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AIR POLLUTION EFFECTS ON FOREST GROWTH AND SUCCESSION: APPLICATIONS OF A MATHEMATICAL MODEL[1]

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ABSTRACT

The information presented in this paper is directed towards plant scientists interested in determining the effects of air pollution stress on forest ecosystems. A mathematical model (FORET) designed to examine the successional dynamics of eastern deciduous forests has been used to study the long-term interactions of air pollution stress and forest community dynamics. Differential levels of growth reduction (0%, 10%, and 20%) were applied to trees in three sensitivity classes to simulate changes in biomass of both individual trees and of the forest stand. Results indicate that the response of individual trees in a forest stand may differ markedly from results predicted on the basis of responses determined in the absence of plant competition. Some species may show growth enhancement in spite of pollutant stress since they may gain a competitive advantage as a result of greater impacts on other species with which they interact in the successional process. Other species may experience much greater than anticipated impacts due to reduced competitive potential. We suggest that simulation models can provide a useful function in integrating the results of past research and by permitting projections thereof to extend our understanding of both the nature and extent of air pollution impacts on forest ecosystems.

INTRODUCTION

The harmful effects of uncontrolled emissions of air pollutants on forest trees have been well documented through investigations conducted around large smelting operations during the first half of this century (1, 2). Recent reviews (3, 4, and 5), however, provide little evidence that our present ability to quantify air pollution impacts on forest ecosystems has progressed much beyond levels generated by these early case studies of point-sources. Our national energy utilization plans have highlighted a need for realistic assessment of both present and future impacts of air quality on forest and agricultural systems. With forest ecosystems the difficulty inherent in this task arises partly because of the complex nature of the stress imposed by the air quality regimes and partly because of the spatial and temporal complexity of forest growth and development.

The application of abatement technology, increased urbanization and industrialization, and the shift to large fossil-fueled electric generating plants has altered both the nature of air quality problems and the focus of air pollution research in recent decades. The problems attendant to large uncontrolled point sources have been replaced with those associated with regional scale elevation of pollutants from multiple sources. This is particularly true in the eastern United States where the high density of fossil fuel combustion plants, a high frequency of air stagnation events, elevated levels of oxidants over widespread areas, and increases in the acidity of precipitation in recent decades combine to expose large acreages of valuable agricultural and forest lands to chronic air pollution stress (6).

Characterization of the expected impacts of current pollutant stress on eastern forests can be conveniently made using the classification system described by Smith (3). In a review of air pollution impacts on temperate forest ecosystems, Smith defines three classes of effects: Class I - Vegetation acts as a sink for pollutants and a vehicle for pollutant transport to soils but is not directly affected; Class II - Individual trees or species may experience subtle and adverse effects due to reduced growth, reduced reproduction, or increased morbidity; and Class III - Individual trees or species experience acute mortality or morbidity. Our present forested areas of the eastern U.S. can be considered to fall in classes I and II. A major uncertainty associated with efforts to quantify present or anticipated damages from air pollutants is evaluation of the significance of the Class II subtle or chronic effects. Evidence for chronic effects of this type on forests is mostly indirect and based on controlled studies with annual plants or tree seedlings where responses of a variety of physiological processes associated with plant growth and development have been identified (See reviews by Ziegler (7), and Mudd and Kozlowski (8)). Documentation of chronic impacts on growth of both agricultural species and tree seedlings exposed in the field to ambient levels of pollutants has increased in recent years. This has occurred largely as a result of the use of open-top field chambers in which growth of plants in ambient and charcoal-filtered air has been compared. Translation of these effects to impacts on forested ecosystems is not a straightforward process for several reasons.

The dynamic nature of forest growth, competition, and the successional processes dictate that any study which is intended to measure air pollution impacts on forests consider multiple stresses over multi-year time scales. An important modifier in community level responses to stress is plant competition. Much of our present day understanding of air pollution effects on plants, however, is based on studies with individual plants or species, and little data exist on responses of natural plant communities to air pollution stress.

The impact of chronic, low-level air pollution effects at the ecosystem level may be considered to be an integration of the aggregate stresses imposed by atmospheric contaminants and other abiotic and biotic stresses inherent in natural systems. Collectively these stresses exert their effects on individual species to differing degrees, and thereby could cause changes in species diversity which would form a basis for altered ecosystem structure. Evidence of these types of changes has come mainly from studies around point sources where pollutant concentration gradients result in decreasing severity of effects with increasing distance from the emission source. Gordon and Gorham (9) found a marked increase in numbers of higher plant species along a 39-mile gradient extending outward from the smelters of Sudbury, Ontario. The changes followed a recognized pattern where more stress tolerant species known as "generalists" replace the more specifically adapted species of the more advanced (i.e., complex) stages of forest succession (10). Evidence of changes of this type over large areas currently impacted by chronic air pollution is relatively rare in the literature, primarily because such changes are subtle, occur slowly, and necessitate long-term studies of a type rarely conducted. There is already evidence, however, that certain species of lichens (11) and white pine (12) may be eliminated or experience reduced growth in response to regional increases of pollutants, primarily sulfur oxides. Changes in structure or diversity of whole ecosystems due to low-level air pollutant effects can be expected initially to be gradual and very subtle. However, Treshow (13) has stressed that ecosystems are delicately balanced with a structure which may depend on a relatively few critical species. The process of environmental deterioration may be slow, but once natural balances are sufficiently disrupted, subsequent alterations may be precipitous because of rapid irreversible changes. The incidence of disease, for example, may be greatly accelerated as plants are gradually weakened to the point where disease resistance is lowered and susceptibility to plant pathogens is increased (14).

This paper describes an approach to the study of air pollution stress on forest stands which permits the consideration of the influence of both plant competition and long-term time scales. It utilizes a forest growth and succession model FORET developed by Shugart and West (15) to examine effects of stress applied differentially to species of differing sensitivity to air pollutants. Mathematical simulations with this model have been performed to determine the time-integrated effects of air pollution stress on the response of both individual species and forest stands. An important aspect of these simulations was consideration of the additional community-level stresses imposed by plant competition.

Methods

Description of the Model

The FORET model (15) is a forest growth simulator which was developed by modifying the forest growth model (JABOWA) of Botkin *et al*., (16). FORET was developed to simulate the dynamics of stand biomass, species biomass, species numbers, and diameters of individual trees of the Eastern Deciduous Forest. It was initially applied to examine the response and recovery of eastern deciduous forests following removal of American chestnut by *Endothia parasitica* (Murr.) the causal agent of chestnut blight. However the model has broad applicability for examining the influence of a variety of stresses on the ecology of forests.

A generalized schematic diagram of the FORET model is shown in Figure 1. The present model considers 33 forest tree species native to the southern Appalachian forests, simulates growth of individual trees on circular 1/12 ha plots, and is designed to model stand development primarily on lower slope positions where water availability does not significantly limit growth. The growth of each tree on a plot is simulated as a function of climate, the leaf area of adjoining taller trees, crowding from other trees, and the size of the tree.

The silvercultural characteristics of each tree species considered in FORET are:

1. Relative shade tolerance
2. Maximum height and diameter recorded for a species
3. Maximum recorded age
4. Relative growth rate - curvilinear growth is implemented by assuming that under optimal conditions a tree should grow to two thirds its maximum height at one-half its maximum age.
5. Sprouting potential
6. Response to temperature-growth responses are based on deviations from the physiological degree day maximum and minimum associated with a species geographical range.

Stand simulation with FORET may be initiated either from a bare soil site or an existing stand of defined composition. The development of the stand is then followed through time in terms of total stand biomass, and the composition and biomass of individual tree species present. Ingrowth of new individuals and mortality within the stand are stochastic processes with probabilities determined by the availability of space and relative growth rate, respectively.

Validation of FORET was accomplished by running the model with and without American chestnut as a viable species. With chestnut included the model produced a forest similar in composition to the relatively undisturbed forests which existed around 1890 to 1910. Simulations with FORET run with the removal of chestnut also produced forests of very similar composition to the contemporary, post-chestnut blight forest. Additional details describing model construction and validation results can be found in Shugart and West (15).

Model Application

Application of FORET to regional scale problems in forest ecology necessitates modification of the growth of one or more species in some logical fashion. To apply the model to a study of the effects of air pollution stress on growth and development of forests, we used the well-recognized fact that species differ widely in sensitivity to air pollutants as a basis for applying differential levels of growth inhibition to individuals within a forest stand. Tree species were assigned to three sensitivity classes (1 = high, 2 = intermediate, 3 = low) based on visible injury data for SO_2 effects reported by McLaughlin and Lee (17) and Davis and Wilhour (18). A list of the 33 species included in the simulation and their sensitivity rankings is shown in Table 1. Although much of the available data on sensitivity was developed from visible injury determinations, our model assumes the relative sensitivity of species to acute effects (visible injury) will generally hold for chronic effects on growth.

Responses of a simulated forest to air pollution stress were examined by varying both the level of stress and the forest age at which the stress was initiated. Growth of sensitive and intermediate species was differentially inhibited at two levels high (20% and 10%) and low (10% and 5%) while resistant species were unaffected. The following six combinations of stress level and initiation time were thus produced:

1. No stress - Begin at 0 years - Run 500 years (control)
2. High stress - Begin at 0 years - Run 500 years
3. Low stress - Begin at 50 years - Run 150 years
4. High stress - Begin at 50 years - Run 150 years
5. Low stress - Begin at 400 years - Run 100 years
6. High stress - Begin at 400 years - Run 100 years

For purposes of this paper we will discuss only results from the first two of these scenarios. Results of the additional simulations will be documented at a later time.

Results and Discussion

A simulation of stand biomass dynamics for a typical eastern deciduous forest is shown in Figure 2. This computer-generated plot describes changes in the relative importance of each of 11 major species (black oak, red oak, chestnut oak, white oak, black cherry, yellow poplar, beech, bitternut and shagbark hickory, sugar maple, and red maple) and 22 "other" species through 500 years of forest succession. Additional plots of biomass of each of the 33 species, total stand biomass, numbers of trees and leaf area index were generated but not included here. The biomass dynamics shown in Figure 2 represent the typical successional pattern in eastern deciduous forests. Early successional stages are characterized by a relatively high biomass value for the "other" category (typically pioneer species) with rapid changes in relative importance of all taxa during the first 100 years. Beginning about 100 years after initiation of forest development, the forest structure begins to stabilize in both composition and total biomass. The mature forest is dominated compositionaly by seven species, yellow poplar, bitternut hickory, black cherry, and white chestnut, red, and black oak.

The results of simulations with species-dependent stress levels (0, 10, and 20% growth reduction applied to trees in sensitivity classes 3, 2, and 1, respectively) are summarized in Figure 3. Increases in biomass of four major species (yellow poplar, white oak, black oak, and black cherry), the collective "other" species category, and total stand biomass are compared with and without simulated air pollution stress. Comparisons of percentage changes in biomass for these species and the "other" species category are summarized in Table II. At 6 intervals during the 500 year simulation.

Yellow poplar, an early successional species with a rapid growth rate shows a rapid positive response to stress with a maximum increase of approximately 50% above the control level. The enhancement of yellow poplar under a regime which inhibits its growth by 10% may be attributed to the relatively greater effect of the stress on other species competing at early stages of the developing forest stand. Thus, yellow poplar with its fast growth has an opportunistic potential favored by stress on other species with which it competes.

Black oak, on the other hand, with the same level of applied growth suppression shows greater than anticipated response. Biomass reductions ranging from about 45% at year 50 to 50% at year 200 were observed for this species. Reductions of this magnitude may be attributed primarily to 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 species not directly impacted by stress in the model, showed a positive response in the simulation. As a late successional species, however, this response becomes evident only as the stand matures and begins to stabilize. The maximum biomass increment for white oak in the stressed forest was approximately +80% and occurred in the 350 year-old stand. The fourth species, black cherry, while less important compositionally, was included as an example of a sensitive but valuable sawtimber species. The effects of a 20% growth reduction on this species were quite dramatic as can be seen in Figure 3. Effects on black cherry were most obvious on stands older than 100 years and resulted in almost total elimination of this species. The maximum reduction in biomass contributed by black cherry was approximately 95% and occurred at year 250. Responses of other species and of the whole stand indicate an overall growth suppression by the simulated stress. It is interesting to note that a maximum stand response of -20% was noted (at year 200) indicating a system level response which was greater than the additive response of its parts. When individual sensitivities were used to predict stand level response, the summed and biomass weighted response of the 7 species comprising 87% of the total biomass of the 200 yr old stand was only -7%.

The results of these simulations offer some interesting insights into responses which might be expected when forests are exposed to air pollution stress. They 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 either much greater or much less than expected impacts due to changes in their relative competitive potential within the forest stand. Both resistant trees and those of intermediate sensitivity may actually experience growth stimulation as a result of relative increases in competitive potential.

Conclusions derived from these simulations agree with those drawn by Botkin (19) in a study of species interactions under uniform stress. In a 13-species simulation of northern hardwood forest dynamics, he found that perturbations that reduced tree growth generally favored growth of shade-tolerant species. He also emphasized the importance of species interactions in understanding the response of forest systems under conditions which either increase or decrease growth of individual species. Additional support of the importance of plant competition has been provided by a recent study by Bennett and Runeckles (20) who compared relative inhibition of growth of rye grass and clover by ozone under single and combined culture. This work provided preliminary evidence of increased competitive potential for rye grass under combined culture when ozone stress (0.09 ppm) was applied.

The selection of the differential levels of growth reduction in our study was of necessity arbitrary and subjective. While it is a well recognized fact that visible injury and growth reduction do not necessarily occur concurrently, the assumption that trees which are most sensitive to visible foliar injury are also most susceptible to growth reduction by chronic air pollution stress appears reasonable. The levels of growth inhibition which were selected also do not appear excessive based on documented growth responses of forest trees. Miller (21), for example, reported a 37% reduction in growth of ponderosa pine in the oxidant-impacted San Bernadino Forest. Recent studies by Kress (23) indicate height growth reductions of up to 45% for sycamore exposed for 28 days to levels of O_3, SO_2, and NO_2 below the current ambient air quality standards and in the absence of visible foliar injury.

Documentation of the response of forest communities under chronic stress from air pollutants will not be easy. Miller (22) cites several lines of evidence supporting the importance of such changes in the San Bernadino Mountains. Current studies underway at that site (21) may add appreciably to our understanding of the nature and extent of such changes. While we would agree with Smith's (3) conclusion that "No quantitative field estimates of the bulk of Class II relationships is possible at present," we suggest that mathematical simulations such as those we have undertaken are both possible and fruitful mechanisms for projecting the potential influence of pollutant impacts on forest ecosystems.

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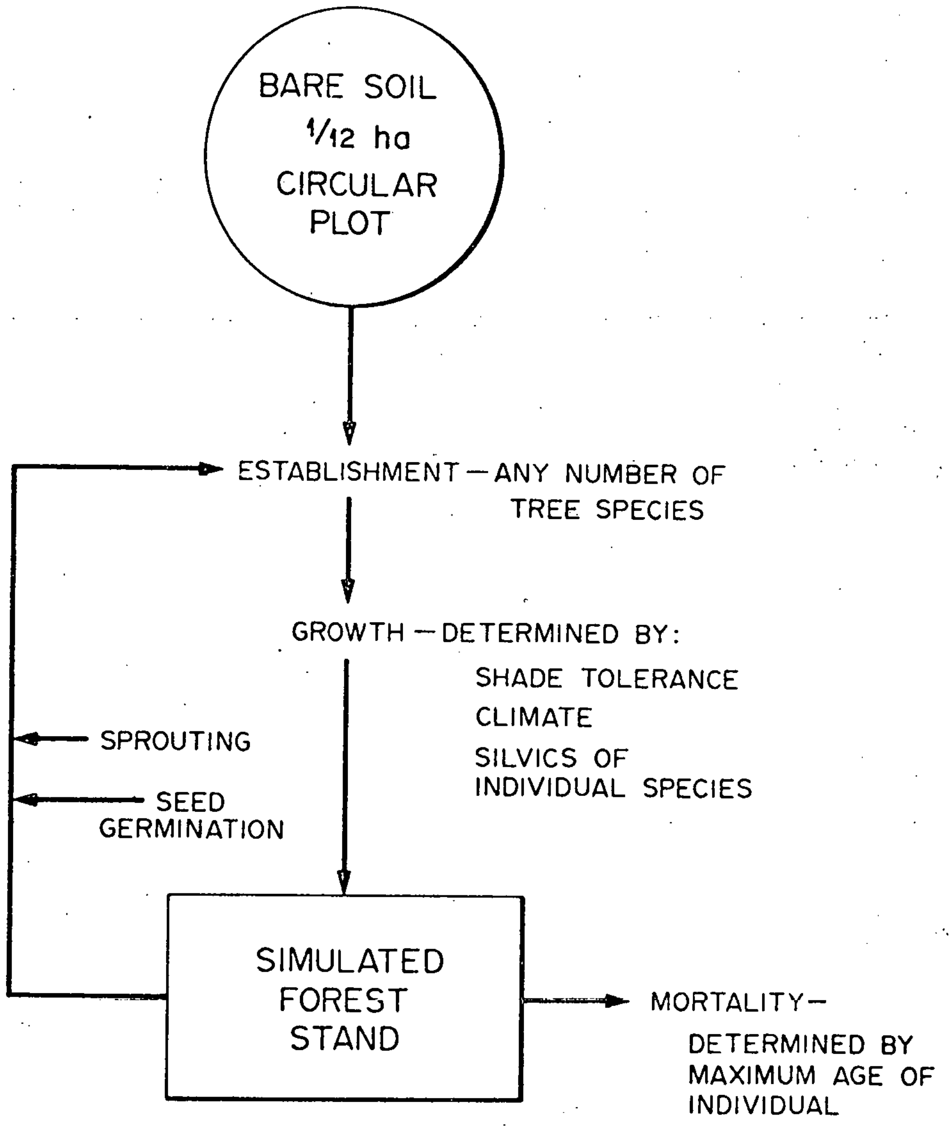

Fig. 1. Generalized Diagram of FORET

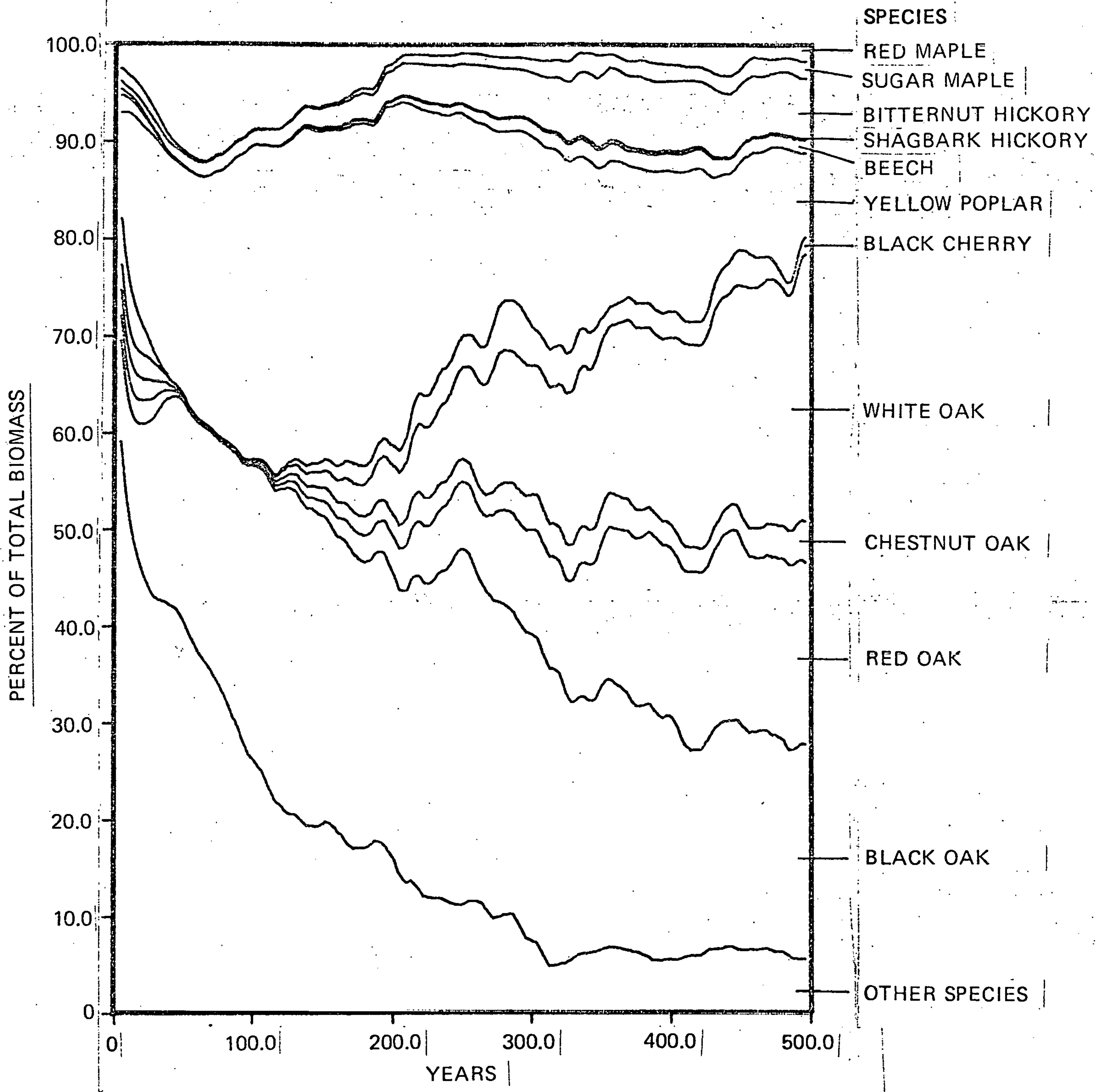

FIG. 2. SIMULATED SUCCESSIONAL DYNAMICS OF AN EASTERN DECIDUOUS FOREST IN THE 500 YEARS FOLLOWING INITIATION FROM BARE SOIL. DATA ARE AVERAGES DERIVED FROM 50 PLOTS — 0.05 HA IN SIZE

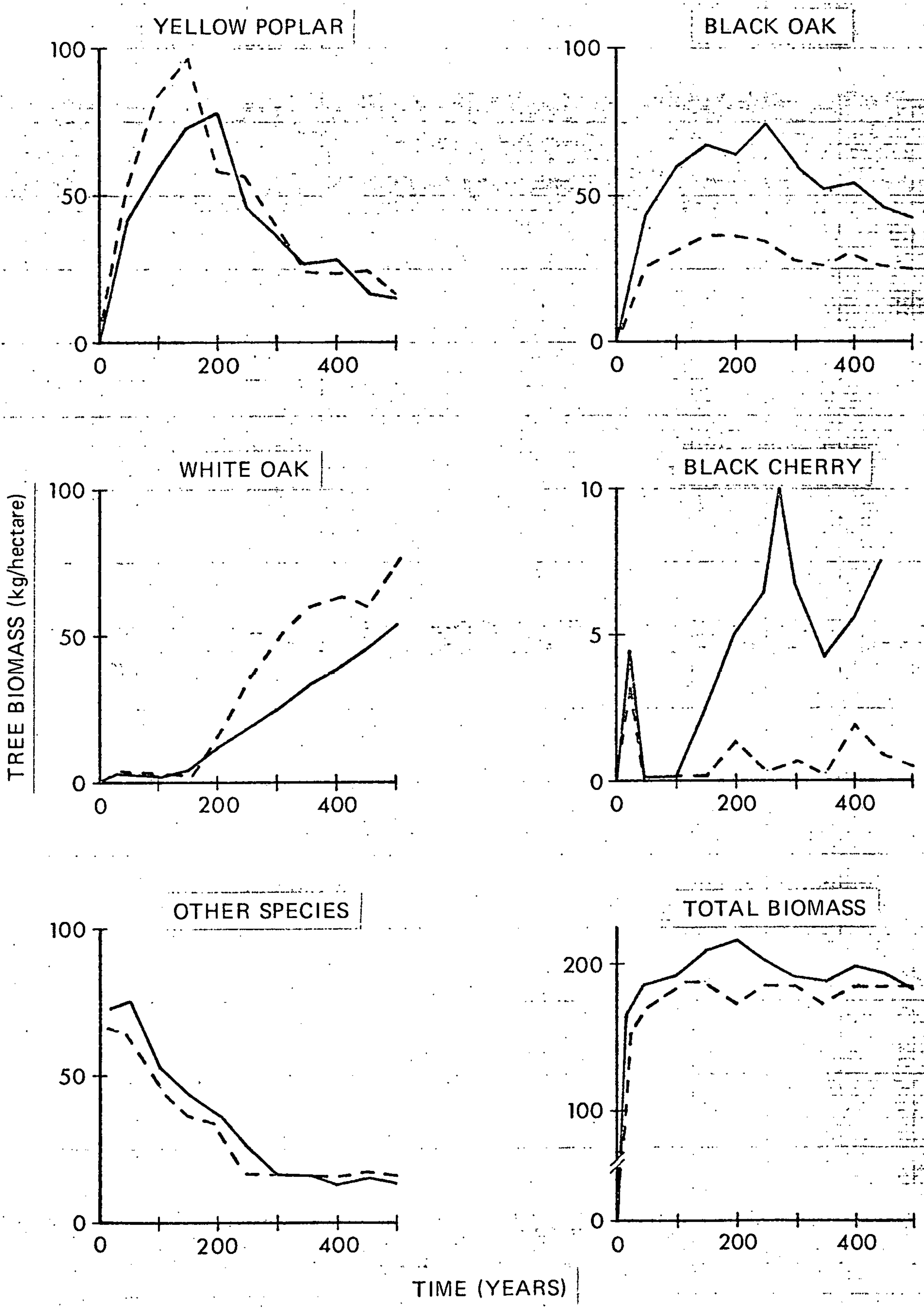

FIG. 3. SPECIES AND STAND DYNAMICS OF A FOREST WITH AND WITHOUT CONTINUOUS EXPOSURE TO AIR POLLUTION STRESS. (——— UNAFFECTED; – – – – AFFECTED)

Table I. Tree species and sensitivity classes included in the FORET simulation of air pollution effects on forest stand growth and development

Species	Effects code[a]
Acer rubrum	3
Acer saccharum	3
Aesculus octandra	2
Carya cordiformis	3
Carya glabra	3
Carya ovata	3
Carya tomentosa	3
Castanea dentata	3
Cercis canadensis	2
Cornus florida	3
Diospyros virginiana	3
Fagus grandifolia	3
Fraxinus americana	3
Juglans nigra	1
Juniperus virginiana	3
Liquidambar styraciflua	2
Liriodendron tulipifera	2
Nyssa sylvatica	3
Oxydendrum arboreum	3
Pinus echinata	1
Pinus strobus	1
Pinus virginiana	1
Prunus serotina	1
Quercus alba	3
Quercus coccinea	2
Quercus falcata	2
Quercus prinus	3
Quercur rubra	2
Quercus stellata	3
Quercus velutina	2
Robinia pseudoacacia	1
Sassafras albidum	2
Tilia heterophylla	2

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[a] 1 = 20 percent growth reduction, 2 = 10 percent growth reduction, and 3 = no growth reduction.

Table II. Effects of simulated air pollution stress on biomass of individual tree species and of the forest stand

		Years Since Stress Began					
		25	50	100	150	300	500
		Percentage Change from Control[1]					
Yellow Poplar	A	+20	+30	+40	+35	+10	0
Black Cherry	A	-29	0	0	-90	-90	-85
Black Oak	A	-30	-45	-5	-50	-45	-40
White Oak	A	0	0	0	-35	+80	+45
All Species	A	-10	-10	-5	-10	-5	-5

[1] Data derived from averages of 50 1/12 ha plots run with and without (control) stress.

[2] A = Stress applied at 0, 10, and 20% to resistance classes 1, 2, and 3 respectively. Stress begun at year 1.