Modeling the Potential Effects of Growth Reductions and Changes in Photosynthetic Efficiency and Needle Retention on the Stand-Level Growth of Loblolly Pine Plantations

by

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(ABSTRACT)

An existing individual tree growth and yield model (PTAEDA2) was modified study the potential effects of air pollution stress on the growth and yield of loblolly pine plantations. These modifications were based on the assumption that pollution stress on older trees could result in reductions in diameter and height growth, decreases in photosynthesis, and increased losses of older foliage, as demonstrated in some seedling studies.

One modification applied differential levels of reductions of diameter and height increments to various percentages of trees. Results indicated no sizeable losses on total volume per acre except at severe stress levels (-32 and -64 percent annual diameter and height increments on 50 and 67 percent of the trees).

Another modification consisted of developing a measure of photosynthetic potential to drive diameter and height growth in the model. This new measure was an estimate of foliage weight which was weighted by a factor of photosynthetic efficiency and needle retention for each age class of needles. Reductions of these weighting factors were applied to simulate air pollution stress. Results of this modification show that if air pollution does cause a decrease in photosynthesis and needle retention rates, the impact on

over-all stand productivity is minimal. These results are not intended to be quantitative estimates of the effect of air pollution on tree growth but to identify potential areas within an existing growth and yield model where biologically-oriented processes to simulate air pollution impact can be incorporated.

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Chapter I

INTRODUCTION AND JUSTIFICATION

One of the more challenging research issues currently facing the forestry profession is the assessment and quantification of the effects, if any, of air pollution on forest growth and productivity. Air pollution, in particular ozone, has been proven the cause of the chlorotic decline of ponderosa pine (*Pinus ponderosa*) near Los Angeles in the San Bernardino Mountains of California (Miller et al., 1963). Recent observations of similar symptoms in the high elevations of the spruce/fir forests of the eastern United States and the frequent occurrence of phytotoxic ambient levels of pollutants in rural and forested areas have caused concern that southeastern forests could experience a similar loss of productivity.

Currently, most research efforts are focusing on establishing dose-response relationships in tree seedling studies using ambient pollutant levels in greenhouses and open-top chambers. Several seedling studies have demonstrated decreases in photosynthate production, diameter growth, and height growth in response to air pollution stress (Kress and Skelly, 1982; Chevone, 1985).

However, there are several difficulties in directly applying quantitative seedling responses to older tree responses. In addition to physiological differences between seedlings and older trees, forest stand dynamics, such as competition, may complicate or mitigate the effects of air pollution stress on individual trees. Stand level experiments are extremely time-consuming and expensive and the control of the appropriate variables as well as the provision of unbiased controls are almost impossible.

Simulation models, with modifications to reflect the effects of possible air pollution stress, have the potential for providing further insight into stand-level responses. On one hand, physiologically-oriented process models may more realistically incorporate the effects of air pollution by modeling changes in photosynthetic rates, but these models generally have time steps as hours or days, making it difficult to project long-term effects on overall stand productivity. Physiological models also often require input variables which are difficult to measure in the field on a broad scale basis. On the other hand, most empirically derived growth and yield models incorporate the input of easily measured variables, such as diameter at breast height (dbh), height, and crown ratio, and are designed to give long-term projections of stand development. In addition, modification of an existing individual tree growth and yield model to incorporate air pollution stress has the following advantages:

- several reliable models are already well-developed and validated with large data sets utilizing a wide range of variables.
- the individual tree can be impacted by simulated air pollution stress, but the effects of stand age, density, and site quality can also be assessed over long periods of time.
- individual trees can be impacted randomly or differentially with varying levels and frequencies of pollutant stress.

- most models contain some measure of photosynthetic potential, usually a crown variable, and several seedling impact studies have shown a decrease in photosynthesis caused by air pollution stress.

Thus, the purpose of this study was to evaluate methods for modeling the potential effects of air pollution on stand-level growth and yield of forest trees, assuming that air pollution stress results in reductions in height and diameter growth, decreases in photosynthesis and losses of older age classes of foliage. A growth and yield model for loblolly pine (*Pinus taeda*) was used since loblolly pine is one of the most important commercial species of the southeastern United States.

To accomplish the overall objective, the following specific objectives were set:

1. to develop an expression of photosynthetic potential based on crown variables which can be used to predict individual tree growth and development;

2. to modify this expression of photosynthetic potential to extrapolate known seedling responses to air pollution to mature trees;

3. to identify areas within an existing growth and yield model framework where biologically-oriented processes to simulate the potential effects of air pollution may be incorporated.

Chapter II

LITERATURE REVIEW

Introduction

Most air pollutants affecting plant growth result from the combustion of fossil fuels, industrial processes, and transportation emissions. These pollutants include carbon monoxide (CO), sulfur dioxide (SO_2), nitrogen oxides (NO_x), hydrocarbons, lead, and fluorides. Ozone (O_3) and peroxyacetyl nitrate (PAN) are two secondary pollutants which result from photochemical reactions involving nitrogen dioxide and hydrocarbons (Manion, 1981; Smith, 1981). Of all of these toxicants, ozone is the most significant and widespread in the United States, primarily because it repeatedly occurs at ambient phytotoxic concentrations over urban and rural areas of the country. Although sulfur dioxide infrequently occurs at toxic levels, its damaging nature to plants has caused scientists to believe that sulfur dioxide and ozone cause more injury to plants that all other pollutants combined (Kozlowski, 1980). There is considerable evidence suggesting the responsibility of acidic rain for damage to aquatic systems; however, data supporting damage to forest trees are often inconclusive or contradictory (Reich and Admundson, 1985).

Smith (1974) classifies the effects of air pollutants on forest trees into three major categories: Class I (low dose); Class II (intermediate dose); and Class III (high dose). Under Class I conditions, forest vegetation and soils act as sources and sinks for pollutants, where the impact can be undetectable or even stimulatory. With Class II conditions, individual trees can be subjected to nutrient stress, impaired metabolism, and predisposition or direct induction to insects and disease. Class III exposure may cause acute morbidity or mortality of individual trees. Other responses attributable to air pollutants include impaired or reduced reproduction processes, suppressed photosynthesis and enhanced dark respiration, abnormal or reduced growth, altered soil conditions, and changes in species composition. Air pollutants have also been reported to be possible contributing factors in forest declines, which are complex diseases that result in a progressive dieback of the crown and accelerated weakening of the tree and are most often associated with mature trees. A gradual loss of vigor leads to decreases in growth rate and increases in susceptibility to secondary biotic and abiotic stresses (Manion, 1981).

Since photosynthesis ultimately provides all products necessary for tree maintenance and growth, many studies have focused on the influence of pollutants on the suppression of photosynthesis. Bennett and Hill (1973) found that ozone damages enzyme systems, cell membranes, and chloroplasts in the leaf, and hence impairs photosynthate production. However, genetic and environmental conditions can influence the amount and degree of impact. Pallardy and Kozlowski (1979) discovered that the effects on photosynthesis varied with differences in stomatal diffusion resistance, which is a function of stomatal size, number, and aperture. Noland and Kozlowski (1979) reported that low concentrations of sulfur dioxide induced stomatal opening in American elm (*Ulmus americana*) seedlings, whereas high concentrations caused stomatal closing. They also found that the effects of sulfur dioxide on stomatal aperture were regulated, and often negated, by low light intensities and drought. Reich and Admundson (1985) discovered that drought-stressed soybean (*Glycine max* cv) plants had lower leaf conductances and more pronounced effects from ozone than similar well-watered plants. Foliar symptoms which affect the amount of leaf area available for photosynthesis include chlorotic and necrotic lesions, shortened needle length, and abnormally high rates of needle abscission (Dochinger and Selikskar, 1970; Usher and Williams, 1982). However, it has frequently been found that there can be a significant reduction in photosynthesis without the development of any foliar symptoms, commonly referred to as "hidden injury" (Barnes, 1972; Botkin et al., 1971, 1972b; Heck et al., 1977).

Most research has been performed with tree seedlings, due to their size, ease of measurement, and level of control, although several studies have been performed with larger forest trees. Work done in the area of modeling the effects of air pollutants on the growth and yield of forest trees has been mainly in the area of successional dynamics of mixed species stands. However, there exists a large body of research in the area of modeling crown development in large forest trees that could possibly be used to extrapolate known air pollution effects on photosynthesis and associated diameter and height growth reductions for seedlings to older tree growth.

Effects of Air Pollutants on Tree Seedlings

Currently, the majority of air pollution research is focusing on the effects of ozone, sulfur dioxide, and nitrogen oxides on tree photosynthesis and resultant changes in biomass and morphology. Tree seedlings, because of their size and ease of measurement, are typically housed in greenhouses, controlled growth chambers, or continuously stirred tank reactors (CSTR's). However, these seedlings may be morphologically and physiologically different from seedlings grown in their natural environment (Lewis and Brennan, 1977). Some studies have also used saplings because they are more physiologically similar than seedlings to older trees. Because measurements of carbon dioxide uptake on saplings may be more difficult than on seedlings, often just portions of foliage are placed in growth chambers.

Open-top chambers are used to examine the differences in effects obtained from use of ambient air and charcoal-filtered air concentrations. However, some artificialities may be associated with the use of such chambers. Plants grown in chambers may have longer needle retention and achieve greater heights than open-grown plants (Wang et al., 1986). Air temperatures within chambers may become higher than ambient temperatures outside of the chambers, and air flow rates within the chamber may differ from flow rates that naturally occur outside (Smith, 1981).

Miller et al. (1969) fumigated three-year-old ponderosa pine seedlings in controlled environmental chambers at ozone levels of 0.15, 0.30, and 0.45 ppm. The seed came from ponderosa pine in the San Bernardino mountains of California which for the past several decades have been documented as being exposed to phytotoxic levels of ozone. After a 30 day exposure, apparent photosynthesis rates decreased by 10, 70, and 85% for the levels of 0.15, 0.30, and 0.45 ppm, respectively. A 25% decrease in photosynthesis occurred after a nine hour per day, 60 day exposure to 0.15 ppm ozone. Several seedlings did not show a reduction in apparent photosynthesis at the 0.15 ppm level but all did at the 0.30 ppm level. Although even the 0.15 ppm level for ozone is rather high for most parts of the United States, the researchers stated that it is comparable to ambient concentrations in that particular region.

Skeffington and Roberts (1985) studied three-year-old Scots pine (*Pinus sylvestris*) seedlings subjected to a 56 day exposure to four levels of ozone (0.0, 0.05, 0.10, and 0.15 ppm) with and without acid mist (pH 3) in outdoor solardome fumigation chambers. The first visible foliar symptoms were observed after one week, which consisted of a severe necrosis of the apical third of the current year's needles at the high level of ozone, the high level of ozone-acid mist, and the medium level of ozone-acid mist. By the end of the experiment, all of the high ozone plants had chlorotic mottling, but only a few had mottling at the low ozone level. Ozone also increased the rate of leaf senescence. Acid mist increased the percentage of needles lost at zero, low, and medium levels of ozone by 8, 19, and 23% respectively.

Seedling studies can also be used to determine the effects of various combinations of pollutants and to rank species, as well as families within species, with respect to air pollution tolerance. Kress (1978) screened several families of loblolly pine families for sensitivity to ozone, nitrogen dioxide, and sulfur dioxide and selected a sensitive and a tolerant family to study the effects of a long-term exposure to these pollutants singly and in combination. He used one to two-week-old seedlings and exposed them to 0.05 ppm ozone, 0.10 ppm nitrogen dioxide, and 0.14 ppm sulfur dioxide for six hours per day, and for 28 or 56 days in CSTR's. Significant height growth decreases for the sensitive family for all treatments except the nitrogen dioxide alone were reported. For the tolerant family, significant height growth suppressions were found only for the pollutant combinations. Less than 5% of the loblolly pine seedlings developed any foliar symptoms.

Effects of ambient air on seedlings, using charcoal-filtered air and non-filtered air were also assessed. Sensitive pine seedlings experienced up to a 40% decrease in height growth in the non-filtered air compared to the filtered air, whereas the tolerant seedlings exhibited a 29% decrease.

Kress and Skelly (1982) used CSTR's to study two to four-week-old seedlings of ten eastern forest species at ozone levels of 0.0, 0.05, 0.10 and 0.15 ppm and two to four-week-old seedlings of seven species at ozone and/or nitrogen dioxide levels of 0.10 ppm for six hours per day for 28 days. At ozone levels of 0.05 ppm, loblolly pine exhibited significant height growth (18%) and total dry weight suppressions (14%) whereas white ash (*Fraxinus americana*) and yellow poplar (*Liriodendron tulipifera*) exhibited significant stimulations of growth. Similarly, at 0.10 and 0.15 ppm ozone, loblolly pine exhibited a 27% and 59%, respectively, decrease in height growth. Results showed that nitrogen dioxide possibly alleviated the effects of ozone when interaction effects between ozone and nitrogen dioxide were less than additive. Only Virginia pine (*Pinus virginiana*) and loblolly pine were suppressed in height growth, 23% and 39% respectively, at 0.10 ppm ozone combined with the nitrogen dioxide. Loblolly pine and Virginia pine were the only species to experience height growth reductions caused by nitrogen dioxide alone. Effects of suppression noted at the lowest level of ozone exposure were not accompanied by any foliar symptoms.

Wang et al. (1986) studied field grown trembling aspen (*Populus tremuloides* Michx.) saplings in open-top chambers over a three year period, using two known pollution sensitive clones and two tolerant clones. Ambient levels of ozone exceeded a maximum hourly average of 0.12 ppm from one to six times during the three growing seasons. Ambient levels of ozone significantly reduced aboveground dry matter production by 12-24% but did not affect root biomass. Mean height and diameter growth was significantly lower in the ambient air than in the charcoal-filtered air treatments. Charcoal filtration resulted in fewer injured leaves per tree, reflecting a reduction but not an elimination of air pollution stress. Effects on leaf senescence did not correlate with the presence of visible symptoms of injury.

Effects of Air Pollutants on Large Forest Trees

Several studies have been done on larger forest trees. Environmental variables such as temperature, humidity, and radiation levels all affect photosynthetic rates and the amount and rate of uptake of different pollutants and favorable environmental conditions may override negative effects on photosynthesis by air pollutants (Townsend and Dochinger, 1974; Karnosky and Steiner, 1981; Garsed and Rutter, 1982). In addition, soil moisture, nutritional status, competition, stand composition, tree developmental stage, and genetic sensitivity to pollution may further influence the impact of air pollution. Thus, experiments with large forest trees are not only hard to control and expensive, but results may not be easily applied to other forest stands since stands vary greatly in structure and ability to recover from stress. Often large tree experiments are performed after visible foliar injury has occurred. By that time, important changes in stand structure may have already been induced. Larger tree studies have generally demonstrated that visible injury may not necessarily correlate with losses in productivity and that different age classes of needles may be impacted differentially.

Perhaps one of the most extensively studied relationships between ambient levels of ozone and large forest trees has been in the San Bernardino Mountains of California.

Easterly flowing air from Los Angeles has produced high ozone concentrations as far away as 120 km. A condition characterized by yellow, shortened needles and premature leaf abscission of ponderosa pine in the San Bernardino National Forest was first recognized in the mid-1950's and termed chlorotic decline (Parmeter et al., 1962). Miller et al. (1963) established ozone as the causal agent after duplications of these symptoms with controlled fumigations of ozone. Documented observations of foliar injury, premature defoliation, decreases in photosynthetic capacity, and decreases in radial growth for ponderosa pine were also made during the 1970's. It is believed that reduced carbohydrate production and nutrient concentrations have resulted in weakened trees, which have become more susceptible to pine bark beetles, increases in mortality, and changes in species composition within the more impacted areas.

Coyne and Bingham (1981, 1982) conducted a study in the San Bernardino National Forest where they observed 18 year-old ponderosa pine trees previously classified into three injury classes determined by foliar symptoms. The study was conducted in an area which had been subjected to heavy ozone concentrations of up to 0.6 ppm. Photosynthesis and stomatal conductances on attached fascicles were measured as well. Height, diameter at breast height, and number of needles per whorl obtained were inversely related to injury severity. Within a needle age class, photosynthesis did not vary significantly with injury class but was different among needle classes within an injury class. Needles tended to be shorter, smaller in girth, and less dense as the chronic injury symptoms of the trees increased in severity. Coyne and Bingham claimed that the decline in photosynthesis and stomatal conductance normally associated with natural aging appeared accelerated as ozone injury symptoms increased.

Williams (1983) evaluated ponderosa pine in the Southern Sierra Nevadas of California with respect to annual radial growth, needle and branch growth, premature defoliation, and general needle health. Using an oxidant disease severity index, 7-10%

of the trees in the sample were of a sensitive genotype based on visible symptoms of injury. No correlation between index rating and annual ring, needle, or branch growth over a four year period was determined. However, general leaf health deteriorated dramatically from current needles to one year and two year needles. Fifteen percent of the current needles and 50% of the one year needles had damage symptoms, whereas 75% of the two year needles had either visible injury or had already abscised. At the sampled elevations, ponderosa pine should retain needles for about six years; however, few fourth year needles were observed.

Several large forest tree studies have also been conducted in the eastern United States. Phillips et al. (1977a, 1977b) conducted studies around the Radford Army Ammunition Plant (RAAP) in Radford, Virginia. The RAAP is an industrial source of nitrogen oxides and sulfur dioxides and has had a unique history with three distinct production periods (WW II, the Korean conflict, and the Vietnam conflict). A significant inverse relationship between annual radial growth and annual pollution production levels for was demonstrated, even when the effects of age were removed for 15-18 year-old loblolly pine trees. The removal of rainfall variables had no significant effect. Only the sample trees in the plot closest to the plant exhibited any foliar symptoms from air pollution stress.

Oleskyn (1984) exposed detached twigs of Scots pine trees growing in a 16 year-old commercial plantation to sulfur dioxide concentrations of 0.5, 1.0, and 2.0 cm^3/m^3 for six hours per day, to nitrogen dioxide of concentrations of 0.05 and 1.0 cm^3/m^3 and to 0.1 cm^3/m^3 of halogen fluoride and measured net photosynthesis and dark respiration rates. With the sulfur dioxide treatment, the greatest reduction in photosynthesis was observed in third year needles (24%) followed by current needles (11%) and second year needles (10%). Dark respiration was stimulated in needles exposed to higher concentrations of sulfur dioxide. Exposure to halogen fluoride resulted in decreased photosynthesis which increased with needle age (38, 42, 65% for current, one year and two year needles respectively). In third year needles, photosynthesis was less than the dark respiration. Nitrogen dioxide did not cause any significant changes in photosynthesis and dark respiration.

Usher and Williams (1982) inspected white pine (*Pinus strobus*) trees in areas of known high concentrations of ozone and sulfur dioxide over a two year period and developed an index of pollution injury based on the degree of chlorotic mottling, tip necrosis, and premature defoliation. Thus, a tree with severe air pollution disease would be dwarfed, have shortened needles, retain none of the second youngest complement of needles, have needles with necrosis more than 5 mm in length on more than 90% of the one year foliage, and have severe mottling or chlorosis on portions of needles not necrotic. In Indiana, 80% of the trees showed tip necrosis on 20% or more of their needles, 14% had no needle necrosis, 81% had chlorotic mottling or flecking, and 8% were classified as severely diseased. In Wisconsin, most trees had only slight symptoms. Premature needle loss appeared to be a general phenomenon in the region but was not strongly correlated to visible disease severity.

McLaughlin et al. (1982) studied the allocation of ^{14}C photosynthate in branches of field-grown white pine trees to determine whether distribution patterns differed between trees with apparent differences in pollution sensitivity. This study was conducted in the area of the Cumberland Plateaus of East Tennessee where the decline of white pine was first studied by the U. S. Forest Service in the 1950's. Later, Berry and Hepting (1964) and Gerhold (1977) documented the regional extent, symptomology and pathological extent of this decline and concluded that atmospheric pollutants, principally ozone and sulfur dioxide, were primarily the causal agents in the development of observed foliar damage. Growth ring analysis of increment cores revealed that average annual radial increment over the past 18 years of intermediate and sensitive trees was

98% and 47%, respectively, of that attained by tolerant trees. The transport patterns of ^{14}C emphasized the role of older needles as sources of photosynthate for new needle growth in the spring and as storage sinks in the fall. Higher retention of ^{14}C photosynthate by foliage and branches of sensitive trees indicated that photosynthate export to boles and roots was reduced. The rate of respiratory to photosynthetic activity was significantly higher for the foliage of sensitive trees. Sensitive trees had mottled, shortened needles and typically cast needles from the previous year during the current growing season. Only tolerant trees consistently retained two year needles. Needles from sensitive trees were 15-45% shorter than those of the other two classes. The data supported the researchers' hypothesis that growth limitations in sensitive trees are a function of stress-induced reductions in photosynthate availability which result from reduced needle length and premature needle abscission.

Kramer (1986) examined five Norway spruce (*Picea abies*) stands over 80 years old in Germany and used stem analysis techniques to establish their volume increment patterns over the past four decades. In each stand he measured diameter, height, crown length, crown projection area, social tree class, percent of needle loss, and distance to neighboring trees. With the removal of age and climatic fluctuations, mean annual increment of the last ten years was significantly lower than the previous nine years. However, there was no correlation between growth rates and evidence of crown damage. A dominant tree with a large crown but a high percent needle loss still had greater increment than a suppressed, crowded tree with a small percent needle loss. Kramer suggested that stem and crown dimensions as well as competitive status can outweigh the influence of needle loss on the increment of an individual tree.

Models for Predicting the Effects of Air Pollution on Forest Trees

Kercher et al. (1980,1984) developed a model to forecast the effects of sulfur dioxide and fire on the growth and succession of the mixed conifer forest type of the Sierra Nevadas in California. The model, SILVA, decreases tree-level growth according to an empirical dose-response relationship. The model is based on the recruitment, growth, and death processes that Botkin et al. (1972a) developed in JABOWA, a northeastern species simulator. Growth is modeled as a difference equation in a tree's diameter at breast height and as a function of environmental variables, such as species-specific parameters describing reproduction, growth, mortality, potential and actual evapotranspiration rates, degree-days, water stress, and number of good and bad seed years. The model simulates the development of each tree from the seedling stage to death and determines the population age and size structure for each species during the period of interest. A dose-response relationship which consists of a decreasing linear pattern in growth with increasing dose and a seasonal average sulfur dioxide concentration is used to decrease growth. Initially Kercher et al. simulated a 10% reduction in growth for ponderosa pine and scaled the response of other species, such as white fir (*Abies concolor*), according to known levels of pollution sensitivity in relation to that of ponderosa pine. The growth and successional dynamics of the stand over several hundred years were then projected. The basal area of ponderosa pine decreased significantly while the basal area of white fir increased dramatically, which was believed due to a greater competitive advantage of white fir over the more dominant, but pollution-damaged, ponderosa pine. The mortality patterns of the ponderosa pine suggested that this species was at a higher risk to pollution damage at higher ages.

West et al. (1980) also modified JABOWA (Botkin et al., 1972a) to develop a model, FORET [FORests of East Tennessee], for determining the influence of sulfur dioxide pollution on the growth and successional development of eastern forest species. Growth reductions were assigned to 33 species which had been categorized in one of three sensitivity classes based on known sensitivity rankings from the literature. By varying the level of impact, the age at which the impact occurred, and the length of occurrence, competition is shown to modify the rate and the direction of change due to the stress. The growth of each tree is a function of total annual degree days, total leaf area of taller trees on the plot, the number of trees on the plot, and the size of the tree. The species to be simulated on each plot is a function of site requirements for germination, palatability of seedlings for browsers, shade tolerance, germination and growth temperature requirements, sprouting potential, and longetivity. Initially the growth of the six most sensitive species was reduced by 20% and ten intermediately sensitive species by 10%. Simulated periods of growth ranged from 50 to 500 years. The introduction of stress into a 50 year-old stand caused a completely different pattern of growth than when the stress was initiated at the seedling stage. When black oak (*Quercus velutina*) was stressed by a 10% growth reduction in the seedling stage, it responded much less favorably than when it was initially impacted at age 50. Yellow-poplar exhibited a positive growth response when the stress was imposed at the seedling level but a growth reduction occurred when the stress was applied when the stand was 50 years old. Both resistant and intermediately sensitive species were found to experience a stimulation in growth as a result of a competitive advantage over the more stressed sensitive species. Black oak showed a growth reduction which was greater than expected considering its sensitivity class and white oak (*Quercus alba*), a late successional species, showed a positive growth response only after about 200 years of simulated growth.

Bossell (1986) developed two simulation models to evaluate the dynamics on individual tree growth subjected to pollution damage on leaves and/or feeder roots. One model, BAUTMOD, is a simple model which describes in relative terms the photosynthesis production, growth of new leaves, shedding of old leaves, and allocation of photosynthate, in order to examine the possible effect on total system structure pollution stress may have. SPRUCE [*Picea abies*], the second model, is more complex and designed to use specific growth parameters for spruce. The SPRUCE model considers leaf aging and efficiency with a breakdown into age classes, the production of assimilate as a function of leaf mass, net photosynthetic production, daylight period, and temperature influence on photosynthesis. The only effects air pollution is assumed to have on these physiological processes are a reduction in photosynthetic efficiency in the foliage and an increase in feeder root turnover rate. For both models, the state variables are the foliage mass, feeder root mass, and remaining biomass (stem, branches, and coarse roots). The model theory is that the production of photosynthate from the foliage requires a certain amount of respiration flow from the feeder roots (to supply water and nutrients) and if the amount of feeder root mass is insufficient, the amount of photosynthate production is decreased. Assimilation demands are a function of the current biomass, current feeder root turnover rate, and fructification demand. Diameter and height increment occurs when there is more assimilate remaining after meeting these demands.

Pollution effects are simulated by decreasing the productivity of the leaves (and therefore reducing the amount of available photosynthate) and by increasing the feeder root turnover rate (which drains the assimilate pool because if insufficient assimilate is available to replace this feeder root drain, the feeder root mass becomes smaller than required for full photosynthate production, and the assimilate production is reduced further). The respiration of leaves, roots, and wood biomass is a function of specific respiration coefficients and temperature.

The SPRUCE model successfully modeled normal growth of spruce both without the influence of air pollution and with slight pollution stress, but exhibited stagnation for moderate stress and eventual breakdown and death of a tree under severe stress. The model also showed a decrease in needle retention with an increase in pollution stress and that older trees were more susceptible to damage than younger trees. Bossel concluded that the two models showed that the breakdown of trees will only occur when the amount of available assimilate falls below a critical level, and may occur after many years of subcritical stress.

Tate (1987) related air pollution stress to a change in crown ratio, a common crown variable used in growth and yield modeling. Since seedling research has shown that air pollution affects photosynthesis and needle retention, she simulated differential levels of air pollution stress in the model Mitchell (1969) developed for Douglas-fir (*Psuedotsuga menziesii*) by modifying the photosynthetic efficiency and needle retention rates. The six scenarios included reduction of photosynthetic efficiency by 0, 7.5, and 15 percent and average needle retention by 0 and 1 year. These levels of simulated pollution stress resulted in total volume per acre losses, which were expressed on a percentage basis of volume reduction as 0, 4.4, 16.6, 17.3, 23.1, and 32.4. Tate then reduced crown ratio in a growth and yield model for loblolly pine plantations developed by Burkhart et al. (1987) to determine the amount of crown ratio reduction required to give similar volume reductions as those observed from the simulations using Mitchell's model. Results indicated that crown ratio reductions of 0, 5, 10, 12, 15, and 22 percent caused total volume reductions of 0, 6.3, 14.9, 18.7, 22.6, and 33.3 percent. Tate concluded that large growth and yield reductions may occur when photosynthetic efficiency and average needle retention rates are reduced and suggested that crown ratio, needle retention, and foliage area as variables to be collected in future vegetation surveys to quantify the effects of air pollution on forest trees.

Relationships Between Crown Productivity and Tree Growth

Crown productivity has been demonstrated to be closely related to tree growth by many applications of predicting diameter and height growth from crown characteristics and vice versa. In 1864, Pressler developed three basic tree growth laws (in Hall, 1965):

1. Tree ring growth at any point along the stem is proportional to the quantity of foliage above that point.
2. Tree ring area is constant in a branch-free bole.
3. Tree ring area decreases with increasing height in the crown in a manner dependent on the distribution of foliage.

Labyak and Schumacher (1954) discovered that for loblolly pine trees, the location of a single branch on the bole and the number of branchlets determine its contribution to bole diameter growth. For example, a branch below 50% of the tree height with fewer than three branchlets supplied almost no resources to the diameter growth of the main stem. Larson (1963) felt that most variations in tree bole form are caused by changes in the size of live crown, form distribution along the stem, and the length of clear bole. Jahnke and Lawrence (1965) suggested four major relationships that govern the productive potential of a plant when water, gas exchange, nutrients, and destructive agents are excluded:

1. the ratio of photosynthetic activity to respiration for the entire plant;
2. the amount of chlorophyll exposed to incoming radiation and the time of year exposed;
3. the geometric form of the crown along with its reflectivity and transmissivity as influenced by leaf shape, surface texture, thickness, and orientation;
4. the density of neighboring plants.

The age and the size of a tree also play a role in determining how a tree may react to environmental stress. As a stand of trees proceeds from the seedling stage to the pole-size stage, current annual increment increases at a steady rate. Competition-induced mortality is highest, and environmental factors, such as light, soil nutrients, and water, are the most limiting. When trees progress from pole-size to thrifty mature size, growth is the most stable and is most limited by environmental factors which reduce carbohydrate production and leaf area. As trees age into mature trees, growth rates decline and trees are most susceptible to climatic stresses, insects, diseases and any factor which increases water stress or reduces photosynthesis and nutrient flow.

Photosynthetic behavior and stomatal conductance have been shown to vary with leaf age and position in the canopy (Woodman, 1971; Kinerson et al., 1974). Woodman (1971) studied net photosynthesis rates of a 38 year-old Douglas-fir and found that net assimilation rates within different positions of the crown were so variable that an average photosynthesis rate for an individual tree could not be predicted. However, zones of differing photosynthesis production efficiencies within a crown were determined. The highest rate of photosynthesis from mature current year needles occurred on the south side of the crown in the area between zones of full sunlight and perpetual shade. The second highest area was the north side of the crown receiving full sunlight. The lowest rates occurred at the bottom of the crown and with the older needles. By the end of the growing season, one year needles had photosynthesis rates that were 72% that of the maximum, two year needles had 50% rates, three year needles had 30% rates and four year needles had 12% rates of the maximum.

O'Neil (1962) performed an artificial defoliation study on 15 year-old jack pine (*Pinus banksiana*) and found that the loss of first year needles decreased height, diameter, and shoot growth but the removal of second or third year needles had no effect. However, the joint removal of second and third year needles did decrease height growth. Removal of current needles increased bud mortality and decreased shoot elongation. Trees which had all but current year needles removed exhibited a significant decrease in height, diameter, and shoot growth.

Since crown productivity is so influential on tree growth and survival, an appropriate way to model the effects of air pollution stress on large tree growth may be through reductions in photosynthesis and needle retention rates which have been demonstrated from seedling studies. Attempts to model and predict crown productivity have consisted of modeling individual branch growth and partitioning assimilate production to diameter and height growth, estimating foliar mass through the pipe model theory and relationships between cross-sectional sapwood basal area and crown volume, and developing probability densities for needle biomass distributions within the crown.

Mitchell (1969) used branch development as the driving variable behind a growth model for white spruce (*Picea glauca*). Total height is modeled as a function of the height of dominant and codominant trees and crown diameter, which is in turn dependent on branch growth. Diameter growth is a function of crown diameter and total height, and tree volume is a function of crown projection area and total height. Later, Mitchell (1975) used a similar approach in developing a growth model for Douglas-fir. In this model he used a measurement of crown productivity to determine diameter and height growth. Since each year a tree adds a new sheath of needles, he modeled the development of a tree's crown as the successive addition of foliage shells, each shell representing a needle age class. However, since needle productivity and number decline with age, the volume of each shell was modified by a weighting factor, which consisted of the multiplication of estimates for photosynthesis efficiency and needle retention rates for each needle age class/foliage shell, as shown in Table [1]. An estimate of the available photosynthate was accordingly obtained by summing the weighted volumes of each foliage shell. A relationship between the estimate of foliage volume and annual bole increment was then developed according to Pressler's growth laws. Thus, age and site quality determined height growth, which influenced branch growth, and which was reflected in the size and shape of the crown. The crown represented the amount of photosynthate available for growth, which determined the quantity and distribution of annual bole increment and which resulted in subsequent height growth.

Shinozaki et al. (1964) developed the pipe model theory in Japan, which is based on the idea that a unit weight of foliage is sustained by a specific cross-sectional area of conducting sapwood in the crown, thus making it analogous to a pipe system. The theory is that since water transport within a tree stem is confined to the sapwood, foliar area might be related to cross-sectional sapwood basal area. These ideas have been used to estimate canopy leaf area from knowledge of sapwood area at breast height or at the base of the live crown. Grier and Waring (1974) were the first to demonstrate a linear relationship between foliar mass and sapwood cross-sectional area at breast height in

Table 1. Factors for weighting foliage volume for each age class of needles for Douglas-fir (Mitchell, 1975).

AGE CLASS OF NEEDLES (1)	PHOTOSYNTHETIC EFFICIENCY (2)	RETENTION RATE (3)	WEIGHTING FACTOR (2)(3)
1	1.00	1.00	1.00
2	0.86	1.00	0.86
3	0.75	1.00	0.75
4	0.63	1.00	0.63
5	0.53	0.75	0.40

Douglas-fir, ponderosa pine, and Noble fir (*Abies procera*) over a range of tree sizes. Whitehead (1978) similarly demonstrated a linear relationship for Scots pine which was independent of stand density. He also found that the same general linear relationship existed across four different sites but the slopes were varied. Waring et al. (1982) applied the pipe model theory to several conifers and determined that the sapwood area at the base of live crown was a better estimate of foliar volume than sapwood area at breast height. This suggested that taper should be taken into account when using sapwood area measurements from below the live crown.

Several studies have attempted to describe the vertical distribution of foliar biomass within crowns, using probability densities. The Weibull distribution has been used to describe 80-year-old lodgepole pine (*Pinus contorta*) (Gary, 1978), the beta distribution for young Scots pine stands (Kellomaki and Hari, 1980), and the normal distribution with the inclusion of a term to accomodate for the significant skewness found in foliar distribution for mature Scots pine (Beadle et al., 1982). Beadle et al. also found that the distribution of leaf area density with height had bimodal and even trimodal distributions. Kinerson et al. (1974) studied loblolly pine trees in the North Carolina Piedmont region and described the vertical distribution of foliage within the crown. Cumulative normalized foliage mass was expressed as a function of the normalized position in the live crown for both new foliage development and the rate of loss of old foliage over time.

The integration concerning the knowledge of the effects of air pollution on seedlings and larger trees together with knowledge of crown relationships should lend insight towards evaluating the potential effects of pollution on tree growth. As knowledge increases concerning the impacts of air pollution on different age classes of needles and position in the crown, the use of known foliage distributions within the crown may provide further refinements to any modeling efforts.

Chapter III

METHODS AND MATERIALS

General Approach and Objectives

The primary purpose of this study was to examine and compare methods for modeling the potential effects of air pollution stress on the growth and yield of cutover, site-prepared loblolly pine plantations. Two general methods were used in accomplishing this objective. The first method was based on the premise that, in some studies, air pollution research has demonstrated a reduction in seedling diameter and height growth. Therefore, Method I consisted of the application of direct reductions to the diameter and height increment equations of an existing growth and yield model for loblolly pine. Since there is no available information concerning the amount and the frequency of reduction that should be applied to larger forest trees, a sensitivity analysis approach was used, representing varying levels and frequencies of diameter and height reductions.

The second method was based upon some research which has shown that air pollution stress decreases the photosynthetic efficiency and needle retention rates of different age classes of foliage. Thus, Method II consisted of modifying the loblolly pine model with a measure of crown productivity that reflected these changes in photosynthetic efficiency and needle retention rates. After modifying the model by both methods, different scenarios were simulated to explore the interactions of stand age, density, site quality, and air pollution stress on stand productivity.

Data

Modifications were performed on the loblolly pine individual tree growth and yield model, PTAEDA2 [*Pinus taeda*], originally developed by Daniels and Burkhart (1975), and revised by Burkhart et al. (1987). This model was chosen because:

1. Loblolly pine is one of the most commercially important tree species in the southeastern United States.
2. Plant-toxic episodes of ozone have frequently been reported over much of the natural range of loblolly pine, and loblolly pine has been shown to be one of the more sensitive southeastern species to ozone.
3. PTAEDA2 is an individual tree model based on even-aged plantation growth of a single species.

4. The growth relationships in the model have been calibrated with a three-year remeasurement dataset.
5. A crown variable (crown ratio) is used in PTAEDA2 to drive height and diameter growth, and to determine the probability of an individual tree's survival.
6. The model, once modified to reflect potential effects of air pollution, provides information to analyze the effects of age, site density, competition, and site quality at varying levels of simulated pollution stress.

The data used to develop and validate PTAEDA2 originated from 186 plot locations in cutover, site-prepared plantations throughout most of the natural range of loblolly pine. Initial measurements were made during the 1980-81 and 1981-82 dormant season and consisted of diameter at breast height (dbh, to the nearest 0.1 inch), total height (to the nearest foot), height to the base of live crown, crown class, and a stem quality assessment. The three plots initially established at each location were remeasured three years later. A summary of the initial measurement and first remeasurement data is presented in Table [2].

Description of the PTAEDA2 Model

PTAEDA2 is an individual tree growth and yield model divided into two main components. The first component is the generation of an initial, pre-competitive stand to the age of eight years. The second component then grows the competitive stand on

Table 2. Summary of the cutover, site-prepared loblolly pine plantation data used to develop the PTAEDA2 model.

	Variable	Minimum Value	Mean	Maximum Value	Standard Deviation
Permanent Plot Data Initial Measurement					
	AGE	8.00	14.87	25.00	4.13
	AVG DBH	0.50	5.63	14.10	1.79
	AVG HT	5.00	37.56	80.00	11.85
	CR	0.00	0.45	0.94	0.13
Permanent Plot Data 3-Year Remeasurement					
	AGE	11.00	17.92	28.00	4.10
	AVG DBH	0.70	6.21	14.90	1.84
	AVG HT	8.00	43.19	86.00	11.44
	CR	0.00	0.40	0.93	0.12

Where:

AGE = Age since planting (years)
AVG DBH = Average diameter at breast height (inches)
AVG HT = Average individual tree height (feet)
CR = Crown ratio

an annual basis to rotation age. At age eight, mortality is assigned at random and individual tree dimensions are assigned to the remaining trees. Diameter at breast height dimensions are determined from a two parameter Weibull distribution with a cumulative distribution function as follows:

$$F(y) = 1 - e^{-ay^b} \qquad [1.0]$$

The parameters a and b are estimated from minimum dbh (DMIN), average dbh (DAVE), and number of trees surviving (TS). DMIN and DAVE are predicted as functions of stand age, height of dominant and codominant trees (HD), and TS (Strub and Burkhart, 1974).

At age eight, intraspecific competition is assumed to begin and each tree is individually grown according to a theoretic growth potential adjusted by a factor based on that tree's crown ratio and competition index. A random component representing microsite and/or genetic variability is added to the predicted growth. The competition index used in PTAEDA2 is a modified Hegyi (1974) index where:

$$CI_i = \sum_{j=1}^{n} (D_j / D_i) / DIST_{ij} \qquad [2.0]$$

where:

CI = competition index for the ith tree

D = dbh of individual tree i

DIST = distance between subject tree i and jth competitor tree

n = number of neighbors with a BAF 10 sweep centered at the subject tree i

The height and diameter increments for each tree is determined by the following equations:

$$HIN = PHIN(0.2632 + 2.1112CR^{0.5619}e^{-0.2637CI-1.0308CR}) \qquad [3.0]$$

$[R^2 = 0.46, s_{y.x} = 0.751]$

$$PDIN = 0.2866HIN + 0.2095 \qquad [4.0]$$

$$DIN = PDIN(0.7251CR^{0.9801}e^{-0.3740CI}) \qquad [5.0]$$

$[R^2 = 0.66, s_{y.x} = 0.085]$

where:

HIN = actual total height increment (feet)

PHIN = potential total height increment (feet)

CR = crown ratio

CI = competition index

PDIN = potential diameter increment (inches)

DIN = diameter increment (inches)

The potential height increment is a function of average height of a dominant and codominant tree which in turn is a function of site index and age (Amateis and Burkhart, 1985). The potential height increment is the first difference of equation [6.0] with respect to age:

$$\ln(HD) = \ln(SI)(25/A)^{-0.0221}e^{-2.8329\times(1/A-1/25)} \qquad [6.0]$$

where:

HD = height of dominant and codominant trees (feet)

SI = site index (feet, base age 25)

A = age (years)

In PTAEDA2, crown ratio represents a measure of photosynthetic potential and is predicted as a function of age, dbh, and height (Dyer and Burkhart, 1987):

$$CR = 1 - e^{(-1.3524-37.0260/A)D/H} \qquad [7.0]$$

where:

CR = crown ratio

A = age (years)

D = dbh (inches)

H = total tree height (feet)

In addition to height and diameter increments being dependent on the competitive status and photosynthetic potential of a tree, the probability that a tree remains alive is determined as follows:

$$PLIVE = 1.0280CR^{0.0379}e^{-0.0023CI^{2.6521}} \qquad [8.0]$$

where:

PLIVE = probability of tree survival

CR = crown ratio

CI = competition index

Thus, PLIVE increases as crown ratio increases and decreases as the competition increases.

Finally, PTAEDA2 calculates the volume of an individual tree as a function of dbh and height, using the combined variable volume equation:

$$V = a + bD^2H \qquad [9.0]$$

where:

V = volume estimate

D = dbh (inches)

H = total tree height (feet)

The model then sums the individual tree volumes to obtain an estimate of volume per acre.

Input variables for PTAEDA2 include the number of simulated growing seasons, site index (feet, base age 25), number of trees planted per acre, whether the stand is thinned or fertilized, and if there is any hardwood competition. A sample output showing the inputs and outputs of the PTAEDA2 model is shown in Figure [1].

Live Trees

INPUTS		PREDICTED	
Site Index =	50.0	Dominant Height =	25.4
Growing Seasons Completed =	10.0	Average DBH =	3.8
Planted Trees =	1210.0	Average Height =	23.3
		Average Crown Ratio =	54.6

DBH Class	Number Trees	Average Height	Basal Area	Total Volume o.b.	Volume o.b. To 4.in	Volume o.b. To 6.in
1	16.1	12.5	.1	3.7	.0	.0
2	107.6	17.7	2.2	38.6	.0	.0
3	209.7	21.9	9.8	138.3	.0	.0
4	306.5	24.2	27.7	365.4	.0	.0
5	204.4	26.3	28.3	378.9	244.8	.0
6	48.4	27.1	8.9	119.4	92.0	.0
Total	892.7		77.0	1044.4	336.8	.0

Acres simulated = .1860
Trees simulated = 166

Figure 1. Sample output from a simulation using the PTAEDA2 model.

Procedures

Method I

The first method involved an annual direct reduction of the diameter and height increment equations beginning at the age of crown closure and continuing through age 40, a typical rotation age. Initially, trees were impacted randomly but the same set of trees were affected throughout the simulation period. Once a tree is stressed, it is more likely to succumb to future stress than an initially healthy tree. The repeated impact on the same individual tree may also reflect the differing levels of sensitivity among families of loblolly pine (Kress, 1978; Ward, 1980). The same random number seed was used for all simulations to allow for comparison across all scenarios. Previous experience with the PTAEDA2 model had shown that if the simulation plot is large, there are no significant differences in outputs due to different random number seeds. The simulation plot used in this study was 15 x 15 (225 trees). Since there was no biological basis for determining appropriate percentages of impact and number of trees to be impacted, various scenarios across a range of site indices and stand densities were simulated. The following scenarios were initialized for each simulated run of PTAEDA2 and one simulation was conducted for each scenario:

1. Site indexes: 50, 60, and 70 (feet, base age 25 years).
2. Initial planting densities: 6x6, 8x8, and 12x12 (approximately 1210, 680, and 300 trees/acre).
3. Percent of trees impacted: 0%, 25%, 50%, and 67%.

4. Percent of impact on diameter and height increments: +4%, 0%, -4%, -8%, -32%, and -64%.

The percent of trees impacted arbitrarily reflected no stand stress (0%), slight stand stress (25%), moderate stand stress (50%), and severe stand stress (67%). The percent of impact on diameter and height increment reflected a slight stimulatory effect (+4%), a slight inhibitory effect (-4%), and exponentially negative effects (-8%, -32%, and -64%). Diameter and height reductions were at the same level, i.e. a 4% dbh reduction and a 4% height reduction. Conclusions which can be drawn from this simulation are the level and frequency of stress required to produce a sizeable reduction in yield, the biological reasonableness of using such an approach, and the trend in impact across site indices and stand densities.

Method II

The second method involved the development of a variable representative of crown productivity which could be substituted for crown ratio, the variable in PTAEDA2 that drives diameter and height increment and tree survival. In a manner similar to Tate's (1987) study for loblolly pine, this new variable was modified to reflect changes in photosynthetic efficiency and needle retention rates as shown to result in some seedlings subjected to air pollution stress.

Since foliage weight and surface area are crown variables which are occasionally measured in biomass studies, these two variables were selected for further study. Although these two variables were not originally measured in the PTAEDA2 data set, several prediction equations using the input variables of dbh, height, and crown length (original PTAEDA2 measured variables) are reported in the literature. For predicting foliage weight for loblolly pine, the following equations from Hepp and Brister (1982) were examined:

$$\ln TWT = -0.1080 + 2.3012 \ln D + 1.1514 \ln CR \qquad [10.1]$$

$[R^2 = 0.9377, s_{y.x} = 0.2456]$

$$\ln BWT = -1.0165 + 2.5803 \ln D + 1.3014 \ln CR \qquad [10.2]$$

$[R^2 = 0.9385, s_{y.x} = 0.2456]$

Therefore,

$$FWT = TWT - BWT$$

where:

TWT = total crown dry weight (pounds)

BWT = weight of branches with bark in the tree crown (pounds)

D = diameter at breast height (inches)

CR = crown ratio

FWT = total foliage weight (pounds)

and from Kinerson et al. (1974):

$$\ln N_W = -0.806 + 3.187 \ln D \qquad [11.0]$$

where:

NW = needle weight (grams)

D = diameter at breast height (inches)

Other foliage weight prediction equations were found but the above two were developed from data similar to that used for PTAEDA2. Hepp and Brister measured branch samples from 364 trees during the summer in site-prepared loblolly pine plantations distributed across North Carolina and South Carolina. These trees represented a wide range of ages, soil types, densities, and site qualities. All plantations were at least ten years old and were unthinned. Sample trees were from the dominant as well as intermediate and suppressed crown classes. Kinerson et al. sampled 18 trees on old-field loblolly pine plantations during and after the growing season in North Carolina and constructed a vertical distribution of leaf biomass.

For predicting foliage surface area for loblolly pine, the following equations from Blanche et al. (1985) were examined:

$$LA = 29.75e^{0.05D} \qquad [12.1]$$

$[R^2 = 0.91]$

and

$$LA = 0.43D^{1.73} \qquad [12.2]$$

$[R^2 = 0.87]$

where:

LA = leaf area (square meters)

D = diameter at breast height (centimeters) and from Kinerson et al. (1974):

for top 1/3 of crown:

$$S_A = 2.861 + 88.83N_W \qquad [13.1]$$

for middle 1/3 of crown:

$$S_A = 4.240 + 95.12N_W \qquad [13.2]$$

for bottom 1/3 of crown:

$$S_A = 1.704 + 120.49N_W \qquad [13.3]$$

where:

SA = leaf surface area (square centimeters)

NW = needle weight (grams)

Blanche et al. sampled fourteen natural stands of loblolly pine in Mississippi during August and September over a wide range of ages. In a manner similar to Mitchell's (1975) use of "weighted" foliage shells, the foliage weight and surface area estimates were then weighted as shown in Table [3]. Since loblolly pine needles typically remain on the tree for two seasons, but rarely three, two age classes were represented. It was assumed that the several flushes of growth for loblolly pine in a single season would be counted as one age class of needles. It was also assumed that the current year's age class of needles exhibited full photosynthetic efficiency and all needles remained on the tree during the growing season. The values for the second year's age class were determined from Metz and Wells (1965) study. Metz and Wells studied the weight and nutrient content of all aboveground parts of ten loblolly pine trees. They listed the weights of the terminal, upper third, middle third, and lower third of the crown for two growing

Table 3. Weighting factors used for each age class of needles for loblolly pine (derived from Metz and Wells, 1965).

AGE CLASS OF NEEDLES (1)	PHOTOSYNTHETIC EFFICIENCY (2)	RETENTION RATE (3)	WEIGHTING FACTOR (2)(3)
1	1.00	1.00	1.00
2	0.50	0.20	0.10

seasons for each tree. An independent analysis of their reported raw data showed that approximately 14 percent of the total foliage weight was in the second year age class, making the current year age class approximately 86% of the total foliage weight. A search of the literature revealed no specific estimates of photosynthetic efficiency and needle retention rate for second year loblolly pine needles, so an estimate of 50 and 20 percent respectively was used.

Using the prediction equations [10.1]-[13.3] and the weighting factors in Table [3], foliage weight and surface area were estimated for each tree in the unthinned remeasurement data set for PTAEDA2. Efforts were then directed to developing two versions of the original PTAEDA2 model, one using foliage weight to drive diameter and height growth and one using foliage surface area.

Evaluation of the performance of foliage weight and surface area in predicting diameter and height growth and survival consisted of examining R-square and standard error values. Candidate models were validated using the growth data from the lightly thinned and heavily thinned plots. Residual analysis compared predicted diameter and height growth estimates to actual observed diameter and height growth values. Overall model performance was also evaluated for the logical trends and relationships that existed in the original PTAEDA2 model.

Since the foliage weight version was the only model found to perform satisfactorily in predicting diameter and height increment within the PTAEDA2 framework, the scenarios of air pollution stress were analyzed using only the foliage weight prediction equations. The scenarios were designed to reflect some research showing the effects of air pollution stress on loblolly pine seedlings with respect to photosynthetic efficiency and needle retention and to reflect the study Tate (1987) performed with the PTAEDA2 model. The six scenarios consisted of reducing photosynthetic efficiency by 0, 7.5, and 15 percent and needle retention by 0 and 1 year as shown in Table [4]. Thus, for each

Table 4. Weighting factors used for each air pollution scenario in Method II.

SCENARIO	CURRENT PHOTOSYNTHETIC EFFICIENCY	CURRENT NEEDLE RETENTION	SECOND YR. PHOTOSYNTHETIC EFFICIENCY	SECOND YR. NEEDLE RETENTION
1	1.000	1.000	0.500	0.200
2	1.000	0.500	0.500	0.100
3	0.925	1.000	0.463	0.200
4	0.925	0.500	0.463	0.100
5	0.850	1.000	0.425	0.200
6	0.850	0.500	0.425	0.100

tree in the simulations, foliage weight was calculated for each age class of needles and then weighted by the appropriate factor according to each scenario. The needle retention reduction was distributed equally over each needle age class.

Each scenario shown in Table [4] was simulated using the foliage weight model for site indexes 50, 60, and 70 over a 50 year rotation. A 15 x 15 matrix of trees (225 trees) was simulated for each run of PTAEDA2. Each stand was planted with 1210 trees per acre with exact regular spacing. For simplicity, no thinning or fertilization treatments were considered and there was no hardwood competition. The results were then analyzed to determine the effects of differential levels of air pollution stress on the growth and yield of an average loblolly pine stand.

Chapter IV

RESULTS

Two methods were evaluated for modeling the potential effects of air pollution stress on the growth and yield of cutover, site-prepared loblolly pine plantations. The first method, based on previous research showing decreases in diameter and height growth of seedlings exposed to air pollution, involved the application of direct reductions in diameter and height increment on the original PTAEDA2 model. The second method, based on several research studies showing decreases in photosynthetic efficiency and needle retention rate of seedlings exposed to air pollution, involved finding a variable representative of an individual tree's photosynthetic potential. Assuming air pollution causes decreases in photosynthetic efficiency and average needle retention, this new variable was modified by varying decreases in photosynthetic efficiency and needle retention rates. The results of each of these two methods will be discussed in turn.

Method I

The following scenarios were initialized for each simulation run of PTAEDA2:

1. Site indexes: 50, 60, and 70 (feet, base age 25).
2. Initial planting densities: 6x6, 8x8, 12x12 (1210, 680, and 300 trees/acre).
3. Percent of trees impacted: 0%, 25%, 50%, and 67%.
4. Percent of impact on diameter and height increments: +4%, -2%, -4%, -8%, -32% and -64%.

The effects of each scenario on cumulative cubic-foot volume (outside bark) per acre at age 40 and average cubic-foot volume per tree were examined for the impacted, non-impacted, and for all the trees combined.

Effects on Volume at Age 40

Cumulative cubic-foot volume per acre at age 40 for the baseline scenarios (no pollution impacts), as shown in Table [5], exhibit the typical trend expected across a range of site indexes and planting densities. As site quality increases, trees are able to put on more diameter growth so volume accumulates in higher diameter classes and can reach a greater total volume per acre. As the initial planting density increases, competition at early ages is greater and diameter growth is slower. There is more total volume per acre at greater stand densities, but it is accumulated in smaller diameter classes.

As expected, a slight stimulatory increase in growth (+4%) results in a slight increase in total volume per acre at age 40, as shown in Table [6]. Sizeable decreases in volume do not occur until the annual impact on growth is -32% and -64%. Even with a 32% decrease in diameter and height increment occurring annually on 25% of the

Table 5. Cumulative cubic-foot volume per acre (o.b.) at age 40 for the baseline scenarios (no pollution impacts) in Method I.

	SITE INDEX								
	SI 50			SI 60			SI 70		
DIAM CLASS	NUMBER OF TREES PLANTED PER ACRE								
	300	680	1210	300	680	1210	300	680	1210
4	15	117	388	13	124	485	4	155	549
6	97	661	1622	97	693	1734	63	753	1841
8	408	1973	3969	419	2073	4196	316	1614	3788
10	1427	3935	5829	1243	4623	6970	1211	4736	7380
12	3328	5718	6328	3487	6969	8158	2938	7100	10029
14	4924	5914	—	5320	8018	8375	5716	9661	10465
16	5157	—	—	6930	—	—	7935	10169	—
18	—	—	—	7187	—	—	9220	—	—
20	—	—	—	—	—	—	9472	—	—

Table 6. Percent change in total cubic-ft. volume per acre (o.b.) at age 40 for the impacted vs. non-impacted scenarios in Method I.

% IMPACT ON GROWTH	% OF TREES IMPACTED	SI 50 TPA 300	SI 50 TPA 680	SI 50 TPA 1210	SI 60 TPA 300	SI 60 TPA 680	SI 60 TPA 1210	SI 70 TPA 300	SI 70 TPA 680	SI 70 TPA 1210
+4	25	+2	+4	+3	+2	+0.1	+0.3	+3	+2	+1
	50	+2	+4	+4	+3	+2	+0.1	+3	+2	+2
	67	+4	+5	+5	+4	+2	+3	+4	+5	+4
-2	25	-0.5	-3	-1	-0.4	-2	-3	-1	-0.5	-0.5
	50	-1	-1	-1	-1	-1	-1	-1	-1	-0.4
	67	-2	-0.3	-0.5	-2	-3	-2	-0.5	-0.2	-0.8
-4	25	-1	-1	-1	-1	-3	-4	-0.3	-1	-1
	50	-3	-2	-1	-3	-3	-2	-3	-2	-1
	67	-3	-2	-0.8	-4	-4	-2	-2	-2	-2
-8	25	-3	-1	-0	-3	-2	-5	-2	-3	-2
	50	-6	-4	-6	-6	-5	-5	-5	-4	-3
	67	-7	-6	-4	-8	-7	-5	-6	-5	-6
-32	25	-10	-9	-7	-10	-8	-12	-8	-8	-5
	50	-19	-13	-13	-18	-16	-17	-18	-16	-12
	67	-24	-20	-19	-26	-22	-17	-24	-21	-21
-64	25	-15	-5	-9	-14	-12	-16	-12	-13	-12
	50	-27	-21	-20	-28	-23	-27	-27	-27	-19
	67	-36	-34	-32	-42	-35	-29	-38	-35	-33

trees, decreases in total volume range from only 5 to 12%. However, with a 64% decrease in diameter and height increment on 67% of the trees, total volume reduction ranges from 29 to 42%.

The impacts for a given site quality, for the most part, showed smaller percentage reductions in volume associated with greater planting densities. This suggests that growth lost on stressed trees may be redistributed on neighboring trees. The smaller percentages of volume reduction for a given planting density over a range of site indexes suggests that the better the site quality, the better the stand can adjust to pollution stress.

Tables [7]-[12] show the distribution of volume over diameter classes for impacts of -32% and -64%, for site indexes 50, 60, and 70, and for 300, 680, and 1210 trees planted per acre on 25, 50, and 67% of the trees. These figures portray the amount of volume of both the impacted and non-impacted trees for each scenario and show that the impacted trees remain in the smaller diameter classes. Therefore, the volume in the smaller diameter classes increases as severity of stress increases.

Effects on Average Cubic-Foot Volume Per Tree

The effects on average cubic-foot volume per tree for site index 60 and 680 trees planted per acre are presented in Tables [13] and [14]. When only 25% of the trees are impacted, the average volume per tree for the non-impacted trees remains about the same, regardless of the severity of stress. This suggests that when relatively few trees are affected, the loss of volume per tree of the impacted trees has no influence on the growth of neighboring non-impacted trees. However, when more of the trees are impacted, the decreased growth of the impacted trees begins to allow the non-impacted

Table 7. Cumulative cubic-ft. volume per acre (o.b.) at age 40 by dbh class (inches) for SI 50 (ft, base age 25) and -32% impact.

SITE INDEX: 50 NUMBER OF TREES PLANTED PER ACRE: 300 IMPACT ON GROWTH: -32%

	PERCENT OF TREES IMPACTED								
	25			50			67		
DIAM CLASS	IMPACT	NON-IMPACT	TOTAL	IMPACT	NON-IMPACT	TOTAL	IMPACT	NON-IMPACT	TOTAL
4	4	9	13	6	10	16	12	3	15
6	44	71	115	128	36	164	99	33	132
8	251	301	552	439	163	602	534	136	670
10	577	996	1573	947	591	1538	1198	409	1607
12	693	2172	2865	1275	1535	2810	1509	1216	2806
14	—	3552	4245	—	2516	3791	1623	2102	3725
16	—	3922	4615	—	2922	4197	—	2316	3939
18	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—

SITE INDEX: 50 NUMBER OF TREES PLANTED PER ACRE: 680 IMPACT ON GROWTH: -32%

4	78	121	199	73	71	144	136	17	153
6	264	419	683	374	321	695	582	164	746
8	535	1071	1606	875	1143	2018	1340	722	2062
10	889	2915	3804	1463	2547	4010	2021	1842	3863
12	—	4311	5200	—	3458	4921	—	2471	4492
14	—	4497	5386	—	3657	5120	—	2689	4710
16	—	—	—	—	—	—	—	—	—
18	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—

SITE INDEX: 50 NUMBER OF TREES PLANTED PER ACRE: 1210 IMPACT ON GROWTH: -32%

4	164	246	410	303	196	499	273	131	404
6	558	1179	1737	918	848	1766	1265	645	1910
8	938	2664	3602	1617	2056	3673	2121	1591	3712
10	—	4438	5376	1743	3261	5004	2249	2312	4561
12	—	4965	5903	—	3618	5361	—	2533	4782
14	—	—	—	—	3781	5524	—	2883	5132
16	—	—	—	—	—	—	—	—	—
18	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—

Table 8. Cumulative cubic-ft. volume per acre (o.b.) at age 40 by dbh class (inches) for SI 60 (feet, base age 25) and -32% impact.

SITE INDEX: 60 NUMBER OF TREES PLANTED PER ACRE: 300 IMPACT ON GROWTH: -32%

	PERCENT OF TREES IMPACTED								
	25			50			67		
DIAM CLASS	IMPACT	NON-IMPACT	TOTAL	IMPACT	NON-IMPACT	TOTAL	IMPACT	NON-IMPACT	TOTAL
4	7	3	10	8	5	13	10	5	15
6	54	37	91	90	32	122	96	18	114
8	231	283	514	269	123	392	413	90	503
10	640	824	1464	1071	462	1533	1274	489	1763
12	900	2056	2956	1587	1581	3168	2346	990	3336
14	1019	3654	4673	1888	2678	4566	2586	1802	4388
16	—	5093	6112	—	3824	5712	—	2387	4973
18	—	5434	6453	—	4001	5889	—	2733	5319
20	—	—	—	—	—	—	—	—	—

SITE INDEX: 60 NUMBER OF TREES PLANTED PER ACRE: 680 IMPACT ON GROWTH: -32%

4	47	80	127	79	74	153	93	35	128
6	253	447	700	491	309	800	519	255	774
8	700	1398	2098	1201	993	2194	1452	703	2155
10	1054	3124	4178	1821	1996	3817	2661	1432	4093
12	—	5181	6235	2144	3526	5670	2997	2614	5611
14	—	6014	7068	—	4447	6591	—	2948	5945
16	—	6337	7391	—	4610	6754	—	3264	6261
18	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—

SITE INDEX: 60 NUMBER OF TREES PLANTED PER ACRE: 1210 IMPACT ON GROWTH: -32%

4	143	316	459	328	190	518	383	180	563
6	674	1224	1898	1068	793	1861	1201	508	1709
8	1187	2719	3906	1861	1834	3595	2291	1408	3699
10	1432	4871	6303	2177	3756	5933	2733	2685	5418
12	—	5946	7378	—	4350	6527	—	3560	6293
14	—	—	—	—	4774	6951	—	4181	6914
16	—	—	—	—	—	—	—	—	—
18	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—

Table 9. Cumulative cubic-ft. volume per acre (o.b.) at age 40 by dbh class (inches) for SI 70 (feet, base age 25) and -32% impact.

SITE INDEX: 70 NUMBER OF TREES PLANTED PER ACRE: 300 IMPACT ON GROWTH: -32%

	PERCENT OF TREES IMPACTED								
	25			50			67		
DIAM CLASS	IMPACT	NON-IMPACT	TOTAL	IMPACT	NON-IMPACT	TOTAL	IMPACT	NON-IMPACT	TOTAL
4	4	6	10	2	1	3	13	2	15
6	21	74	95	73	21	94	62	10	72
8	187	222	409	312	178	490	395	126	521
10	586	880	1466	915	581	1496	1318	447	1765
12	909	1922	2831	1981	1240	3221	2526	719	3245
14	1335	4003	5338	2448	2456	4904	3360	1709	5069
16	—	6062	7397	2569	4078	6647	3489	2724	6213
18	—	6998	8333	—	4991	7560	—	3410	6899
20	—	7385	8720	—	5227	7796	—	3665	7154

SITE INDEX: 70 NUMBER OF TREES PLANTED PER ACRE: 680 IMPACT ON GROWTH: -32%

4	37	111	148	80	77	157	96	36	132
6	208	535	743	408	226	634	532	177	709
8	645	1323	1968	1294	949	2243	1529	579	2108
10	1332	3018	4350	2400	1926	4326	2708	1633	4341
12	1614	5502	7116	2711	3275	5986	3668	2733	6401
14	—	7011	8625	—	4758	7469	—	3538	7206
16	—	7747	9361	—	5863	8574	—	4323	7991
18	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—

SITE INDEX: 70 NUMBER OF TREES PLANTED PER ACRE: 1210 IMPACT ON GROWTH: -32%

4	164	342	506	245	207	452	324	173	497
6	582	1141	1723	904	904	1808	1171	649	1820
8	879	3093	3972	1912	2476	4388	2586	1743	4329
10	1315	5247	6562	2369	3859	6228	3659	2813	6472
12	—	7629	8944	—	5625	7994	3785	4081	7866
14	—	8335	9650	—	6857	9226	—	4520	8305
16	—	8619	9934	—	—	—	—	—	—
18	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—

Table 10. Cumulative cubic-ft. volume per acre (o.b.) at age 40 by dbh class (inches) for SI 50 (feet, base age 25) and -64% impact.

SITE INDEX: 50 NUMBER OF TREES PLANTED PER ACRE: 300 IMPACT ON GROWTH: -64%

	PERCENT OF TREES IMPACTED								
	25			50			67		
DIAM CLASS	IMPACT	NON-IMPACT	TOTAL	IMPACT	NON-IMPACT	TOTAL	IMPACT	NON-IMPACT	TOTAL
4	11	10	21	32	6	38	33	3	36
6	135	78	213	214	42	256	240	28	268
8	303	258	561	506	163	669	633	141	774
10	314	793	1107	572	534	1106	737	304	1041
12	—	2093	2407	—	1216	1788	—	1039	1776
14	—	3543	3857	—	2343	2915	—	1955	2692
16	—	4065	4379	—	3098	3670	—	2585	3322
18	—	—	—	—	3172	3744	—	—	—
20	—	—	—	—	—	—	—	—	—

SITE INDEX: 50 NUMBER OF TREES PLANTED PER ACRE: 680 IMPACT ON GROWTH: -64%

4	70	65	135	124	41	165	186	25	211
6	287	519	806	438	351	789	557	143	700
8	404	1357	1761	689	1153	1842	1009	724	1733
10	—	3191	3595	—	2350	3039	—	1573	2582
12	—	4522	4926	—	3657	4346	—	2675	3684
14	—	4802	5206	—	3963	4652	—	2901	3910
16	—	—	—	—	—	—	—	—	—
18	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—

SITE INDEX: 50 NUMBER OF TREES PLANTED PER ACRE: 1210 IMPACT ON GROWTH: -64%

4	187	292	479	345	191	536	417	130	547
6	493	1138	1631	795	867	1662	1117	726	1843
8	—	2600	3093	914	2156	3070	1237	1555	2792
10	—	4418	4911	—	3179	4093	—	2452	3689
12	—	5123	5616	—	3981	4895	—	2697	3934
14	—	5293	5786	—	4151	5065	—	3046	4283
16	—	—	—	—	—	—	—	—	—
18	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—

Table 11. Cumulative cubic-ft. volume per acre (o.b.) at age 40 by dbh class (inches) for SI 60 (feet, base age 25) and -64% impact.

SITE INDEX: 60 NUMBER OF TREES PLANTED PER ACRE: 300 IMPACT ON GROWTH: -64%

	PERCENT OF TREES IMPACTED								
	25			50			67		
DIAM CLASS	IMPACT	NON-IMPACT	TOTAL	IMPACT	NON-IMPACT	TOTAL	IMPACT	NON-IMPACT	TOTAL
4	16	5	21	26	2	28	31	1	32
6	120	53	173	126	20	146	154	11	165
8	324	271	595	553	108	661	728	107	835
10	458	824	1282	778	534	1312	1173	310	1483
12	—	1913	2371	839	1442	2281	1192	886	2078
14	—	3798	4256	—	2740	3579	—	1435	2627
16	—	5225	5683	—	4055	4894	—	2373	3565
18	—	5681	6139	—	4301	5140	—	2987	4179
20	—	—	—	—	—	—	—	—	—

SITE INDEX: 60 NUMBER OF TREES PLANTED PER ACRE: 680 IMPACT ON GROWTH: -64%

4	57	81	138	103	33	136	129	39	168
6	349	432	781	689	378	1067	751	196	947
8	535	1307	1842	1028	844	1872	1407	583	1990
10	—	3025	3560	1061	1972	3033	1469	1329	2798
12	—	5055	5590	—	3585	4646	—	2876	4345
14	—	6217	6752	—	5086	6147	—	3464	4933
16	—	6543	7078	—	—	—	—	3755	5224
18	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—

SITE INDEX: 60 NUMBER OF TREES PLANTED PER ACRE: 1210 IMPACT ON GROWTH: -64%

4	213	370	583	391	194	585	420	120	540
6	652	1215	1867	1031	772	1803	1185	441	1626
8	718	2643	3341	1246	2077	3323	1474	1330	2804
10	—	4705	5423	—	3255	4501	—	3405	4879
12	—	5934	6652	—	4605	5851	—	4257	5731
14	—	6321	7039	—	4605	5851	—	4257	5731
16	—	—	—	—	4883	6129	—	4504	5978
18	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—

Table 12. Cumulative cubic-ft. volume per acre (o.b.) at age 40 by dbh class (inches) for SI 70 (feet, base age 25) and -64% impact.

SITE INDEX: 70   NUMBER OF TREES PLANTED PER ACRE: 300   IMPACT ON GROWTH: -64%

	PERCENT OF TREES IMPACTED								
	25			50			67		
DIAM CLASS	IMPACT	NON-IMPACT	TOTAL	IMPACT	NON-IMPACT	TOTAL	IMPACT	NON-IMPACT	TOTAL
4	8	2	10	22	0	22	26	5	31
6	102	55	157	151	6	157	183	5	188
8	311	305	616	498	136	634	660	65	725
10	606	730	1336	1034	475	1509	1431	390	1821
12	—	1885	2491	1151	1081	2232	1627	685	2312
14	—	3603	4209	—	2430	3581	—	1346	2973
16	—	5659	6265	—	4338	5489	—	2525	4152
18	—	7060	7666	—	5518	6669	—	3837	5464
20	—	7730	8336	—	5775	6926	—	4196	5823

SITE INDEX: 70   NUMBER OF TREES PLANTED PER ACRE: 680   IMPACT ON GROWTH: -64%

4	60	70	130	159	53	212	173	49	222
6	318	446	764	562	309	871	655	160	815
8	721	1402	2123	1251	836	2087	1523	653	2176
10	794	3023	3817	1363	2396	3759	1887	1217	3104
12	—	5216	6010	—	3506	4889	—	2573	4460
14	—	6978	7772	—	4992	6355	—	3878	5765
16	—	8029	8823	—	5840	7203	—	4248	6135
18	—	—	—	—	6065	7428	—	4681	6568
20	—	—	—	—	—	—	—	—	—

SITE INDEX: 70   NUMBER OF TREES PLANTED PER ACRE: 1210   IMPACT ON GROWTH: -64%

4	193	285	478	301	239	540	425	137	562
6	610	1369	1979	958	885	1843	1217	709	1926
8	777	2914	3691	1289	2305	3594	2041	1546	3587
10	—	5433	6210	—	4189	5478	—	2803	4844
12	—	7837	8614	—	6010	7299	—	4484	6525
14	—	8048	8825	—	7146	8435	—	4714	6755
16	—	8371	9148	—	—	—	—	5002	7043
18	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—

Table 13. Average cubic-foot volume per tree (o.b.) for baseline scenarios in Method I.

SITE INDEX	AGE	NUMBER OF TREES PLANTED PER ACRE 300	680	1210
50	10	2.6	4.4	6.5
	15	6.4	9.6	12.9
	20	10.8	16.3	21.4
	25	15.5	22.6	30.5
	30	20.5	32.9	45.5
	35	27.1	43.2	64.2
	40	34.8	58.5	84.4
60	10	3.6	6.0	8.1
	15	9.0	13.5	16.7
	20	15.4	22.0	28.9
	25	22.6	31.4	42.8
	30	30.1	45.8	62.5
	35	40.2	59.1	83.9
	40	50.3	76.4	108.8
70	10	4.9	7.5	10.1
	15	12.4	17.3	22.8
	20	20.9	30.7	37.7
	25	31.3	45.5	60.5
	30	41.2	64.1	84.7
	35	55.3	85.1	117.2
	40	71.2	107.0	151.7

Table 14. Average cubic-foot volume per tree (o.b.) for pollution impacted scenarios in Method I.

SITE INDEX 60, NUMBER OF TREES PLANTED 680

% IMPACT ON GROWTH	AGE	PERCENT OF TREES IMPACTED 25 IMPACT	25 NON-IMPACT	25 TOTAL	50 IMPACT	50 NON-IMPACT	50 TOTAL	67 IMPACT	67 NON-IMPACT	67 TOTAL
+4	10	5.6	6.1	6.0	5.9	6.2	6.1	6.1	5.9	6.0
	15	13.1	13.6	13.5	13.5	14.0	13.7	14.6	12.8	13.9
	20	22.1	22.7	22.6	22.5	22.5	22.5	24.0	21.5	23.1
	25	34.8	34.8	34.8	31.6	32.6	32.1	34.7	31.7	33.6
	30	50.0	47.6	48.2	46.3	47.7	47.0	46.9	43.0	45.5
	35	70.3	60.5	62.9	60.7	61.2	60.9	65.9	57.0	62.5
	40	96.5	72.7	77.8	79.8	88.5	83.8	88.7	75.1	83.6
-2	10	5.6	6.1	6.0	5.8	6.2	6.0	6.0	5.9	6.2
	15	12.4	13.7	13.3	12.8	14.1	13.4	13.8	13.1	13.5
	20	20.5	22.8	22.2	21.0	22.7	21.9	22.7	21.3	22.2
	25	31.9	35.0	34.2	29.1	33.0	31.0	32.4	30.8	31.8
	30	45.4	47.9	47.3	42.3	48.3	45.2	46.7	42.3	44.9
	35	61.3	61.8	61.6	55.7	61.1	58.4	58.4	54.1	56.9
	40	83.5	74.1	76.2	73.7	76.9	75.3	75.7	65.7	71.7
-4	10	5.5	6.1	6.0	5.8	6.2	6.0	6.0	5.9	5.9
	15	12.2	13.7	13.3	12.5	14.1	13.3	13.5	13.1	13.3
	20	20.0	22.8	22.1	20.5	22.8	21.6	22.2	21.4	21.9
	25	31.0	35.1	34.0	28.3	33.1	30.7	31.6	30.9	31.3
	30	44.0	48.0	46.9	41.1	48.5	44.7	45.4	42.5	44.1
	35	59.2	61.9	61.2	53.9	61.4	57.6	56.9	54.4	55.9
	40	80.5	74.3	75.7	71.2	77.4	74.3	73.3	66.2	70.4
-8	10	5.5	6.1	5.9	5.8	6.2	6.0	5.9	5.9	5.9
	15	11.8	13.7	13.2	12.1	14.1	13.1	13.1	13.1	13.1
	20	19.5	22.9	22.0	19.5	22.9	21.2	21.2	21.5	21.3
	25	26.4	33.9	31.8	26.7	33.3	30.0	30.0	31.2	30.4
	30	36.7	46.9	44.1	39.1	48.2	43.6	42.8	43.0	42.9
	35	50.5	60.5	57.9	53.5	61.7	57.7	53.5	55.1	54.1
	40	67.4	81.4	77.8	76.2	77.3	76.8	68.7	67.1	68.1
-32	10	5.2	6.1	5.9	5.4	6.2	5.8	5.6	5.9	5.7
	15	9.0	13.8	12.5	9.6	14.3	12.0	10.0	13.4	11.3
	20	13.3	22.7	20.2	14.5	23.6	19.2	14.8	23.4	17.9
	25	18.5	32.4	28.8	19.7	35.4	27.9	21.1	33.5	25.8
	30	26.5	44.1	39.9	26.5	49.3	38.2	27.4	50.5	35.7
	35	35.9	61.0	55.3	36.0	61.6	50.0	35.5	69.3	47.4
	40	45.8	77.3	70.4	46.6	82.3	66.2	43.4	85.9	58.5
-64	10	4.8	6.1	5.8	5.0	6.2	5.6	5.2	5.9	5.4
	15	6.6	13.9	11.9	6.9	14.1	10.6	7.3	13.7	9.7
	20	8.5	23.1	19.1	8.7	24.1	16.5	9.5	24.9	15.2
	25	10.8	33.1	27.3	10.8	37.2	24.1	11.6	37.6	21.1
	30	14.5	45.2	37.9	12.9	51.8	32.5	14.6	56.4	29.2
	35	18.9	62.8	52.8	14.9	71.5	42.1	17.1	74.2	36.9
	40	23.3	79.8	67.4	18.9	86.2	53.4	21.6	93.9	48.4

trees more room to grow, but only in the later age classes. This is evidenced by the increase in average volume per tree in non-impacted trees when 50% and 67% trees are impacted at -32% and -64% growth reductions. Similar trends at other site indexes and planting densities were also observed.

Method II

Development of a Modified Model

The first step involved in modifying PTAEDA2 to incorporate changes in photosynthetic efficiency and needle retention consisted of developing diameter and height increment and survival equations using either foliage weight or surface area as the main driving variable, rather than crown ratio as in the original PTAEDA2.

Two estimates of foliage weight were evaluated:

1. FW1 = Foliage weight estimate from Hepp and Brister (1982) equations [10.1] and [10.2]
2. FW2 = Foliage weight estimate from Kinerson et al. (1974) equation [11.0]

Three estimates of surface area were evaluated:

1. SA1 = Surface area estimate from Blanche et al. (1985) equation [12.1]
2. SA2 = Surface area estimate from Blanche et al. (1985) equation [12.2]
3. SA3 = Surface area estimate from Kinerson et al. (1974) equations [13.1]- [13.3]

Initially, the same model forms as in the original PTAEDA2 equations [3.0]-[5.0] were examined. When none of these model forms converged for any of the estimates of foliage weight or surface area, other model forms were evaluated, until the following equations converged:

Using Foliage Weight:

$$HIN = PHIN(b_1 FW^{b_2} e^{-b_3 CI - b_4 FW}) \qquad [14.0]$$

$$DIN = PDIN(b_5 FW^{b_6} e^{-b_7 CI}) \qquad [15.0]$$

$$PLIVE = b_8 FW^{b_9} e^{-b_{10} CI^{b_{11}}} \qquad [16.0]$$

and using Surface Area:

$$HIN = PHIN(b_{12} SA^{b_{13}} e^{-b_{14} CI}) \qquad [17.0]$$

$$DIN = PDIN(b_{15} SA^{-b_{16}} e^{-b_{17} CI}) \qquad [18.0]$$

$$PLIVE = b_{18} SA^{b_{19}} e^{-b_{20} CI} \qquad [19.0]$$

Tables [15]-[16] contain the parameter estimates for each model for the foliage weight and surface area estimates used. All parameter estimates were significant.

Analysis of the residuals versus the predicted values for determining height increment in all equations showed a slightly right downward aggregation about zero. Residuals for diameter increment showed random variation about zero. The behavior of the equations while holding particular variables constant, led to the elimination of certain

Table 15. Parameter estimates for PTAEDA2 equations using the FW1 and FW2 values in Method II.

	FW1	FW2
HIN EQUATION [14.0]		
b1	0.8751	0.5901
b2	0.0951	0.0563
b3	0.1368	0.1393
b4	-0.1216	-0.3037
R^2	0.1115	0.1117
Sy.x	0.7200	0.7206
DIN EQUATION [15.0]		
b5	0.5199	0.7523
b6	0.0073	-0.0530
b7	0.7872	0.7430
R^2	0.5678	0.5755
Sy.x	0.0961	0.0953
PLIVE EQUATION [16.0]		
b8	0.9873	0.9718
b9	0.0157	0.0039
b10	-0.0026	-0.0062
b11	2.5498	2.1109
R^2	0.0551	0.0485
Sy.x	0.1002	0.1005

Table 16. Parameter estimates for PTAEDA2 equations using the SA1, SA2, and SA3 values in Method II.

	SA1	SA2	SA3
HIN EQUATION [17.0]			
b12	0.5047	0.8172	0.9652
b13	0.1886	0.0797	0.0433
b14	0.1862	0.1849	0.1852
R^2	0.1129	0.1126	0.1126
Sy.x	0.7246	0.7235	0.7235
DIN EQUATION [18.0]			
b15	1.4656	0.7228	0.5950
b16	-0.2578	-0.0977	-0.0531
b17	0.7503	0.7424	0.7430
R^2	0.5751	0.5755	0.5755
Sy.x	0.0953	0.0953	0.0953
PLIVE EQUATION [19.0]			
b18	*	0.9764	0.9895
b19	*	0.0073	0.0039
b20	*	-0.0062	-0.0062
b21	*	2.1110	2.1111
R^2	*	0.0485	0.0484
Sy.x	*	0.1005	0.1005

* Model form would not converge.

equations. The 3-D plots in Figures [2]-[10] show these relationships between variables for the original model versus the foliage weight and surface area models. Height increment should decrease as the competition index increases and this relationship was true for all equations. As foliage weight or surface area increases, i.e. as photosynthetic potential increases, height increment should increase and this held true for all equations. Similarly, diameter increment should decrease as the competition index increases, but this did not hold true for the equations using the FW2, SA1, and SA3 estimates. Therefore, these equations were not examined further. For PLIVE prediction, as the competition index increases, PLIVE should decrease and this held true for FW1 and SA2. As FW1 and SA2 increase, PLIVE should increase and this relationship was true.

Finally, using the data from the lightly thinned and heavily thinned plots of original data for PTAEDA2 as validation datasets, the mean residuals for the foliage weight and surface area models as shown in Table [17] were obtained. The height and diameter increment equations using foliage weight and surface area as derived from the unthinned plots slightly overpredict the growth on the thinned plots. The overprediction is greater for the heavily thinned plots, although the residuals are approximately zero.

Several simulation runs of PTAEDA2 were performed to observe the effect of introducing the new DIN, HIN, and PLIVE equations using FW1 or SA2, instead of the original crown ratio. Results showed that the PLIVE equations using FW1 or SA2 were not behaving properly. For site index 60 and 680 trees planted per acre, the number of trees surviving at age 40 was 356 for the original model, 487 for the foliage weight model, and 210 for the surface area model. Therefore, the original PLIVE equation using crown ratio was substituted back into the FW1 model and SA2 model. Thus, the models selected for further study consisted of the FW1 and SA2 models where foliage weight or surface area was used to drive diameter and height growth and crown ratio was used to predict the probability of a tree's survival.

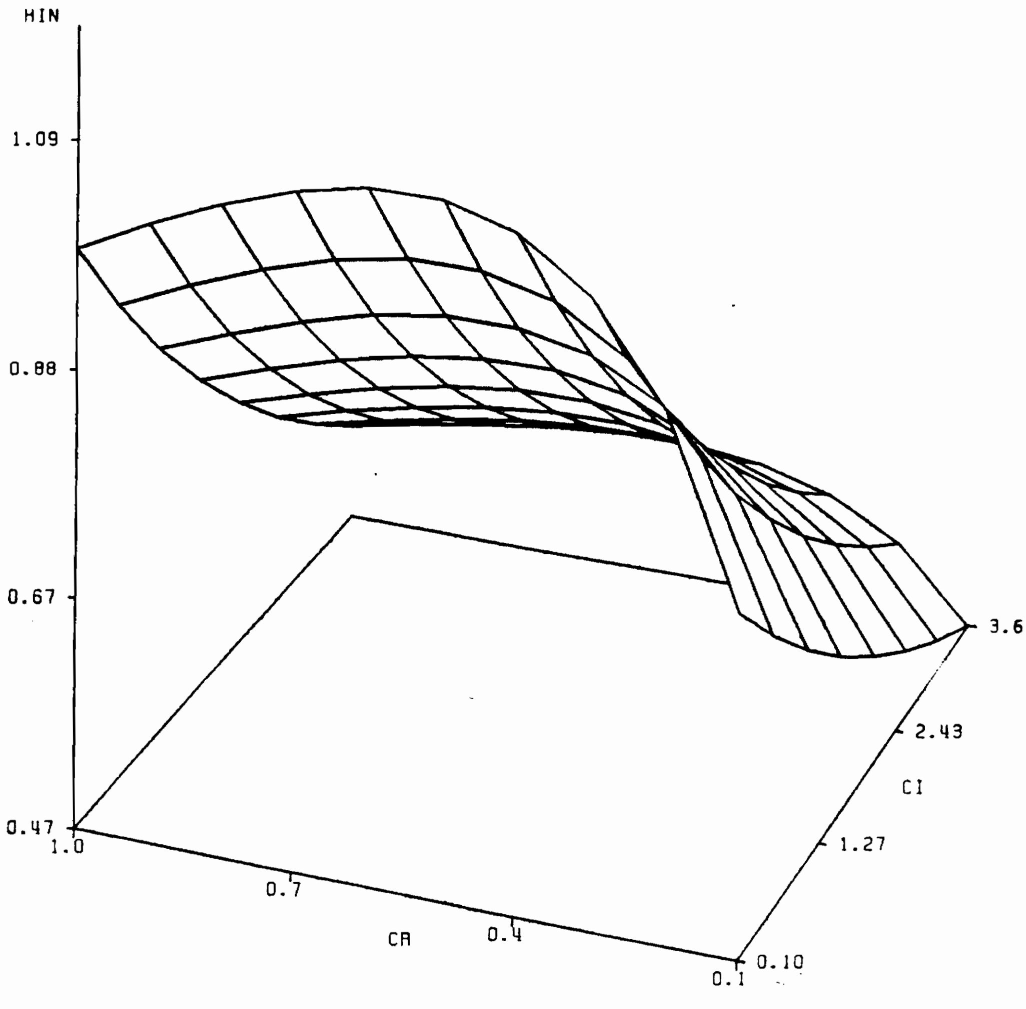

Figure 2. Relationship between height increment (HIN), competition index (CI), and crown ratio (CR) in the original PTAEDA2 model.

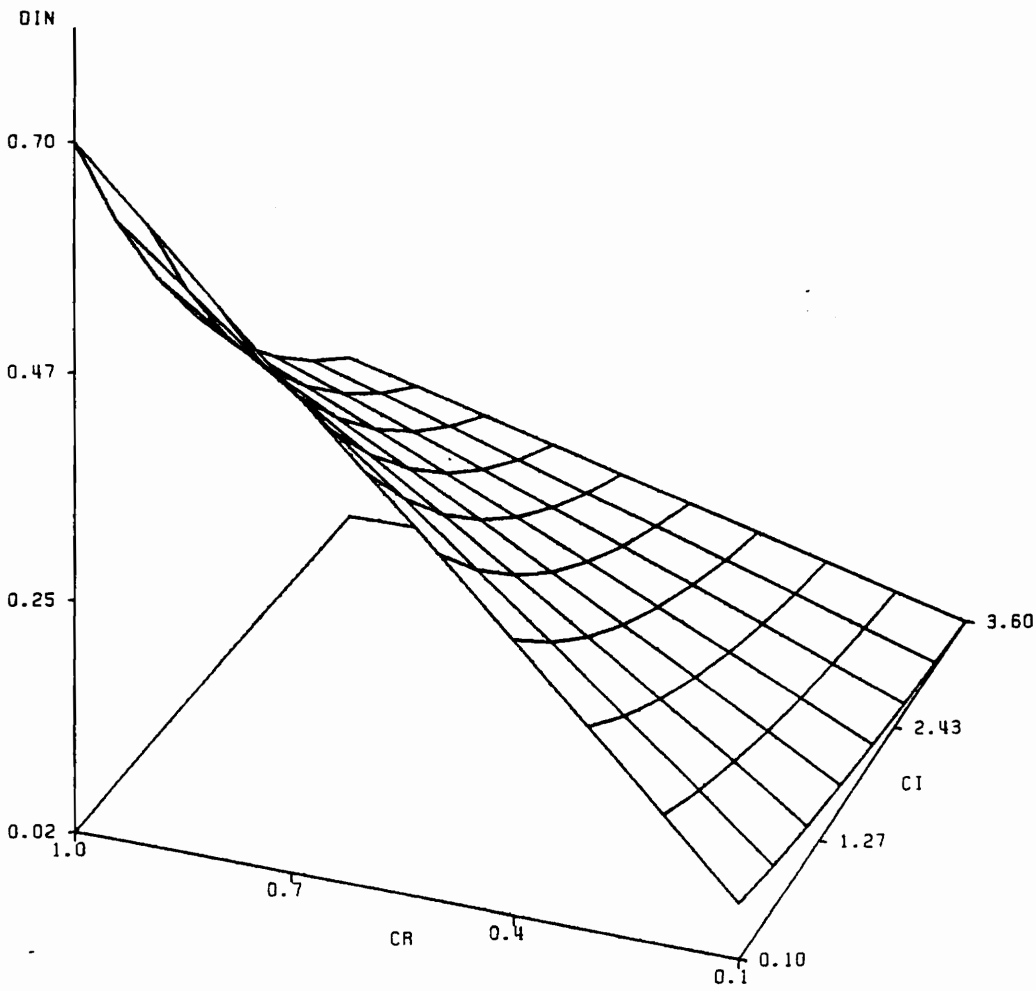

Figure 3. Relationship between diameter increment (DIN), competition index (CI), and crown ratio (CR) in the original PTAEDA2 model.

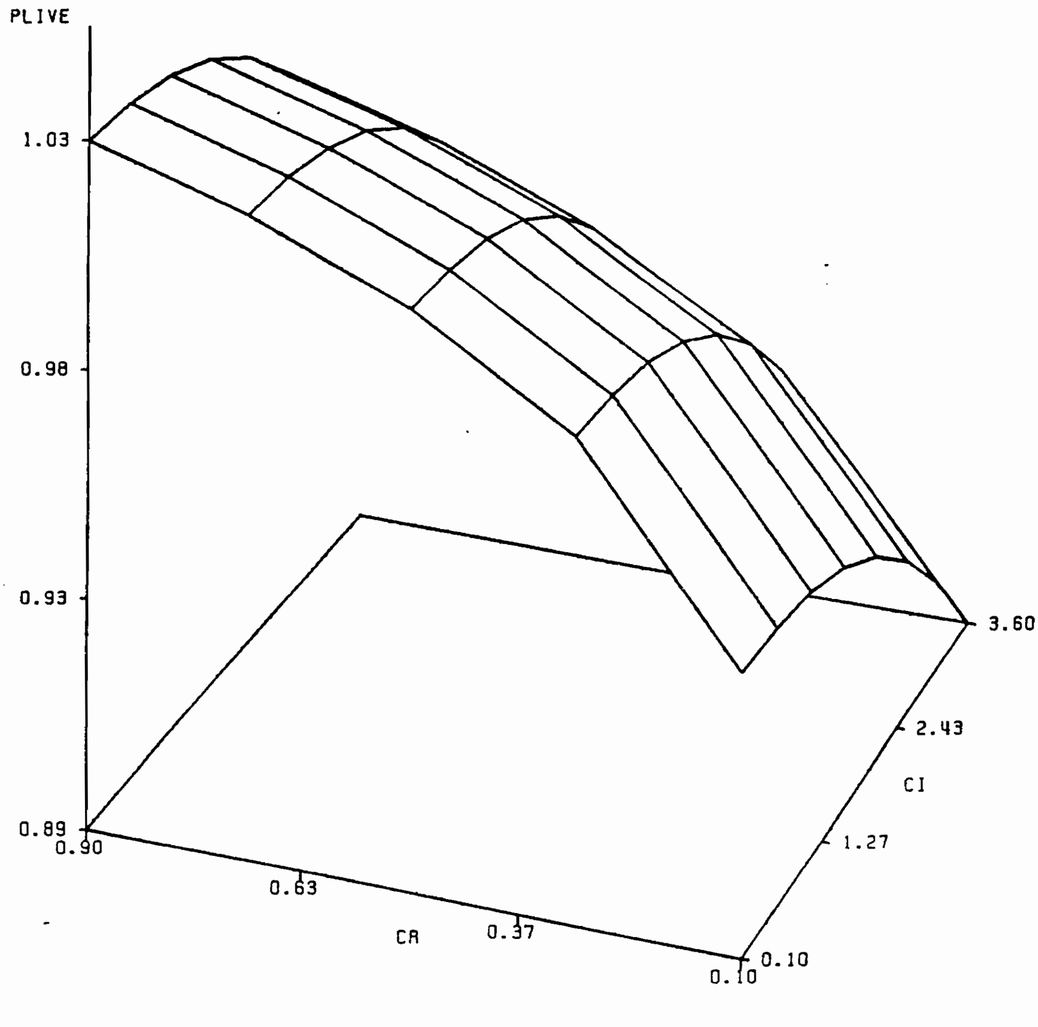

Figure 4. Relationship between the probability of survival (PLIVE), competition index (CI), and crown ratio (CR) in PTAEDA2.

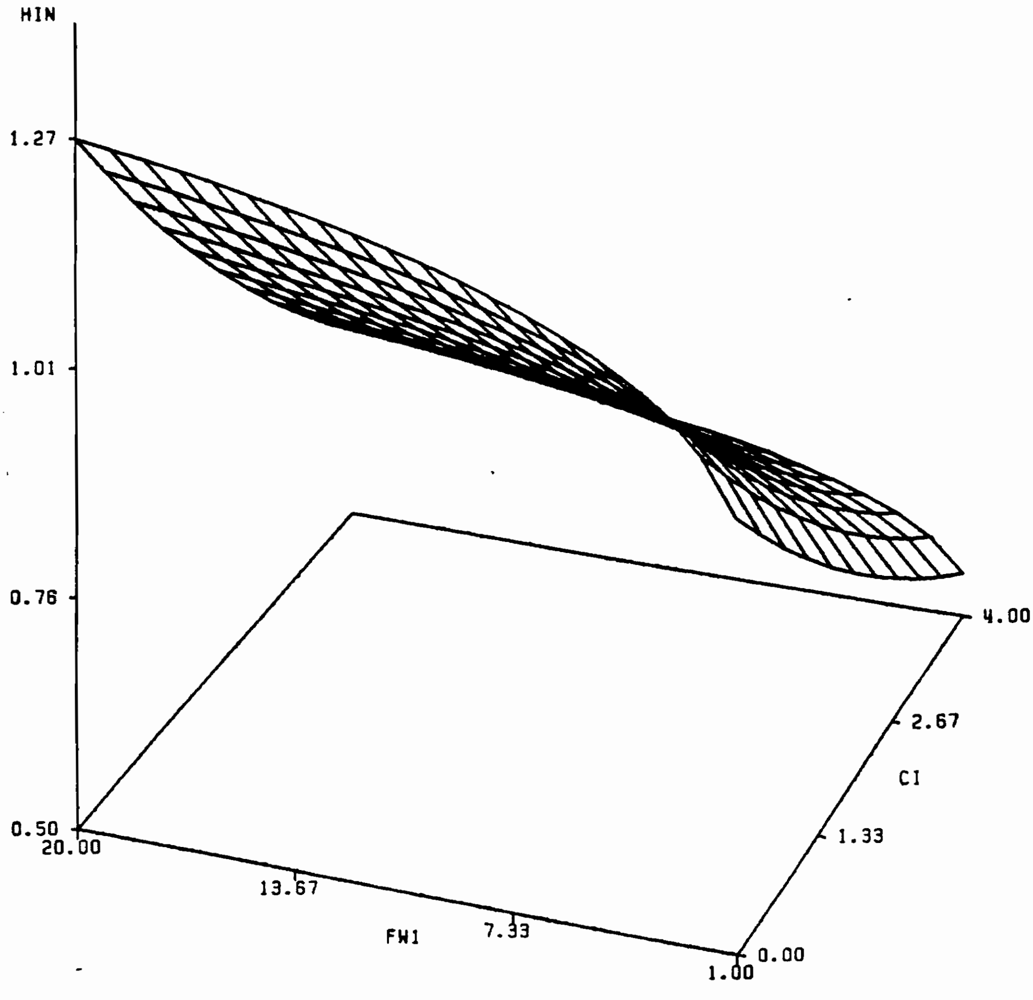

Figure 5. **Relationship between height increment (HIN), competition index (CI), and foliage weight (FW1) in the FW1 model.**

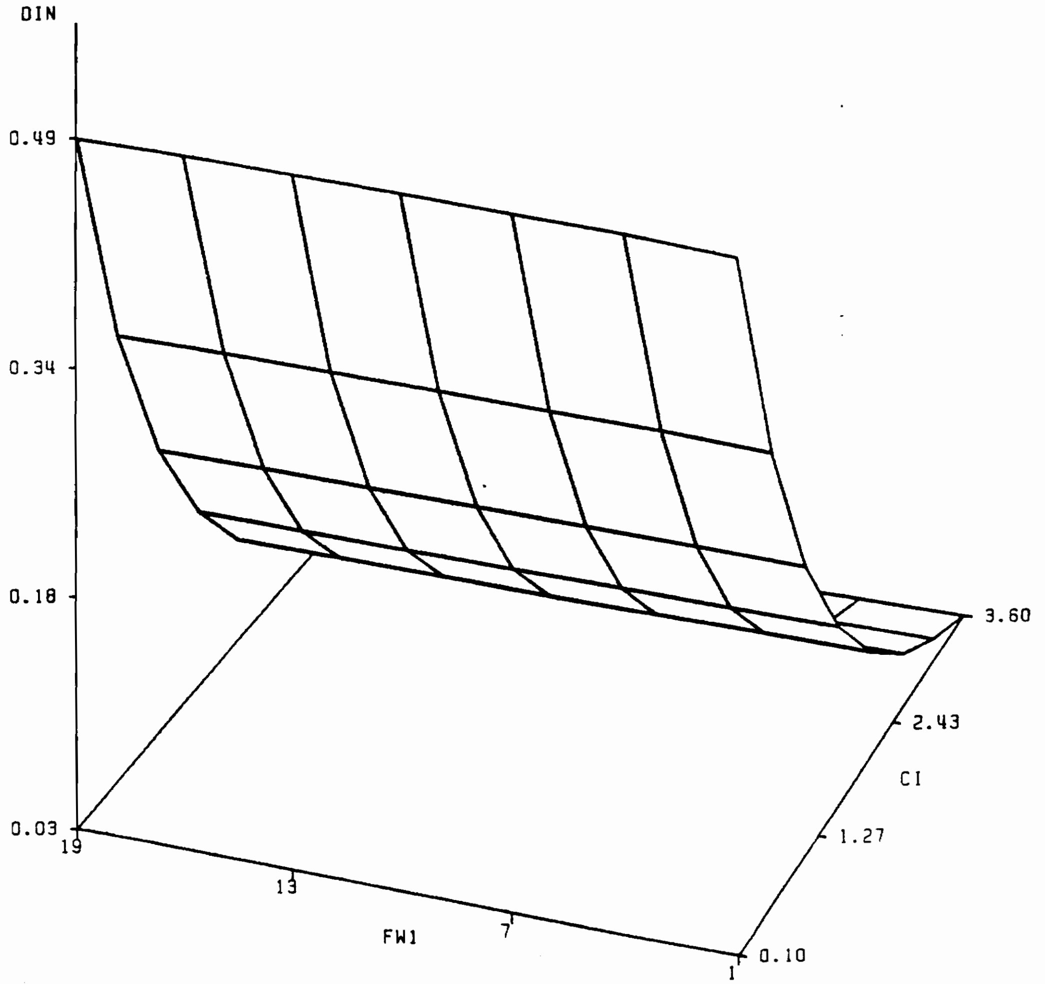

Figure 6. Relationship between diameter increment (DIN), competition index (CI), and foliage weight (FW1) in the FW1 model.

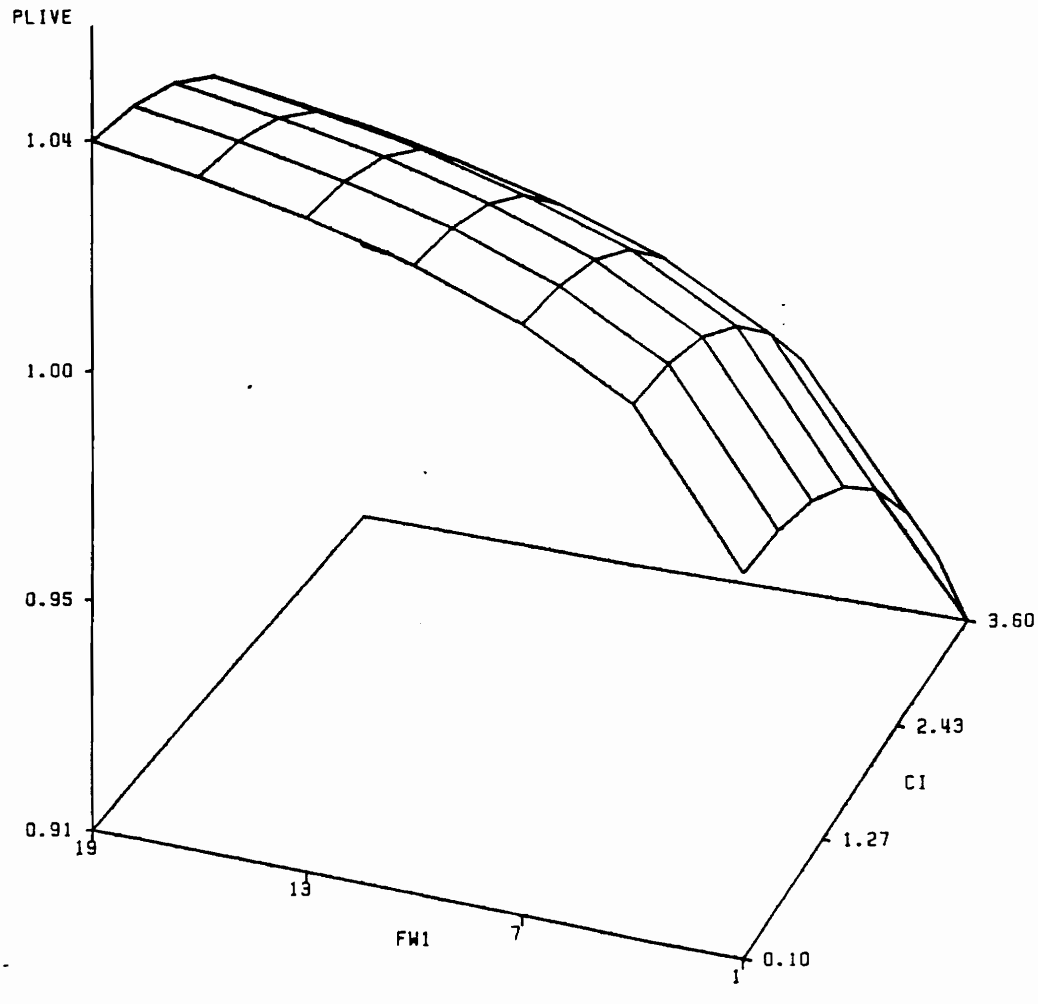

Figure 7. Relationship between the probability of survival (PLIVE), competition index (CI), and foliage weight (FW1).

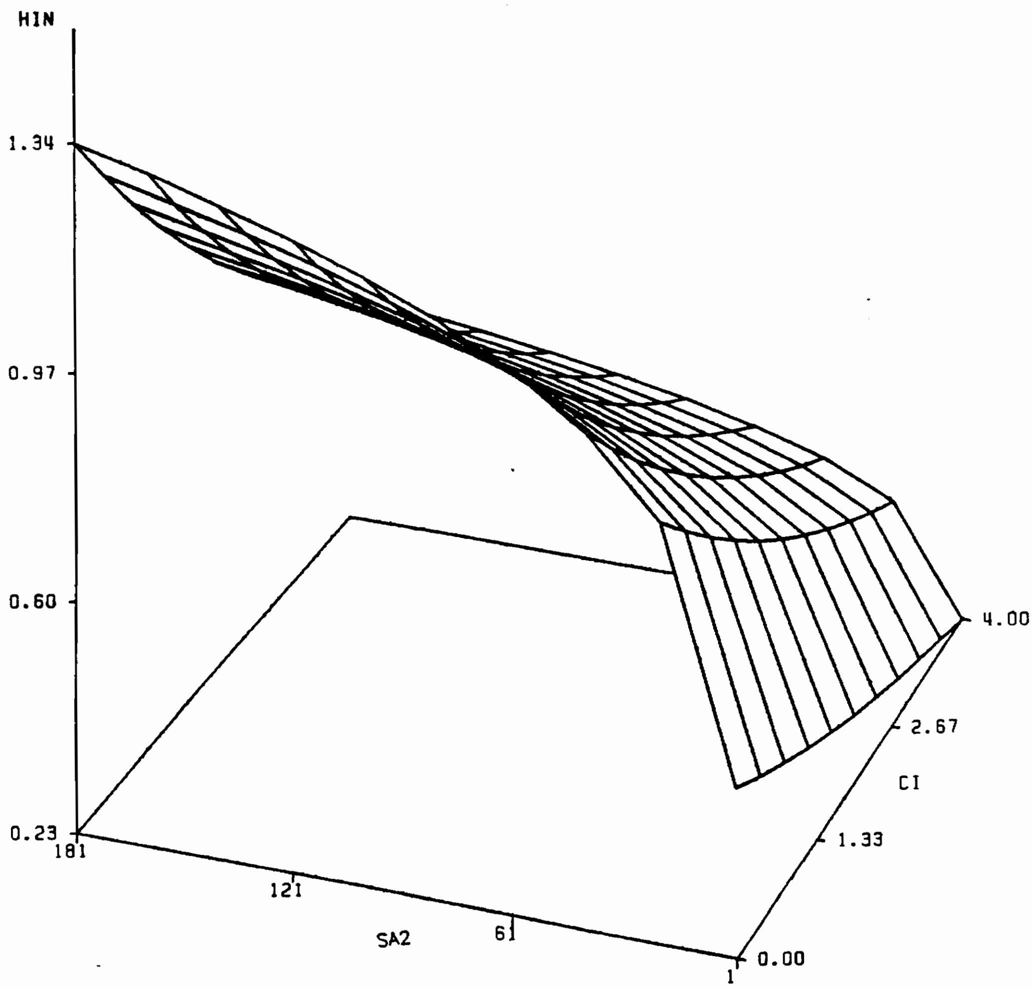

Figure 8. Relationship between height increment (HIN), competition index (CI), and surface area (SA2) in the SA2 model.

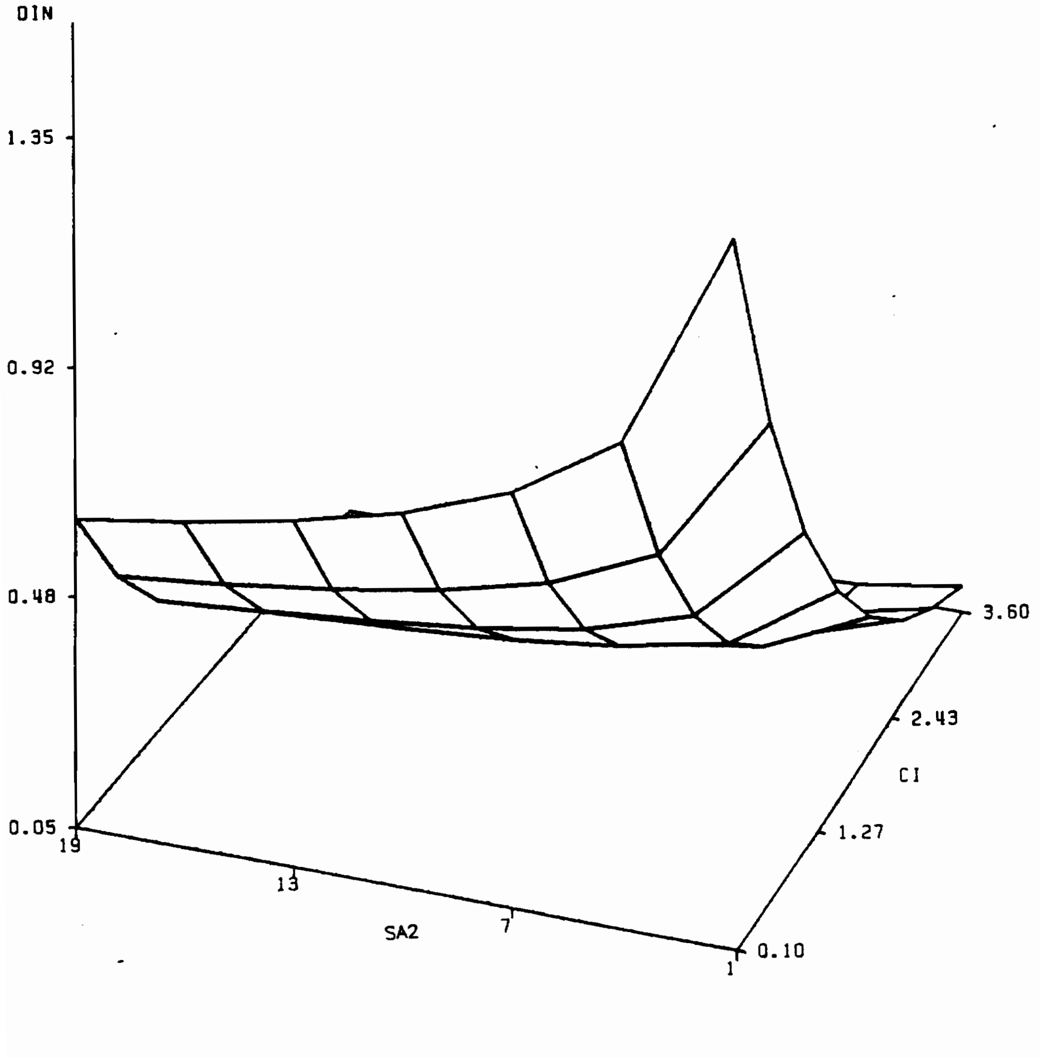

Figure 9. Relationship between diameter increment (DIN), competition index (CI), and surface area (SA2) in the SA2 model.

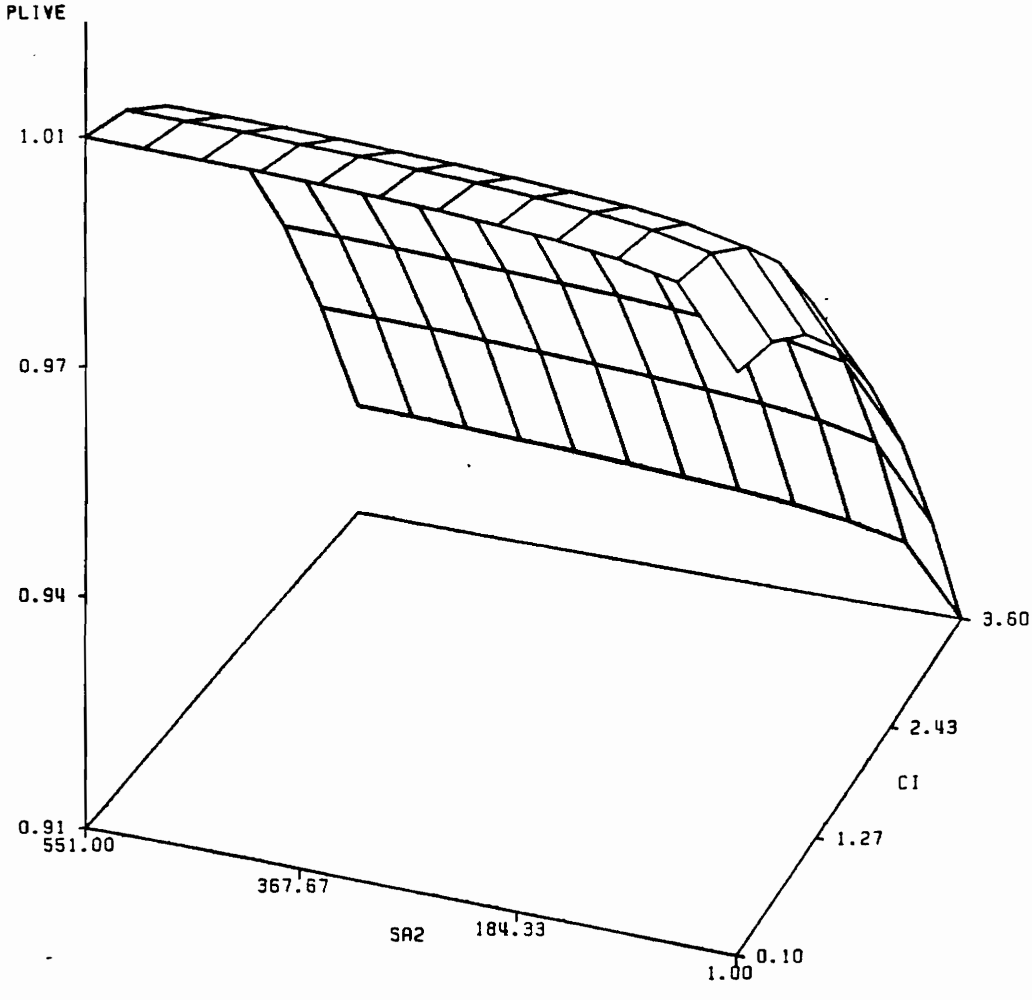

Figure 10. **Relationship between the probability of survival (PLIVE), competition index (CI), and surface area (SA2).**

Table 17. Mean residuals for the height and diameter increment (HIN, DIN) equations for the original PTAEDA2, FW1 and SA2 models.

VARIABLE	LIGHT THIN HIN	LIGHT THIN DIN	HEAVY THIN HIN	HEAVY THIN DIN
CR	-0.1728	0.0296	-0.1899	0.0664
FW1	-0.4278	0.0482	-0.4612	0.0824
SA2	-0.3208	0.0511	-0.3443	0.0868

Comparison of the FW1 and SA2 Models with the Original PTAEDA2 Model

Once the foliage weight and surface area versions of PTAEDA2 were developed, the performance of each model over time was compared to the original PTAEDA2. Projections of mean annual increment, basal area, total volume, average stand diameter and height, and mortality were compared for 50 years, across site indexes 50, 60, and 70 and for planting densities of 300, 680, and 1210 trees per acre.

Projected Mean Annual Increment, Basal Area, and Total Volume Per Acre

The foliage weight and surface area versions of PTAEDA2 generally overpredicted growth and yield estimates when compared to the original PTAEDA2 when the models were initialized with 300 and 680 trees planted per acre. The magnitude of overprediction decreased with an increase in initial planting density and with a decrease in site index. At 1210 trees planted per acre, both models initially underpredicted at early ages and overpredicted at later ages. The closest approximation to the original model occurred with the foliage weight model for 1210 trees planted per acre and site index 60.

Figures [11]-[12] compare the projection of mean annual increment (cubic-foot volume) over time for the FW1 and SA2 models to the original model at site index 60 and 1210 trees per acre planted. For both models, the culmination of mean annual increment occurred earlier for the higher site indexes, as expected. Although both models underpredicted at early ages, the models approximate the original PTAEDA2 by ages 25 and 30.

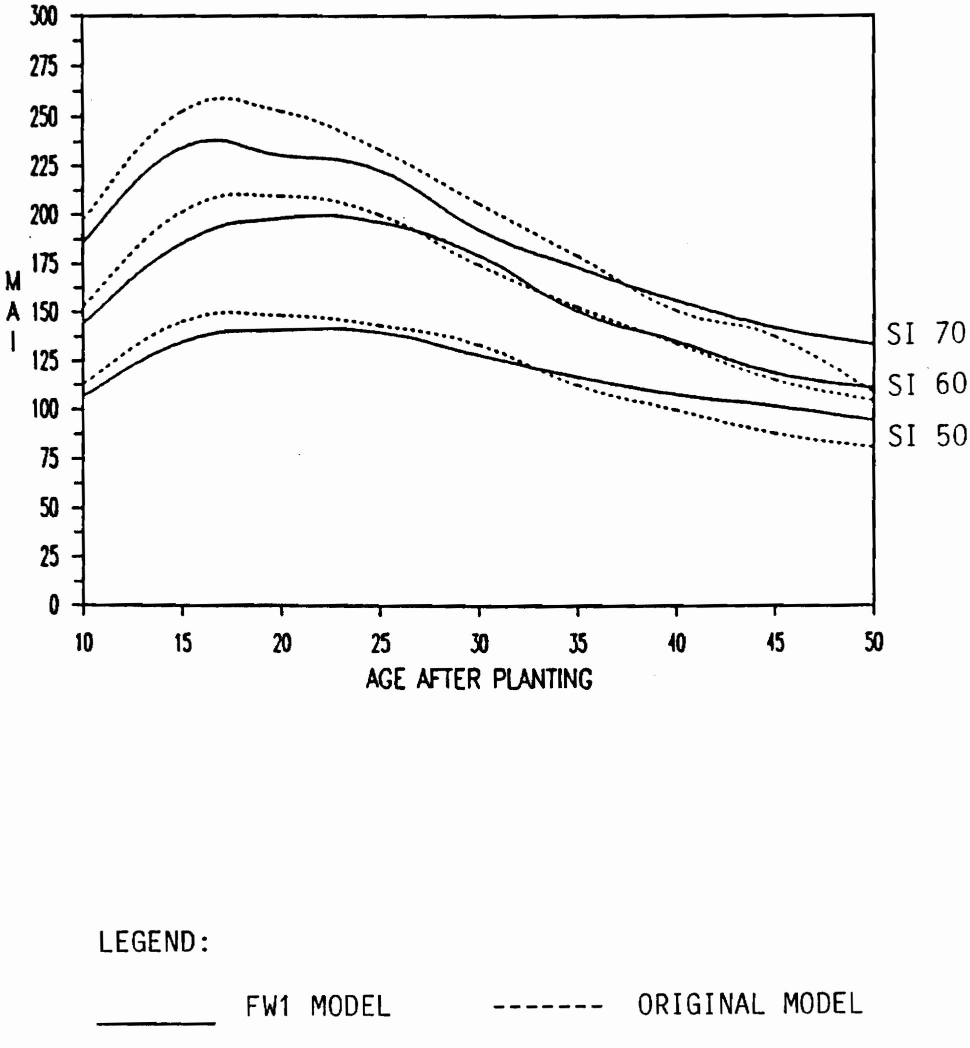

Figure 11. Projections of mean annual increment for the original and FW1 versions of PTAEDA2 at 1210 trees/acre.

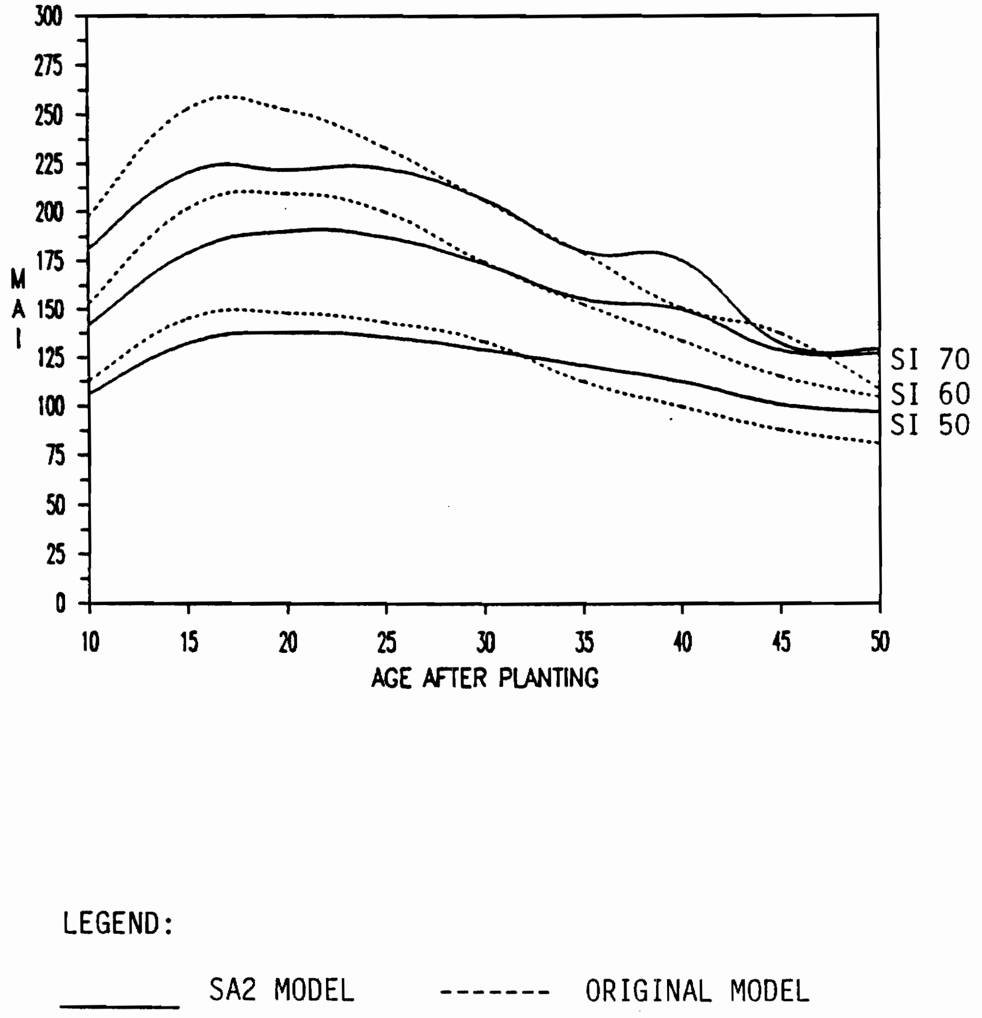

Figure 12. **Projections of mean annual increment for the original and SA2 versions of PTAEDA2 at 1210 trees/acre.**

The FW1 model, particularly at site index 60, performs better than the SA2 model. At other planting densities, both models grossly overprojected mean annual increment but the FW1 model still performed better than SA2, as shown in the Appendix. Similar conclusions can be made concerning the projection of basal area and total cubic-foot volume as seen in Figures [13]-[16] and in the Appendix.

Projection of Average Stand Diameter and Total Height

Both the FW1 and SA2 models project a larger average stand diameter at breast height, particularly after age 20, than the original PTAEDA2. The closest approximation occurred at site index 60 and 1210 trees planted per acre as shown in Figure [17]. The FW1 model projected average stand total height at all levels fairly close to the original model, whereas the SA2 model underpredicted total stand height at all levels, as presented in Figure [18] and the Appendix.

Projection of Mortality

Figure [19] portrays the mortality function in the original versus the FW1 and SA2 models at SI 60 and 1210 trees planted per acre. The PLIVE equation was the same for all three models, i.e. the probability of a tree's survival was a function of its crown ratio and competition index and the same set of coefficients was used for all three models. The mortality within the foliage weight model approximated the mortality within the original model at the higher site indexes and the greater planting densities, as shown in the Appendix. Except for SI 50 and 60 with 1210 trees planted per acre, the surface area model underestimated mortality.

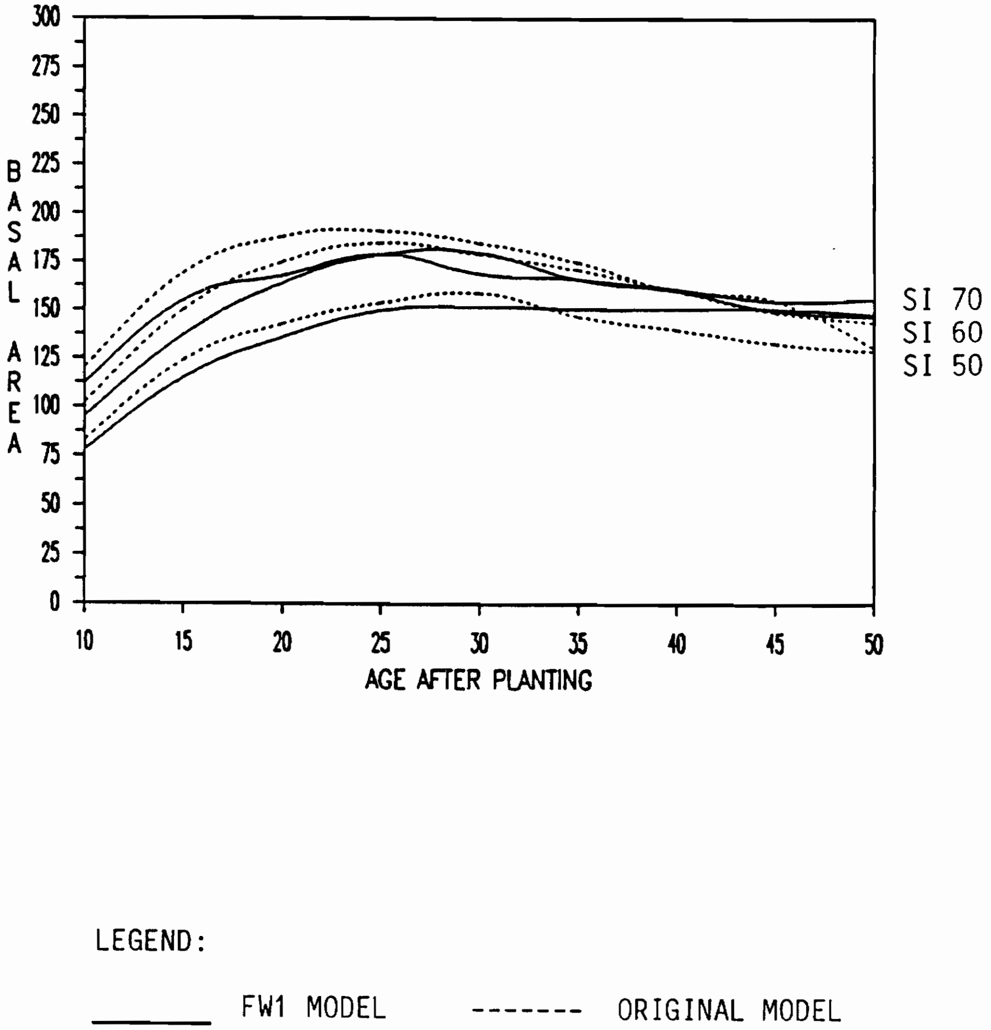

Figure 13. Projection of basal area for the original and FW1 versions of PTAEDA2 at 1210 trees planted per acre.

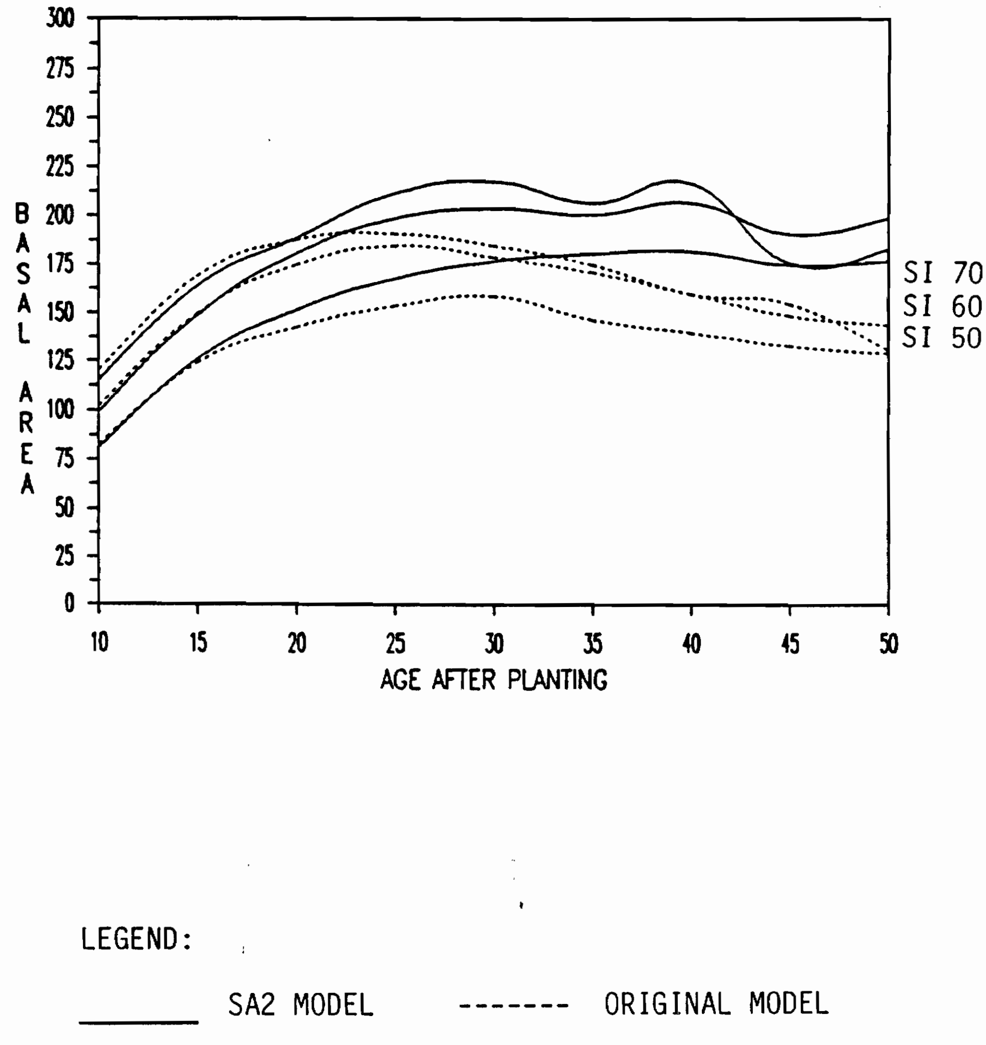

Figure 14. **Projection of basal area for the original and SA2 versions of PTAEDA2 at 1210 trees planted per acre.**

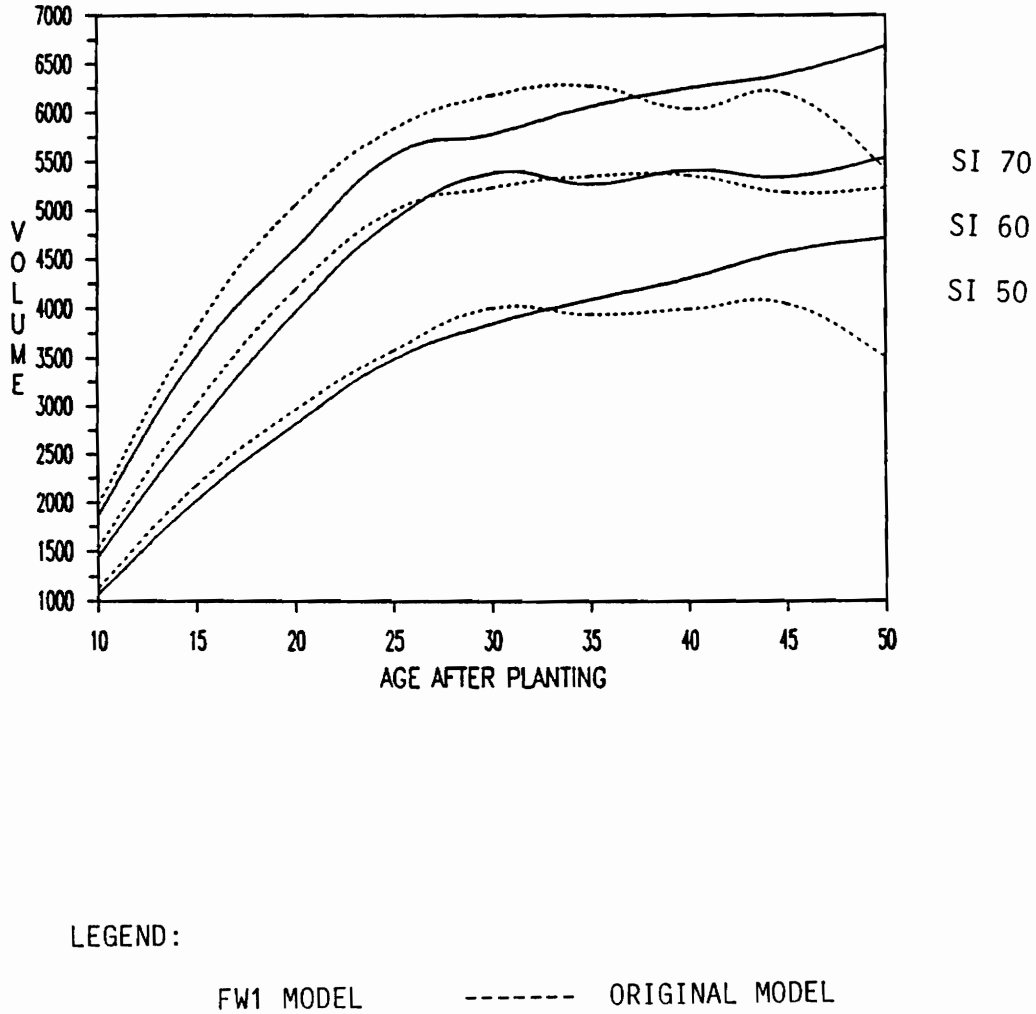

Figure 15. Projection of total volume for the original and FW1 versions of PTAEDA2 at 1210 trees planted per acre.

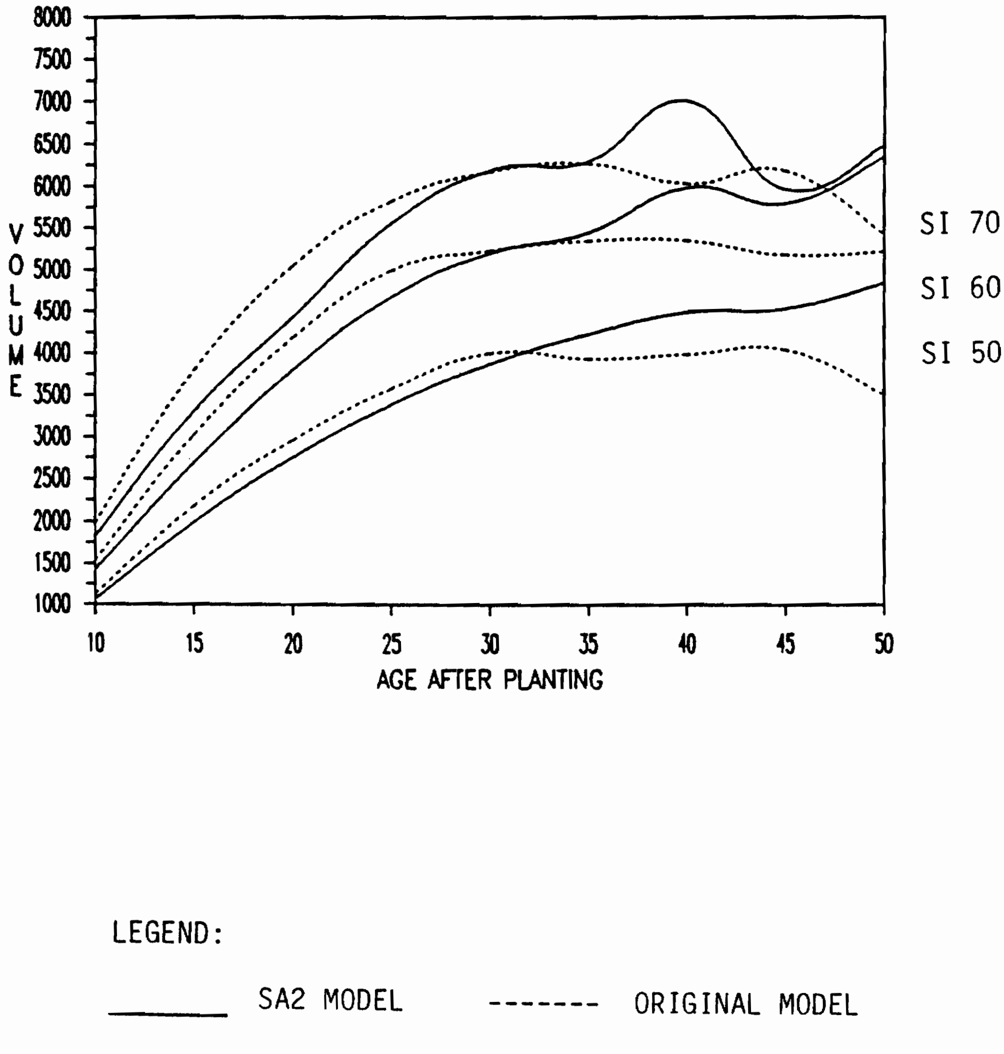

Figure 16. Projection of total volume for the original and SA2 versions of PTAEDA2 at 1210 trees planted per acre.

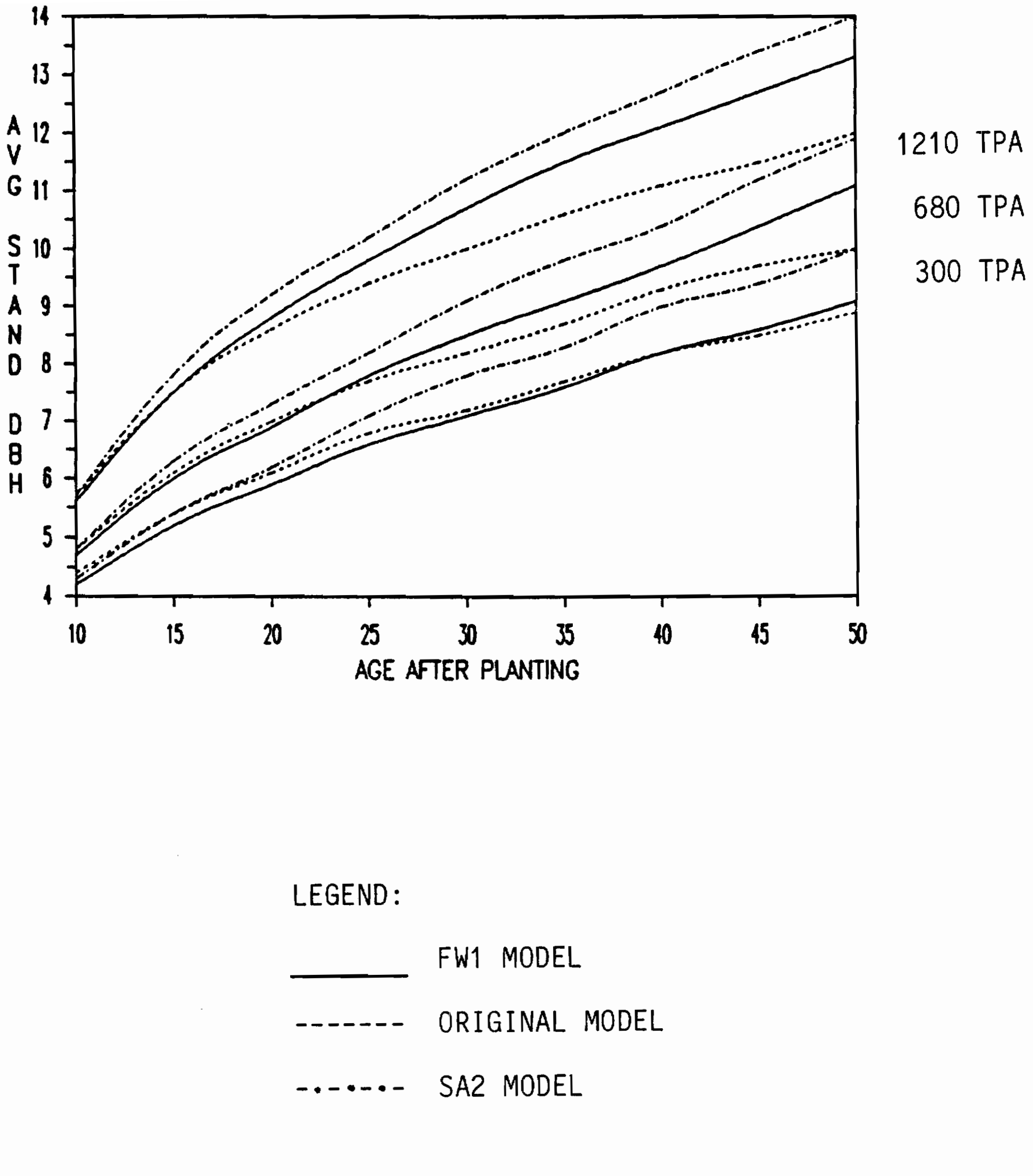

Figure 17. Projection of average stand dbh for the original, FW1, and SA2 models at SI 60 and 1210 TPA.

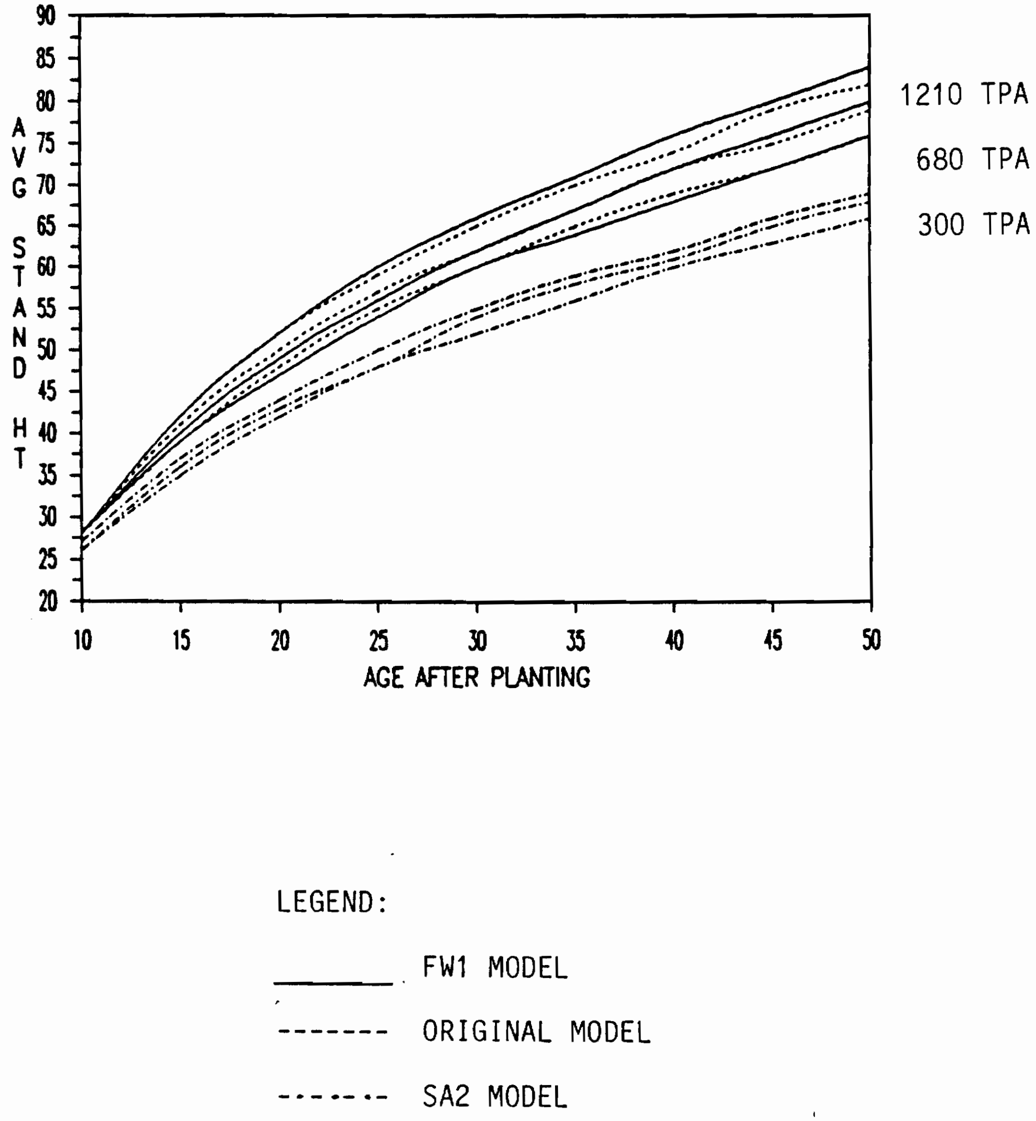

Figure 18. Projection of average stand height for the original, FW1, and SA2 models at SI 60 and 1210 TPA.

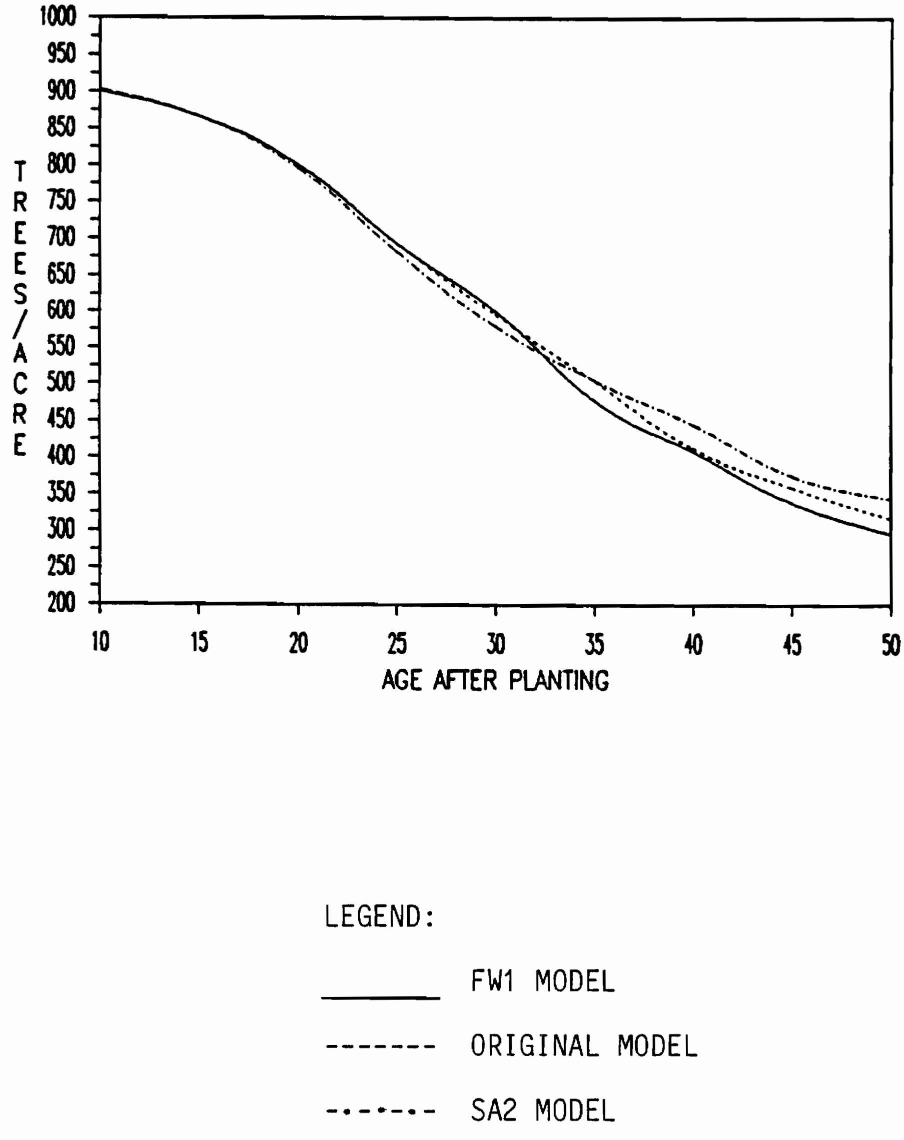

Figure 19. Projection of number of trees surviving per acre for the original, FW1, and SA2 models at SI 60 and 1210 TPA.

Simulation of Air Pollution Effects on Photosynthetic Efficiency and Needle Retention

Based on the comparison of the FW1 and SA2 models to the original PTAEDA2 model, it was decided that the FW1 version provided a better model that the SA2 version and approximated the original model growth relationships most closely at site index 60 and 1210 trees planted per acre. Thus, the simulations of air pollution stress were performed using the FW1 model at site index 60 and 1210 trees planted per acre. Assuming that air pollution stress could result in reductions in photosynthetic efficiency and average needle retention, these reductions applied to the photosynthetic efficiency and needle retention weighting factors were designed to reflect literature studies and Tate's (1987) research. Tate used six scenarios which included a reduction in photosynthetic efficiency by 0%, 7.5% and 15% and average needle retention reduction by 0 and 1 year. The needle retention reduction was distributed evenly over each age class of needles. Thus, the scenarios defined in Table [4], as previously shown, were simulated. Scenario 1 represents a baseline scenario (no impacts from air pollution). Scenarios 1 and 2 represent no decrease in photosynthetic efficiency, Scenarios 3 and 4 represent a 7.5% decrease in photosynthetic efficiency and Scenarios 5 and 6 a 15% decrease. Scenarios 1, 3, and 5 represent no decrease in needle retention while Scenarios 2, 4, and 6 represent a one year reduction in needle retention. The results of each scenario included an examination of projected basal area and total volume, average stand diameter and total height, diameter distribution at age 40, and mortality over a 40 year rotation.

Effects on Total Volume and Basal Area

Table [18] shows the percent volume change over time for each impacted scenario as compared to the baseline scenario. The only scenario that showed a sizeable decrease in volume was scenario 6 (a 15% decrease in photosynthetic efficiency and a one year reduction in needle retention). For that scenario, the greatest percent change in volume reduction was 12% at age 30, but by the end of the rotation, there was only a 6% loss in volume. It appeared that a reduction in the needle retention resulted in a greater loss of volume that did a decrease in photosynthetic efficiency.

Figure [20] shows the projected basal area per acre over time for each scenario. Scenarios 1, 3, and 5 (those with no needle retention impacts) initially carried more basal area at earlier ages than scenarios 2, 4, and 6 (those with needle retention impacts). However, after age 35, the scenarios with a one year needle reduction carried more basal area than the baseline scenario. The most severe stress, in scenario 6, showed a substantial decrease in basal area until age 40, where the stand appeared to recover and approximate the basal area of the baseline stand.

Effects on Average Stand Diameter and Total Height, Diameter Distribution, and Mortality

The projections of the average stand diameter and total height for all scenarios are portrayed in Figures [21]-[22]. There were no sizeable differences in average diameter or height between the impacted scenarios and the baseline scenario. Figure [23] presents the diameter distribution at age 40 for all scenarios. Scenarios 1, 3, and 5 (no needle retention impacts) have about the same distribution but scenarios 2, 4, and 6 (needle

Table 18. Percent changes in total cubic-foot volume/acre for impacted scenarios 2-6, using the FW1 model at SI 60, 1210 TPA.

SCENARIO	AGE AFTER PLANTING 10	15	20	25	30	35	40
2[a]	-2.2	-4.6	-5.5	-6.0	-7.5	-0.1	+2.6
3[b]	-0.3	-0.6	-0.6	-0.7	-0.7	-0.7	-0.8
4[c]	-2.5	-5.1	-6.1	-6.7	-8.1	-0.8	-0.4
5[d]	-0.5	-1.1	-1.3	-1.4	-1.5	-1.5	-1.5
6[e]	-2.8	-5.6	-6.5	-7.4	-12.2	-9.5	-5.6

a: 0% decrease in photosynthetic efficiency, 1 year decrease needle retention.
b: 7.5% decrease in photosynthetic efficiency, 0 year decrease needle retention.
c: 7.5% decrease in photosynthetic efficiency, 1 year decrease needle retention.
d: 15% decrease in photosynthetic efficiency, 0 year decrease needle retention.
e: 15% decrease in photosynthetic efficiency, 1 year decrease needle retention.

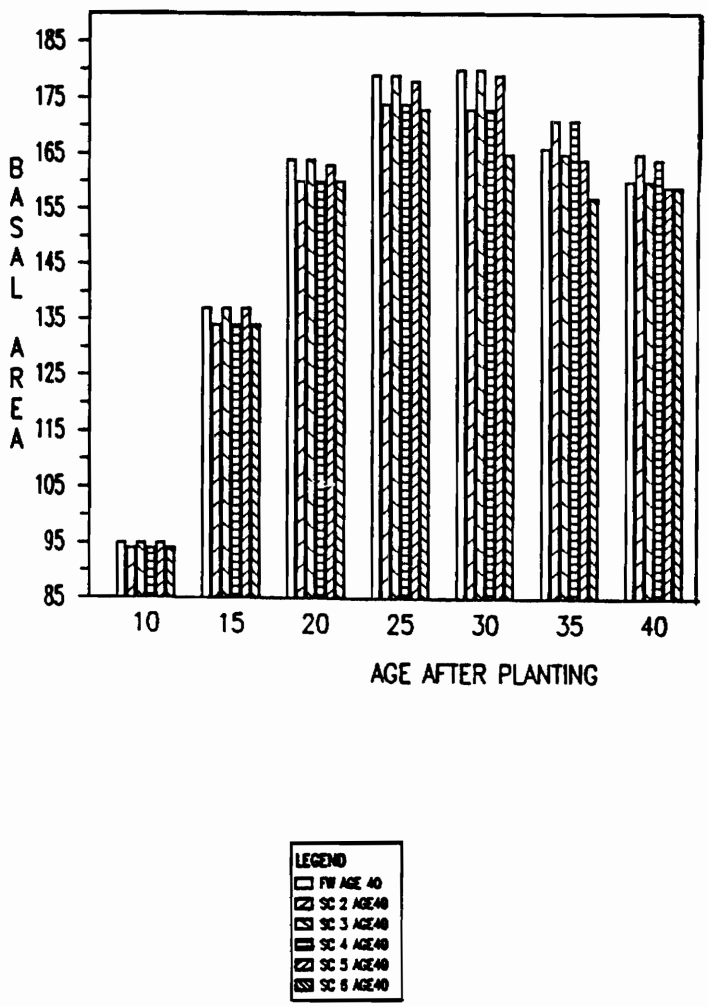

Figure 20. Projection of basal area for each air pollution scenario at SI 60 and 1210 TPA.

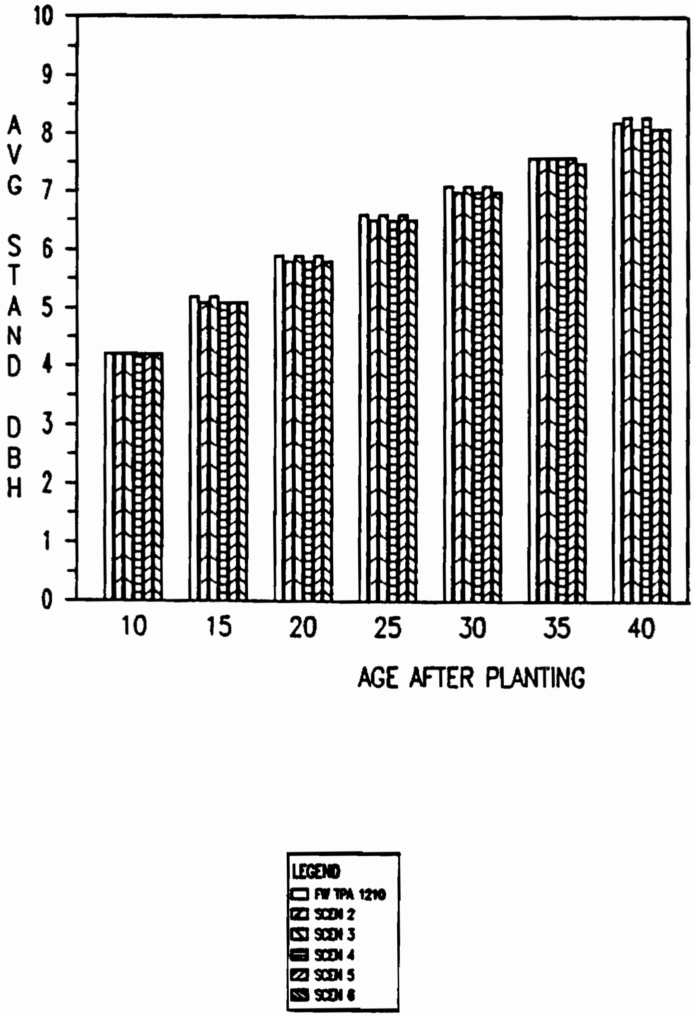

Figure 21. Projection of average stand diameter for all scenarios, using the FW1 model at SI 60 and 1210 TPA.

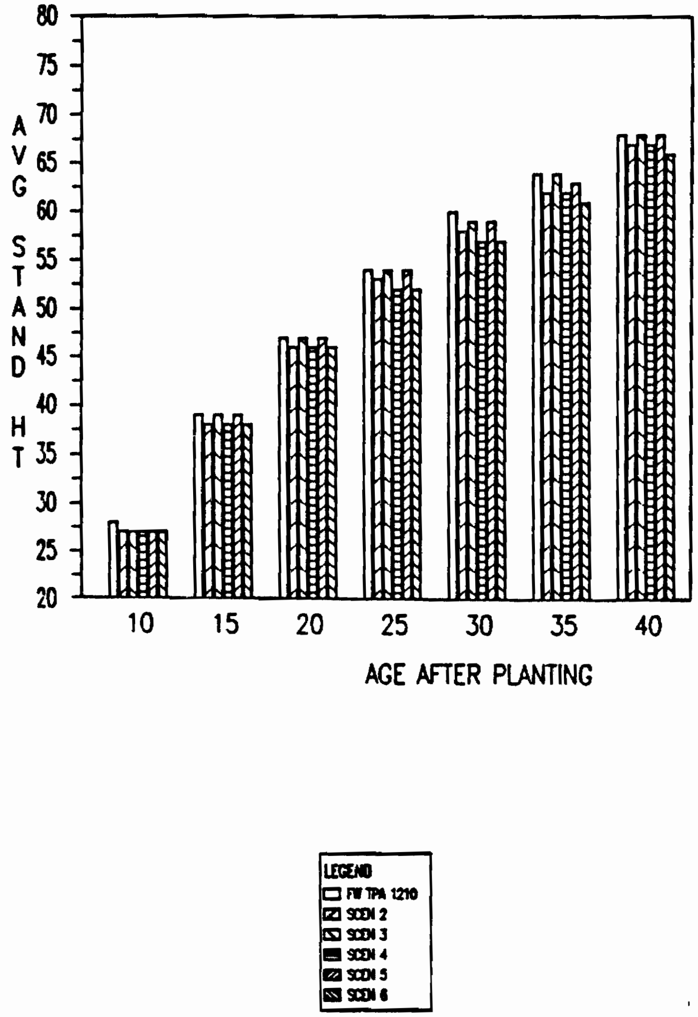

Figure 22. Projection of average stand total height for all scenarios, using the FW1 model at SI 60 and 1210 TPA.

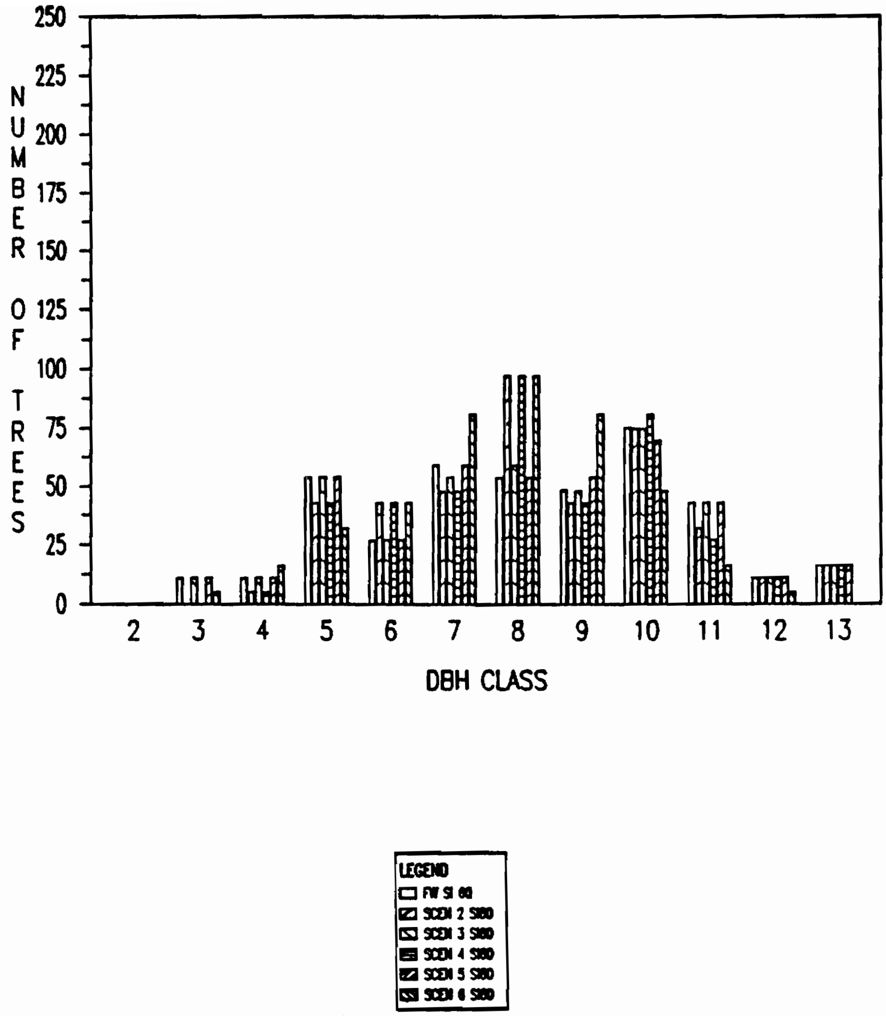

Figure 23. Projections of diameter distributions at age 40 for all scenarios, using the FW1 model at SI 60 and 1210 TPA.

retention impacts) show more variability. The most severely stressed scenario (6) resulted in a greater number of trees in the mid-range diameter classes and very few in the larger diameter classes when compared to the baseline scenario. Figure [24] presents the trend in mortality over time for all scenarios. There is little difference in the number of trees surviving per acre across the scenarios, even for the most severely stressed scenario.

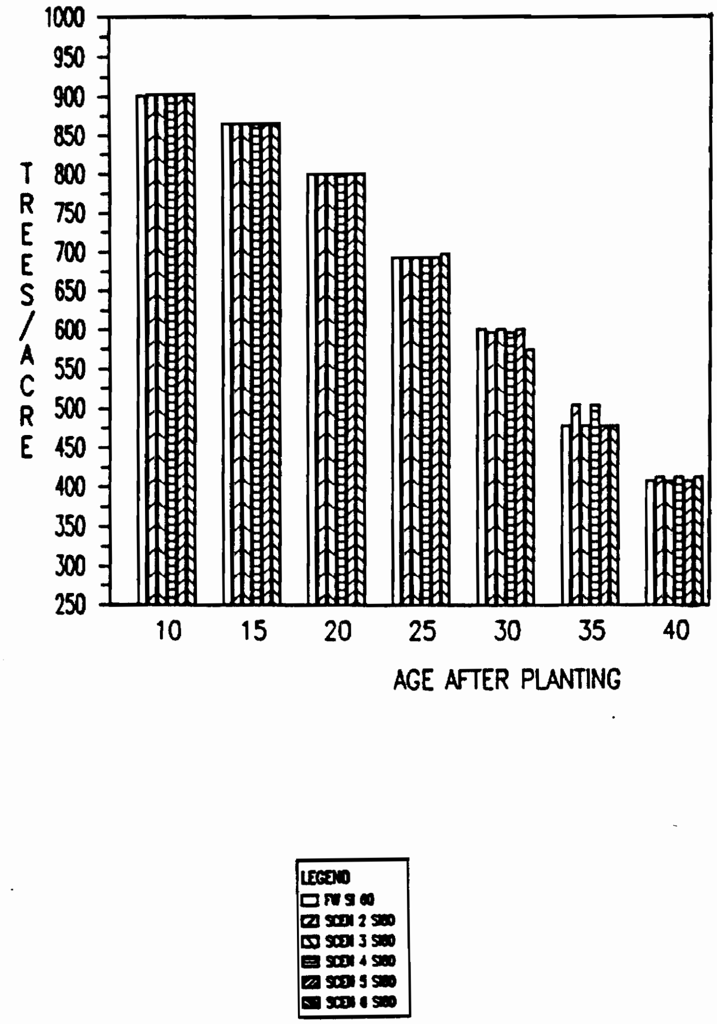

Figure 24. Projections of mortality for all scenarios, using the FW1 model at SI 60 and 1210 TPA.

Chapter V

SUMMARY AND CONCLUSIONS

Some research studies have revealed that seedlings exposed to air pollution experienced decreases in diameter and height growth, reductions in photosynthesis, and/or losses of older age classes of needles. This study investigated two methods for incorporating these possible effects of air pollution into an existing growth and yield model for loblolly pine. Due to a lack of understanding how seedling responses can be translated into mature tree responses, several assumptions were made in developing these methods. Efforts were made to identify areas in the model where improvements can be made, such as further data collection or the refinement of the relationships between crown development and growth. Therefore, this study was not intended for providing quantitative answers as to the effects of air pollution on stand-level growth, but rather for suggesting biological process-oriented hypotheses for developing a statistically sound empirical growth and yield model framework.

Limitations of Method I

In the first method, a sensitivity approach was used to apply varying levels of reductions in height and diameter increments for varying percentages of trees across a wide range of site indexes and initial planting densities. This method assumed that a certain percentage of the trees were impacted while the others continued to be totally unaffected. The result could be interpreted as air pollution causing a thinning effect on the stand. However, placing the stress continually on some trees and not on others, reflects some studies showing different pollution sensitivity levels among families of loblolly pine (Kress, 1978). This was a crude attempt to see at what level would sizeable losses in stand productivity occur, given that air pollution stress would result in such annual losses in growth. One major limitation in this approach is that even though no sizeable losses in stand volume were observed until half of the trees were impacted with a 32% or greater reduction in growth, it is still unknown what level of air pollution this represents. There is still no means for simulating ambient levels of pollution since there are no quantified relationships between diameter and height growth reductions and the level of pollution. However, this method did provide insight into over-all stand-level relationships. If reductions in diameter and height increment do occur, the loss in volume by the end of rotation may not be substantial but the shift in volume to smaller diameter classes may be of concern to those more interested in the sawtimber market.

Limitations of Method II

In the second method, efforts focused on developing a crown variable to drive growth within the model that could be more easily modified by changes in photosynthesis and needle retention than the original crown ratio variable. Although foliage weight and surface area of an individual tree were not measured variables in the data for the development of the original model, their estimated values performed fairly well in predicting diameter and height increments at some site indexes and planting densities. Foliar surface area did not perform as well as foliage weight, but improvements may be observed with better data.

Assuming that the effects of air pollution can be represented as a decrease in photosynthesis and needle retention rates, there were no substantial losses in over-all stand growth and yield. One major limitation in this method involved the determination of appropriate photosynthetic efficiency and needle retention weighting factors by needle age class to apply to the foliage weight estimates. These factors were indirectly derived from data presented in a study using only ten sample trees. These factors then were used to develop a weighted foliage weight estimate from which new diameter and height increment equations were derived. Any errors associated with these factors may have substantially affected the performance of foliage weight and surface area as predictor variables. To further evaluate subjective changes in these weighting factors to simulate the effects of air pollution stress may be only compounding the errors associated with these unknown biological parameters.

Another limitation with the modified models was the use of the original equation calculating the probability of a tree's survival, based on its crown ratio and competition index. If pollution does increase the rate of abcission of older needles, the effect may be a thinning of the crown from the inside out. A stressed crown may have the same crown ratio as a healthy crown, but just more sparse. Thus, in this model, a tree's photosynthetic potential based on crown ratio may not be adequately determining a tree's potential for survival. Similarly, within the models, the effects of a stressed crown show up indirectly as a decrease in diameter increment. Since a tree's competition index is based on the ratio of diameters of neighboring trees and their distances from the individual tree, a stressed tree's loss in competitive advantage may not be accurately represented. A competition index based on crown surface area exposed to sunlight (Hatch et al., 1975) may offer a better measure of a tree's vigor when air pollution is simulated as causing changes in the crown structure.

Future Modeling Considerations

This study was intended to be an initial attempt to identify areas within an existing growth and yield model framework that could be modified, or expanded upon, to study the potential effects of air pollution stress. A simplified approach was taken concerning both the nature of that stress and the growth of an individual tree. In this study, a level of pollution was never explicitly expressed as x ppm, but rather with a qualitative connotation of "slight" (7.5% decrease in photosynthetic efficiency) or "severe" (15%). "Ambient" level of air pollution can change daily and even hourly, depending on such environmental influences as wind, air temperature, and the presence of an inversion layer. Therefore, pollution levels reported in the literature can be hourly averages, daily averages, or peak values. Research has shown that the length of exposure at a certain level can have different effects on seedlings. Seedlings exposed to short-term, high levels of pollution tend to recover more than those exposed to long-term, low levels concentrations (Kress, 1978; Reich and Admunson, 1985). This creates a problem in trying to simulate exposure to air pollution on a yearly time step on which most growth and yield models operate. Similarly, this study expressed foliage weight and surface area, as well as photosynthesis and needle retention rates, as yearly averages. These values also change more frequently. A tree exposed to air pollution when dormant may not be as affected as one exposed early in the growing season. All of the above considerations suggest the need for of using a finer time step for simulations of some processes. It may be necessary to use more physiologically-oriented models for hourly, daily, or monthly time steps and then aggregate estimates for input into a growth and yield model.

The scope of this study was limited to the potential effects of air pollution to foliar-related responses. However, research has suggested that there are changes in carbon-allocation patterns in trees stressed by air pollution and that pollution may affect the root growth of impacted trees (McLaughlin, 1982). Further modeling attempts should address these considerations, perhaps in a manner similar to Bossell's (1986) approach, which attempted to model the carbon-allocation for diameter, height, and root growth.

One assumption made in this study was the homogeneous effect on the trees selected for pollution impact. The amount of pollution absorbed by an individual tree may be affected by environmental factors, stomatal conductances, and the position in the crown. Environmental factors, such as wind or air temperature, above the stand canopy can be different from within the canopy. Photosynthesis and needle retention rates also vary by position in an individual crown. Knowledge of crown architecture may help determine a better estimate of photosynthetic potential, such as foliage weight, if the new needles (sun leaves) in the upper crown can be weighted more that the older needles (shade leaves) in the lower crown. To address these considerations in future modeling efforts, thought must be given to the level of detail possible in a growth and yield model, the known parameterization of biological values, and the temporal resolution necessary.

Recommendations for Further Research

Current empirical growth and yield models do not have the growth relationships defined in sufficient detail to model the complexities of air pollutants and their potential effects on tree growth to enable many hypotheses of interest. Conversely, at present, process-oriented models do not have the statistical rigor of growth and yield models to allow for quantitative conclusions. However, to adequately address the potential effects of air pollution stress on stand-level growth, the long-term projection of growth for an individual tree as it is affected by neighboring trees is necessary. A compromise between an empirical growth and yield model and a process-oriented model is needed.

Since most mensurational data involve simple above-ground variables, modeling efforts should initially focus on developing stronger relationships between foliar productivity and growth. This may entail measuring foliage weight or surface area in future data collection efforts for the PTAEDA2 model, as well as estimates of photosynthesis and needle retention rates. If foliage weight or surface area prediction equations could be developed from this data, and diameter and height growth could be predicted from these estimates, the methodology in Method II could be used. Data collected from various positions in the crown may enable the calculation of a better measure of an individual tree's photosynthetic potential for growth. Development of a competition index and mortality function should also be based on this measure of growth potential. Additional knowledge of carbon-allocation patterns and root impacts may lend insight into how this photosynthetic potential is distributed for diameter and height growth.

Modeling efforts should be directed to the possibility of using process-oriented models with finer time steps for determining effects on photosynthesis by air pollution. Then these outputs could be aggregated into a larger time estimate for input into PTAEDA2.

In conclusion, a concerted research effort will be required to quantify the possible effects of air pollution on the growth of forest stands. The observed responses in studies of seedlings and trees subjected to air pollution are often contradictory. The interaction of complex biological processes with environmental influences must be better understood to effectively model air pollution stress on tree growth. However, the development of a hybrid growth and yield model and a process model may provide insight for possible hypotheses for the effects of stress, be it air pollution or other factors, on individual tree growth and over-all stand productivity.

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Appendix

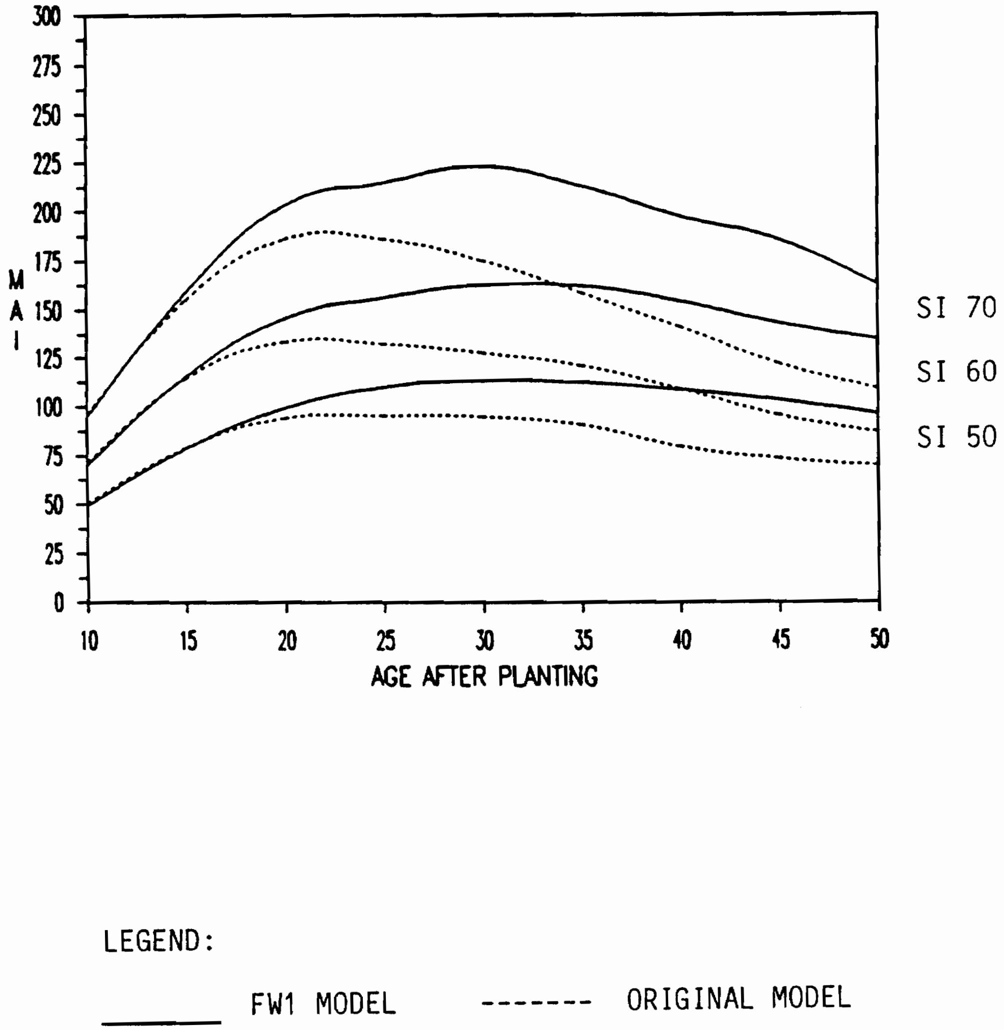


Figure 25. Projection of mean annual increment for the FW1 and original version of PTAEDA2 for 300 trees/acre.

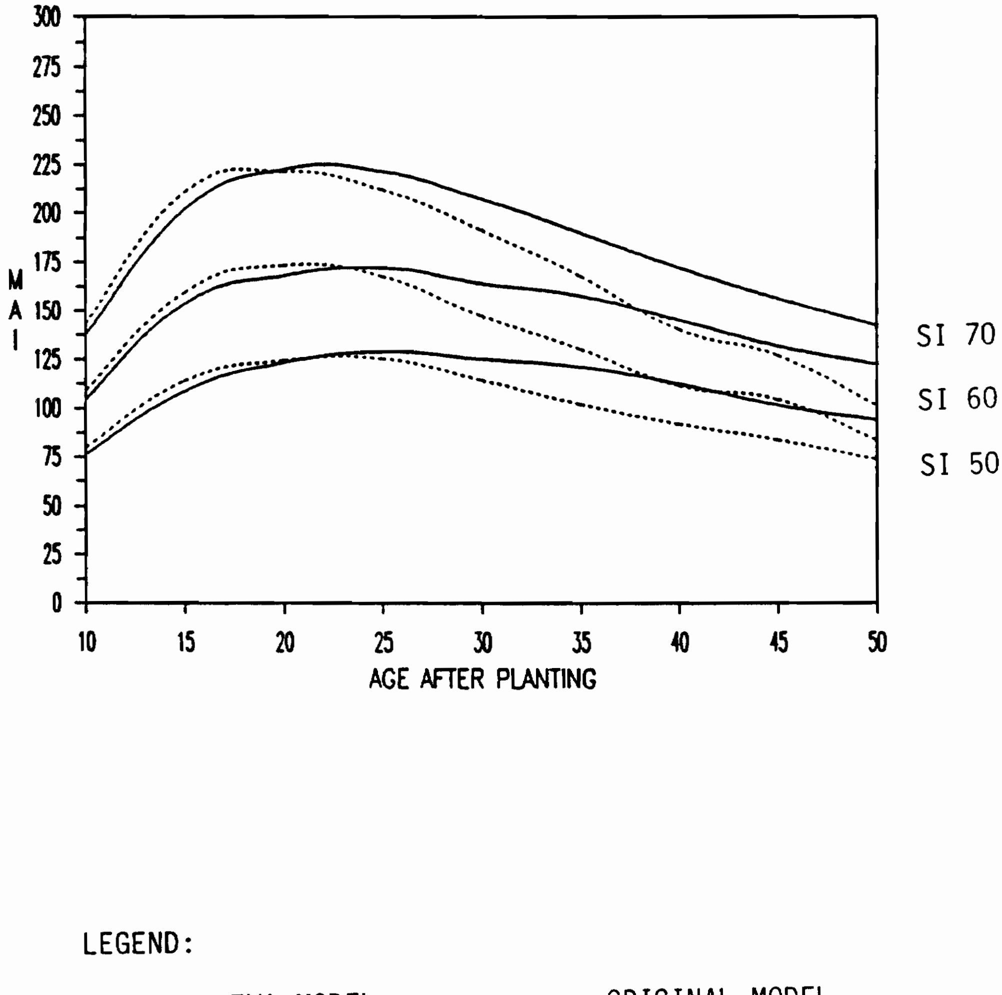


Figure 26. Projection of mean annual increment for the FW1 and original version of PTAEDA2 for 680 trees/acre.

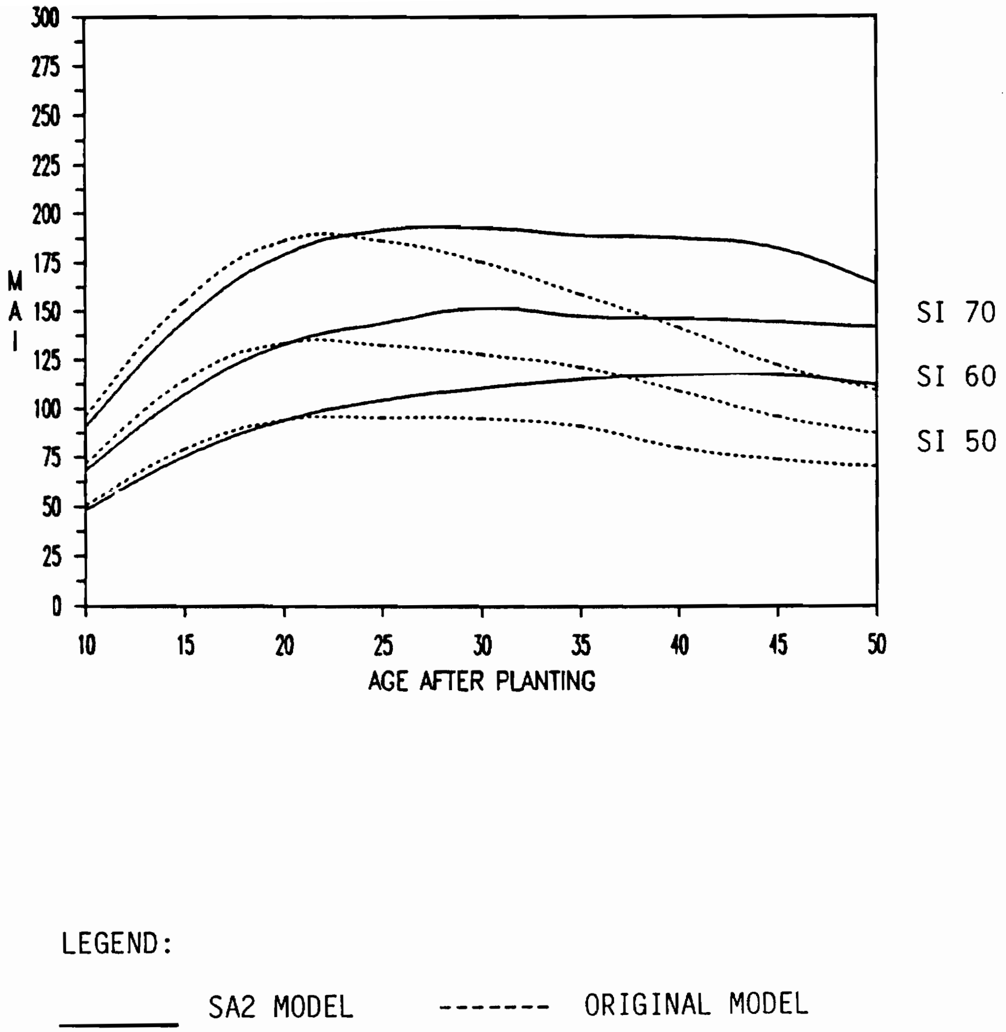


Figure 27. Projection of mean annual increment for the SA2 and original version of PTAEDA2 for 300 trees/acre.

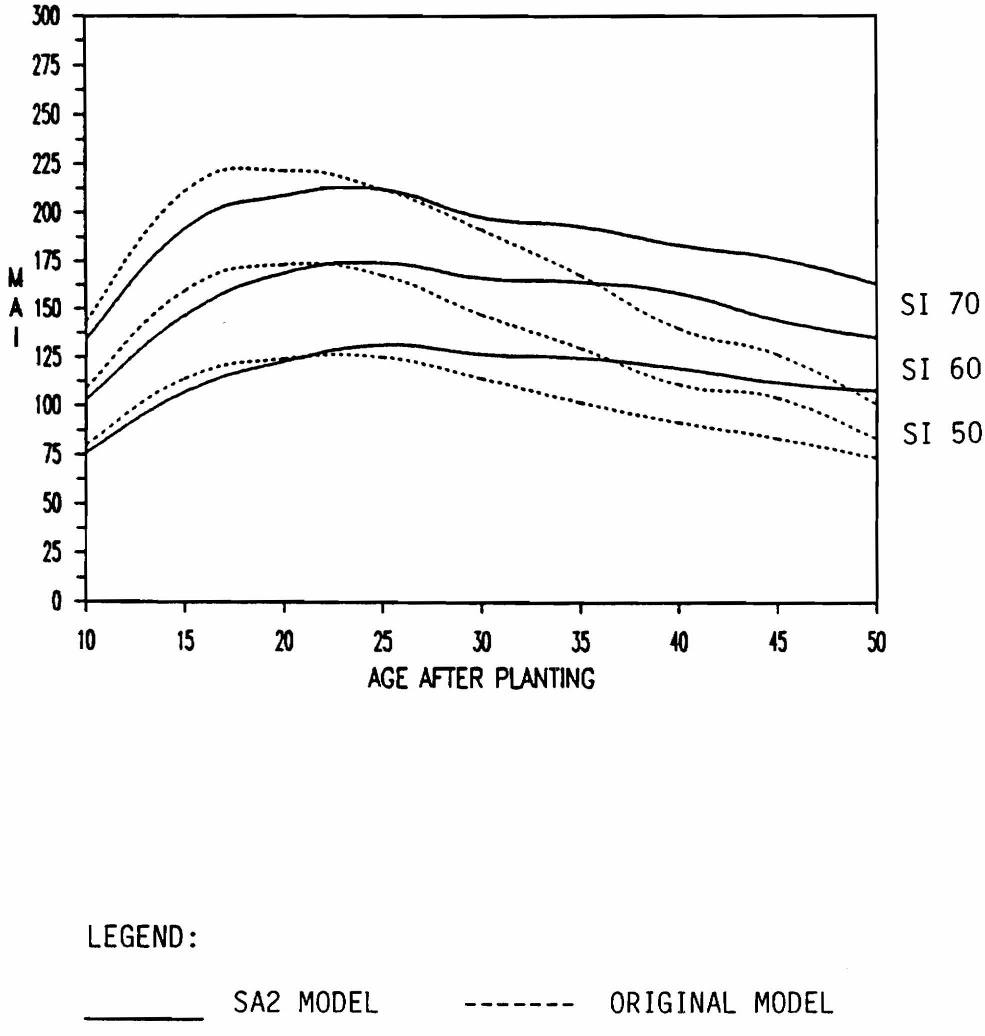


Figure 28. Projection of mean annual increment for the SA2 and original version of PTAEDA2 for 680 trees/acre.

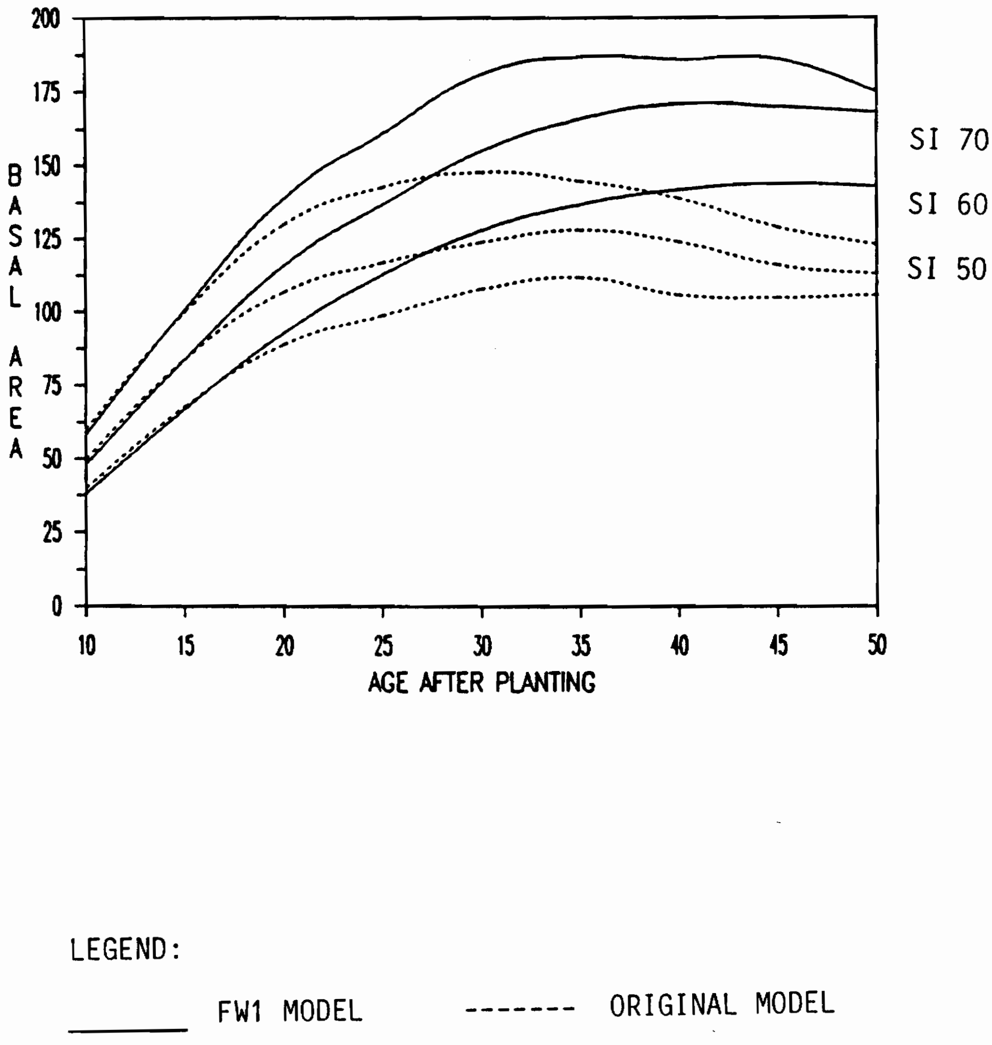


Figure 29. Projection of basal area per acre for the FW1 and original versions of PTAEDA2 for 300 trees/acre.

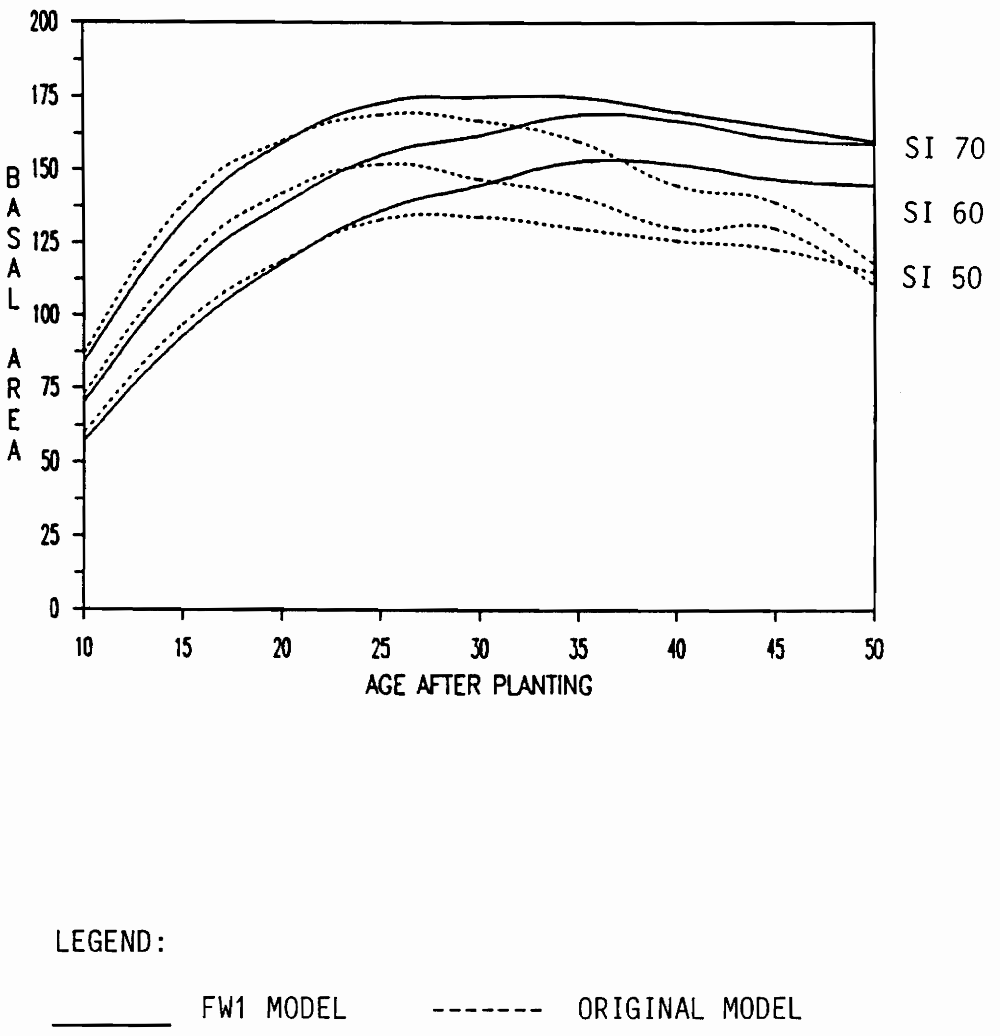


Figure 30. Projection of basal area per acre for the FW1 and original versions of PTAEDA2 for 680 trees/acre.

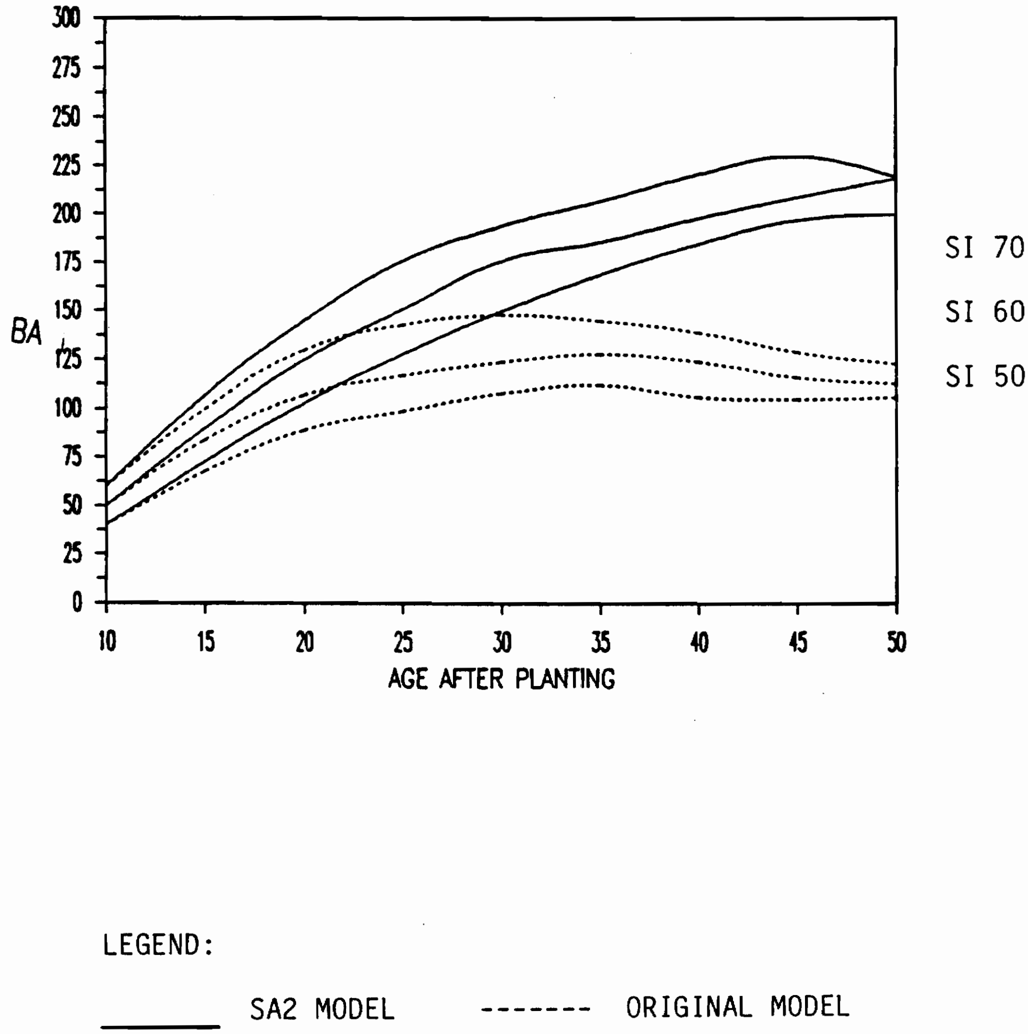


Figure 31. Projection of basal area per acre for the SA2 and original versions of PTAEDA2 for 300 trees/acre.

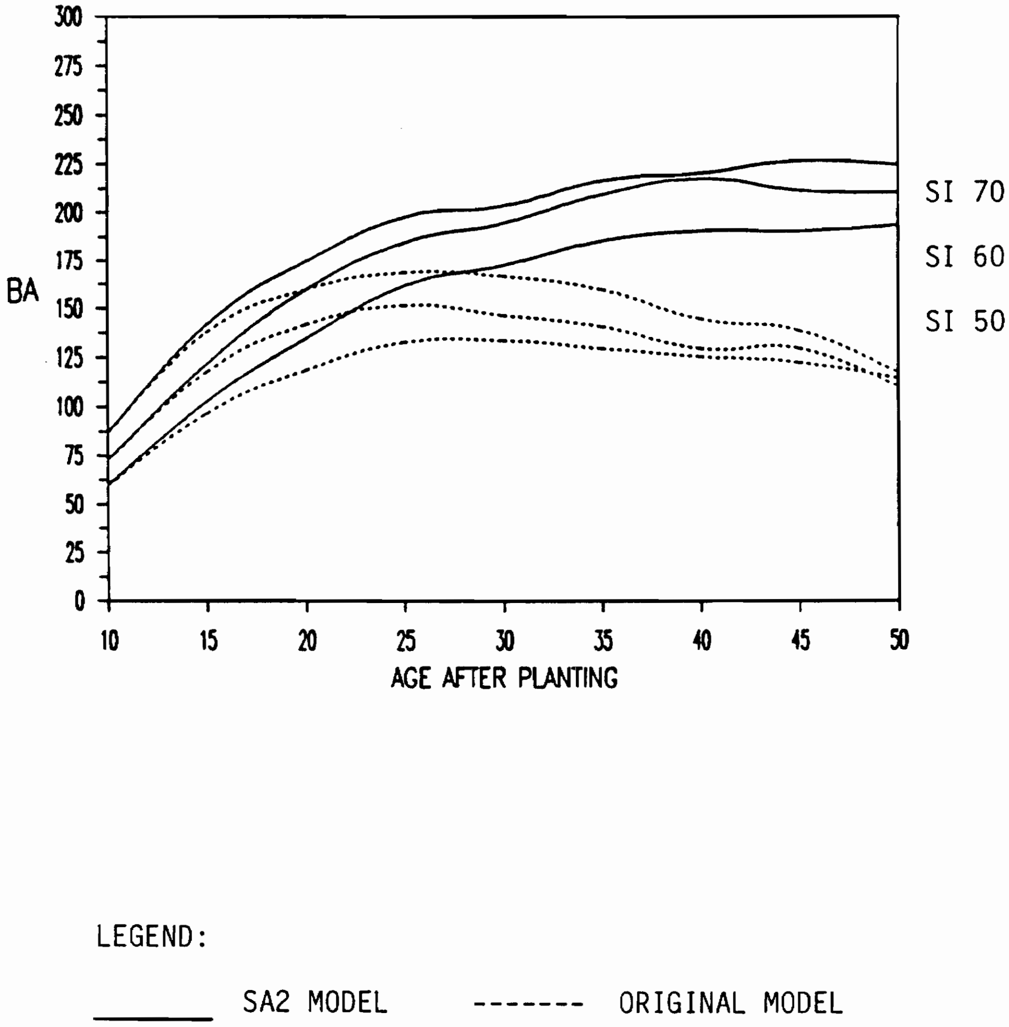


Figure 32. **Projection of basal area per acre for the SA2 and original versions of PTAEDA2 for 680 trees/acre.**

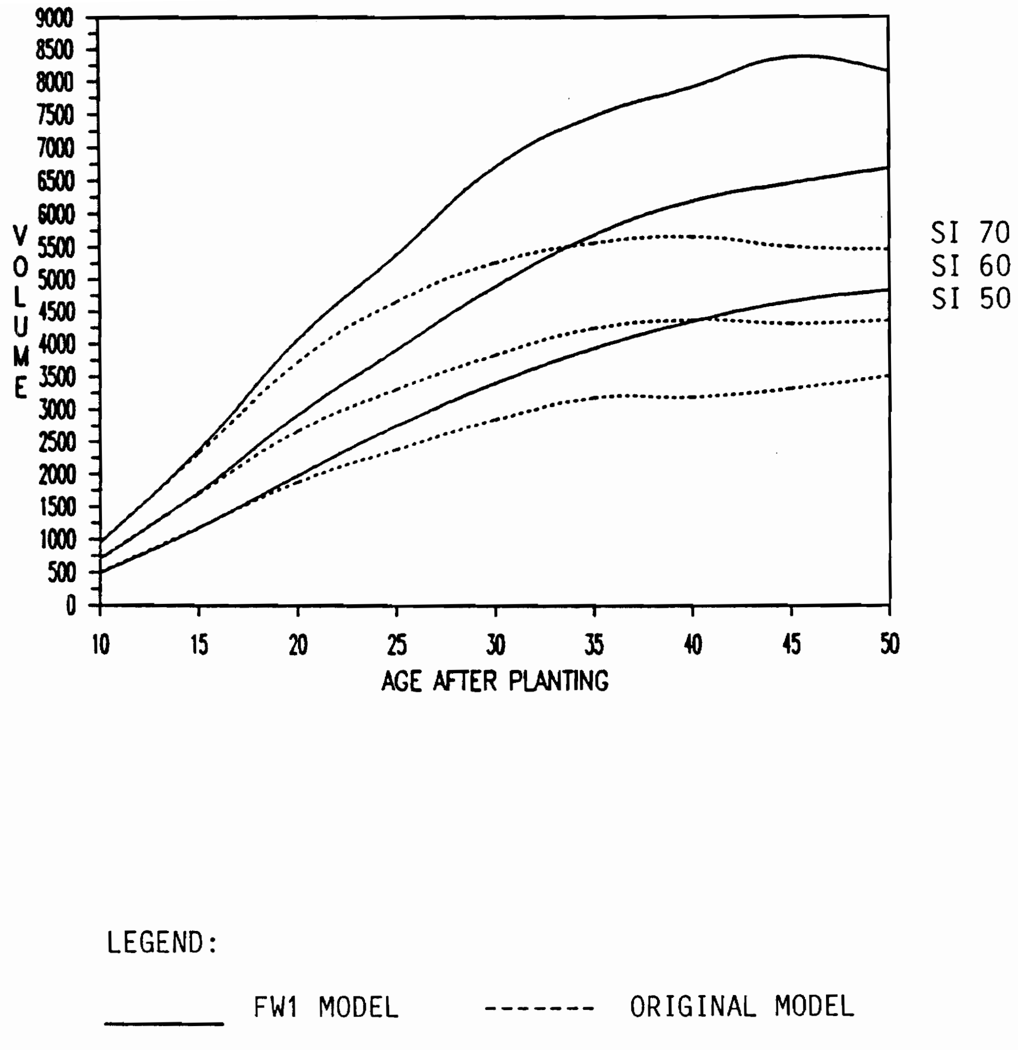


Figure 33. Projection of total cubic-ft. volume/acre for the FW1 and original versions of PTAEDA2 for 300 trees/acre.

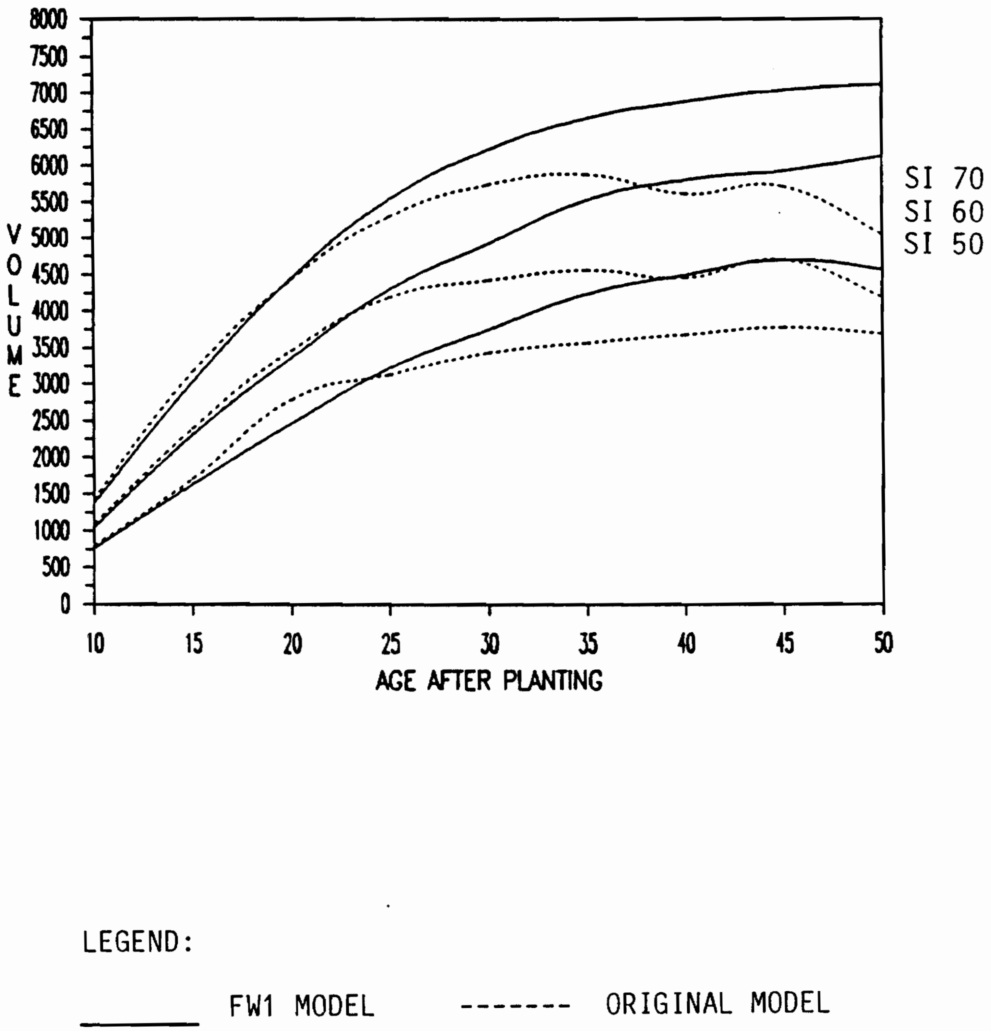


Figure 34. Projection of total cubic-ft. volume/acre for the FW1 and original versions of PTAEDA2 for 680 trees/acre.

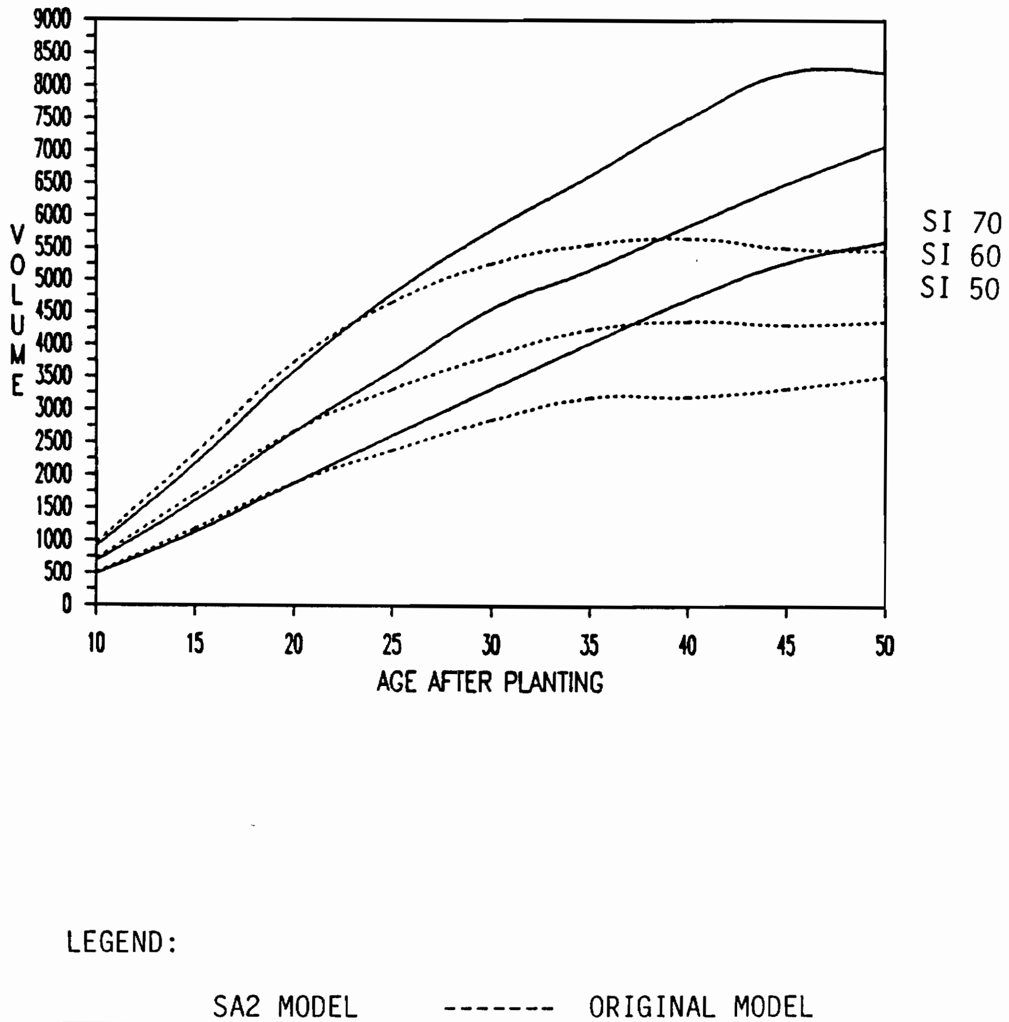
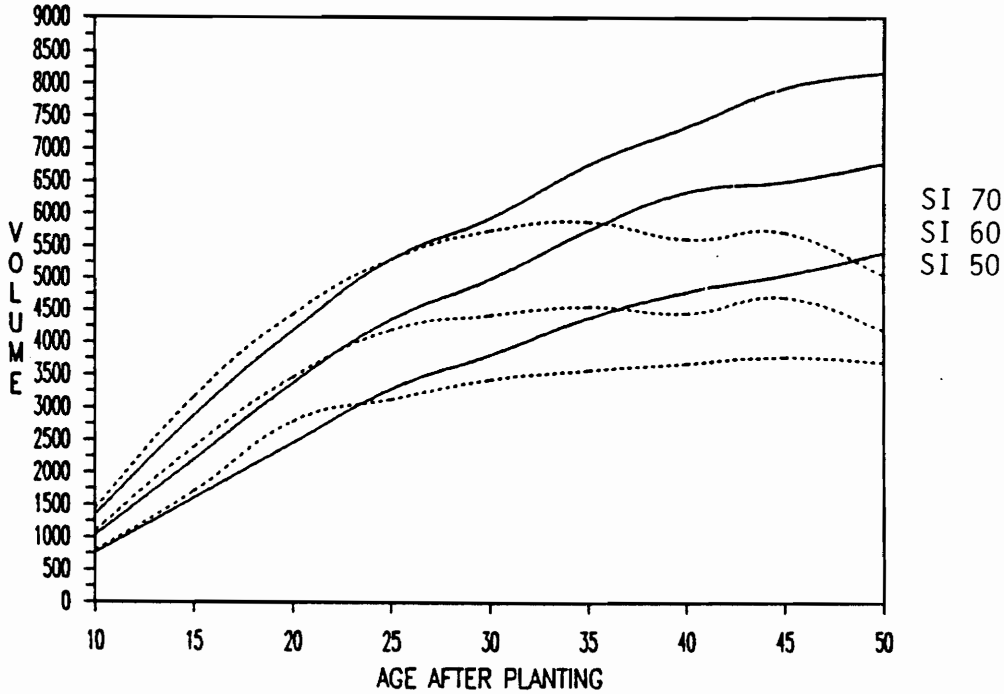


Figure 35. Projection of total cubic-ft. volume/acre for the SA2 and original versions of PTAEDA2 for 300 trees/acre.



LEGEND:

_______ SA2 MODEL ------- ORIGINAL MODEL

Figure 36. Projection of total cubic-ft. volume/acre for the SA2 and original versions of PTAEDA2 for 680 trees/acre.

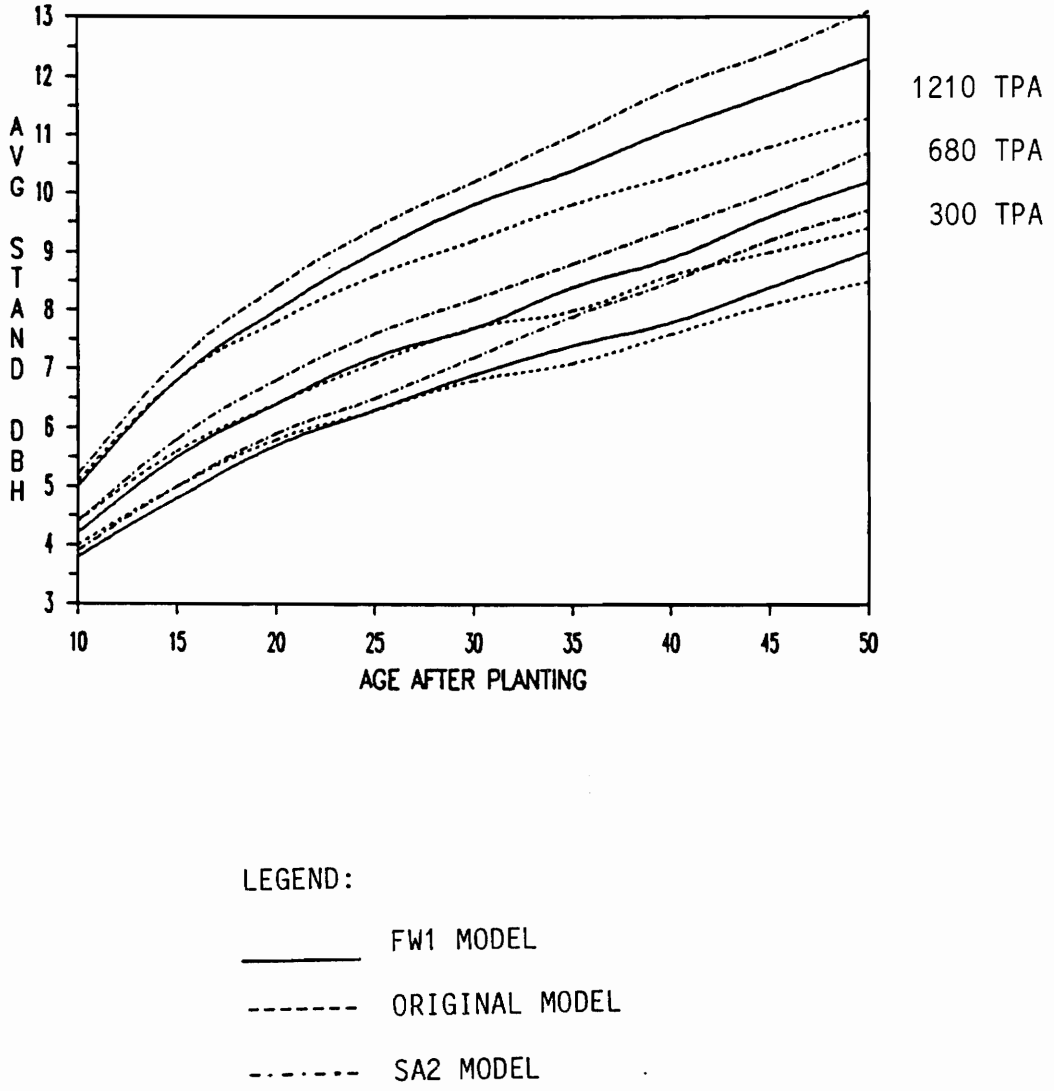


Figure 37. Projection of average stand dbh for the FW1, SA2, and original PTAEDA2 versions of PTAEDA2 for SI 50.

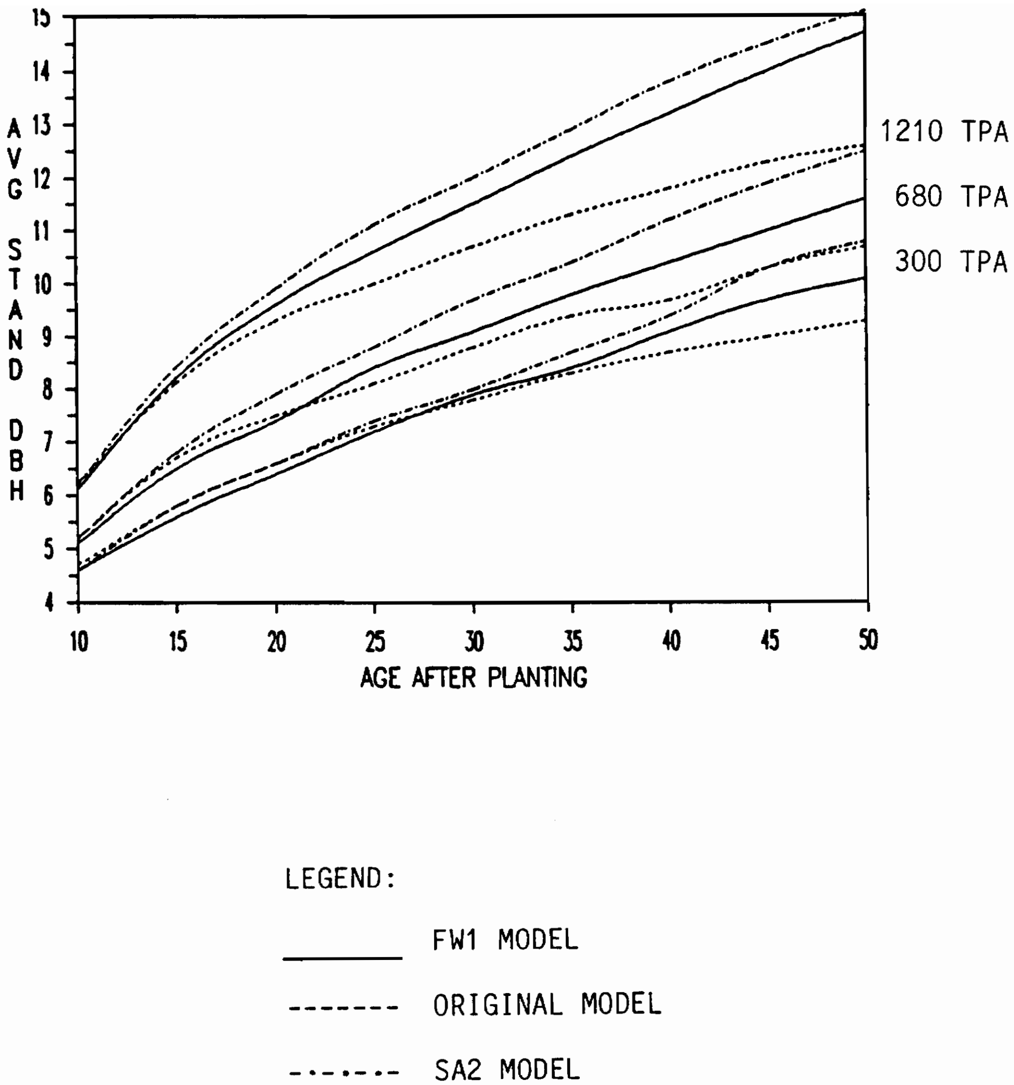


Figure 38. Projection of average stand dbh for the FW1, SA2, and original PTAEDA2 versions of PTAEDA2 for SI 70.

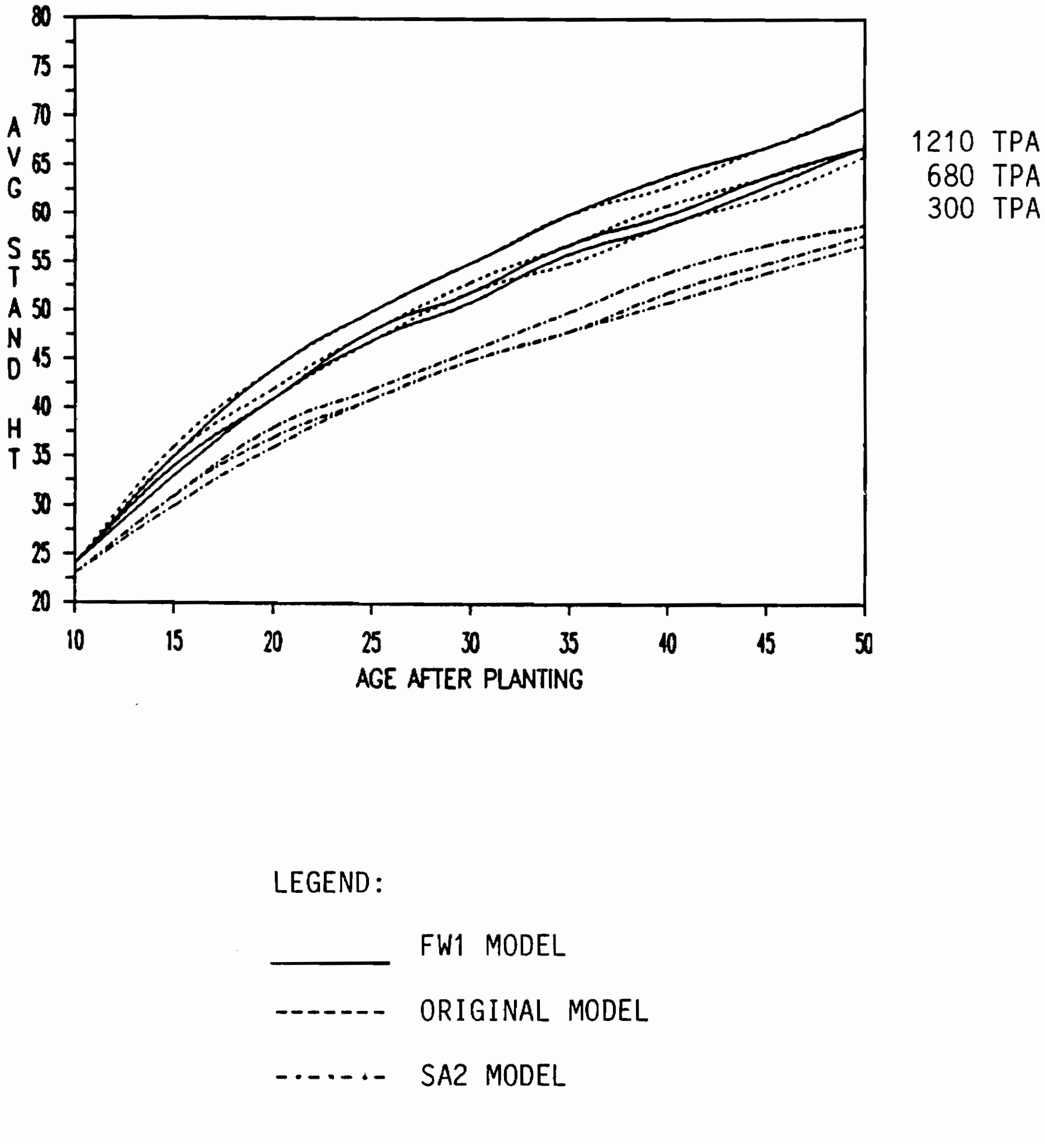


Figure 39. Projection of average stand height for the FW1, SA2, and original versions of PTAEDA2 for SI 50.

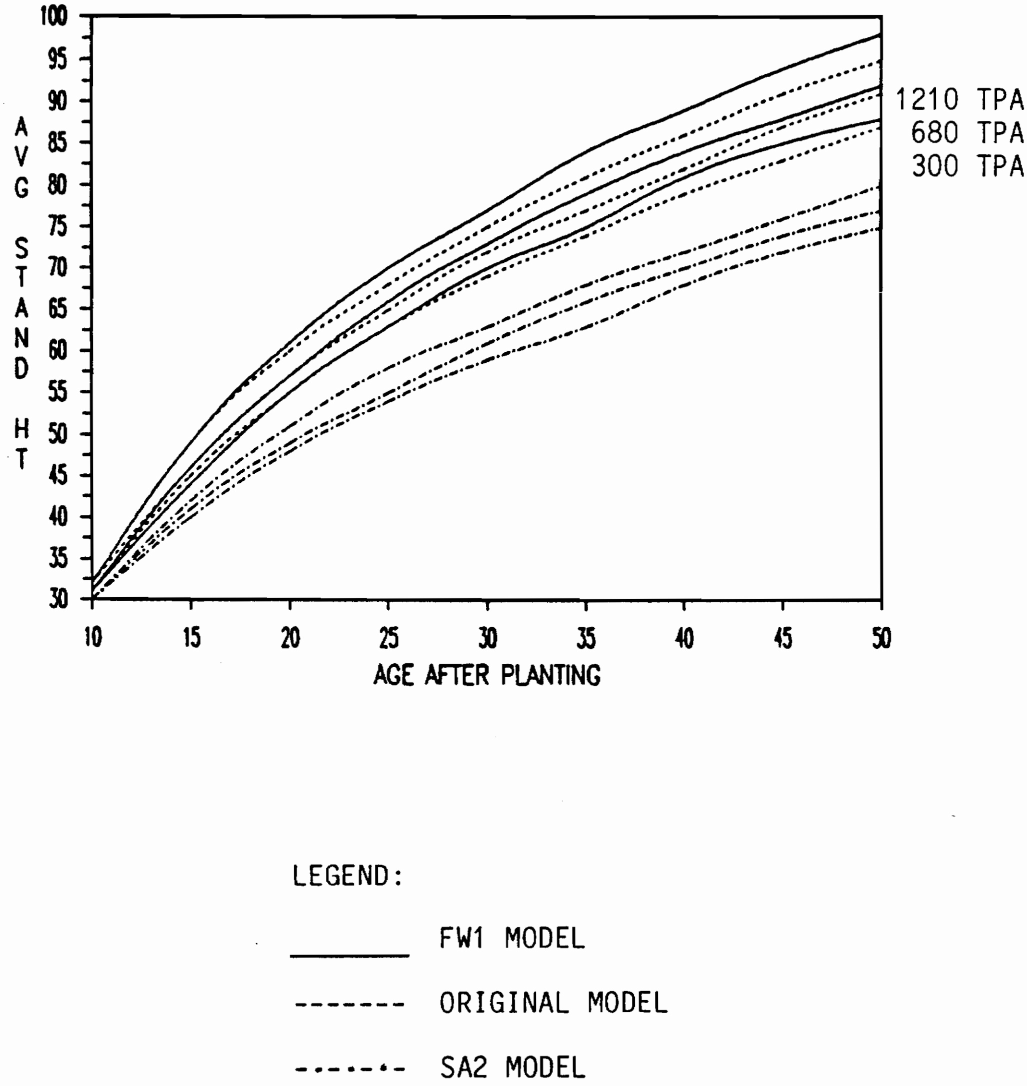


Figure 40. Projection of average stand height for the FW1, SA2, and original versions of PTAEDA2 for SI 70.

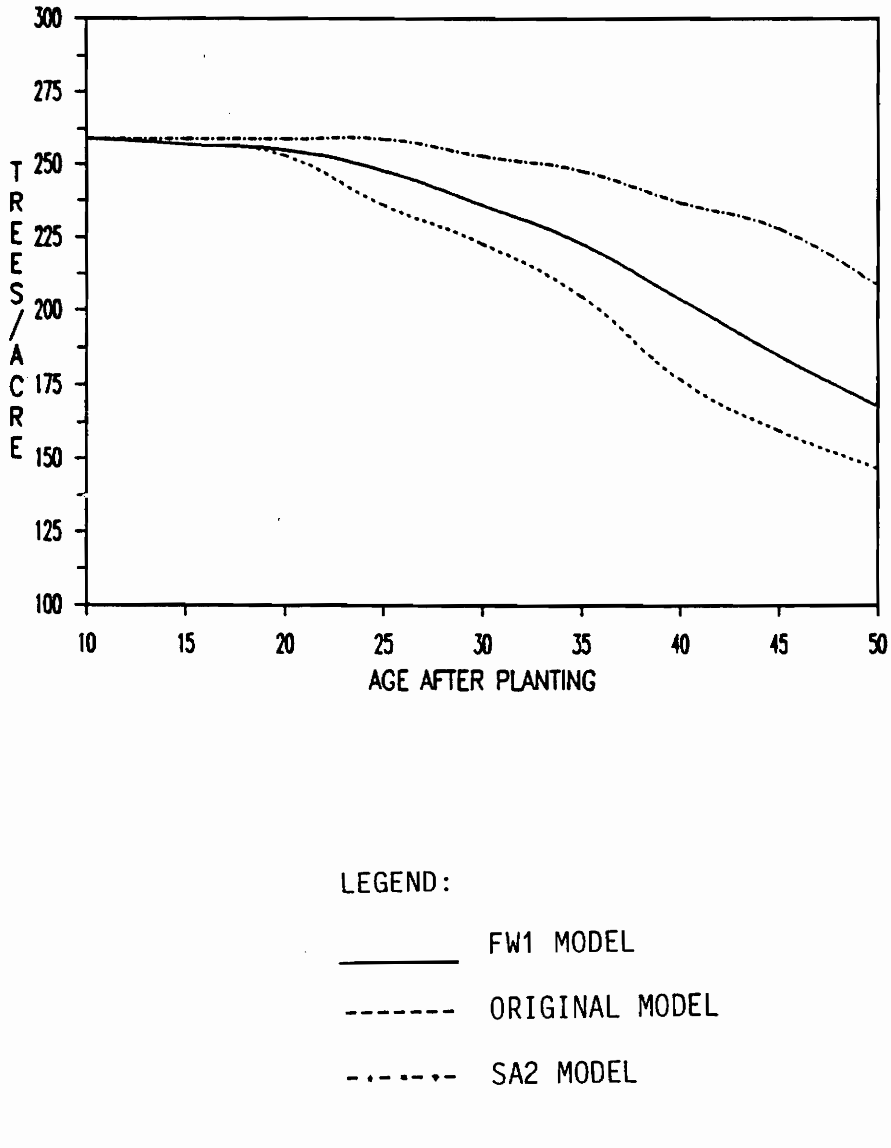


Figure 41. Projection of mortality for the FW1, SA2, and original versions of PTAEDA2 for 300 TPA and SI 50.

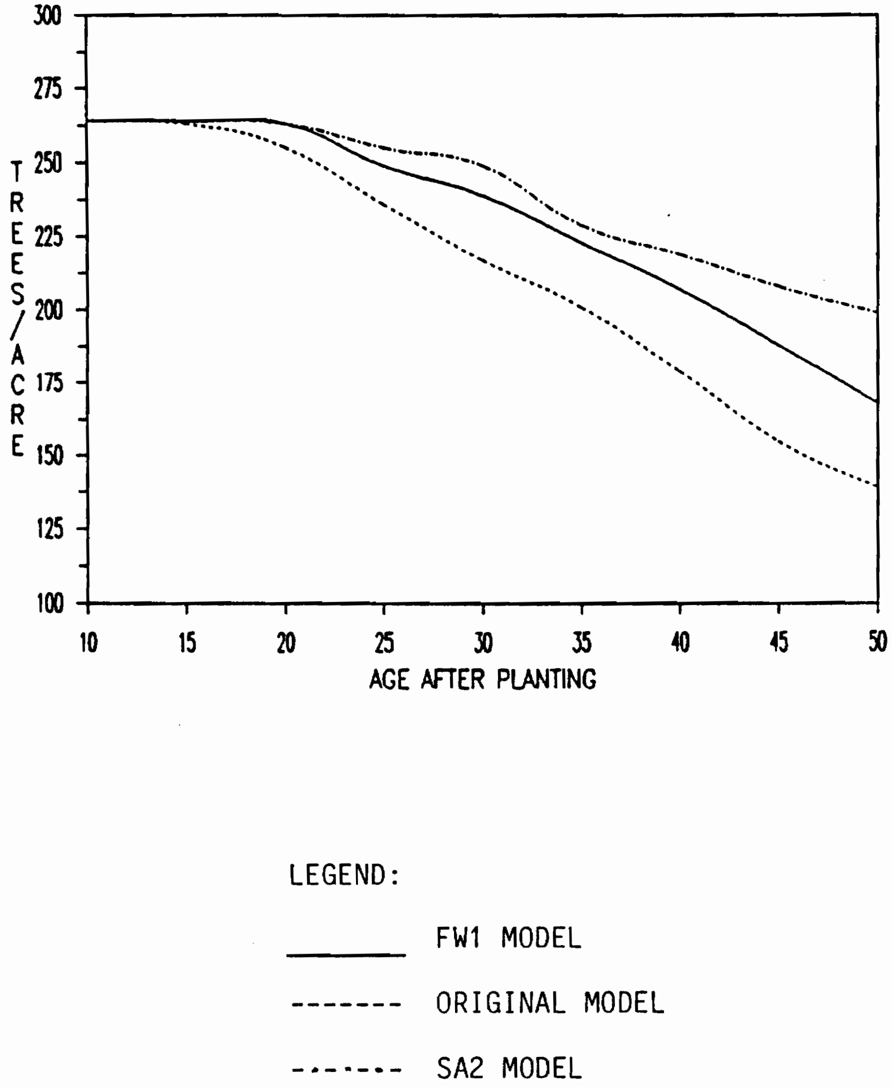


Figure 42. Projection of mortality for the FW1, SA2, and original versions of PTAEDA2 for 300 TPA and SI 60.

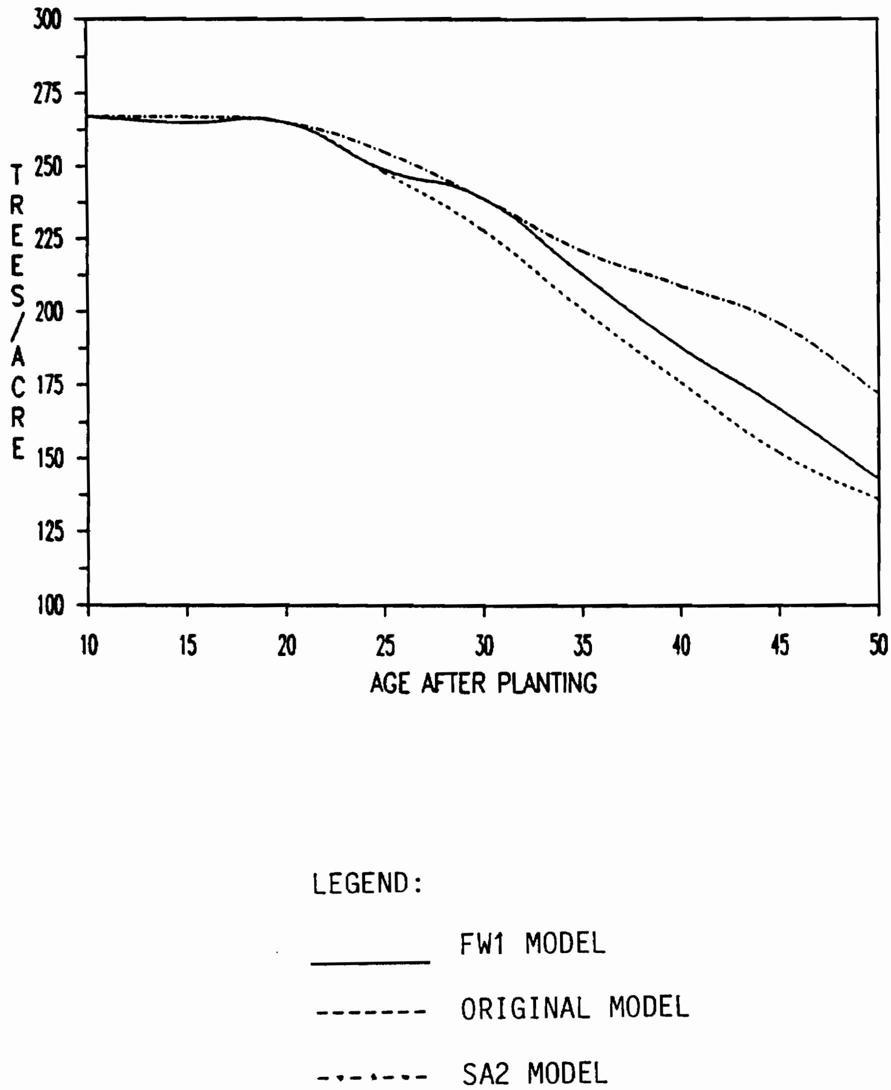


Figure 43. Projection of mortality for the FW1, SA2, and original versions of PTAEDA2 for 300 TPA and SI 70.

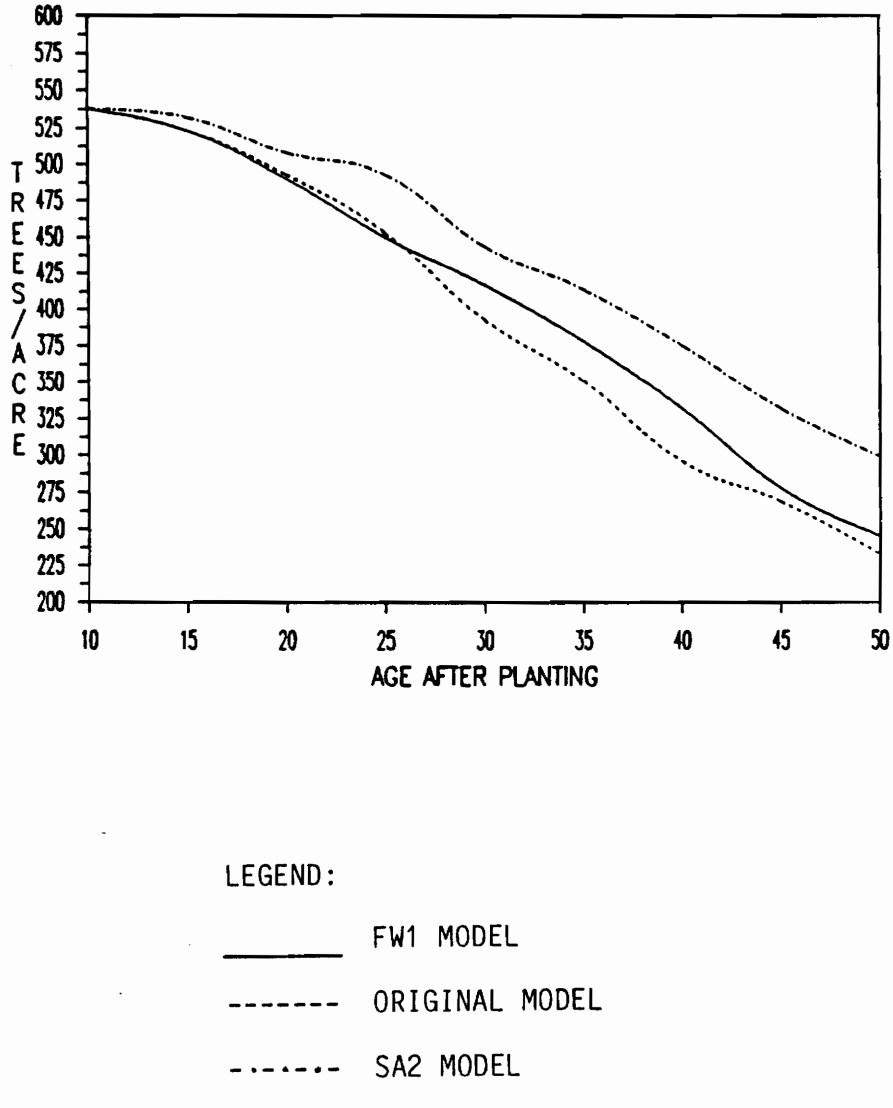


Figure 44. Projection of mortality for the FW1, SA2, and original versions of PTAEDA2 for 680 TPA and SI 50.

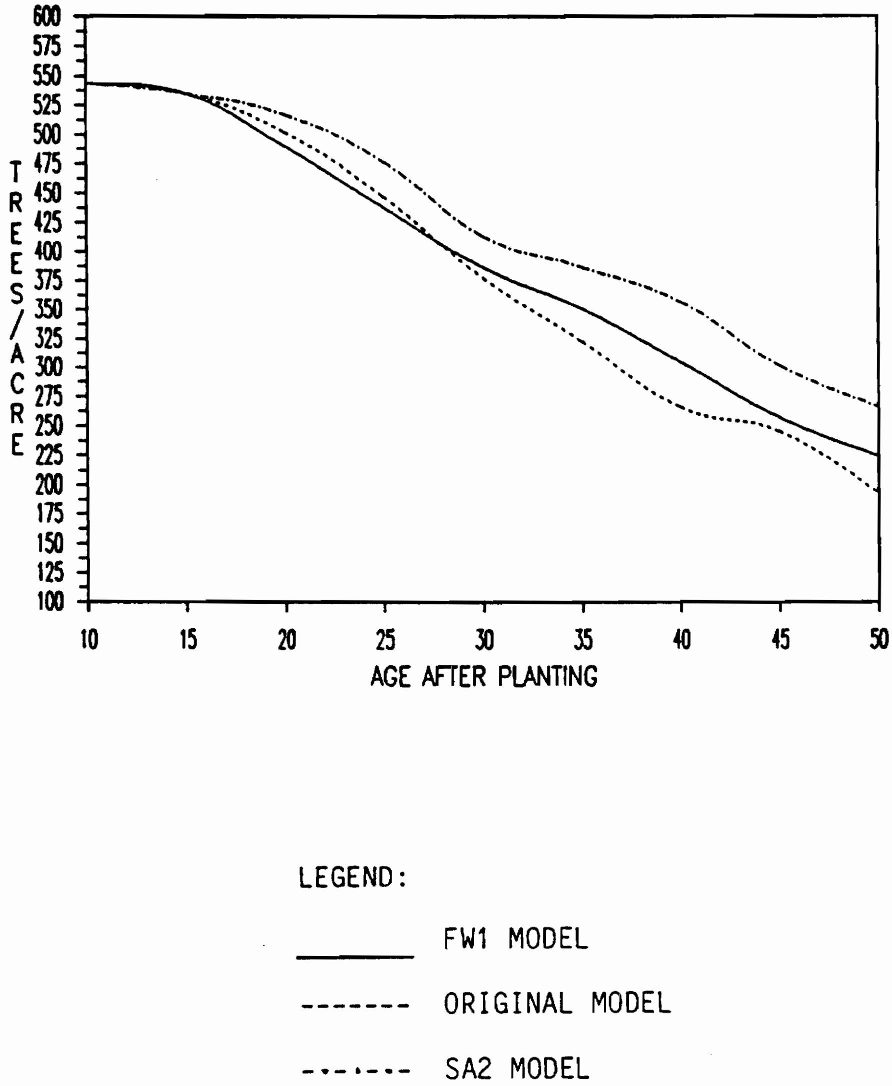


Figure 45. Projection of mortality for the FW1, SA2, and original versions of PTAEDA2 for 680 TPA and SI 60.

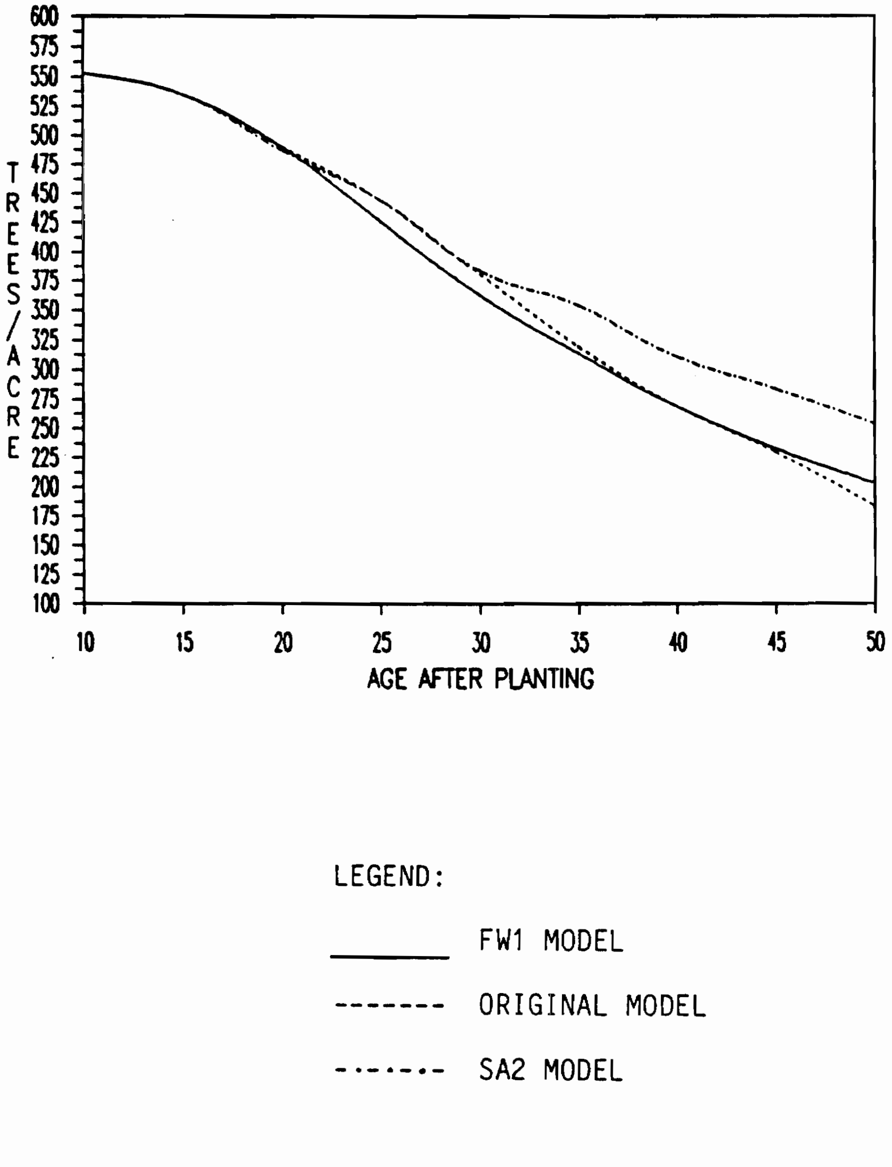


Figure 46. Projection of mortality for the FW1, SA2, and original versions of PTAEDA2 for 680 TPA and SI 70.

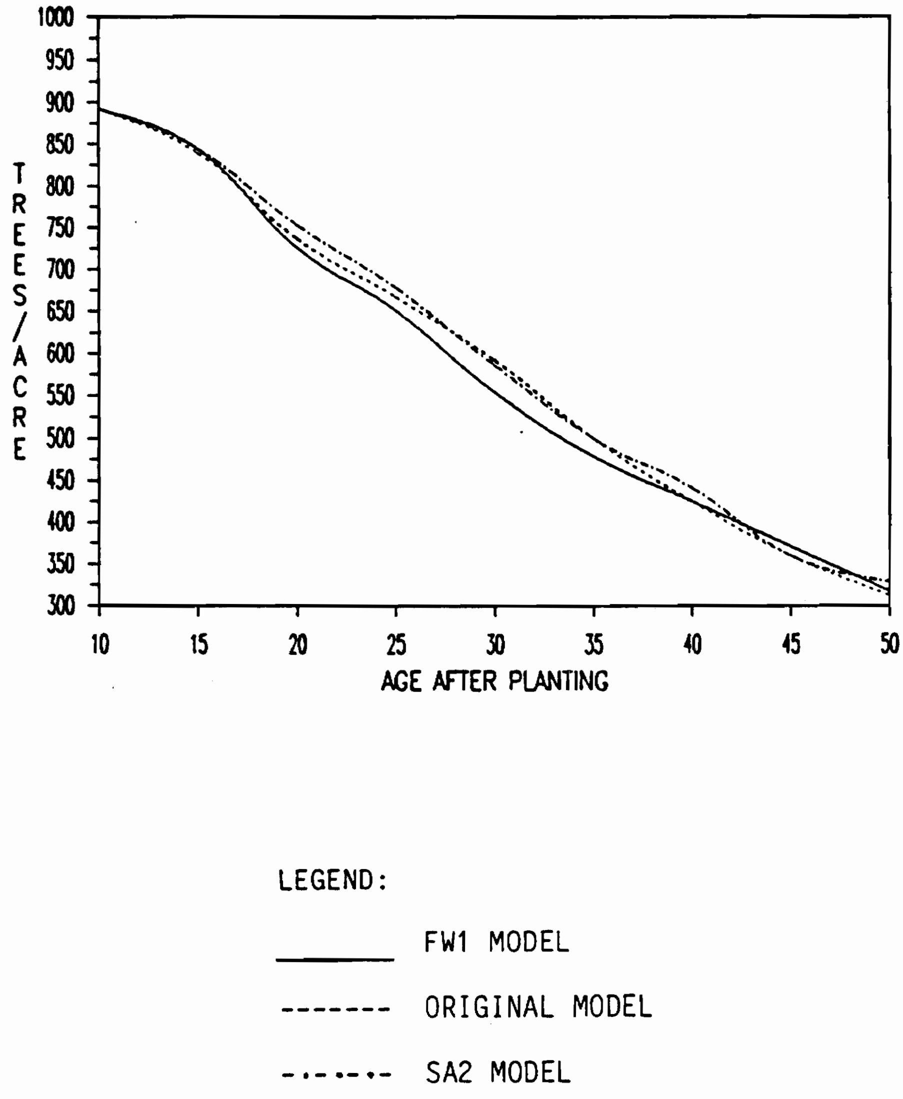


Figure 47. Projection of mortality for the FW1, SA2, and original versions of PTAEDA2 for 1210 TPA and SI 50.

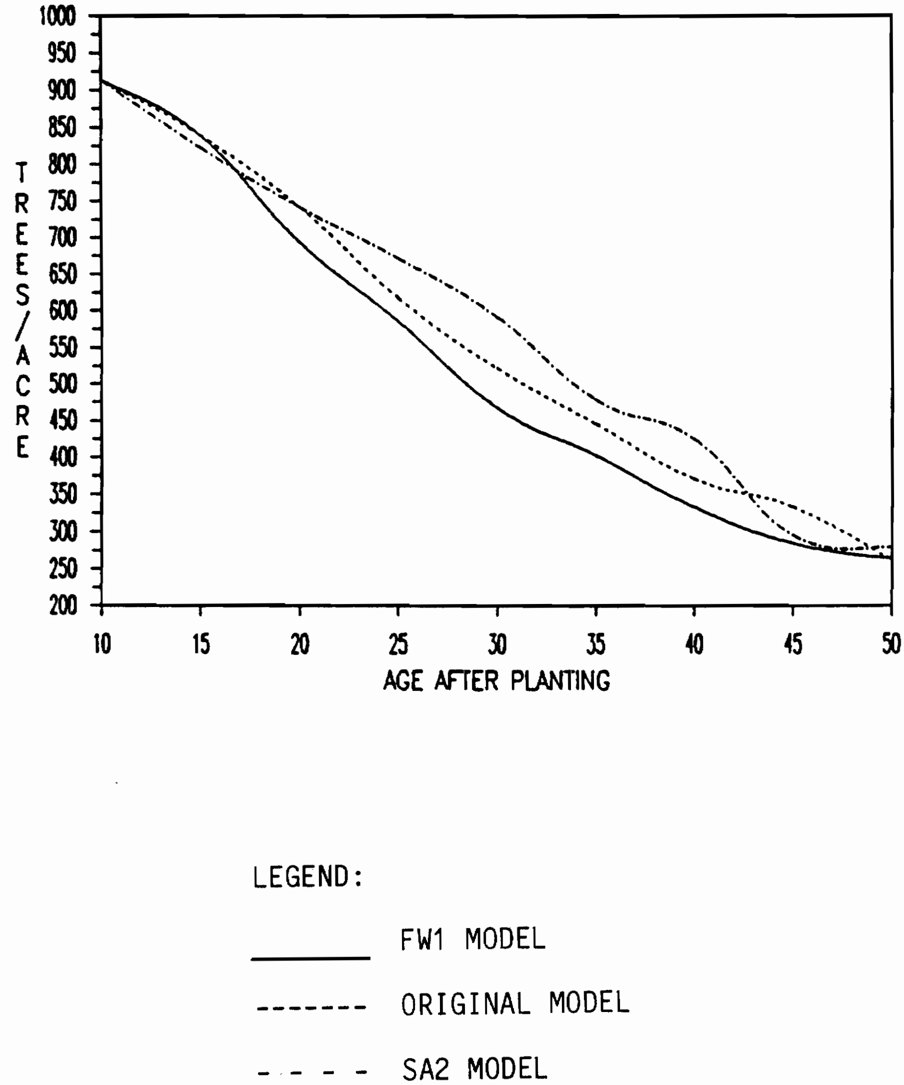


Figure 48. Projection of mortality for the FW1, SA2, and original versions of PTAEDA2 for 1210 TPA and SI 70.

VITA

The author was born in the heart of "Pigtown", Baltimore, Maryland in 1961 and was raised in Winchester, Virginia. After graduating from John Handley High School in 1980, she entered VPI & SU where her studies emphasized forest resource management. As an undergraduate, she participated in the Cooperative Education program with the U.S. Forest Service and worked nine quarters in the George Washington National Forest. She received her Bachelor of Science degree in Forestry from VPI & SU in 1985 and subsequently began a Master of Science program at VPI & SU in Forest Biometrics. Karen began employment with the U.S. Forest Service on the Jefferson National Forest in 1987 in Roanoke, Virginia. Her duties include resource information management, land management planning, geographic information system coordination, and computer modeling.

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