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MASTER

FOREST - SUCCESSION MODELS AND THEIR ECOLOGICAL AND MANAGEMENT IMPLICATIONS

by

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ABSTRACT--Computer models of forest succession have been developed to an extent that allows their use as a tool for predicting forest ecosystem behavior over long periods of time. This paper outlines the use of one approach to forest succession modeling for a variety of problems including: (1) determining the effect of climate change on forests, (2) integrating information on wildlife habitat changes with the changes in forest structure associated with timber management, (3) assessing the potential effect of air pollutants on forest dynamics, and (4) determining the theoretical importance of disturbance on forest community diversity and function.

Keywords--Modeling, forest succession, deciduous forest.

INTRODUCTION

Vegetation communities are formed by replacement of species by others more adapted to the prevailing environmental conditions. Often these conditions are in turn modified by species themselves, provoking new replacement. However, the sequence of species replacement is thought to be determined to a large extent by the tolerance to shading of the individual taxa. For this reason, once a community reaches the forest stage of development the sequence of events is more predictable (MacArthur and Connell 1966). This holds because trees respond to establishment and growth according to their tolerance to shading. The more tolerant species replace the less tolerant ones until the most tolerant individuals within the region have established a "climax" forest (Whittaker 1975). Some misconceptions have been formed with regard to some of the finer points of the tolerance-intolerance hypothesis concerning forest succession. For example, MacArthur and Connell (1966) state that "...the climax forest is composed of the most tolerant species..." when in fact the uneven-aged nature of a mature forest stand permits the presence of an array of species with a relatively broad spectrum of tolerance characteristics (Braun 1950).

An obvious problem with forest succession studies is the slowness of change associated with the replacement sequence in comparison to the life span of research studies. For example, during the seventy-five years which have elapsed since Clements first began publishing his work, only a small percent of the time required for a mature forest to develop from an old field has passed. To cope with this problem, forest ecologists examine a spatial sequence of similar communities that are in different stages of development. From this, inferences are made that the spatial heterogeneity of sites represents a temporal continuum of the successional sequence. However, the lack of accurate historical information concerning specific communities adds to the uncertainty of making valid comments about the forest's future behavior. An even more serious constraint associated with forest succession studies is that the predictability of taxonomic sequence discussed by MacArthur and Connell (1966) assumes relative constancy of environment and that the growth and behavior of the individual taxa will adhere to some known set of characteristics.

Modeling techniques have been used to explicitly examine the behavior of a forest community over time and can thus add the dimension that is unavailable from field studies. Further, models can predict the effects of changing environmental conditions on successional sequences. Calibrated in conjuction with observations of forest communities in various stages of succession, models can extend these observations to a more complete explanation of successional dynamics. The case studies below are presented as examples of how modeling has used this temporal dimension to examine the results of the competitive interaction of species.

THE GENERAL FORM OF THE MODEL

The type of model which will be discussed throughout this paper is referred to as a gap replacement model (Shugart and West 1980). In general, these models simulate succession by calculating the competitive interrelations among trees in a restricted spatial unit equivalent to the size of a gap created by the death and removal of a canopy tree. The models simulate the annual change of a forest stand [one-fifth acre, one-twelfth hectare (ha), circular plot] by calculating the growth increment of each tree on the stand, by tabulating the addition of new saplings to the stand, and by tabulating the death of trees present on the stand (Fig. 1). These processes are simulated, based on general silvicultural information that includes site requirements for germination, palatability of seeds to browsers, sprouting potential, shade tolerance, temperature requirements for germination and growth, inherent growth potential, longevity, and sensitivity to crowding stress. The maximum growth of each tree on a plot is computed from the inherent radial and height increment potential and longevity of the tree species. This maximum growth is modified by the response of the tree to such environmental conditions as light availability, annual temperature and growing degree days, and spatial crowding and root competition. These environmental factors are considered to be homogeneously distributed over the plot (Shugart and West 1977). Seed and sprout establishment is based on the availability of light, proper temperatures, substrate requirement for germination, and sprouting capabilities of dying or harvested trees. Mortality is a function of the growth and expected maximum age of the tree. Each growth response to environmental conditions is described as a probability function. Therefore, the models are of a stochastic nature, allowing for a wide variation in the response of any individual tree. Provided that the mean and variance of the biological response of an individual tree to a management technique are known, the model can be used to simulate the subsequent effect on the forest community.

PREDICTING CLIMATE CHANGE EFFECTS ON FORESTS

The ability of models to simulate forest dynamics over long time periods makes them ideal for examining the response of vegetation communities to climate change. Characterizations of past climates can be made by analyzing fossil pollen found in the different sediment layers in lakes and bogs (Webb and Bryson 1972, Brubaker 1975). Pollen composition changes as tree species near the lake change over the years, and it is possible, using ^{14}C dating, to accurately date different levels in the sediments.

Solomon et al. (1980) compared characteristics of the output of the FORET model (Shugart and West 1977) to actual pollen records from Anderson Pond in central Tennessee (Delcourt 1979). Long term changes in climatic regime were simulated by shifts in the mean number of growing degree days (temperature). Temporal shifts in individual pollen taxon frequencies from the pond sediments were compared to predicted shifts in individual plant taxa frequencies simulated by the FORET model for the last 16,000 years. Correlations between pollen abundance in pond sediments of different ages (determined by ^{14}C dating) and biomass simulated by the FORET model for comparable times were as high as correlations between recent pollen influx in lake sediments and actual forest compositions (Janssen 1967, Ogden 1969, Webb and Bryson 1972). The model output appears to be a plausible description of the vegetation at Anderson Pond for the past 16,000 years. Along with successfully predicting the changes in vegetation from the last continental glaciation to the present, the model provides insights into dynamics of the entire forest -- not just the species that produce airborne pollen. Figure 2 illustrates the changes in species biomass predicted by the model for the Anderson Pond site. The oaks are not presently distinguishable, one from another, in fossil pollen, but the model predicts a shift from red to white oaks at the site over the past 16,000 years. Yellow poplar, sweet buckeye, and white basswood are rarely represented in pollen samples and are "masked" from pollen profiles even though they may be fairly abundant. The model indicates that these species generally increased over the past 6 to 8 thousand years. The forest at this location has been in a state of change for the past several thousand years.

THE USE OF FOREST SIMULATION MODELS TO INTEGRATE WILDLIFE HABITAT AND TIMBER MANAGEMENT

Forest succession models provide a means of assessing the effects of forest management schemes on specific forested sites through the use of habitat simulation (Smith et al., in press). Habitat simulation integrates the use of habitat classification with the predictive ability of the forest simulation model (Shugart and West 1980). This process involves (a) the structural classification of forest stands in terms of suitability to provide habitat for a given animal species, and (b) a forest simulator with the ability to generate the specific structural variables on which the classification is based. By introducing proposed management strategies to the model, we can evaluate the long-term effects of timber harvest on the availability of habitat for a specific avian species.

FORLOB, a modified version of FORAR (Mielke et al. 1977), simulates a loblolly pine forest on upland forest sites typical of south central Arkansas. The model was used by Mielke to determine the effects of various forest management schemes on both the availability of red-cockaded woodpecker nesting sites and timber production. In addition, the model was used to simulate several management strategies (Table 1) consisting of thinning and controlled burning at different stand ages. All stands were "planted" with an initial stocking density of 1500 stems per acre. At year 100 all stands were clear-cut independent of previous management. It was assumed that the stand was unsuitable as red-cockaded woodpecker habitat until at least year 60 (Jackson et al. 1979). Habitat was further defined as low stocking density (preferably less than 18.60 m^2 basal area per hectare) and low or nonexistent understory. The five management schemes reflect various cutting schedules with periodic burning to clear the understory of hardwood invasion. Timber production is expressed as average basal area and number of trees removed per one-twelfth hectare stand over all cuts. The availability of potential nest trees is expressed as the average number and basal area of the trees greater than 60 years of age on the plots at year 100.

Results (Table 1) show that management scheme number 3, which involved cuts at years 25, 40, and 60, resulting in a basal area of 18.60 m^2 per hectare, gave maximum timber production as well as availability of potential nest trees. Management scheme number 2, which involved only a thinning cut at year 60, resulted in older and larger potential nest trees, but timber yield in both number of trees and basal area were considerably less. Management scheme number 1, in which there was no thinning or burning prior to clearcut, resulted in the largest available nest trees. In this case, however, the understory was very dense (as a result of no burning over the 100 year simulation) and would potentially limit the use of these trees as nest sites.

Despite the wide variation in timber production for the various management schemes, the variation in cutting schedules appears to have only a limited effect on the availability of potential nest trees. This may be misleading, because the number and size of potential nest trees may not necessarily reflect their quality and ultimate use as nesting sites. Also, the suitability of a tree is dependent upon the presence of red heart fungus, a factor very much related to the age of the tree. The model does provide a means by which various management schemes can be assessed as to their potential to maximize timber production as well as provide habitat for the red-cockaded woodpecker.

A second example, FORHAB (Smith et al., in press), a modified version of FORET (Shugart and West 1977), was used to predict the impact of certain forest management decisions on the availability of breeding habitat for the avian community inhabiting the Walker Branch Watershed in east Tennessee (Grigal and Goldstein

1971). FORHAB integrates the multivariate statistical procedure of discriminant function analysis to classify avian habitat based on variables describing structure of the forest with the ability of the forest succession model to predict changes in those structural variables through time (for a detailed explanation of this process see Smith et al., in press).

Figure 3 shows the dynamics of the forest structure from 120 year simulations of the Walker Branch Watershed. Forest structure is expressed as the average number of stems, foliage, and branch biomass over all species per one-twelfth ha. Year zero represents the structural configuration of the present forest on the watershed. This was accomplished by initializing the model with 298 randomly chosen census plots from the watershed, using the vegetation data collected on those plots in 1977. Results are given for both timber management and undisturbed conditions. Sawtimber cuts were made at years 1 and 60 of the simulation. Cuts consisted of removing all commercially valuable timber > 27.9 cm.

Figure 4 shows the availability of potential breeding habitat for the red-eyed vireo (Vireo olivareus) and ovenbird (Seiurus aurocapillus) for the same 120 year simulations. These results show the importance of historical considerations in determining the effects of a particular timber management practice on a given forested area. The structural configuration of the forest prior to cutting is of utmost importance in this case of repeated long-term management plans. To date, this type of information has been lacking. Forest succession models of this type can be used to provide the information on long-term management plans and combinations of management schemes before their actual implementation.

ASSESSING AIR POLLUTION EFFECTS ON FORESTS

Another application of models involves evaluating the impacts of the man-induced disturbance of SO_2 on localized stands. In the eastern United States, the high density of multiple point sources and the high frequency of air stagnation events have led to elevated levels of pollutant oxidants over large regions. Abundant evidence exists documenting the harmful effects of those pollutants on individual trees (Zeigler 1973, Mudd and Kozlowski 1975, Heck and Brandt 1977). The use of this information in an assessment of the forest community response to multiple stresses over multiple year-time scales has been hampered by the complexity of intracommunity competition dynamics.

An investigation into this problem was conducted by West et al. (1980). FORET, which considers 32 tree species of the east Tennessee region, was used to study the effects of air pollution stress on the growth and development of eastern forests. Species were classified with respect to their relative sensitivity to the stress on growth and development induced by SO_2 pollution. Although no two species exhibit identical tolerance levels to this stress, the range of behavior was simplified to three classes of responses: resistant, intermediate, and sensitive. Species were placed in one of these classes based on their relative susceptibility to visible foliar injury. The sensitivity classification was based on 10 years of field survey data of vegetation near a coal-fired electric plant (McLaughlin and Lee 1974) and an extensive summary of field and laboratory data on the susceptibility of woody plants to SO_2 and photochemical oxidants reported by Davis and Wilhour (1976). Species-specific growth reductions based on their sensitivity ranking were incorporated into the model to reflect the expected behavior of individual trees observed under field conditions. The basic assumption of this approach was that reductions in physiological function under chronic stress regimes would parallel sensitivity to visible foliar injury from SO_2.

Responses of a simulated forest to air pollution were examined for varying levels of stress and for the forest ages at which the stress was initiated. An initial simulation imposed a maximum growth stress of 20% on the six most sensitive species. The 10 intermediate species received a 10% stress, and the 16 resistant species were unstressed. Stress was begun at year 1, when trees were still in the seeding stage.

The results of these simulations are summarized in Fig. 5. Increases in the biomass of four major species are compared with and without simulated air pollution stress. These species show representative responses of the three tolerance classes: yellow poplar (intermediate), white oak (resistant), black oak (intermediate), and black cherry (sensitive). The collective "other" species category and total stand biomass are shown as well.

Yellow poplar, an early successional species with a rapid growth rate, shows rapid positive response to stress. The enhancement of the total biomass of yellow poplar on the plot, despite a 10% growth stress, may be attributed to the relatively greater effect of the stress on other species competing at early stages of the developing forest stand. Black oak, on the other hand, with the same level of applied growth stress (10%), shows biomass reductions in excess of 10%. Reductions of this magnitude may be attributed primarily to intrinsically slower growth and response, suggesting the inability of black oak to compete with other species such as yellow poplar and white oak under the additional stress imposed by air pollution. White oak, a tolerant but late successional species, shows a positive response in the simulation which, however, becomes evident only as the stand matures and begins to stabilize. The effects of a 20% growth stress on black cherry, a sensitive species, are quite dramatic, particularly on stands older than 100 years; the result was almost total elimination. Responses of other species and of the whole stand indicate an overall growth suppression by the simulated stress. These results strongly suggest that the response of trees to air pollution may be quite different under the competitive conditions in a forest stand than would be expected from experiments conducted with single individuals or single species. Trees of intermediate sensitivity may experience impacts either much greater or much lower than expected, due to changes in their relative competitive potential. These results offer a different view of air pollution effects than the traditional view constructed from single species response data.

ASSESSING THE ROLE OF DISTURBANCE IN MAINTAINING PLANT COMMUNITIES

The forests of Great Smoky Mountains National Park have traditionally been managed to maintain the existing vegetation communities in a natural undisturbed state. The spread of forest fires, a principle agent of disturbance, has been restricted according to this policy. Yet there are indications that the absence of fire is radically changing these communities.

The frequency of fire in this region previous to enforcement ranged from one fire burning each plot of land every 500 years to one fire every 20 years. The former frequency was experienced on low elevation stands and the latter in the high elevation dry ridge forests. In the years since the beginning of the application of fire prevention policy, the frequency of fires has been reduced to one very 1000 years. Associated with this drop have been signs of a gradual disappearance of virginia pine (Pinus virginiana) and pitch pine (Pinus rigida), vegetation types commonly found occupying the dry ridge environments. Old pine stands are being decimated by pine bark beetle outbreaks, and although the area records indicate that these outbreaks are not uncommon, the scarcity of young pine stands does seem to be new. Sites with exposed soil and abundantly available light are much more infrequent in the absence of forest fires. These environmental changes enhance the establishment of light-tolerant oaks over intolerant pines.

The competitive dynamics of the species can be evaluated by the modeling approach. The region can be divided into cells, isolating the important environmental types, such as dry ridges in one cell and wet coves in another. The management policies that will be applied over the entire region can then be evaluated for each cell. Initial investigations have suggested that in high elevational forests the dominance relationships are greatly affected by the fire frequency.

A simulation was conducted of the ridge top forests of the Hannah Branch watershed in Great Smoky Mountain National Park. The dynamics in twenty-five existing communities (Harmon 1980) were simulated for a period of 500 years. The vegetation presently found on each of 25 plots (1/12 ha) was simulated 500 years into the future. Simulations for such long time periods are necessary if dynamics related to the long life span of the trees are to be uncovered. Figure 6 consists of the average biomass of Pinus echinata, the major pine species found on the 25 plots. Curve A shows the change in average biomass of this species during a simulation when periodic fire is excluded from the model. The pine presence in this community is greatly reduced. Curve B shows the biomass change with fire now permitted to occur in the simulation at the estimated pre-management rate of 1 fire every 50 years (Harmon 1980). The presence of fire dramatically enhances the ability of this pine to maintain a presence in the community. The slight decrease in pine biomass during the simulation is likely related to the difficulty of estimating the actual fire frequency which the area experiences. Pine species regeneration ability may be very sensitive to this frequency.

CONCLUSION

The range of scientific and management problems that can be attacked, using these detailed models, is large and warrants the effort needed to develop such models. Having been involved with the testing and application of these sorts of models for the past several years, we are naturally enthusiastic about their importance --

particularly in terms of building a real capacity to project the pattern of dynamics of forest ecosystems. The potential of these (and related) forest succession models for testing the consequences of theories about the functioning of forests seems large.

However, we would be remiss not to inject a cautionary note with regard to the uses of these models. Gap replacement models make certain strong assumptions about what is important in the control of the dynamics of forest ecosystems. These assumptions are conjectures about forest function that over time and with increased instances of successful applications may become a theory of forest function and structure. It appears to us that these theories, if they develop, will be special rather than general theories. The successes of gap replacement models have been in solving problems within the range of this evolving special theory. We know already the sorts of problems that are outside this range -- any problem that requires a knowledge of exact locations of trees; any problem that is strongly interactive across the mosaic elements of a landscape; any problem where the ecological consequences of a major abiotic disturbance are poorly known.

Gap replacement models are a powerful tool in the ecologist's search to understand forest dynamics and in the manager's need to project the consequences of decisions over time or space. The utility of gap replacement models should not overshadow the need to test these models against independent data, particularly in new situations. Testing of models such as these is difficult, and the data for such tests are often difficult to obtain. Often the best tests of the models involve manipulations of information about real forest dynamics into inferential tests on the models. We have in our own work attempted to maintain at least a 1:1 ratio of model tests:model applications and would recommend such a practice to others.

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FIGURE 1. Representation of the processes considered in tree growth on a 32-m-diam plot in the gap replacement model, FORET (Shugart and West 1977).

FIGURE 2. Simulated distribution of biomass from one-twelfth-ha plot near Anderson Pond, White County, Tennessee. Species immigration and climate vary according to historical record.

FIGURE 3. Structural dynamics of the Walker Branch Watershed as predicted by FORHAB for both undisturbed and timber harvest conditions. Biomass measurements are expressed as kilograms dry weight per one-twelfth ha. Results are grouped into three size classes: —— less than 7.6 cm dbh, --- 7.6 to 22.8 cm dbh, ... greater than 22.8 cm dbh.

FIGURE 4. Percent available habitat for red-eyed vireo and ovenbird as predicted by FORHAB for both undisturbed and timber harvest conditions. Percent available habitat expressed as percent of the total land area of the watershed. Undisturbed simulations are expressed as a solid line, results of the timber harvest simulations are shown as a dashed line.

FIGURE 5. Species and stand dynamics of a forest with and without continuous exposure to air pollution stress (—— unaffected; --- affected) (after West et al. 1980).

FIGURE 6. Total biomass of short leaf pine (*Pinus Echinata*) during 500 year simulation without periodic fires (curve A) and with periodic fires (curve B).

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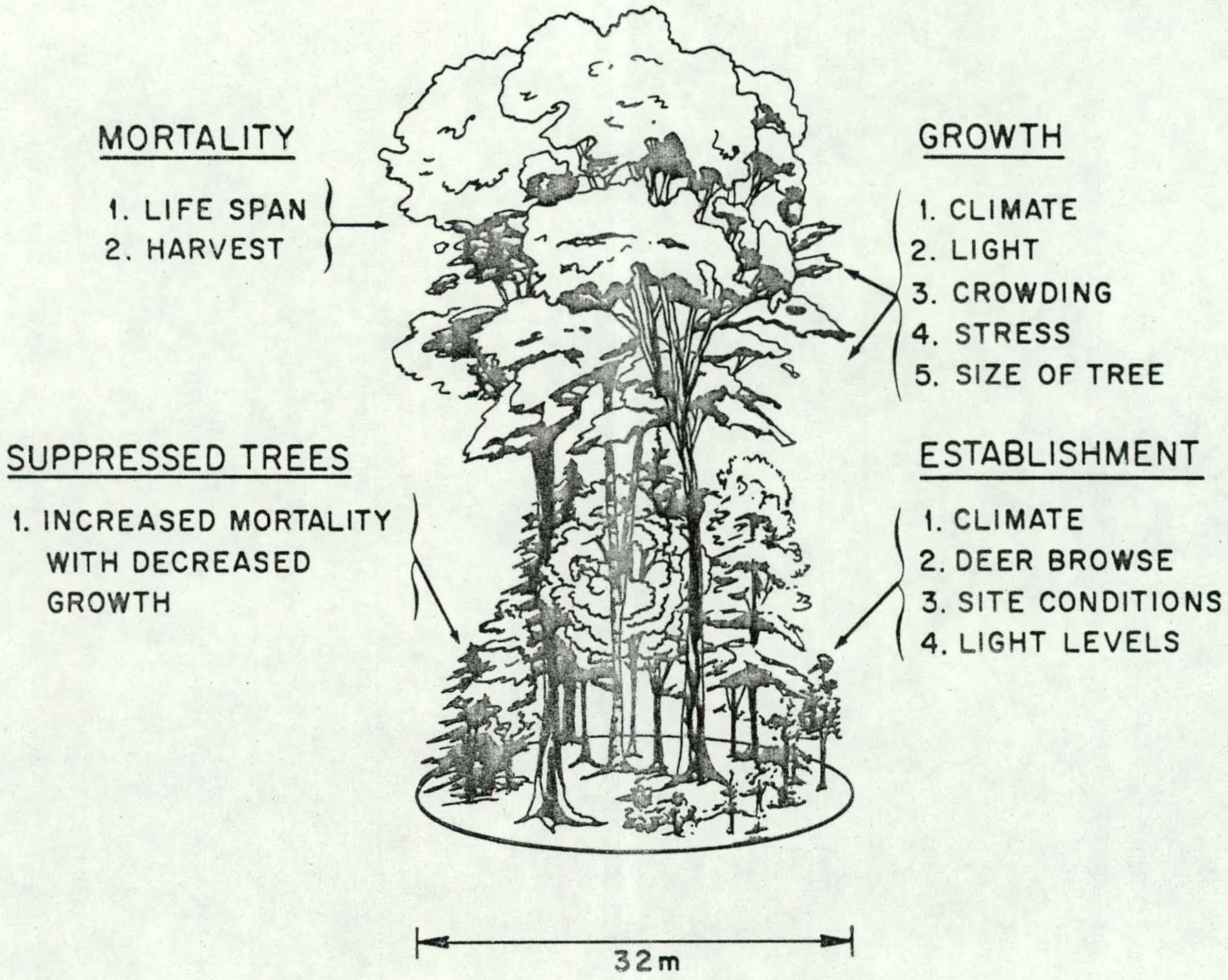

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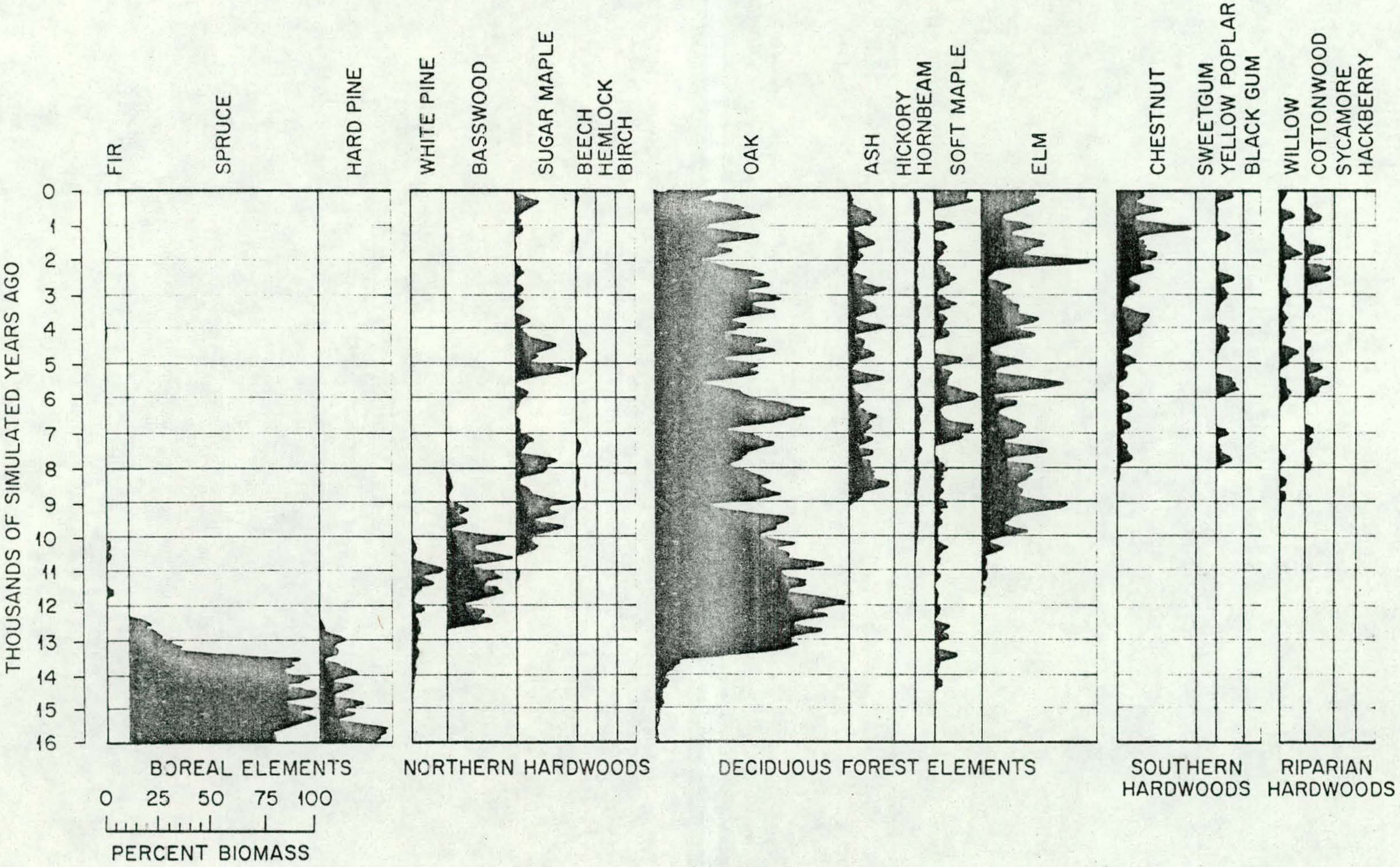
SIMULATED FOREST COMPOSITION: IMMIGRATION AND CLIMATE VARY



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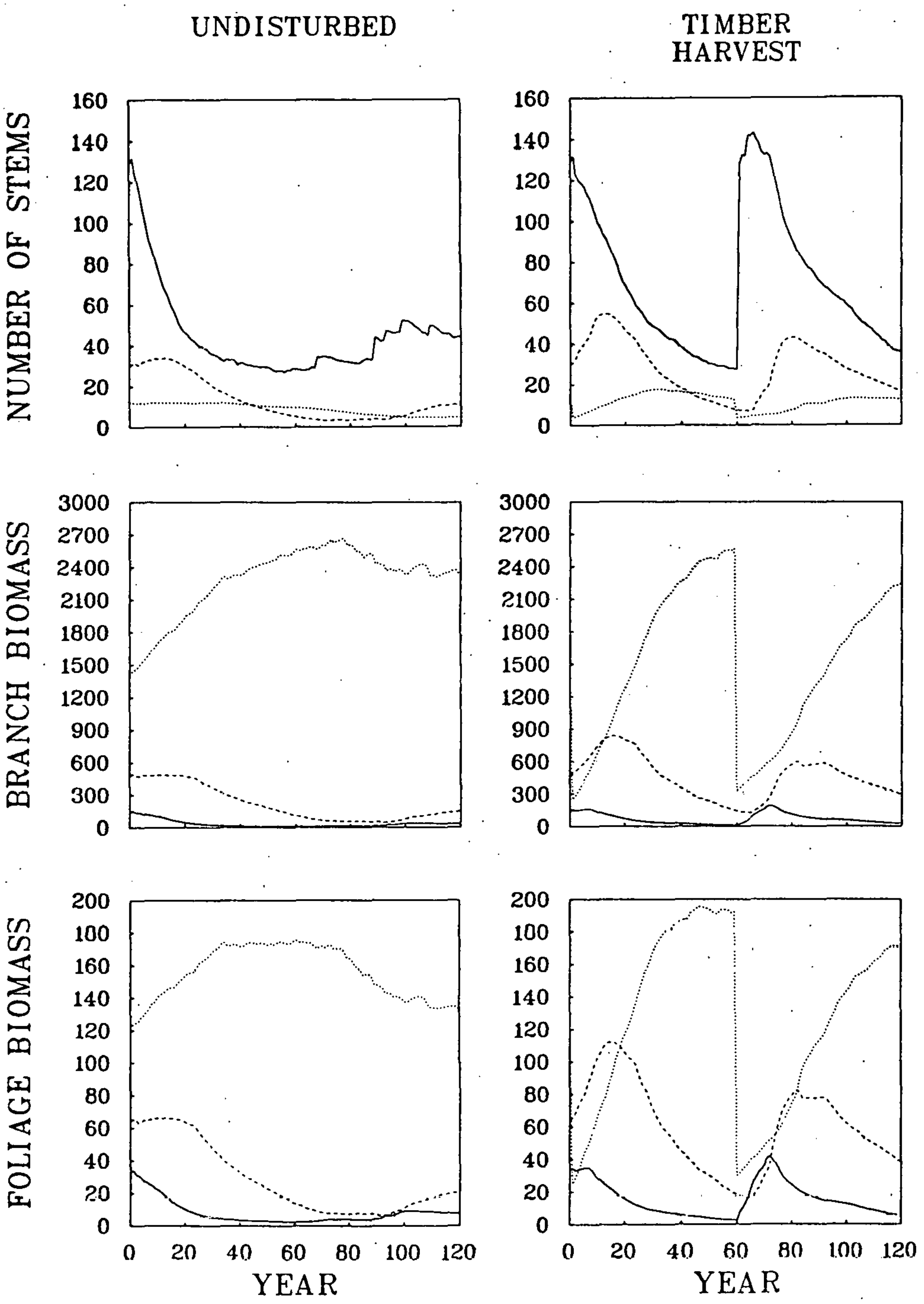

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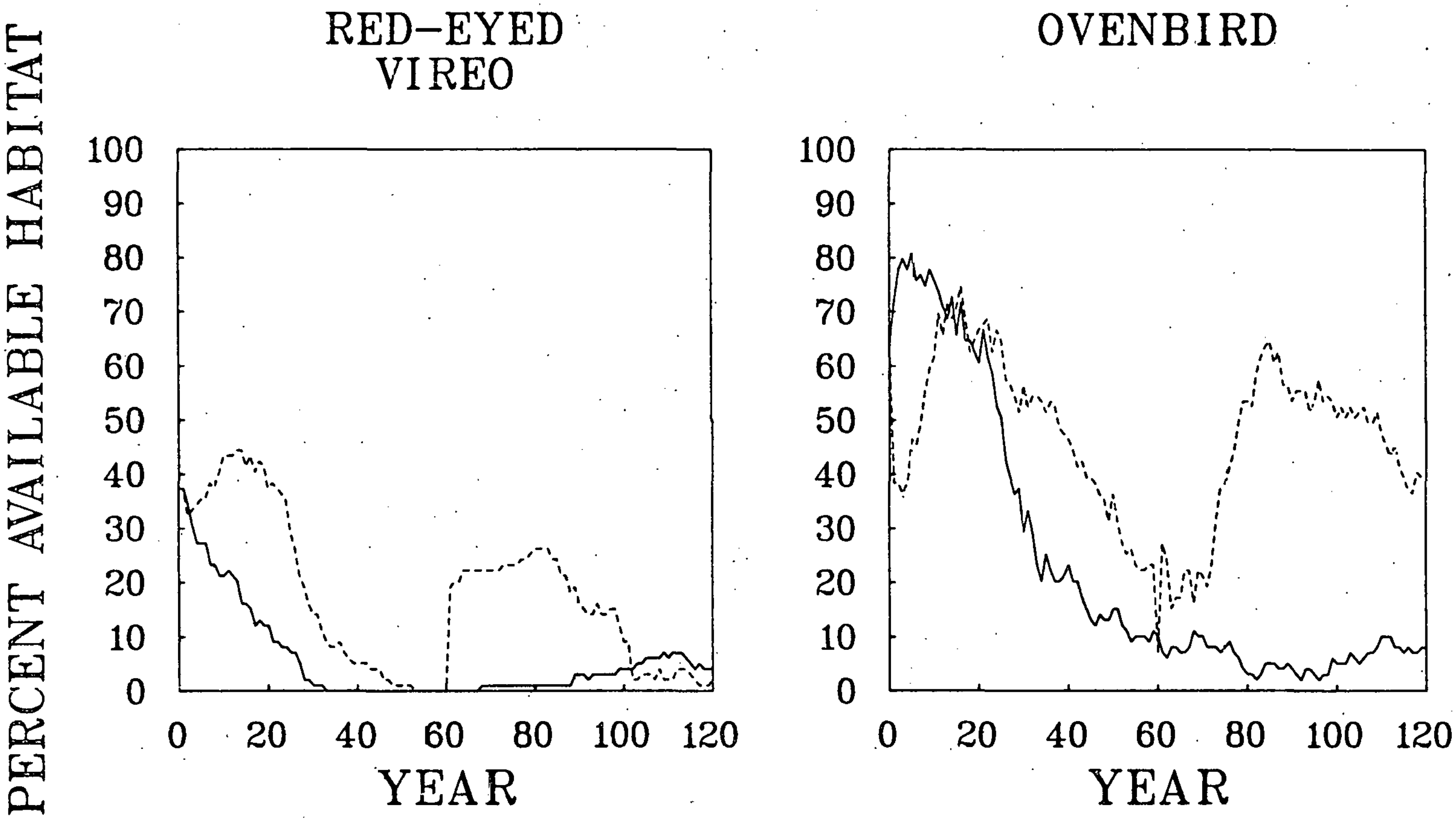

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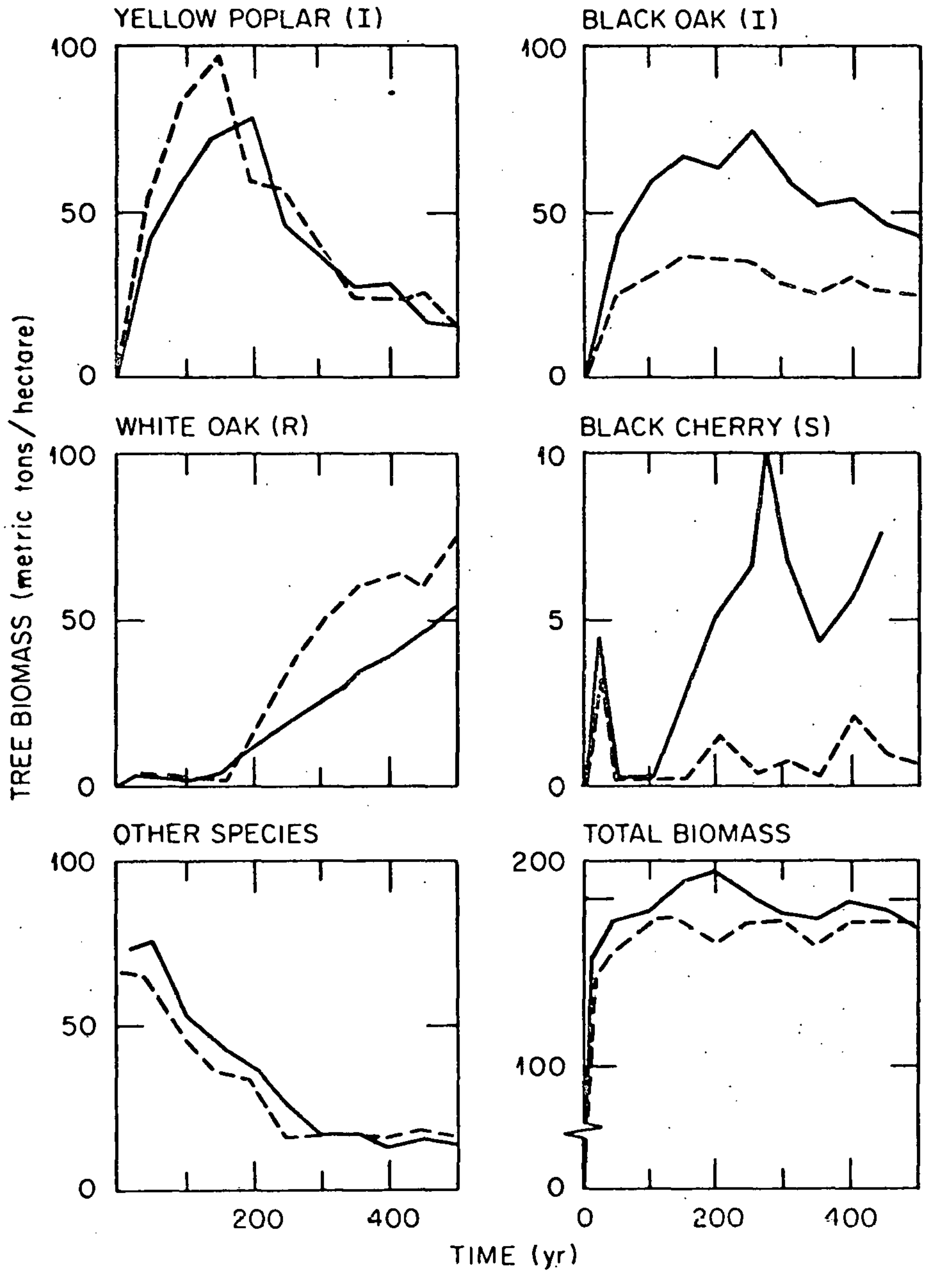
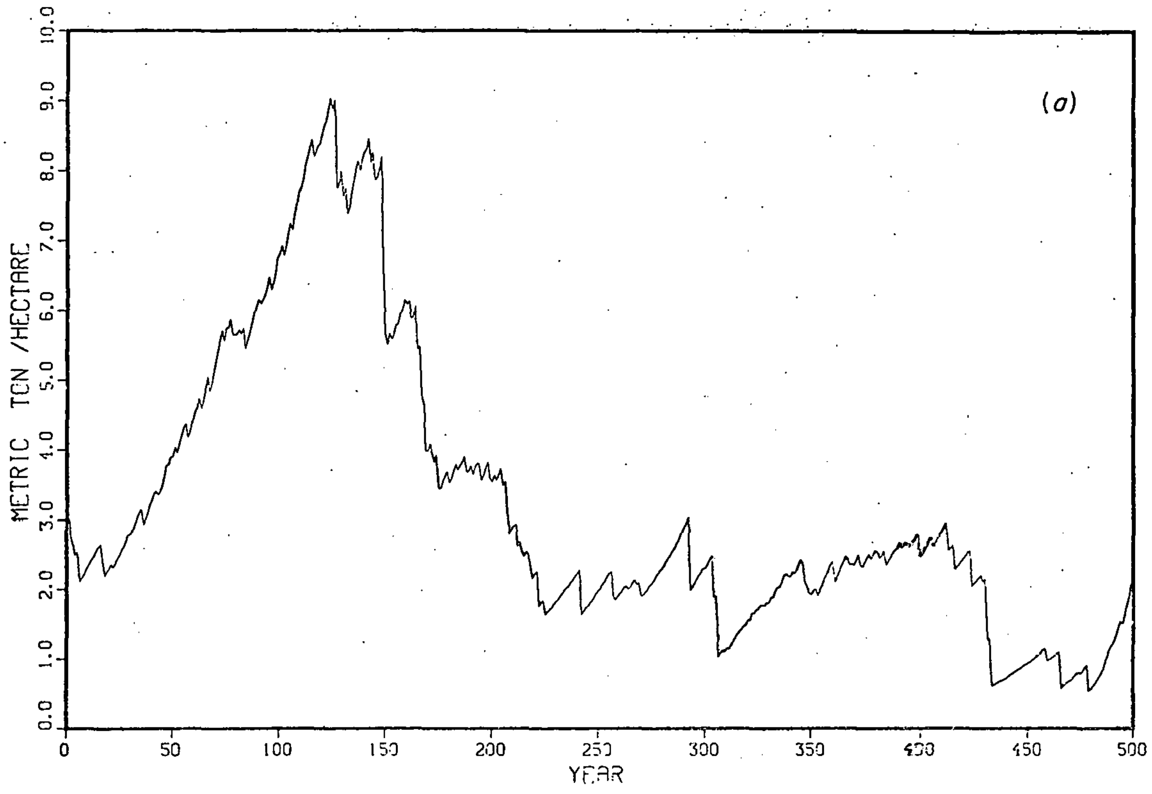


Species and Stand Dynamics of a Forest with and Without Continuous Exposure to Air Pollution Stress (—— Unaffected; – – – Affected) (After West et al. 1980).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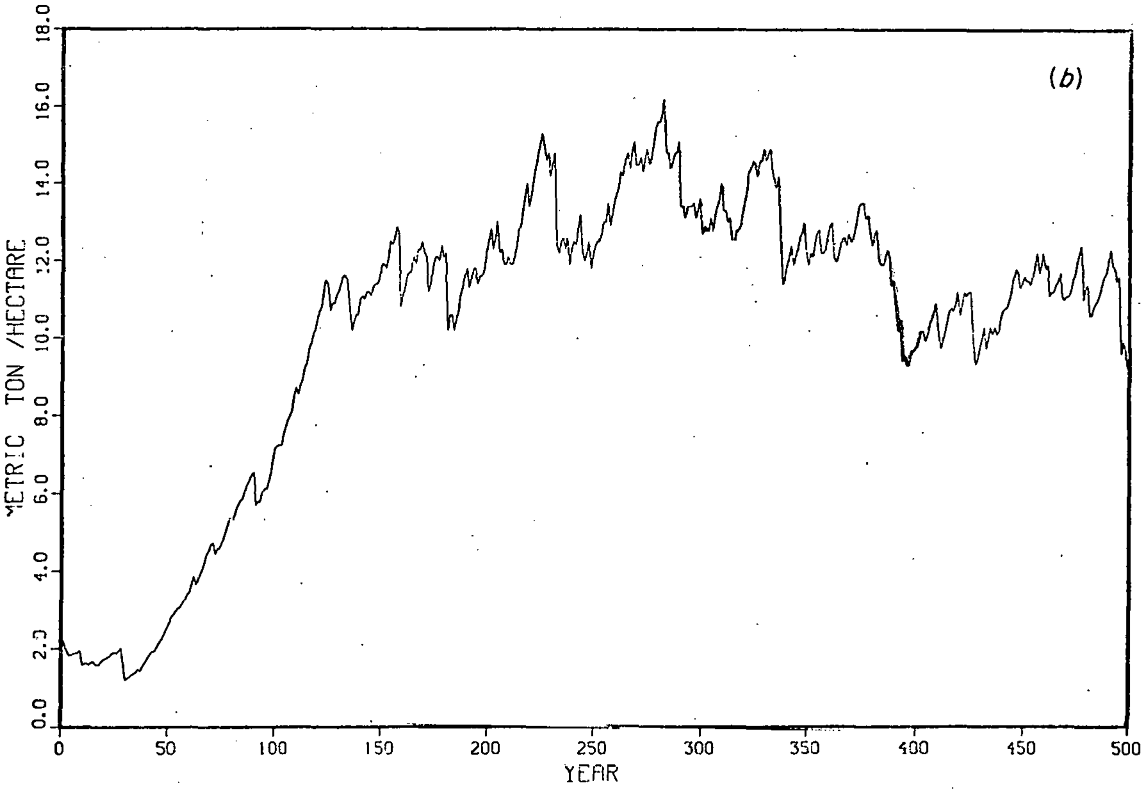
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TABLE 1.

RESULTS OF FORLOB FOR FIVE SIMULATED FOREST MANAGEMENT SCHEMES.

Type of management	Mean basal[a] area removed (m^2)	Mean number[a] of trees cut	Number of potential[a] nest trees at year 100	Mean basal area of nest trees (m^2)
Scheme No. 1 No thinning cuts. No fire. Clearcut at year 100.	18.36	42.50	42.50	.44
Scheme No. 2 Thinning at year 60 to basal area of 18.60 m^2 per hectare. Periodic fire. Clearcut at year 100.	28.11	76.25	41.25	.37
Scheme No. 3 Thinning at years 25, 40, and 60 to a basal area of 18.60 m^2 per hectare. Periodic fire. Clearcut at year 100.	47.98	467.50	48.75	.10
Scheme No. 4 Thinning at years 30, 45, and 60 to a basal area of 18.60 m^2 per hectare. Periodic fire. Clearcut at year 100.	39.45	342.50	32.50	.12
Scheme No. 5 Thinning at years 25, 40, and 60 to a basal area of 13.95 m^2 per hectare. Periodic fire. Clearcut at year 100.	165.54	225.0	15.5	0.74 ft^2

[a] Values expressed on a per-ha basis.