppressed. Actually, since Douglas-fir typically carry more leaf biomass than pine; we would expect more Douglas-fir leaf biomass on the wet site. Dissimilarities between Figure 4.4a and typical forestry stocking curves occur because all trees are represented, not just the dominant and codominant trees.

To summarize these results, browse damage causes rapid population drops on both plots. A heavy seed year at year 9 results in a great ponderosa pine population explosion, but the dry site seeding is approximately half that of the wet site because the climate inhibits seedling establishment. On both sites, Douglas-fir establishment is minimal. As the stand ages, the microclimate is modified, and successive seed years are more successful on the dry site until, at approximately year 30, the population curves cross. Mortality is greater on the set site owing to faster growth of the dominant cohorts, which shade out the smaller cohorts. The dense shade prevents establishment of new cohorts, resulting in a steady population decline. The dry site remains open much longer with less leaf biomass (Figure 4.4b). The maximum total leaf biomass of the wet site is reached around 30 years, while the dry site leaf biomass continues to increase slightly from year 45 through year 85. The values appear reasonable (see Turner and Long 1975), although they were higher than observed by Grier and Logan (1977) on old-growth Douglas-fir forests. Comparisons of height, diameter, diameter growth, and bole volume are also shown in Figure 4.4c to f.

The SUCSIM algorithm allows specification of height of seedlings in order to simulate planting of larger seedlings. This is illustrated in Figure 4.5, where we simulated the planting of 500 pine seedlings 30 cm tall and 500 pine seedlings 3 cm tall on the warm, dry site. Only the heights of the tallest pine cohorts are illustrated. The larger seedlings had a head start that produced larger trees and had other minor effects on the stand (not illustrated). These effects included a reduction in pine mortality due to browse, because the bigger seedlings were less vulnerable and volume was greater. Growth of the 3-cm seedlings was progressively less than that of the bigger seedlings, because of direct competition.

The second set of demonstration runs was devised to address the question: What level of stocking will produce the greatest yield of Douglas-fir on good and poor sites? Simulated height, diameter at breast height, diameter growth, leaf biomass, and basal area as a function of time and stocking levels on a good



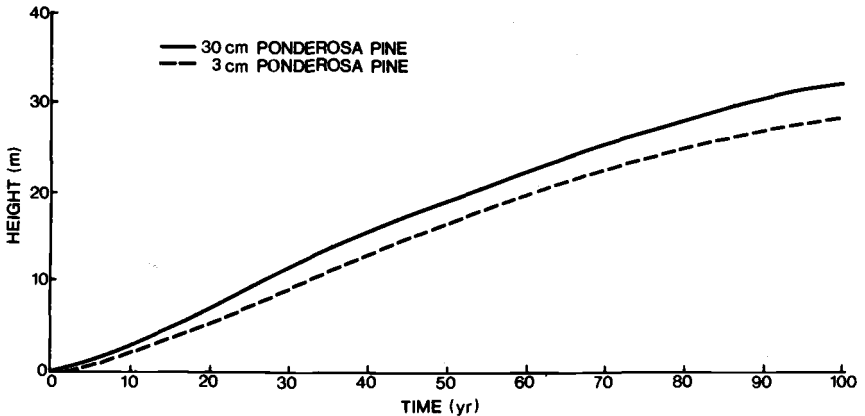


FIGURE 4.5 Comparison of simulated height of ponderosa pine “planted” at initial heights of 30 cm and 3 cm on an optimal pine site. Only the two tallest cohorts were plotted.

site are shown in Figure 4.6a to e, respectively. Figure 4.7 compares the impact of stocking levels on cubic volume of the good site and a poor, dry site.

The environmental coordinates of the simulation for the good site were 70 OTD, full sun, and transpiration ratio of 1. These conditions are optimal for Douglas-fir in this version of the model. In these runs, mortality, seeding, and browse routines were turned off; only the growth routine was active. Program SUCSIM keeps track of individual crown area and leaf biomass in twenty strata, which allows simulation of crown closure. Crown closure results in lower available light, which reduces growth, thus allowing comparison of the effects of stocking level.

Four stocking levels are compared, ranging from 240 to 1440 stems/ha. Decreased stocking produces larger trees (mean height, Figure 4.6a), but reduces total basal area per hectare (Figure 4.6e) because of the lower population. Crown closure (indicated by the break in the leaf/biomass curves) in the lowest stocking level is 10 years later than in the highest (Figure 4.6d). The differences between the poor, dry site and the good site are summarized in Table 4.2, and the volume curves are compared in Figure 4.7a and b. Aside from the lower values on the poor site, a significant difference is that the volume curves of the good site cross at year 40, while the poor site curves are just beginning to converge at year 100. The crossing at year 40 suggests that the high site stand should be thinned no later than year 40, if volume is the decision criterion, while the dry site yields more at high stocking.

The examples of SUCSIM runs presented here demonstrate only a few of the simulation experiments possible with the model. Thinning can be simulated using a given set of criteria, and the harvested “wood” can be left on the plot (as input to a decomposition model yet to be developed) or removed. Manage-

TABLE 4.2 *Comparison of simulated production on good and poor, dry Douglas-fir sites.*

Stock level (stems/ha)	DBH (cm)	Height (m)	Basal area (m ² /ha)	Leaf biomass (t/ha)
High site: temp. index = 70 OTD, $\tau/\tau_p = 1$				
1440	44.5	23.6	224	24.2
960	52.2	27.1	205	22.8
480	68.2	34.2	175	20.7
240	87.7	42.4	145	18.5
Low site: temp. index = 80 OTD, $\tau/\tau_p = 0.6$				
1440	36.6	19.4	151	19.7
960	42.4	22.2	135	18.2
480	54.6	27.7	112	16.1
240	69.5	34.3	91	15.0

Note: Temperature is expressed in optimum temperature days (OTD); moisture regime is defined in terms of a ratio of transpiration over potential transpiration (τ/τ_p), as discussed in the text.

ment can be simulated by selective planting, thinning, and even pruning. The simulated stand can be clearcut, partially cut, high-graded harvested by species, or some combination thereof. Insect defoliation can be simulated. Natural forest conditions (as in Figure 4.4) or ideal experimental conditions (as in Figures 4.6 and 4.7) can be simulated. Given realistic parameter values, the model can “grow” any species of tree. All parameter values can be easily changed, and modification of submodels is a relatively simple task.

One of the principal goals of modeling work is the development of a model that can be used to generate data for optimization and decision routines. Here a criterion is established and the model is exercised to produce results that can be mathematically analyzed to optimize the system with respect to the criterion of interest. Such routines are exceedingly expensive and would require a very efficient model. We believe that the speed and efficiency of SUCSIM, coupled with the considerable degree of biological reality, will make optimization experiments possible.

Further, the theoretical concepts of niche, adaptation, competition, and succession can be studied with a model that is far more complex and realistic than the simple differential equations most often used. Such studies should provide a better understanding of the nature of forest ecosystem dynamics and lead to the clarification of many concepts that are now poorly understood. This better understanding could give rise to land management systems that are more ecologically sound, and would reemphasize the importance of ecology in land management problems.

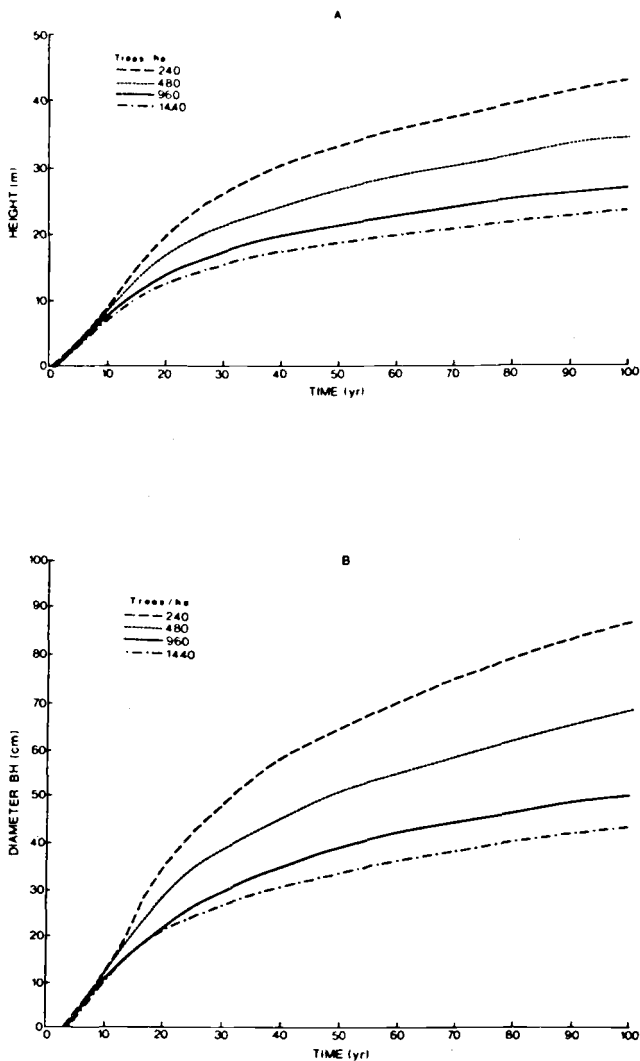
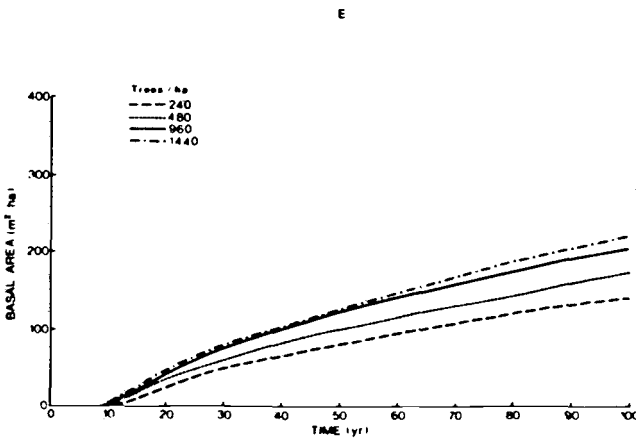
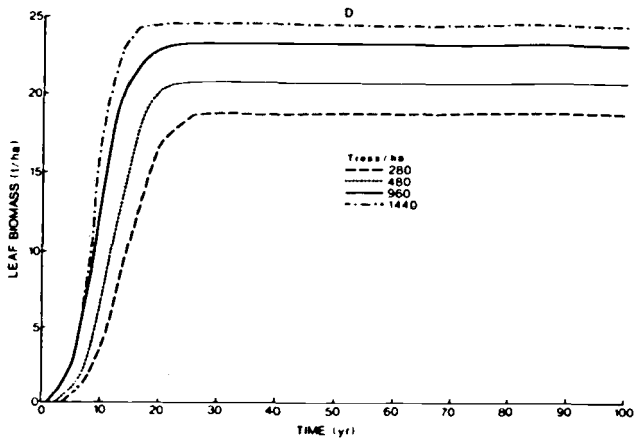
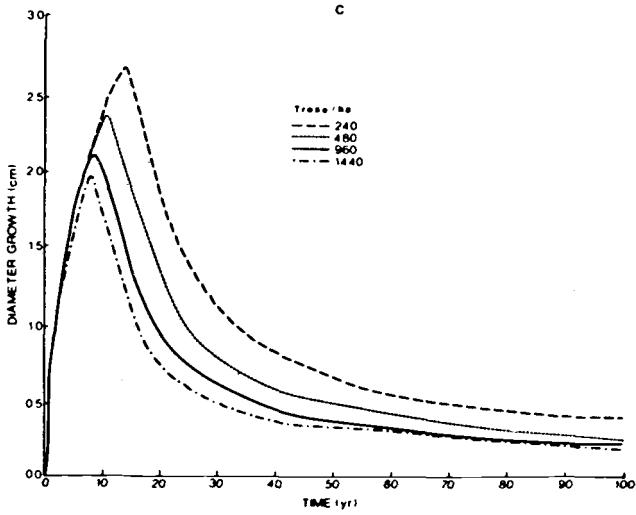


FIGURE 4.6 Comparison of productivity on a good Douglas-fir site as affected by stocking levels (population density; lines represent numbers of trees per hectare). (a) height (meters); (b) basal diameter (centimeters); (c) basal diameter growth (centimeters per year); (d) leaf biomass (tons per hectare); (e) basal area at breast height (square meters per hectare).



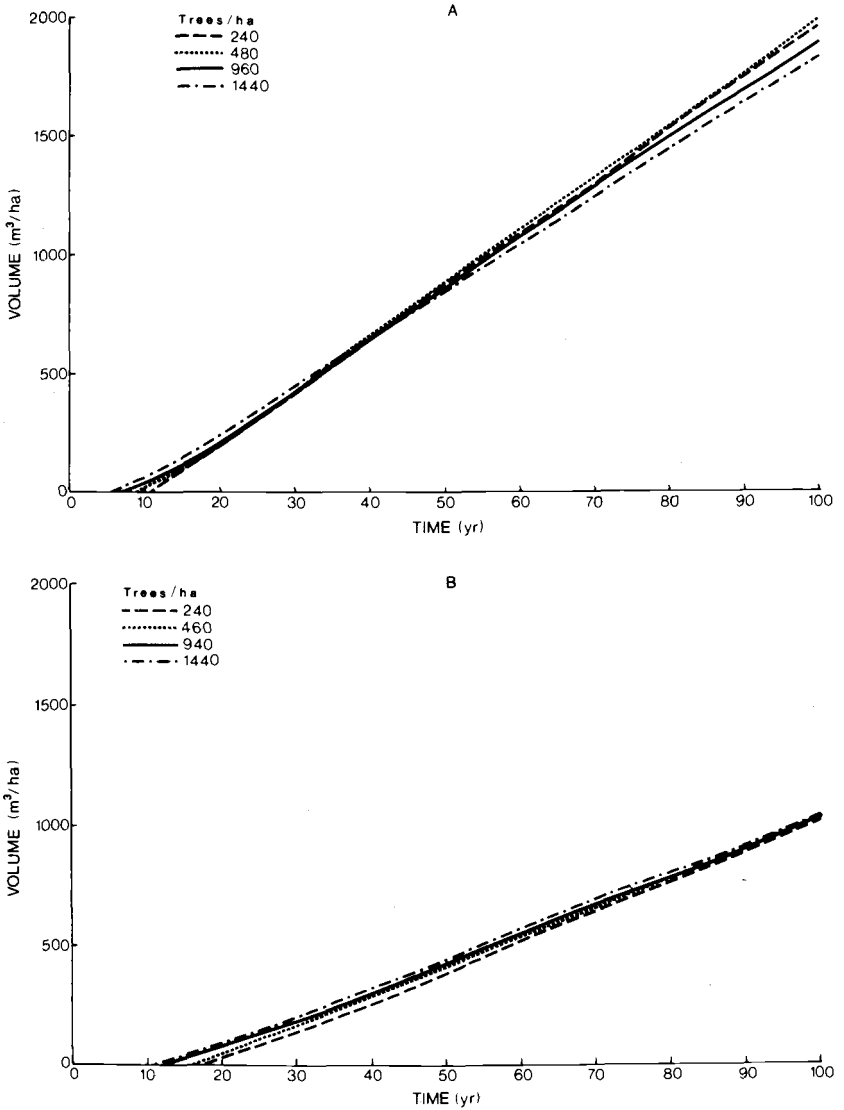


FIGURE 4.7 Comparison of simulated cubic volume yields on a good Douglas-fir site and a poor site as affected by stocking levels (population density; lines represent numbers of trees per hectare). (a) good site; (b) poor site.

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