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Examination of optimal energy allocation patterns in lodgepole pine-mountain pine beetle systems through the use of dynamic programming and computer simulation

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AN EXAMINATION OF OPTIMAL ENERGY ALLOCATION PATTERNS IN LODGEPOLE PINE - MOUNTAIN PINE BEETLE SYSTEMS THROUGH THE USE OF DYNAMIC PROGRAMMING AND COMPUTER SIMULATION

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An Examination of Optimal Energy Allocation Patterns for Lodgepole Pine-Mountain Pine Beetle Systems through the Use of Dynamic Programming and Computer Simulation (125 pgs.)

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Optimal energy allocation patterns for lodgepole pine in a mountain pine beetle stressed system were examined using dynamic programming coupled with simulation modeling. The risks modeled were vegetative competition and beetle attack. Because energy was modeled as a finite resource, allocating energy to protect against one risk meant that there was less energy available to protect against the other. The best energy allocation choice, defined as the choice that maximized probability of survival, was determined for each potential height and age through the use of a discrete Markov chain system.

The model used two simulation programs to determine the choices that were taken, generate beetle production data and test the accuracy of the optimization model. The first program utilized data generated by the optimization model. The second allowed the input of allocation strategies based on constants and smooth or discontinuous functions. Because it lacked the error build up that plagued the recursion process, the second simulation program was considered to be more reliable. Testing of the validity of the allocation choices created in the dynamic program, therefore, was conducted by importing data into this program and comparing the probability of survival with the probability generated by the best constant allocation strategy.

The dynamic program produced a consistent three stage pattern of choices. This pattern was characterized by allocation to growth in the juvenile period, an allocation to defense in the old growth period and a stable equilibrium level in the mid-life. This indicates the existence of a locally stable equilibrium that can shift suddenly with perturbation.

The model predicts that old growth stands can become resistant to beetle attack if they are able to shift their energy allocation optimally. This would be the case if competitive pressure were removed through extensive thinning, a prediction that is supported by recent field work. The model also shows that optimal tree survival strategies allow for large beetle production levels even though a consistent high allocation to defense can eliminate beetles from the system.

Contents

Introduction.....1
Bark Beetle Biology.....5
Beetle Population Dynamics.....9
Energy Allocation and Tree Resistance.....13
Model Objectives.....21
Model Design and Structure.....22
    Tree Growth and Energy Production.....22
    Beetle Production.....27
    The Optimization Process.....30
    Setting the Probability Values.....33
    Model Structure.....35
Model Results 38
    Patterns of Energy Allocation.....38
    Beetle Production.....41
    Sensitivity Analysis.....42
Conclusions.....48
Modeling Problems and Future Needs.....53
Possibilities for Experimental Verification.....57
Tables.....60
Figures.....65
Appendix A.....90
Appendix B.....97
Appendix C.....105
Appendix D.....116
Literature Cited.....120

List of Tables

Table 1: A presentation of the matrix of optimal energy allocation choices obtained through dynamic programming.....60

Table 2: Sensitivity analysis holding energy allocation at fixed levels.....61

Table 3: Sensitivity analysis shifting various parameters and using dynamic programming.....63

Table 4: Model assumptions and constraints.....64

List of Figures

Figure 1: Energy Available for Allocation.....65

Figure 2: Energy Cost of Height Growth.....66

Figure 3: Potential Height Growth.....67

Figure 4: Available Phloem.....68

Figure 5: Area Available for Beetle Attack.....69

Figure 6: Beetle Production.....70

Figure 7: Maximum Beetle Production.....71

Figure 8: Probability of Beetle Survival.....72

Figure 9: Risk of Being Killed by Overtopping.....73

Figure 10: Probability of Beetle Attack.....74

Figure 11: Available Energy per Unit Volume.....75

Figure 12: Probability of Survival.....76

Figure 13: Mean Probable Beetle Production.....77

Figure 14: Three Stage Allocation Strategy.....78

Figures 15-20: This is a graphical presentation of the data contained in table 2.....79

Figure 21: Mean Probable Maximum Beetle Production.....85

Figure 22: Flow Chart for TREEGR.FIL.....86

Figure 23: Flow Chart for TREEGR.SIM.....87

Figure 24: Flow Chart for TREEGR.EQU.....88

Introduction

The mountain pine beetle, *Dendroctonus ponderosae* (Hopkins), has always been an integral part of lodgepole pine, *Pinus contorta* (Douglas var. *latifolia* Engelmann), ecosystems. Since 1895, the mountain pine beetle has killed an estimated average of two billion board feet per year (Cole and Amman 1980). Recently, two changes have combined to bring to bring mountain pine beetle-lodgepole pine interactions to the attention of forest managers. The first has been the increasing value of lodgepole as a commercial timber species. Yearly losses of the magnitude mentioned above cannot be tolerated if the timber being destroyed is marketable. The second is that a series of fires around the turn of the century, such as the 1910 burn that covered approximately three million acres of forested land in Montana and northern Idaho, resulted in numerous pure lodgepole pine stands. These areas have become susceptible to beetle attack in recent years and large outbreaks have occurred. Recent outbreaks, such as the one that began in the 1970's in the Targee National Forest, have been large and spectacular. At its peak in 1976, this

outbreak lead to the destruction of nearly 4 million trees per year (Klein et al. 1979).

In the last 20 years, a tremendous amount of research has been done to ascertain the characteristics and dynamics of the lodgepole pine - mountain pine beetle interactions, but the research has failed to produce anything more effective than a heuristic risk rating system that depends upon the multiplication of ordinal numbers (Cole and Amman 1980). This system, modified by habitat type stratification (Cole and McGregor 1983), is presently used by Region One of the United States Forest Service (USFS) to risk rate all the lodgepole pine stands in the region.

The primary reason that the early attempts to model beetle dynamics mechanistically (Anderson et al. 1976, Berryman and Pienaar 1974) failed is that they did not take into account the resistance of the trees to attack. This failure was carried over into the 1980's because one school of thought, lead by Gene Amman and Walter Cole, was that the dynamics of bark beetle outbreaks could be explained entirely by the age and phloem thickness of the trees attacked (Cole and Amman, 1980) and that conditions such as stand density were immaterial.

Berryman (1982) hypothesized that the epidemic cycles of bark beetles were controlled by a dynamic relationship between food availability (phloem thickness) and tree resistance. He hypothesized that the attack density of beetles necessary to kill a tree increased exponentially with the tree's resistance. According to this model, there were narrow "windows" in time in which the phloem was thick and the resistance of the trees was low. These windows would be the periods during which outbreaks could occur. Either high resistance or thin phloem could create a resistant stand. These theories are elegant and served to explain conceptually the existence of durable, old large diameter stands that should have been destroyed according to the Amman risk rating system. There was, however, no clear idea of how resistance could be defined.

Early research (Reid 1963) noted that "resinosis" had an important effect on mountain pine beetle brood survival, but the first link between lodgepole pine resistance and the production of resin came in the mid 1970's (Safranyik et al. 1975). The key to understanding the relationship was the discovery that the reaction was not to the beetles *per se* but to their associated symbiotic fungi. This allowed the bark beetle research

to tie into a large body of pre-existing knowledge. The existence of hypersensitive response systems that were triggered by the presence of fungal pathogens was well established in the literature of tree pathology (Shigo and Marx 1977). Work carried out by Raffa and Berryman (1982,1983) provided definitive evidence that the ability to activate hypersensitive response mechanisms was the key to beetle resistance in lodgepole pine.

The question is really one of energy. Beetles attack quickly and, because they utilize a sophisticated system of pheromones, in great force. In order to provide protection, the hypersensitive response of the tree must be equally rapid. Hypersensitive response to beetle attack, therefore, utilizes stored sugars in the tissues surrounding the attack site (Raffa and Berryman 1983, Miller and Berryman 1985). If the sugar is available, then the tree can resist the beetles; when the sugar is exhausted the tree loses its resistant qualities. This explains both the existence of a resistance threshold (point of energy exhaustion) and the effectiveness of mass attack strategies by the beetles.

The model that is presented in this paper is designed to explore conceptually energetic allocation in trees facing both competitive stress and beetle attack.

It utilizes dynamic programming techniques to determine the optimal energy allocation choices. An allocation to growth decreases the probability that the tree will be killed by competition with its neighbors. An allocation to defense decreases the probability that the tree will be killed by beetles if attacked. The optimal strategy shifts with the condition of the tree, which is represented in the model by height and age. Simulation models are employed to determine the energy allocation choices that will be made by a tree, the probability of survival, and mean probable beetle production.

Bark Beetle Biology

The mountain pine beetle, *Dendroctonus ponderosae* is a member of the family Scolytidae that attacks virtually all species of pine in the western United States (Cole and Amman 1980). The mountain pine beetle is univoltine, and there is little generational overlap from year to year (Amman 1973). The population, therefore, can be said to have no age structure. In the normal bark beetle life cycle, the adults emerge in late July or August, select trees to attack, mate monogamously, and the females lay up to 200 eggs in galleries that are

constructed under the bark of the tree (Reid 1962). The eggs hatch between 10 and 20 days after oviposition, depending on temperature (Reid and Gates 1970), and the larvae construct horizontal galleries using the phloem layer for food.

Because the success of the attack depends upon killing of the tree, it can be viewed as a zero sum game; either the tree wins or the beetles win. The beetles determine the attack density necessary to kill an individual tree by utilizing a system of secondary oxidation by-products that are created in the hind gut of the beetles. The tree's monoterpenes are converted either to aggregation or disaggregation pheromones, depending upon whether the female has mated or not. The aggregation pheromone, *trans*-verbenol, is volatilized by the tree's production of monoterpenes and is carried throughout the stand. The attractant is, therefore, very powerful while the tree is responding hypersensitively to the attack. When resin production ceases, the *trans*-verbenol is no longer volatilized and the attractive power of the tree declines. The disaggregation pheromone, *exo*-brevicomin, is produced primarily by the males after the female has created an initial gallery and the host tree's defenses have been overcome. *Exo*-

brevicomin, therefore, is not volatilized but, rather, creates a local region of repulsion (Pitman and Vité 1969). This prevents the males from attempting multiple mating with the same female and serves to spread the attack galleries evenly around the bole. The end result of this system is that the beetles aggregate around a tree until the attack density is great enough to kill it, and then the disaggregation pheromone becomes dominant and prevents over-colonization. Theoretically, any tree can be killed if the attack density is great enough, but densities higher than 200 beetles per square meter are seldom seen in the field (Waring and Pitman 1980).

There is evidence that the beetles attack trees in densities that maximize the fitness of the individual attackers (Berryman et al. 1985). This density is usually around 70-80 beetles per square meter. If this is indeed the case there may be a level of resistance at which a tree may be considered completely resistant.

Bark beetles show a preference for larger diameter trees. The percent of trees killed during an outbreak increases sigmoidally with diameter, rising sharply between 13 and 38 centimeters and then leveling off at larger diameters (Klein et al. 1978). There has been much speculation concerning the causal mechanism behind

this behavior. Basically there are two views. The first is that the beetles show a positive taxis towards large vertical black objects, though the taxis displayed is not very strong (Amman and Cole 1983). The other view is that all trees have an equal probability of attack but that there is some quality that the larger trees possess that keys the beetles into the fact that they are better for brood production. There has, therefore, been a considerable effort directed towards the analysis of the monoterpene composition of resistant and non-resistant trees (Cole 1981).

Recent studies by Raffa and Berryman (1982,1983) have found no significant differences in initial phloem composition or amount in resistant and non-resistant stems. Borden (1983) found that the diameter preference was exhibited on trees that were baited with *trans*-verbenol. Since the baiting presumably masked what ever minor differences existed between the natural odors of the stems, this seems to support the diameter preference theory. Because of this evidence and because there is no evidence to the contrary, preference based on a positive visual taxis is at present the best theory.

Beetle Population Dynamics

The population dynamics of mountain pine beetle are of the eruptive type. In most stands, few if any beetles are present. These normal endemic conditions are punctuated by occasional epidemics in which billions of beetles are produced. These epidemics usually last approximately 10 years and then come to a sudden end. This scenario, of course, is subject to exceptions; the Yellowstone Park area seems to be in a perennial epidemic state (Cole and Amman 1980).

Beetle populations rise or fall as a consequence of dynamic interactions on a individual tree level. If we assume that a tree has been attacked successfully by a number of female beetles at time t ($ATTACK_t$), then the maximum number of beetles (Bmax) that can emerge the following August (t + 1) equals $ATTACK_t$ * E, where E equals the mean egg production per female. Each tree that is attacked, however, has a finite carrying capacity (K) and it can support only a limited number of beetles. If Bmax > K then the maximum beetle production will be limited by K and K ≈ Bmax. The potential number of attackers that will emerge at time t+1 ($ATTACK_{t+1}$) will equal Bmax * the percent of the emerging beetles that are

female or approximately 0.6 * Bmax (Amman and Cole 1983). If this number is larger than $ATTACK_t$ then a rise in population is possible. Whether or not actual population levels in the field rise depends upon a number of mortality factors that will act to decrease Bmax. The general equation for the finite rate of population change (R) is:

$$R = 0.6 * [Bmax - (D + W + P + O)] / ATTACK_t \quad (1)$$

Where:

D = the number of beetles killed due to desiccation
W = " winterkill
P = " predation/parasitism
O = " other misc. mortality factors

First let us look at Bmax. Usually, except at very low attack densities, Bmax is defined by the amount of food available in the tree rather than the insects' fecundity. There are many facets of bark beetle behavior that allow them to utilize the food supply in a tree nearly optimally; disaggregation pheromones and stridulation cause the entry holes to be scattered evenly over the bole, oviposition decreases as attack density increases, and larvae display a negative taxis to the sound of other larvae. Unlike many populations in which overcrowding leads to starvation, the number of beetles

approaches a maximum as attack densities increase, a stability for which cannibalism may be largely responsible (Amman and Cole 1983).

The food supply for bark beetles is the phloem volume of the successfully-attacked tree. This is equal to the area attacked times the phloem thickness. Cabara (1978) found that phloem thickness remained reasonably constant up to 60 percent of the tree height and then decreased sharply. Since beetle attacks occur in the lower part of the bole, the assumption of even phloem thickness over the entire area under attack is justified.

If we assume that the proportion of phloem utilized by the beetles is constant and does not shift with phloem thickness, then the volume of beetles produced in a given area of bark should be a function of the volume of phloem in that area. If the beetles are assumed to be constant in size then beetle numbers can be substituted directly in place of beetle volume. With these assumptions, the beetle numbers produced by a tree may be modeled as a linear function of phloem thickness. Measurements of larval emergence in the laboratory have been made (Amman 1972) and a linear regression was derived:

$$Y = -23.91 + 947.74X \qquad (2)$$

Where:

Y = beetles/ft^2

X = phloem thickness in inches

$r^2 = 0.69$

This rate of production can be considered to be the maximum potential production: Bmax.

Of the various larval mortality factors, two are dominant, at least in epidemic populations of beetles: desiccation and winterkill. The others may be effective controls at low population levels, but the necessary research has not been done to determine if this is true (Amman and Cole 1983).

Field studies have shown that trees smaller than 18 centimeters in diameter desiccate during the year and that this desiccation can cause total larval mortality. With a few assumptions, this problem can be modeled fairly simply. Moisture escape from a log can be described in a one dimensional sense by the equation:

$$E = (Vs - Va)/r \quad \text{(Campbell 1977)} \qquad (3)$$

Where:

E = moisture exchanged

$Vs - Va$ = the moisture difference between the log and the atmosphere

r = the resistance to transfer

In this case, the resistance to moisture transfer lies primarily in the bark. If we hold this fixed and assume that the moisture content in the wood is initially constant then, for a given site, the loss of water can be viewed as being strictly proportional to the ratio of external surface to internal volume of the affected portion of the stem. If trees with larger diameters are taller than trees with smaller diameters, the volume will increase in proportion to the cube of diameter and surface area in proportion to the square. The ratio of surface area/volume, therefore declines hyperbolically with increasing diameter.

Energy Allocation and Tree Resistance

An understanding of energy utilization in plants must be based on the knowledge that plants have finite resources available to allocate and various sinks into which those resources can be allocated (McLaughlin and Shriner 1980). In this model the two sinks that are recognized are energy allocation to defense and to the production of growth related tissues. It is important to keep in mind the finite nature of the resources to be allocated. If more energy is allocated to one sink then,

necessarily, less is left to be allocated to the other sinks. Energy to any sink will have benefits to that specific compartment. If this were not the case energy would not be allocated. But, due to the limited resources at hand, the benefits that are derived from an energy allocation choice will be balanced against the negative effects that result from a lack of energy allocation to another compartment. An energy allocation to defensive chemistry necessitates a lack of energy allocation to growth and vice versa. The benefits associated with energy allocation to growth are that the tree will be able to compete for light and nutrients and that, being large, it will be able to produce a greater volume of seed and therefore increase its fitness. The benefits associated with energy allocation to defensive chemistry are that the tree will increase its chances of survival if it is attacked by insects or pathogens and therefore live to produce seeds and improve its fitness. Within this equilibrium there will be an optimal energy allocation choice for a given time and condition. To survive, a tree must allocate its resources so that it can maximize its chances of survival in a highly stochastic world and this means that the energy allocation choice must maximize the probability of

survival based on the mean probability of the occurrence of specific risks. This assumption of optimal response to stimuli is not based on the tree's ability to think, but rather the fact that those trees that respond in a more optimal fashion will survive and reproduce in greater numbers than those that respond in less optimal ways. Tree response to survival threats will take two forms.

The first must be a genetically conditioned energy allocation pattern that the tree will adopt without stimuli. A tree must, for instance, grow so as to avoid being shaded. It cannot wait until a shading stimulus occurs to begin growth because by that time it is too late. The same thing is true of beetle attack. Beetle attack occurs suddenly (mass attack) and either the tree is prepared for the attack through a previous allocation of energy or the tree dies. The second is an active response to stimuli when it occurs. In terms of energy allocation, there will be a genetically set strategy that is the "default" for the tree and this default will be conditioned by actual events that occur. Probability of death through beetle attack, for instance, can be modeled as the conditional probability:

$$P(\text{death}) = P(\text{attacked}) * P(\text{killed if attacked}) \quad (4)$$

Genetically, the tree's default must be to maximize the probability of survival based on the mean probability of both of these events occurring. If the tree is attacked unsuccessfully, however, P(attack) will become 1 and the optimal allocation strategy will shift.

Within the confines of defensive chemical allocation strategies, there are two approaches that plants utilize. Compounds that have no function other than defense, such as phenolics, may be held in inhibitory concentrations throughout the life cycle of the plant (constitutive resistance) or energy allocated to defense may be held as a mobile source of energy; as starch or sugar reserves in the parenchyma cells. When an attack occurs, these carbohydrate reserves can be metabolized into defensive compounds (hypersensitive response) (McLaughlin and Shriner 1980). If the probability of attack is low and the consequences of the attack are extreme, the second of these two strategies is the more flexible and efficient one (Matson and Hain 1985). If the probability of attack is high and the consequences of the attack are minor, then a high energy allocation to constitutive defense systems will be more effective.

Given the nature of bark beetle attacks on western pine species, it is not surprising that species such as *Pinus contorta* depend almost exclusively on hypersensitive response to resist beetle attack.

Constitutive resistance to bark beetle attack in conifers is accomplished by a system of resin ducts. In *Pinus contorta*, the system of resin ducts is poorly formed and integrated. Resin ducts are created by the secretion of oleoresin into the spaces between the ray cells and, in time, a mature duct develops. There are two systems of ducts: horizontal ducts within the ray tissues that are connected to ducts in the bark and vertical ducts within the sapwood. The system lacks the integration necessary to successfully defend against an attack by bark beetles because bark beetles primarily sever the resin ducts in the bark and leave the internal system in the sapwood intact. The response within the system of bark ducts is limited because it is, for the most part, separate from the rest of the tree. For this reason, the exudation of resin from wounds caused by bark beetle attack ceases after 1 to 3 days, the time that it takes to exhaust the resin in the affected area of bark (Shrimpton 1978). This is the total effect of the preformed defense system. No significant

relationships have been discovered between resistance to beetle attack and rates of daily resin flow, resin crystallization, monoterpene content or current growth rate (Raffa and Berryman 1982). The major difference between resistant and non-resistant trees is their ability to respond dynamically to the beetle attack.

Most of the hypersensitive response seems to be quantitative rather than qualitative; the tissue surrounding the wound becomes resin soaked and callus tissue is produced by the cambial layer to isolate the various fungi (*Ceratocystis spp.*) that the beetles vector into the tree (Raffa and Berryman 1983, Wong 1977). There are, however, increases in specific monoterpenes. Slight increases in α-pinene were noticed as well as a four-fold increase in limonene. The increase in limonene, even though it is still an extremely minor component in the oleoresin, may be significant. Limonene is the most toxic and repellent of the monoterpenes to bark beetles (Raffa and Berryman 1983). In *Pinus ponderosa*, the greatest resistance to the western pine beetle (*Dendroctonus brevicomis*), as measured by mean gallery length, was observed in a bole that displayed the poorest resin flow of all the trees tested but was abnormally high in limonene (Smith 1975).

Hypersensitive response is very energy-intensive. The cost of monoterpene production is approximately 90 molecules of ATP per molecule of terpene (Miller and Berryman 1985). Since 36 molecules of ATP are produced per molecule of glucose via glycolysis, the Krebs cycle and the electron transport system, the production of each molecule of monoterpene requires approximately 2.5 molecules of glucose. The biosynthesis of toxic terpenes in dynamic response to beetle attack,therefore, will be very sensitive to the level of stored carbohydrates and specifically the stored sugars in the plant tissue at the time of the attack (Miller and Berryman 1985, Wright 1979). *Pinus contorta* responds to fungal inoculation within 3 days with increases in acetone soluble extractives and can continue these increases for an additional 7 day period (Raffa and Berryman 1983). For this rapid response mechanism to operate during the water stress of late summer, the carbohydrates that are metabolized in this process must be allocated to storage prior to attack as photosynthetic activity is limited by moisture stress during this period of the year (Running 1984).

The ability to respond to attack declines as the density of the attack increases (Raffa and Berryman 1983). The theory is that the defensive abilities of the plant become overwhelmed by the attack. In energetic terms, the available carbohydrate reserves in a given area of bark cannot be concentrated sufficiently at any given attack site to stop gallery construction by the beetle or the spread of the associated blue stain fungus. The production of sufficient defenses, therefore, appears to be a threshold phenomenon (Raffa and Berryman 1983).

Because the energy utilized in hypersensitive response is a mobile pool of sugar (Raffa and Berryman 1982), the resistance to beetle attack will be adversely affected by a wide range of stresses. Decreases in plant resistance associated with shading, drought stress, and nutrient limitations will, therefore, be linked either to decreases in the pool of non-structural carbon or an inability to metabolize those reserves into toxic monoterpenes. The production of resin acids, for example, has been shown to be important to the wound response of *Pinus sylvestris* (Gref and Ericsson 1985). Resin acids are also the most energetically costly of the oleoresin compounds to produce. Studies of *Pinus taeda*

found that resin acid production decreased sharply during drought stress and returned to normal levels when the soil moisture recovered (Hodges and Lorio 1975). It is safe to conclude that wound response would have been less effective during the period of drought stress and therefore beetle resistance would decline as well. The linkage between drought stress and beetle epidemics is, in fact, so strong that some researchers have come to the conclusion that beetle epidemics cannot occur without some form of stress to weaken the trees first (Thompson et al. 1985).

Model Objectives

The objectives of this study are to create an idealized tree that will respond optimally to the risks of overtopping and beetle attack. The probabilities of overtopping risk and beetle attack will be designed to emulate the actual risks encountered. After the initial values of the constants have been set, a sensitivity analysis will be executed to determine the sensitivity of the model to shifts in these constants. Because the sensitivity analysis is designed primarily to test model behavior rather than emulate actual shifts in the tree's

environment, the constant values will be halved and doubled in order to obtain a standard by which the sensitivity of the model can be judged.

Model Design and Structure

Tree Growth and Energy Production

In the model, the relationships of height to diameter and crown form are held constant throughout the life of the tree. The crown form and the stem form are both conic. The base of the cone that represents the crown has a radius of 1/6 the height. The radius of the cone representing the bole equals 1/150 the height. A tree 30 meters tall would have a diameter at the ground of 20 centimeters a crown width at the base of 10 meters.

The energy production of a tree through photosynthesis (GPP) can be described by the equation:

GPP = Leaf Area * Mean Productivity/Unit Leaf Area (5)

The leaf area of any stand of trees increases quickly after perturbation such as logging and then, as the site reaches full occupancy, levels off at an

asymptote that can be considered the carrying capacity of the stand (Gholz 1982). The composition and relative abundance of the plants that hold the leaf area on the site will vary but the total leaf area remains constant except in areas of extremely high tree density, where it drops somewhat (Waring 1983). This model assumes that the ground area that is covered by the base of the crown is fully occupied by the tree and that the leaf area index (LAI) can therefore be held constant. In the model, the leaf area of the tree equals the surface area of the cone. Using this relationship, the LAI becomes ≈ 6. Normal LAI's for lodgepole forests range from 4.5 to 9.9 (Pearson 1983).

The photosynthetic efficiency of each unit of leaf area is dependent upon the effects of many factors: temperature, moisture, light intensity, nutrient availability etc.. Because these factors are related to site, this model assumes that the yearly mean photosynthetic productivity of a unit of leaf area will be constant on a specific site. The maintenance respiration for a given leaf area is also considered to be constant. The amount of energy produced per year by a unit of leaf area minus the energetic costs of maintaining that unit therefore may be standardized to 1

unit. When energy is referred to in the model, it is always the units: 1 unit = Net energy fixation per square meter of leaf area per year (NEF).

The maintenance respiration costs for the woody portion of the tree are considered to be directly proportional to the sapwood volume. This assumption presupposes that there is a constant relationship between above-ground living biomass and below-ground living biomass throughout the lifespan of the tree (a constant root/shoot ratio). This, in fact, is not the case. The percent of biomass allocated to the roots increases with age (Grier et al. 1981) drought stress (Keyes and Grier 1981) and stocking density (Pearson et al. 1984, Worrall 1985). Of these shifts, only the shift with age is within the scope of the model. Because of the lack of a clear rationale as well as available data for pines, this shift is ignored in this study.

The leaf area of trees can be accurately approximated by measurement of the sapwood basal area (SWBA) at some point on the stem such as dbh (1.37 meters) or the base of the crown (Waring 1983). The relationship varies greatly with species and with the moisture regime on the site, as well as with the location on the stem at which the sapwood basal area is measured.

It can be stated with a high degree of confidence, however, (r^2 = .98 for lodgepole pine; Waring et al. 1982) that for a given site, species and measurement location, the leaf area of the tree exists in a linear proportionality with sapwood basal area. In the model, this relationship is turned around and the leaf area is used to predict the Sapwood basal area. Sapwood volume (SWV) is, therefore:

$$SWV = C * LA * H \quad (6)$$

Where:
C = a constant
LA = leaf area
H = tree height

The energy available for allocation (NPP) to either growth or defenses is the NEF minus the respiration costs of the woody tissues. Because of the assumptions made in the preceding paragraphs, both the NEF and the respiration costs are functionally related to the height of the tree and can be modeled in the equation:

$$NPP = C * H^2 - H^3 \quad (7)$$

Where:
NPP = yearly net primary productivity
H = height
C = a constant

Since the leaf area is proportional to the sapwood basal area and the maintenance respiration costs are proportional to the sapwood volume, the tree cannot compensate for the vertical growth of sapwood in the stem or longitudinal growth of sapwood in the roots by the production of additional leaf area. Vertical stem growth and associated woody root growth can only be accomplished at the cost of a decrease in the overall NEF/Respiration cost ratio. Height growth, therefore, becomes increasingly expensive and eventually, the tree will approach a maximum height at which NEF = Respiration; a compensation point. (Figure 1)

To keep the crown form fixed, additional height growth requires lateral growth as well as vertical growth. Both lateral and vertical growth involve the production of new needles and the branches to support them. In the model, the energy cost of an additional unit of height growth is a function of the energy required to produce the additional conic volume required to keep the dimensions of the crown constant. The energetic cost of producing new tissue can be varied with a constant. (Figure 2)

In this model, the tree has an energy allocation choice between growth and defensive chemistry. To gauge the costs of an energy allocation for non growth, it is necessary to know what the potential growth of that tree could have been if all of its energy had been allocated to growth. In the model, this is referred to as the potential height. The equation for maximum height growth is:

$$MG = \sum_{i}^{n} NPP_i / \text{Marginal growth cost}_i \quad \text{(Figure 3)} \quad (8)$$

Where:
MG = maximum height growth
n = the number of years in the growth period
NPP = net primary productivity in the i^{th} year

Beetle Production

Beetle production is a function of the total phloem volume available for colonization. The assumption is that there is a constant relationship between the volume of beetles produced and phloem volume consumed. Because attack behavior is near optimal, and consumption efficiency is constant and does not vary with phloem thickness (Amman and Cole 1983), the volume of beetles

can be derived directly from the volume of phloem. If the beetles are considered to be the same size, then beetle numbers can be substituted for beetle volume.

Phloem thickness for a given year is related to xylem growth in that year. In this model, phloem production is held as a fixed proportion of xylem production (1:6; Brown 1970) and may, therefore, be determined from total diameter growth in a given year. This in turn is linked to height growth due to the fixed height-diameter relationship.

The thickness of phloem that is usable by the bark beetles is related not only to the present year's production but also the production that occurred for up to 40 years into the past (Cabara 1978). The phloem produced in past years, however, is compressed and incorporated into the bark. The compression, according to Cabara, doubles with each year since the phloem was produced. The volume that the beetles can utilize is, therefore, all of the present year's phloem (P_t) + 1/2 * (P_{t-1}) + 1/4 * (P_{t-2}) and so on. For n years into the past the equation for phloem thickness is:

$$\text{PHLOEM} = \sum_{t=0}^{n} (0.0011 * \text{HEIGHT GROWTH})_t * 1/2^t \quad (9)$$

This equation does not quite match with the supposition that beetles can utilize growth up to 40 years back (the average was 21 years); $1/2^{40}$ is a very small number. In the model, $1/1.5^{t}$ is used as the depreciation factor and n is set equal to 10 to reduce execution time.(Figure 4)

The area available for colonization is considered to be the lower 1/3 of the bole.(Figure 5) From field studies it has been found that smaller diameter trees in the 20-23 centimeter diameter class were attacked to an average height of 6.1 meters or less and that trees in the 51 centimeter diameter class were colonized to an average height of 12.2 meters (Amman and Cole 1983). In the model, because the diameter of the trees was assumed to be proportional to its height, height could be substituted for diameter. In the model, a tree with a diameter of 51 centimeters has a height of 38.1 meters; a tree with a diameter of 20 centimeters has a height of 15.2 meters. The bole height available for beetle colonization is, therefore, 12.7 and 5.1 meters respectively.

If area available for colonization is held fixed (on a given tree) then beetle numbers will vary in a linear fashion with phloem thickness. The model, therefore,

utilizes a linear regression based on laboratory hatching data (Equation 2, page 12) to estimate maximum potential beetle numbers, with the constraint that the equation is not allowed to become negative. (Figures 6 and 7)

Actual production of beetles in the field will, of course, be less than the production achieved in the laboratory. The maximum potential beetle production, which is defined by the regression, will be decreased by a number of field related factors such as weather events, predation etc. The only factor contributing to beetle mortality that is modeled is desiccation in smaller diameter stems. The mortality from desiccation is considered to be directly proportional to the ratio of surface area/internal volume of the stem. (Figure 8)

The Optimization Process

The model uses a discrete time Markov decision process (Mangel and Clark 1985, Clark 1985). The fundamental property of Markovian models is that the probability of a phenomenon occurring within a system is related to the state of the system. Weather, for instance, can be considered to be a Markovian process if the probability of clear weather at time t + 1 is linked

to the weather at time t. In the modeling approach developed by Mangel and Clark, the assumption is that the optimal (and presumably observed) behavior pattern of an organism at time t + 1 is related to the state of the organism at time t. The variables that define the state can be anything, but usually they are such things as energy or age.

For an optimum to exist, the system must have opposing risks and benefits that can be altered by available behavioral choices. For an animal, a benefit might be the probability that it will acquire food, and the risk the probability of death through predation while searching for that food. In plants, the benefits and risks lie in the energy partitioning strategy that is chosen. Acquired energy can be allocated to growth (which can be sub-partitioned into roots, leaves, etc.), to storage as a mobile carbohydrate pool or converted to defensive chemicals that are very expensive to create and cannot be re-metabolized into energy for growth. The chief benefit derived from allocation of a given amount of energy to growth is that the tree avoids being overtopped; it is able to acquire the light that it needs to survive. Because the amount of energy is finite, allocating a unit of energy to the production of

structural tissues means that a unit of energy is not available for allocation to plant defense systems. The tree therefore must choose between opposing risks and, whatever the choice, there will be survival consequences. When the problem is stated in this manner, it becomes clear that, for any given time and state, there will be an allocation strategy that will be best, a choice that will maximize the probability of survival.

In the model, the trees have 10 options concerning energy allocation ranging from allocating all their energy to growth or diverting up to 0.9 of it to defense.

The optimization equation is:

$$P(H,t) = \max_i [\mu_i \quad \delta_i \quad P(H'_i, t+1)] \qquad (10)$$

Where:

- P = the probability of survival from age t through to the terminal age T assuming optimal choices at all ages t+1 → T
- H = height at age t
- H'= height at age t+1
- t = the age
- i = the discrete allocation choice
- β = the probability of beetle attack at a given Height
- σ = the probability that, if attacked, the tree is killed
- μ = 1 - (β σ) ; probability of survival (beetle) during a given time step
- δ = the probability of being overtopped and dying in a given time step

For a given height, age and allocation choice, the tree will face a specific beetle risk, a risk of being overtopped and killed in that time step and, coming into the next timestep with the acquired growth ($H + Energy_i$), the probability of surviving the remaining steps. The trade-offs can be viewed as a balance between short and long term survival goals.

Setting the Probability Values:

The probability of being overtopped is a function of the height difference between the height that is achieved at a given time and the height potential, the height that could have been achieved at that same age if all available energy had been allocated to growth. The greater the difference between the actual and the potential height, the greater the chance that another plant will be able to overtop the tree and cause it to fall below compensation point and die. As this difference increases, the probability of being overtopped increases exponentially. (Figure 9) The probability of being overtopped in a given year is always computed as a function of the distance below the potential height for that particular timestep. The rationale for this is that

the ability of a tree to obtain light is related to the position of its competitor trees in relation to the position of the sun. Sun angle does not shift with canopy height and therefore it may be supposed that a tree that is 10 feet below a 50 foot canopy will be exposed to the same risk as a tree that is 10 feet below a 20 foot canopy. The exponential nature of the curve is based on the diffusion of light as it passes through a canopy. This follows Beer-Lambert's law. The general equation is:

$$dI/dz = -K * \Sigma LA \qquad (11)$$

Where:

I = light intensity
z = vertical distance into the canopy
Σ LA = sum of the leaf area above z
K = a constant

(Adapted from Waring 1983)

The probability of beetle kill has two parts: First, the probability that the tree is attacked and second, the probability that, if attacked, the tree is killed. The probability of attack is a function of diameter. (Figure 10) The probability of tree death if attacked by beetles is a function of energy allocation per unit volume of sapwood. (Figure 11) The available energy per unit volume of sapwood declines rapidly with size, but since

the resistance of the tree to beetle attack is viewed as a threshold phenomenon, the energy level is allowed to get quite low before the probability of the tree's increases appreciably. After that threshold has been crossed, the probability of death increases rapidly. (Figure 12)

Model Structure

The programs used to generate the data presented in this thesis are written in Turbo Pascal (Turbo Pascal is a registered trademark of Borland International, Inc.) and can be executed on any micro-computer running under MS-DOS (MS-DOS is a registered trademark of Microsoft Corp.).

The model consists of three separate modules. In the first module, TREEGR.FIL, the optimal energy allocation choices are determined by dynamic programming.(Figure 22; Appendix A) The maximum potential height is computed first. The program then computes the probability of survival for all ages, heights and energy allocation choices. Because most optimal energy allocation strategies produce growth patterns that are not far from the height potential, probabilities are only

computed for heights between height potential and 6 meters below the height potential in 1/3 meter increments. This limits the matrix size, and so reduces execution time and saves computer memory space. The energy allocation choices are limited to discrete intervals of 10 percent for the same reason. For each age and height, the energy allocation choice that gives the highest probability of survival is selected and is stored with its associated probability in an array for the next recursion. As the program executes, the energy allocation choices, and probabilities of survival through the final time step are displayed.

At the program's conclusion, the best choices, probability of overtopping, probability of beetle kill and the probability of survival through the last timestep, for each age and height are stored in binary files for use by the second module. Because of error buildup in the recursion program, TREEGR.FIL uses a five-year time step.

The second module, TREEGR.SIM, is a simulation and data display program. (Figure 23; Appendix B) The simulation procedure utilizes the data generated in TREEGR.FIL. In the simulation, a tree is grown using the optimal energy allocation choices generated previously.

At each time step, the probabilities of death through beetle kill or overtopping generated in TREEGR.FIL are compared with numbers created by a random number generator and the tree either lives or dies. The output of the simulation run can be viewed individually, or the data generated by multiple simulation runs (up to 32767) can be saved in standard ASCII text files for importation into Lotus 123, a spread sheet and graphics program (Lotus 123 is is a registered trademark of Lotus Development Corp.). In addition to these forms of output, the module allows one to look at the array of allocation choices generated by TREEGR.FIL and the choices that the simulated tree takes during its lifetime.

The third module TREEGR.EQU is similar to TREEGR.SIM with the exception that it utilizes allocation choices that are generated by pre-specified equations rather than by optimization. (Figure 24; Appendix C) This makes this module a stand- alone program that may or may not be tied to the optimization process. In this module, allocation choices can be generated by constants, smooth curves, or simplifications of the output from TREEGR.FIL. Simulation runs can be viewed individually or multiple runs can be saved and imported into Lotus 123 (See

above). Because this program does not employ a recursion formula to derive the allocation choices, it is numerically stable and can be run using a one year time step. This sensitivity allows the computation of beetle production as well. If the simulated tree is killed by beetles, the program computes beetle production based on the tree's size and phloem thickness at the time of death.

The use of equations to generate the allocation choices also allows the computation of mean probabilities of survival and mean probable beetle production as well as the age and diameter of maximum probable beetle production for a given allocation strategy. This mean data can also be saved in text files for importation into Lotus 123 (See above).

In addition to these three modules there is a peripheral module ARRCHK.PAS that can be used to view any of the data generated by TREEGR.FIL. (Appendix D)

Model Results

Patterns of Energy Allocation

When a tree is small, the potential rate of height growth is large and the beetle risk is insignificant.

When the tree is large, height growth is expensive and the risk of beetle attack is high. Since risk of overtopping is a function of the distance between the actual height and the height maximum, an allocation to defensive chemistry in the early years will put the tree permanently at risk. Height loss cannot be made up by a later allocation to growth. If a tree is 2 meters shorter than the height maximum at age 10, then it will be at least 2 meters shorter at age 125. Falling behind in growth in the juvenile period, therefore, will permanently increase the probability of overtopping death and the tree will be forced to allocate energy towards growth regardless of the risk of beetle kill.

With increasing size, the potential growth rate declines and the probability of beetle attack increases. This in turn causes a characteristic shift in energy allocation strategies as is seen in the array of allocation choices generated by TREEGR.SIM. (Table 1) In early life, the allocation is primarily to growth; in later life the allocation is primarily to defensive chemistry. The pattern of choices that a simulated tree takes through the course of its life exhibits three stages. (Table 3) The first, the juvenile stage, is characterized by a total domination of the risk of being

overtopped and 100 percent of the energy allocation is to growth. The middle period, the mature stage, is characterized by a constant allocation strategy that represents an equilibrium between the two risks of overtopping and beetle attack. This equilibrium occurs because allocation to growth means allocation away from defense and vice versa. A tree that allocates all of its energy to growth in one time step will place itself in an area of the matrix in which the optimal allocation is heavily shifted to defense. This allocation choice will, in the next time step, leave the tree further from the potential maximum height and shift the allocation back towards growth. This process will seek an equilibrium and that equilibrium will be maintained until the tree is unable to maintain it through shifting allocation. Ideally, oscillations should converge rapidly to an equilibrium, but in the model the limitation of discrete 10 percent allocation choices causes overshooting. The middle period, therefore, is characterized by a stable oscillation around this equilibrium. The last stage is characterized by a domination of beetle risk and a total allocation to defensive chemistry. This is due to the small shifts in potential height from year to year and the greatly increased beetle risk due to the inability to

allocate sufficient resources per unit of sap wood volume and greater probability of attack due to the larger diameter size. This three stage energy allocation strategy is very robust and exists unless one of the probabilities completely overwhelms the other. If the risk of overtopping is too high, for instance, optimal allocation will be 100 percent to growth at all stages of life.

Beetle production

Mean probable beetle production over time always forms a mound shaped curve with a clearly defined maximum. If the allocation strategy is a constant allocation or a smooth function, then the curve form of maximum probable beetle production is simple and is very closely linked to the available energy curve. If the allocation is discontinuous, such as is the case with the three stage allocation strategy generated by dynamic programming, then the curve is oddly shaped and has interesting properties. (Figures 13 and 14) In either case, the energetics of the system dominate the probable beetle production except at very small tree sizes where

desiccation begins to dominate beetle production dynamics.

Whatever the allocation strategy, there will be a point at which the surface area of the bole is large, phloem is still thick, and energy per unit volume drops off sharply. When the tree is smaller than the height at which maximum beetle production occurs, energy per unit volume is high and probability of attack is low. At sizes above this maximum, risk of death through beetle attack is high regardless of allocation strategy, but the thin phloem limits beetle production. It is in this "window" (Berryman 1982) that the risk of epidemic beetle outbreak is the highest.

Sensitivity Analysis

Two sensitivity analyses were performed, one using the optimization model (TREEGR.FIL) and the other using fixed allocation strategies (TREEGR.EQU). In the first, probabilities of beetle attack and of overtopping were shifted. (Table 3) In the first analysis, model behavior was very predictable. Either an increase in overtopping or a decrease in probability of beetle attack caused the allocation of energy to shift toward growth; a decline of

overtopping risk or an increase of beetle attack risk caused an allocation shift toward defensive chemistry. The three-stage pattern of allocation strategy was very durable and remained in tact over the range of the parameter shifts tested.

The second sensitivity analysis looked primarily at shifts in beetle production and probability of survival. In this analysis, energy allocation is held constant over time and various parameters are shifted. (Table 2 and Figures 15 - 20). Allocation to growth is fixed at four levels: 100, 85, 70, and 55 percent (0, 15, 30, 45 percent to defense). Greater allocations to defense cause an exponential decline in the survival probabilities in all cases and therefore were not included as reasonable alternatives in the analysis.

Those strategies allocating from 100 to 70 percent to growth yielded the highest probability of survival under all tested conditions. Here again the model behaves in a reasonable manner: increases in the risk of beetle risk attack cause the best allocation choice to shift toward defense; increasing overtopping risk causes the best constant allocation strategy to shift toward growth. The variable that has the largest impact on survival is the probability of beetle attack, but this

parameter has little effect on the behavior of the tree. Shifting the risk of overtopping has the greatest effect on the optimal energy allocation strategy, but has no effect on the numbers of beetles produced or the age at which maximum beetle production occurs.

The condition that has the greatest effect on overall system behavior is the photosynthetic efficiency of the leaf area. The reason that this parameter is so influential is that it shifts the energy curve and this in turn affects the behavior of all other parameters in the model. If the photosynthetic efficiency is doubled, the best allocation strategy is 100 percent to growth due to the rapid growth rate that is possible. The maximum probable beetle production is a factor of 10 higher than any other strategy due to the large diameter (65.9 cm) and thick phloem. Interestingly, the probability of survival goes down with increasing photosynthetic efficiency. This is due to the greater risk of overtopping (steeper slope of the potential growth curve) and the number of time steps that the tree spends in high risk diameter classes. A highly productive site will produce larger trees but the potential for beetle outbreak is greater. The presence of outbreaks on droughty sites cannot, therefore be explained by mean

water availability but rather by the probability of occasional severe drought, a conclusion that is incorporated into the Canadian risk rating system (Safranyik et al. 1975). Changing the resistance to beetle attack had little influence on survival probability at various levels of allocation to growth. Changing the phloem retention affected beetle production but not survival probability.

In the optimization algorithm, storage of energy is impossible because of the backwards recursion. Because this sensitivity analysis was independent of the dynamic programming, the ability to store energy allocated to defense in past years was modeled. It was assumed that not all of the past energy would be available, that some would be lost through incorporation into the heart-wood or the bark as well as through wounding, drought stress and other stresses that occur yearly and would serve to deplete the mobile reserves. Storage is, then, modeled as having a depreciation factor built in. Two types of depreciation were modeled: an exponential decline which holds most of the recent years' energy and then declines sharply, and a linear depreciation that loses 10 percent for each year one moves into the past. Both of these strategies decrease the beetle production, move the

optimal allocation toward defense and cause the maximum beetle production to be at a slightly later age (due to energy carried over from previous years).

Two things become clear when one views the data in Table 2. The first is that the energy status of the tree, which is dependent upon leaf area and respiration costs, is of overriding importance to the system. If energetic conditions are right, the beetles will be produced. Looking at the graphical displays of the sensitivity analysis, this becomes even more clear. (Figures 15-20) If one compares the energy curve (Figure 1) to the beetle production curves, the relationship becomes obvious. The only curves that are very different are those in which the energetics of the system are radically altered by shifting the photosynthetic efficiency.

The second is that, while the trees can completely eliminate beetles from the stand by allocating energy to defense (Figure 21), it is not of survival value to do so. The energy allocation strategies that optimize the survival of the trees also produce large vulnerable trees and high beetle production levels. Elimination of the beetles simply costs the trees too much in terms of growth and competitive ability.

In order to apply the results of this sensitivity analysis to actual stand conditions, it is important to understand that the tree that is modeled is not incorporated into a stand. There is no direct competition or unsuccessful beetle attack that would trigger a energy allocation shift. Shifting a risk parameter is, therefore, artificial. Increases in competitive stress in a stand should, however, cause similar shifts in allocation priorities. If a tree is affected by shade competition or is attacked by beetles, allocation should shift away from the optimal choice determined in the model and toward total energy allocation to guard against the perceived threat. A closed stand, for instance, should be allocating nearly all of its energy to growth; a residual tree that has been strip attacked by beetles and has had its neighbor trees killed should allocate nearly all of its energy to defense.

The shift in allocation in a closed stand to growth does not, however, mean that the trees will grow taller than open grown stock, it merely means that they will allocate more of their energy to height growth. Due to the limitations of water, light and total leaf area that a closed stand exhibits, there may be less total energy

to allocate. Under these circumstances, even with a total allocation to growth, the growth rate may be less in a closed stand.

Conclusions

The conclusions that can be drawn from a theoretical model such as this are in the form of trends, patterns, system strengths, weaknesses and sensitivities. One of the model's most interesting aspects is the three stage allocation strategy. Simulation runs using simplified three stage strategies have higher survival probabilities than the best constant strategies. A crude three stage strategy of 100, 80 and 10 percent to growth (standard parameter settings) produces a probability of survival of 0.03. The best fixed allocation, 86.5 percent to growth, produces a survival probability of 0.028.

It is legitimate to question the extent to which this three stage pattern is an artifact of the model. The fact that it has three stages is, it seems, clearly caused by the presence of two competing risks. How would the pattern shift if there were many competing risks? Modeling a multi-risk system is beyond the scope of this study, but an understanding of the driving mechanisms

that create the three-stage pattern allows one to hypothesize about more complex systems. The clearly defined juvenile period in which allocation to growth dominates should be present in almost any system of competing risks. The dominance of juvenile energy allocation to growth is caused by the slope of the growth curve at this period of the life of the tree. This pattern should, therefore, remain intact in any system where vegetative competition is an important factor. The mid-life equilibrium should also be present in multi-risk systems. A locally stable equilibrium that exists during much of the tree's life will exist whenever there is a balance between risks. One aspect of this equilibrium, however, that may change with the addition of other risks is its stability. If the region of local stability becomes too narrow, then the mid-life period may be characterized by a series of rapid shifts in energy allocation. The late period of total domination by beetle risk is probably artificial. With many competing risks, one would expect the late life allocation patterns to be complex.

The pattern of a locally stable mid-life will create a system in which minor perturbations can lead to major energy allocation shifts. This pattern would allow the

trees to respond suddenly and with force to threats when they first occur rather than waiting for the stress to become serious and then reacting, a pattern that would prove prove to be highly advantageous in the case of bark beetle attack.

The role of the innate strategy in terms of stand dynamics and stand management is that if the allocation is being shifted away from the norm by an increase in a particular risk factor, then the removal of that risk factor will shift the tree to the innate strategy. Thinning a large old growth stand, for example may not produce a marked increase in growth but should create a very beetle-proof stand. One of the interesting predictions of the model is that the trees can prevent beetle production through a reallocation of energy into defensive chemistry in the larger diameter classes. (Figure 14) If this is in fact the case, then allowing the trees to move toward their innate strategies by thinning should create a beetle-resistant stand even if no growth release is seen.

The ability of trees to allocate their resources to defense could help to explain why many trees survive beetle epidemics even though they have been strip attacked during the outbreak (Stuart et al. 1983). One

might suppose that trees that were attacked by beetles and whose cambium was killed by *Ceratocystis spp.* infection on up to 1/2 of the lower bole would be extremely susceptible to future attack. However, the combination of thin phloem, increased light due to the death of competitor trees and an ability to shift their energy allocation to defense could make the stand suddenly quite durable. The idea that old growth stands can become beetle-resistant if thinned was verified by recent work done by Waring and Pitman (1985). They found that old growth lodgepole stands could be made beetle resistant by removing 80 percent of the canopy.

The model suggests that thinning in large diameter stands will have a greater effect on the stand's resistance to beetles and that thinning a smaller stand will cause a greater growth response. In large diameter stands, the innate allocation strategy is shifted toward the production of defensive chemistry. Because the innate allocation strategy in small diameter trees is 100 percent to growth, thinning should not cause a similar shift towards an allocation to defensive chemistry and a height response should be seen.

Another robust property of the model is that the optimal allocation strategies are also strategies that lead to the production of large numbers of beetles, even though a heavier allocation to defense can entirely eliminate beetles from the system. Bark beetles are and will be an intrinsic part of lodgepole pine ecosystems because the survival costs involved in eliminating them are simply too high. When the best allocation strategies are chosen, the mean probable beetle production reaches a clearly defined maximum when the trees achieve diameters of ≈ 30 cm and ages of ≈ 70 years. This is very similar to the classification (greater than 8 inches (20 cm) and older than 80 years) that defines a high risk tree in Amman's risk rating system (Cole and Amman 1980).

Perhaps the most dominant aspect of the model is the extent to which the balance between energy production and respiration controls every aspect of the system, and in particular controls beetle production. A mound shaped available energy curve will produce a mound shaped beetle production curve. The steeper the slope of the energy curve, the more volatile the beetle population dynamics will be. Steep energy curve slopes translate into periods of thick phloem with rapidly declining energy per unit volume of sapwood. A tree that is at a low energy state

for an extended period of time, cannot produce beetles in any quantity due to thin phloem. Reductions in growth, therefore, such as are caused by a reduction in photosynthetic efficiency dramatically decrease the probable beetle production. (Figure 19) For this reason, open grown stands can be expected to become high risk as the trees approach their size maximums. The model suggests that early thinning and stand density control will not produce a durable stand.

Modeling Problems and Future Needs

For modelers, this model suggests a few cautions. First, behavioral equilibriums may be, and in fact probably are, the result of very fine tuned balances; locally stable equilibria that will collapse and act erratically if the system is not modeled with precision. Without the inclusion of some sort of optimization in a model it will be difficult for the modeler to find the balance points. Consider the problems facing a normal sensitivity analysis if there are multiple allocation choices. There will be millions of potential strategies and no way to choose between them except to simulate multiple times and maximize. If the program takes

several minutes to run, the approximation method can take days of computer time before closure is achieved. In more complex models with multiple equilibria, this simulation approach may be impossible; it is simply too bulky.

If optimization algorithms are to be included into models, then there is a heavy price to be paid. The total number of parameters that can be addressed in dynamic programming is extremely limited. Each new parameter must be entered as a separate dimension in a matrix. If, for instance, one wished to model allocation using age, height and crown condition as the "state" variables, then for every age, height and total leaf area there would be a optimal allocation choice. This seems simple, but the matrix that would be created would be three dimensional rather than two. If one allowed 100 possibilities per dimension (100 different heights for instance), the matrix would contain $1 * 10^6$ locations. Even a small fourth dimension ,for instance, 10 levels of stocking density would create a matrix that exceeds the hard disk capacity of most micro computers. In short, dynamic programming involves an extremely inefficient use of computer memory space.

There are other problems as well. Phenomena that occur during the lifespan of the organism are almost impossible to model dynamically. For instance, a tree should be able to store energy allocated to defensive chemistry from year to year with some rate of depreciation for incorporation into bark and heart-wood and the draining of these reserves by other stresses such as defoliation or drought. The equation for stored energy would involve the sum of the past years allocations multiplied times a depreciation factor:

$$\text{Energy} = \sum_{i=0}^{n} \text{Allocation}_i * 1/z^i \qquad (12)$$

Where:

n = the number of years prior to the present age

z = the depreciation constant

This will affect the optimal allocation choice at any point in time because it shifts the probability of death if attacked. This seems simple, but it cannot be modeled using a recursion algorithm that iterates backwards to age zerobecause the amount of energy saved is itself a secondary product of the allocation choices that have not yet been made in the recursion process.

Another disadvantage of dynamic programming is that recursive processes tend to be unstable; the errors build up exponentially because the errors of one step are used in the computing of the next step and, so on. Since errors in the preceding step always out weigh errors in the present step, there is no mechanism for self correction. In the algorithm that I was using, the results were not trustworthy at 125 time steps (confirmed by simulation). The optimal allocation patterns were, therefore, constructed on a 5-year rather than an annual time step. This problem can, unlike the two previously mentioned problems, be addressed through improved programming - more precise interpolation would help - but no matter how precise the interpolation, the choice will have to be made between the precision derived from shortened time steps and the imprecision that results from error build up.

A limitation of the model as it stands is that it is not designed to simulate the energy allocation of trees in a closed stand. In a stand, the leaf area per tree, stem form, above ground/below ground NPP ratio, photosynthetic efficiency and other physiological processes shift as the level of competitive stress increases. If the model is to be of greater utility, it

must be able to accurately shift these parameters so as to emulate an average codominant tree in stands of varying site qualities and densities.

Competition is never directly addressed in this model, and this is in part because the dynamic programming algorithm will not allow it (shifts in competition are the sort of secondary phenomena that were mentioned above.) One way to approach competitive simulation is to create a group of trees with various strategies and rules concerning competition (light allocation, leaf area allocation etc.). The trees' growth could then be simulated as a group and the individual with the highest probability of survival would have the best strategy in a competitive system.

Possibilities for Experimental Verification

The actual probabilities of beetle attack and of competitive stress that a tree is programmed to respond to can probably never be found. The actual numbers, however, are not important to model performance. What is important is the relative size of the risks and the anticipated shifts in allocation if these probabilities are changed. Because the model is defining a default

strategy, one that will be taken in the absence of stress, experimental verification of the model would be best tested under carefully controlled greenhouse conditions. Lacking these, a plantation setting in which the trees are widely spaced would probably make an acceptable substitute. The following model conclusions can be tested:

1. There will be a sharp shift in percent allocation to mobile carbon that is associated with tree size. If a plantation contained trees of various age classes (and therefore sizes), above ground NPP, sapwood volume, and mobile carbon per unit volume of sapwood could be measured and the relative allocation to this compartment could be determined. The hypothesis to be tested: No difference in percent allocation with size.

2. A similar experiment could be done to test the premise that thinning large diameter trees would cause a greater allocation shift to the mobile carbon compartment than thinning smaller trees. The measurements and hypothesis would be the same. In this experiment, the trees could not be too suppressed at the time of thinning or the shift in crown area would invalidate model results. This experiment might, therefore best be done after variable crown size and the various shifts in

physiology associated with competitive stress were incorporated into the model.

3. Trees that are adapted to areas of high levels of persistent beetle attack, such as the Yellowstone Park area, should have default strategies that are shifted toward an allocation to defence when compared with trees that are adapted to a low beetle risk area. This experiment would best be done in a greenhouse with seedlings grown from various stocks. Once again, the above ground NPP, sapwood volume and mobile carbon per unit volume of sapwood would be measured. The hypothesis would be: No difference between different genetic stocks.

Table 1

The matrix of optimal energy allocation choices generated by TREEGR.SIM. A choice of 10 means that 100% of the available energy is allocated to growth, 1 means that 10% of the available energy is allocated to growth.

	Distance Below Height Maximum (meters)									
	0.0	0.6	1.2	1.8	2.4	3.0	3.7	4.3	4.9	5.5
Age										
20	8	8	9	10	10	10	10	10	10	10
25	7	7	8	9	10	10	10	10	10	10
30	6	7	8	9	9	10	10	10	10	10
35	5	6	8	8	9	10	10	10	10	10
40	4	5	7	8	9	9	10	10	10	10
45	4	5	7	8	8	9	10	10	10	10
50	3	4	6	7	8	9	10	10	10	10
55	2	4	6	7	8	9	10	10	10	10
60	2	3	7	7	8	9	10	10	10	10
65	1	3	7	7	8	9	10	10	10	10
70	1	1	7	8	9	10	10	10	10	10
75	1	1	6	7	9	10	10	10	10	10
80	1	1	6	7	8	9	10	10	10	10
85	1	1	5	6	7	9	10	10	10	10
90	1	1	5	4	6	6	10	10	10	10
95	1	1	1	2	4	7	10	10	10	10
100	1	1	1	1	1	7	9	10	10	10
105	1	1	1	1	1	5	7	8	8	10
110	1	1	1	1	1	1	1	3	8	9
115	1	1	1	1	1	1	1	1	1	3
120	1	1	1	1	1	1	1	1	1	1

Table 2

Shifts in Beetle Production and Probability of Survival
Obtained by Changing Key Parameters
Energy Allocation Held Constant Over Time
Maximum Probabilities of Survival are Underlined

Percent Allocation to Growth	Maximum Beetle Production: Diameter(cm)	Age	Beetles Produced	Probability of Survival
Original Settings:				
100	34.4	69	245	0.0204
85	30.3	74	109	<u>0.0277</u>
70	25.2	76	34	0.0162
55	19.9	77	6	0.0029
Double Probability of Beetle Attack:				
100	34.4	69	491	0.0003
85	30.3	74	219	0.0011
70	25.2	76	69	<u>0.0021</u>
55	19.9	77	12	0.0011
Halve Probability of Beetle Attack:				
100	34.4	69	122	<u>0.1456</u>
85	30.3	74	54	0.1293
70	25.2	76	17	0.0439
55	19.9	77	3	0.0046
Increase Probability of Death Through Overtopping: (Double Exponential Decline)				
100	34.4	69	245	<u>0.0204</u>
85	30.3	74	109	0.0162
70	25.2	76	34	0.0018
55	19.7	76	6	0.00002
Decrease Probability of Death Through Overtopping: (Halve Exponential Decline)				
100	34.4	69	245	0.0204
85	30.3	74	110	0.0362
70	25.4	77	35	<u>0.0477</u>
55	19.9	77	6	0.0347
Resistance to Beetle Attack Increased; $1 - e^{(-2 * EPUV)}$: (EPUV = Energy per Unit Volume Sapwood)				
100	34.4	69	245	0.0204
85	30.7	76	99	<u>0.0383</u>
70	25.9	80	26	0.0272
55	20.5	82	3	0.0045

Table 2 Continued

Percent Allocation to Growth	Maximum Beetle Production: Diameter(cm)	Age	Beetles Produced	Probability of Survival
Resistance to Beetle Attack Decreased; $1 - e^{(-0.5 * EPUV)}$:				
100	34.4	69	245	0.0204
85	30.1	73	115	0.0231
70	24.9	74	40	0.0115
55	19.5	74	9	0.0019
Photosynthetic Efficiency Doubled:				
100	65.9	63	2511	0.0086
85	57.4	66	1306	0.0022
70	48.0	68	524	0.00001
55	39.1	73	137	0.0000
Photosynthetic Efficiency Halved:				
100	17.0	69	8	0.1859
85	14.2	68	2	0.2784
70	11.5	66	0	0.3053
55	8.5	61	0	0.2295
Ploem Retention Increased (Depreciation = 1.2^n):				
100	35.5	73	488	0.0204
85	31.3	79	228	0.0277
70	26.5	84	78	0.0162
55	21.1	87	16	0.0029
Phloem Retention Decreased(Depreciation = 2^n):				
100	34.4	69	245	0.0204
85	30.3	74	109	0.0277
70	25.2	76	34	0.0162
55	19.9	77	6	0.0029
Energy Storage Allowed; Exponential Depreciation:				
100	34.4	69	245	0.0204
85	31.1	78	89	0.0517
70	26.5	84	19	0.0396
55	21.0	86	1	0.0057
Energy Storage Allowed; Linear Depreciation:				
100	34.4	69	245	0.0204
85	32.1	83	69	0.0915
70	27.5	91	9	0.0687
55	21.9	94	0	0.0071

Table 3

Percent Allocation to Growth

Optimal Allocation Choice Trajectories Shifting

Probabilities of Beetle Attack and Risk of Overtopping

	Original	Probability of Beetle Attack		Risk of Overtopping	
	Values	Halved	Doubled	Halved	Doubled
Age	Choice	Choice	Choice	Choice	Choice
20	100%	100%	100%	100%	100%
25	100	100	50	100	100
30	100	100	50	50	100
35	50	100	50	50	100
40	50	100	60	60	100
45	70	100	60	60	100
50	70	50	70	60	50
55	70	50	60	60	50
60	70	60	60	60	70
65	70	60	10	70	60
70	90	70	10	70	60
75	70	70	10	10	60
80	70	50	10	10	50
85	70	40	10	10	40
90	60	70	10	10	60
95	50	60	10	10	40
100	10	70	10	10	80
105	10	70	10	10	80
110	10	20	10	10	80
115	10	10	10	10	10
120	10	10	10	10	10

Table 4

Model Assumptions and Constraints.

Assumptions:

1. Crown form remains fixed throughout the life of the tree.

2. Stem form remains fixed throughout the life of the tree.

3. Mean photosynthetic production per unit leaf area remains constant.

4. Respiration costs per unit of leaf area remain constant.

5. The tree captures 100 percent of the leaf area available on the site in the area covered by the base of the crown.

6. The ratio of above ground live biomass to below ground live biomass remains constant throughout the life of the tree.

7. The sap wood basal area exists in a linear proportionality with the leaf area.

8. Energy allocation possibilities allow up to 90 percent of the NPP to be diverted from growth to defense.

9. Trees behave in such a way as to optimize their chances of survival.

Constraints:

1. Trees modeled are not under competitive stress. The model assumptions will not hold in a closed stand.

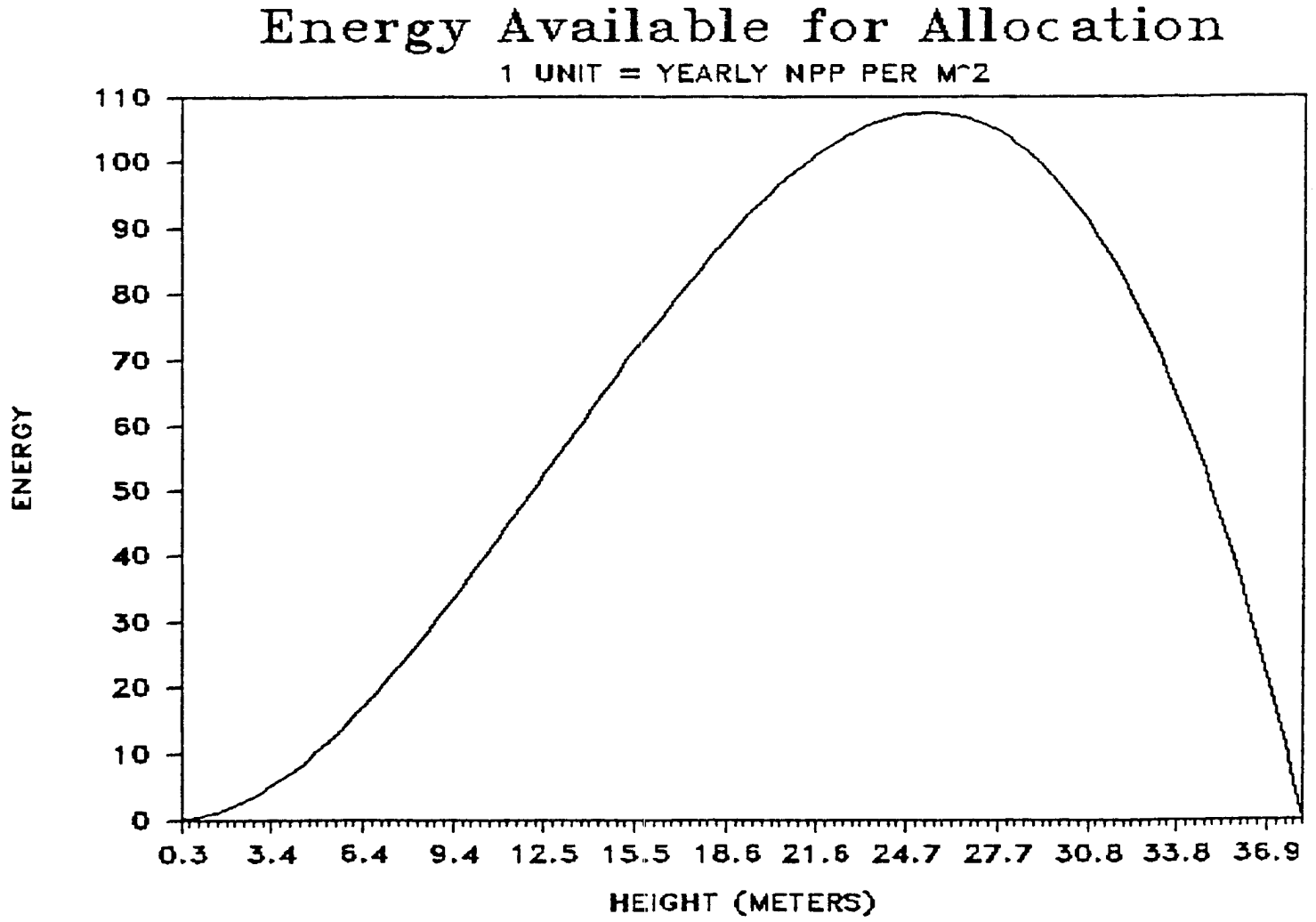

Energy Available for Allocation
1 UNIT = YEARLY NPP PER M^2
ENERGY
110
100
90
80
70
60
50
40
30
20
10
0
0.3
3.4
6.4
9.4
12.5
15.5
18.6
21.6
24.7
27.7
30.8
33.8
36.9
HEIGHT (METERS)

FIGURE 1

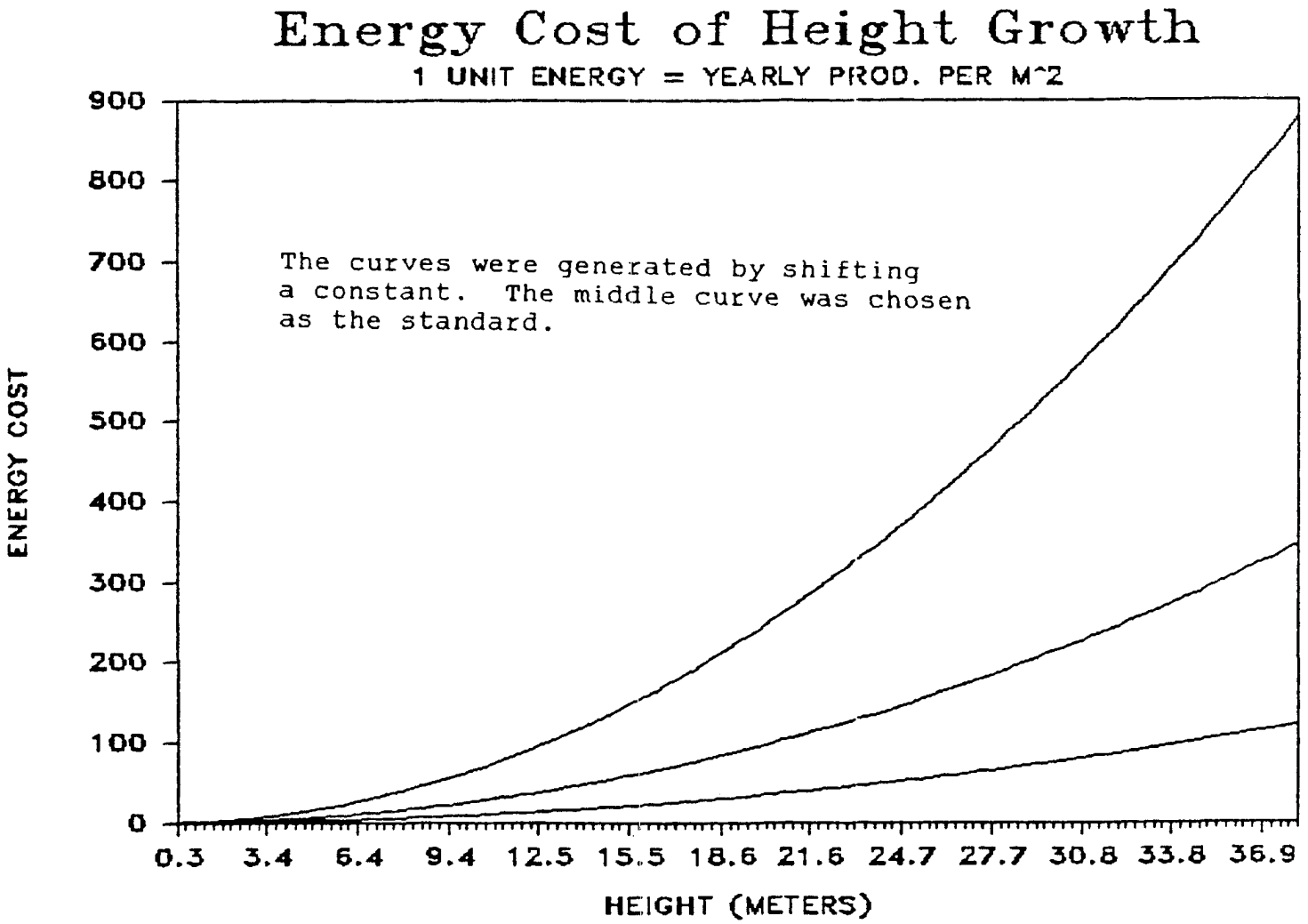

Energy Cost of Height Growth
1 UNIT ENERGY = YEARLY PROD. PER M^2
The curves were generated by shifting a constant. The middle curve was chosen as the standard.
ENERGY COST
900
800
700
600
500
400
300
200
100
0
0.3
3.4
6.4
9.4
12.5
15.5
18.6
21.6
24.7
27.7
30.8
33.8
36.9
HEIGHT (METERS)

FIGURE 2

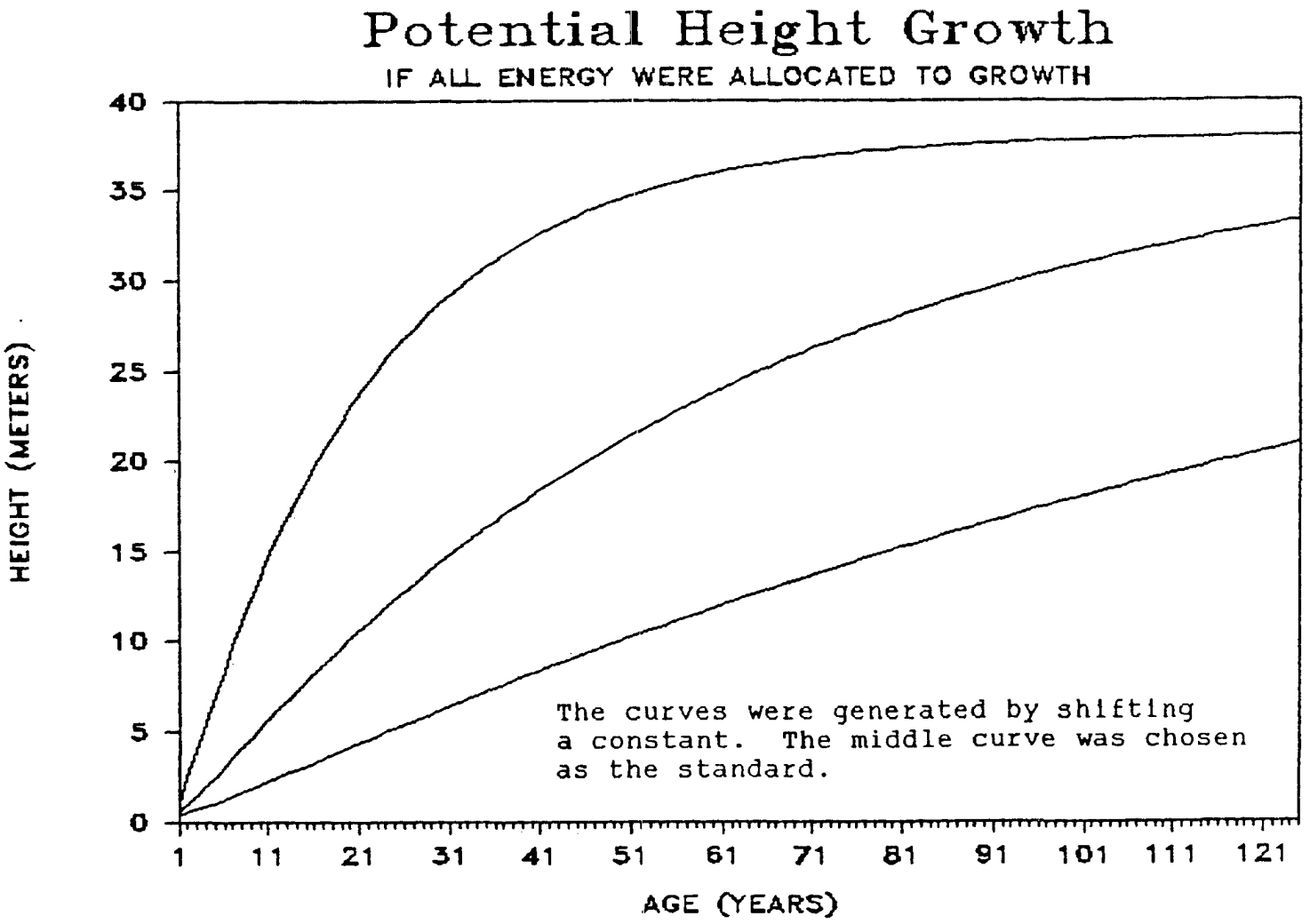

Potential Height Growth
IF ALL ENERGY WERE ALLOCATED TO GROWTH
HEIGHT (METERS)
40
35
30
25
20
15
10
5
0
1
11
21
31
41
51
61
71
81
91
101
111
121
AGE (YEARS)
The curves were generated by shifting a constant. The middle curve was chosen as the standard.

FIGURE 3

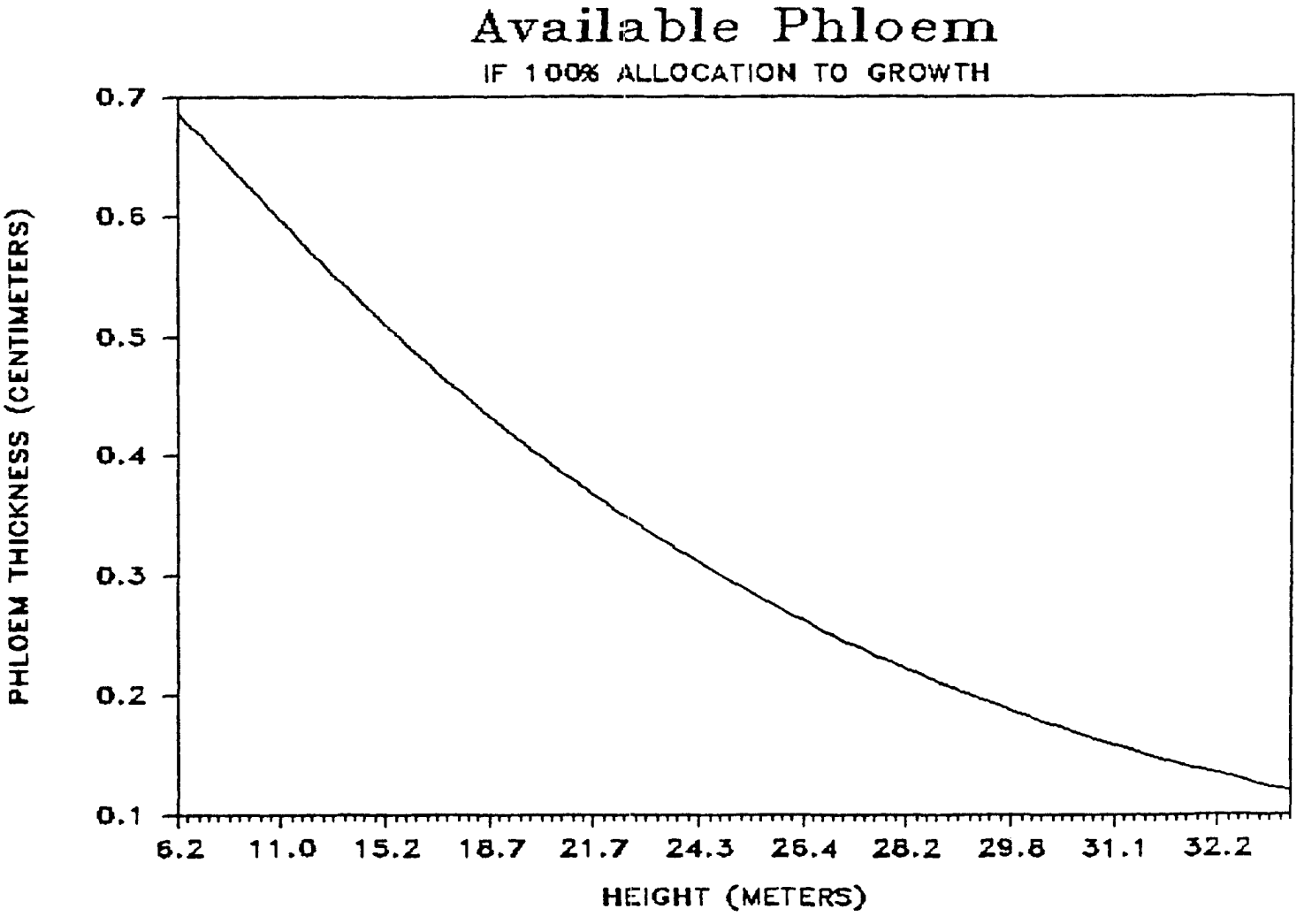

Available Phloem
IF 100% ALLOCATION TO GROWTH
PHLOEM THICKNESS (CENTIMETERS)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
6.2
11.0
15.2
18.7
21.7
24.3
26.4
28.2
29.8
31.1
32.2
HEIGHT (METERS)

FIGURE 4

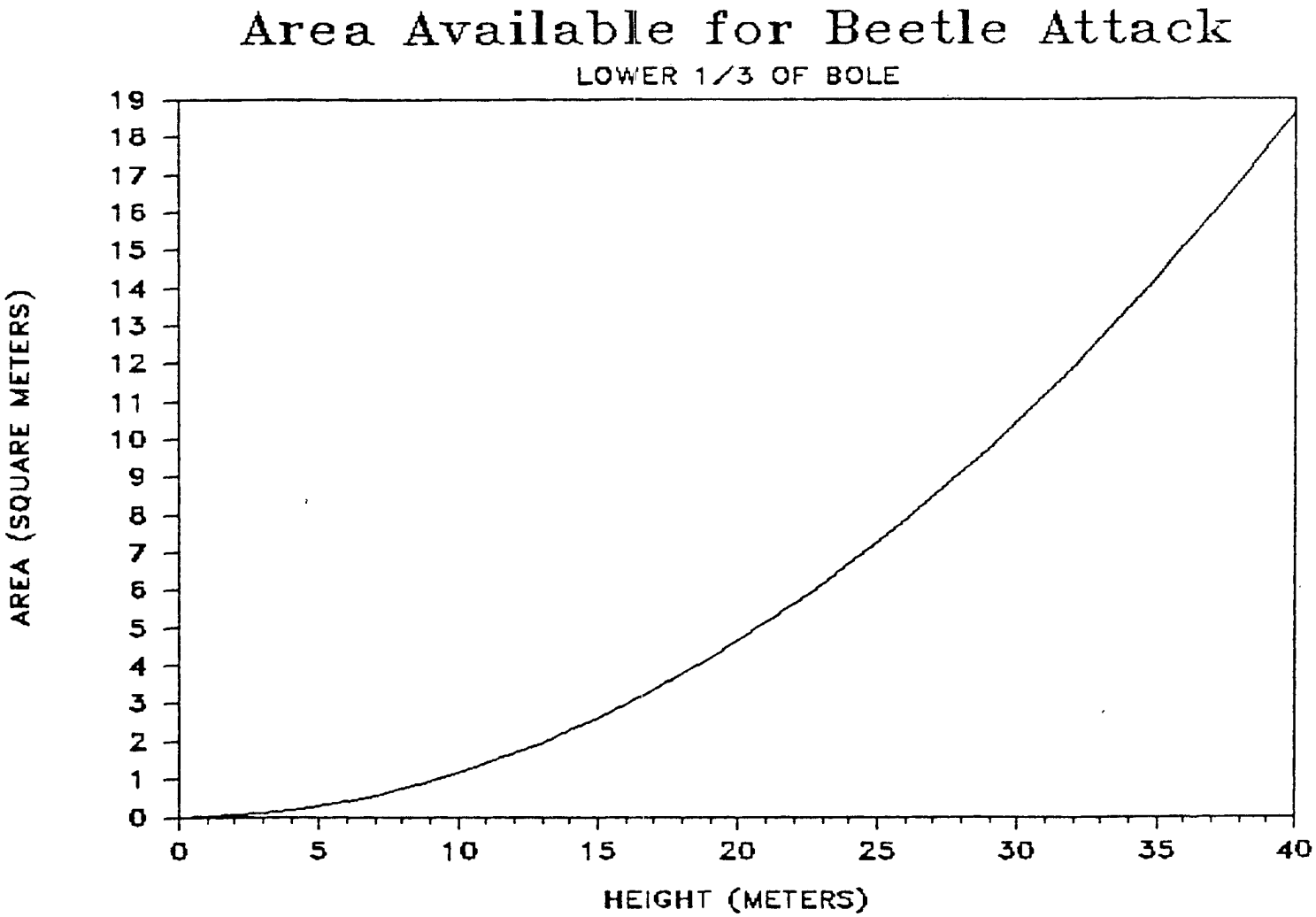

Area Available for Beetle Attack
LOWER 1/3 OF BOLE
AREA (SQUARE METERS)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
0
5
10
15
20
25
30
35
40
HEIGHT (METERS)

FIGURE 5

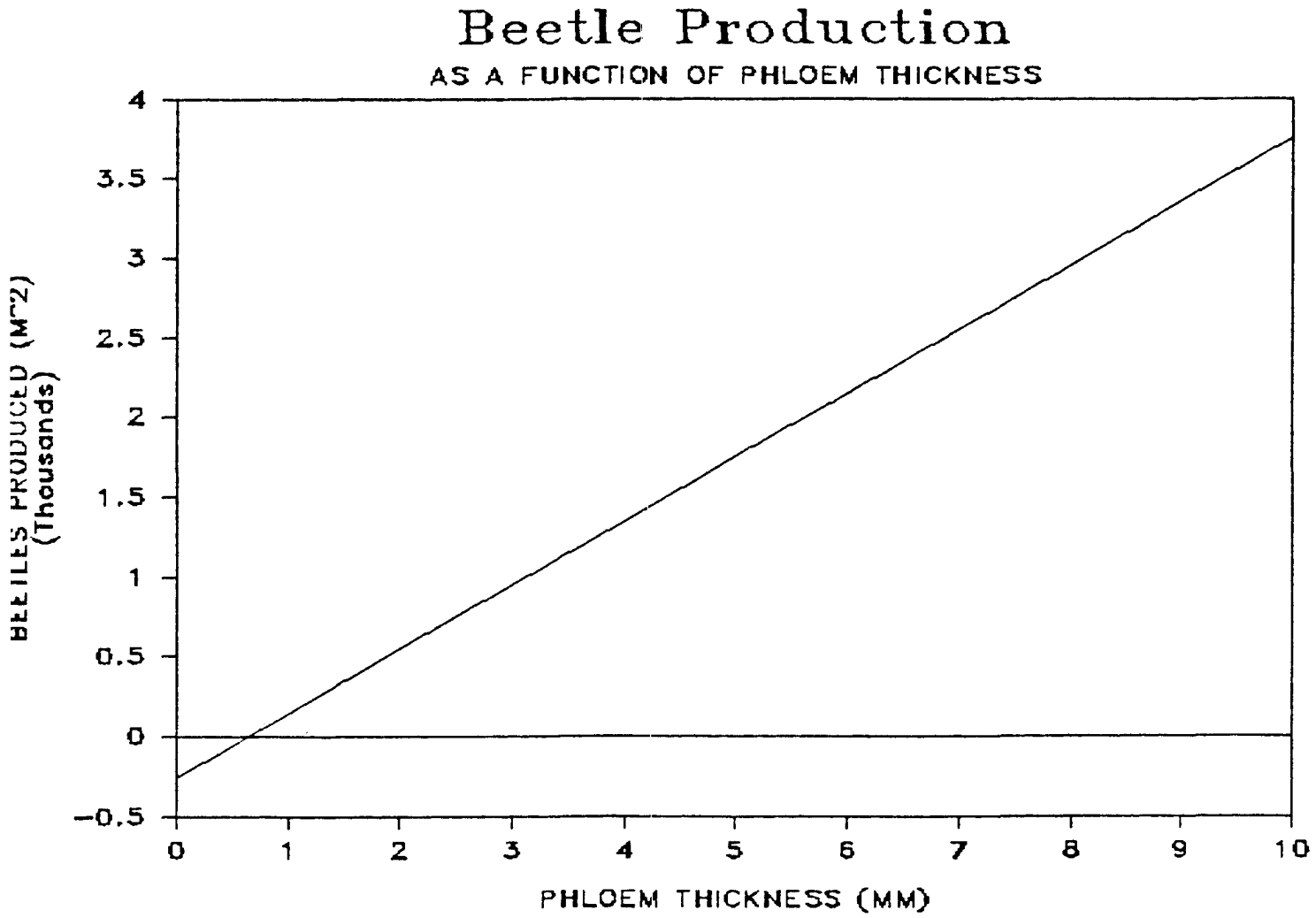

Beetle Production
AS A FUNCTION OF PHLOEM THICKNESS
BEETLES PRODUCED (M^2)
(Thousands)
4
3.5
3
2.5
2
1.5
1
0.5
0
-0.5
0
1
2
3
4
5
6
7
8
9
10
PHLOEM THICKNESS (MM)

FIGURE 6

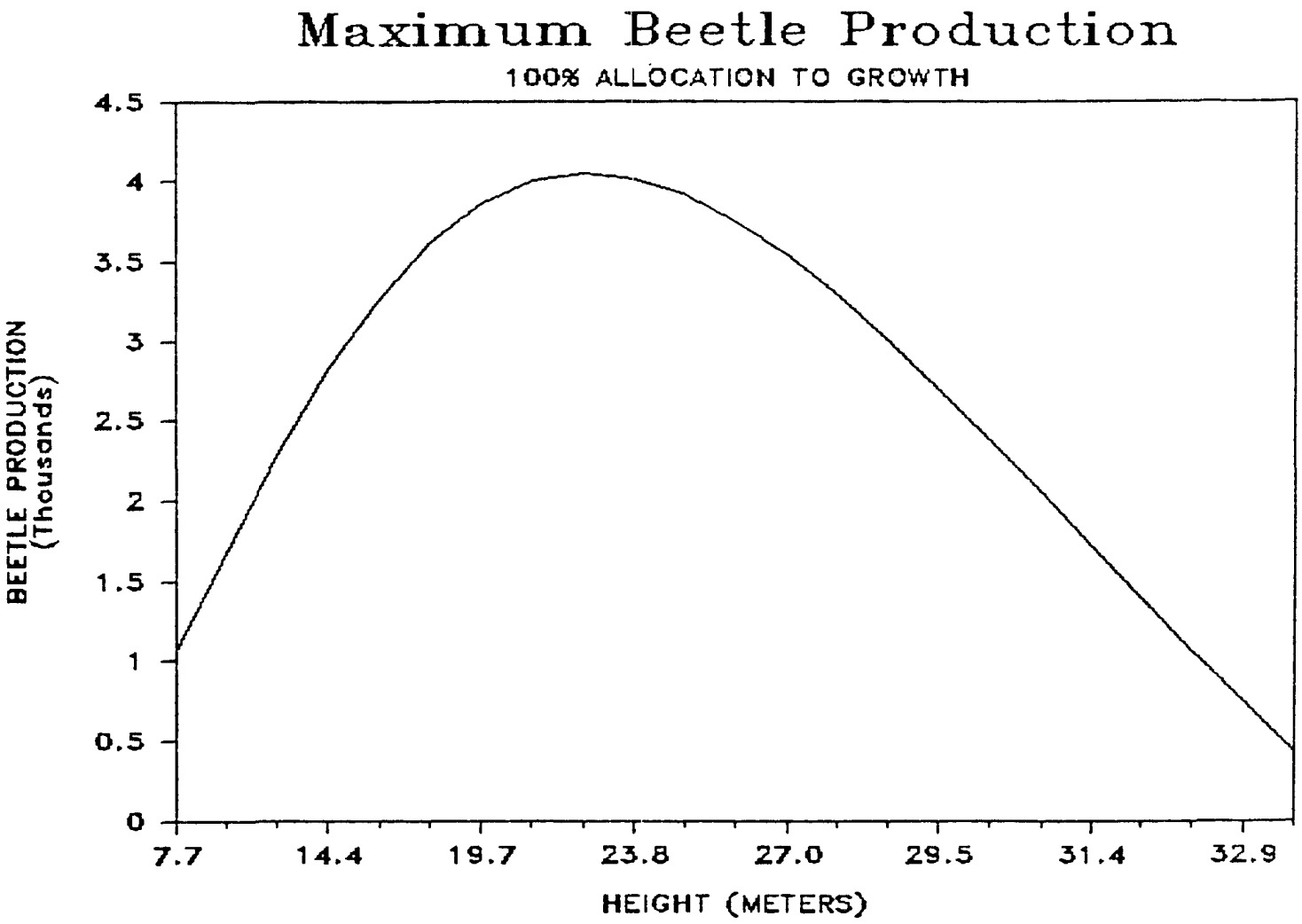

Maximum Beetle Production
100% ALLOCATION TO GROWTH
BEETLE PRODUCTION (Thousands)
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
7.7
14.4
19.7
23.8
27.0
29.5
31.4
32.9
HEIGHT (METERS)

FIGURE 7

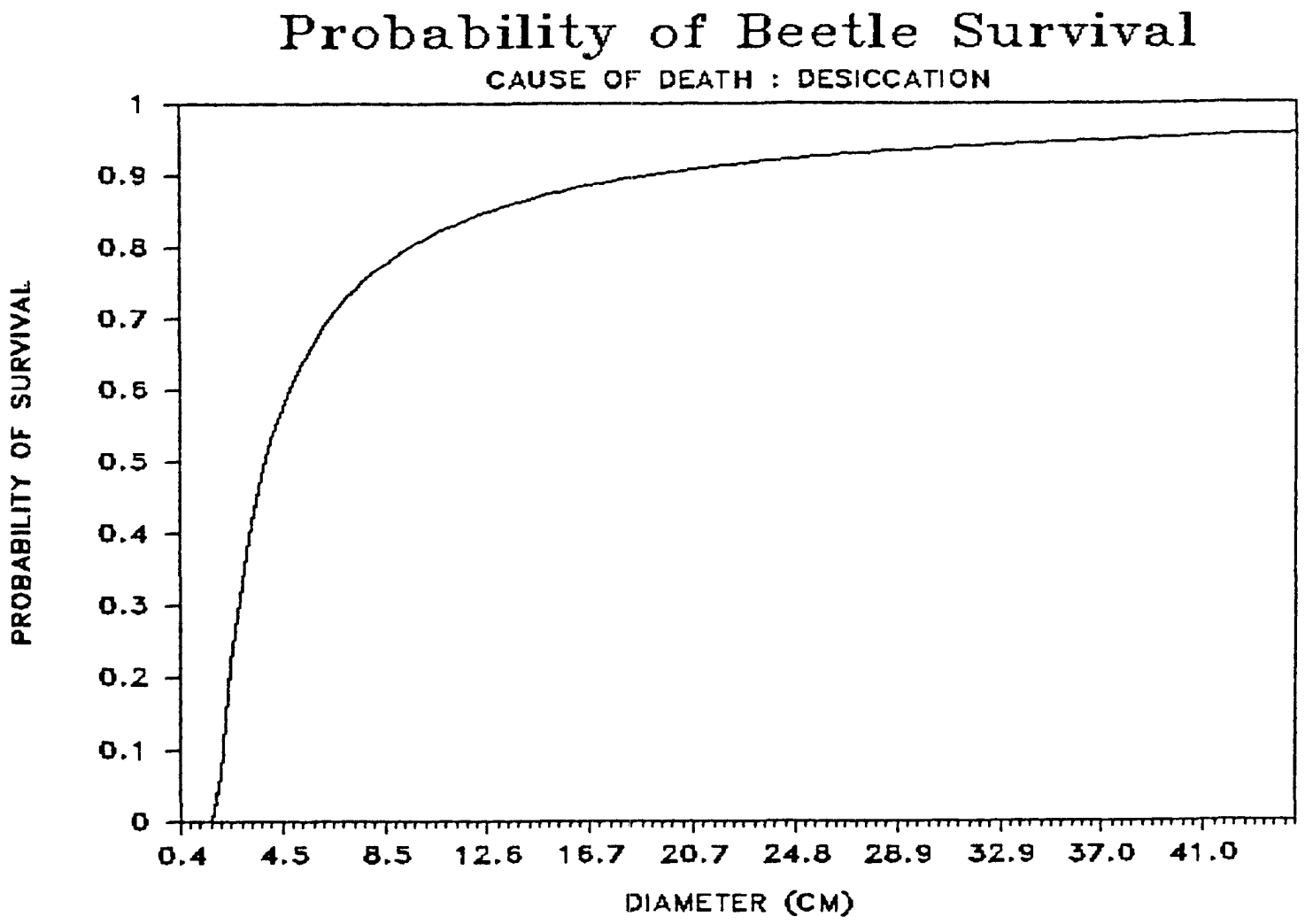

Probability of Beetle Survival
CAUSE OF DEATH : DESICCATION
PROBABILITY OF SURVIVAL
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0.4
4.5
8.5
12.6
16.7
20.7
24.8
28.9
32.9
37.0
41.0
DIAMETER (CM)

FIGURE 8

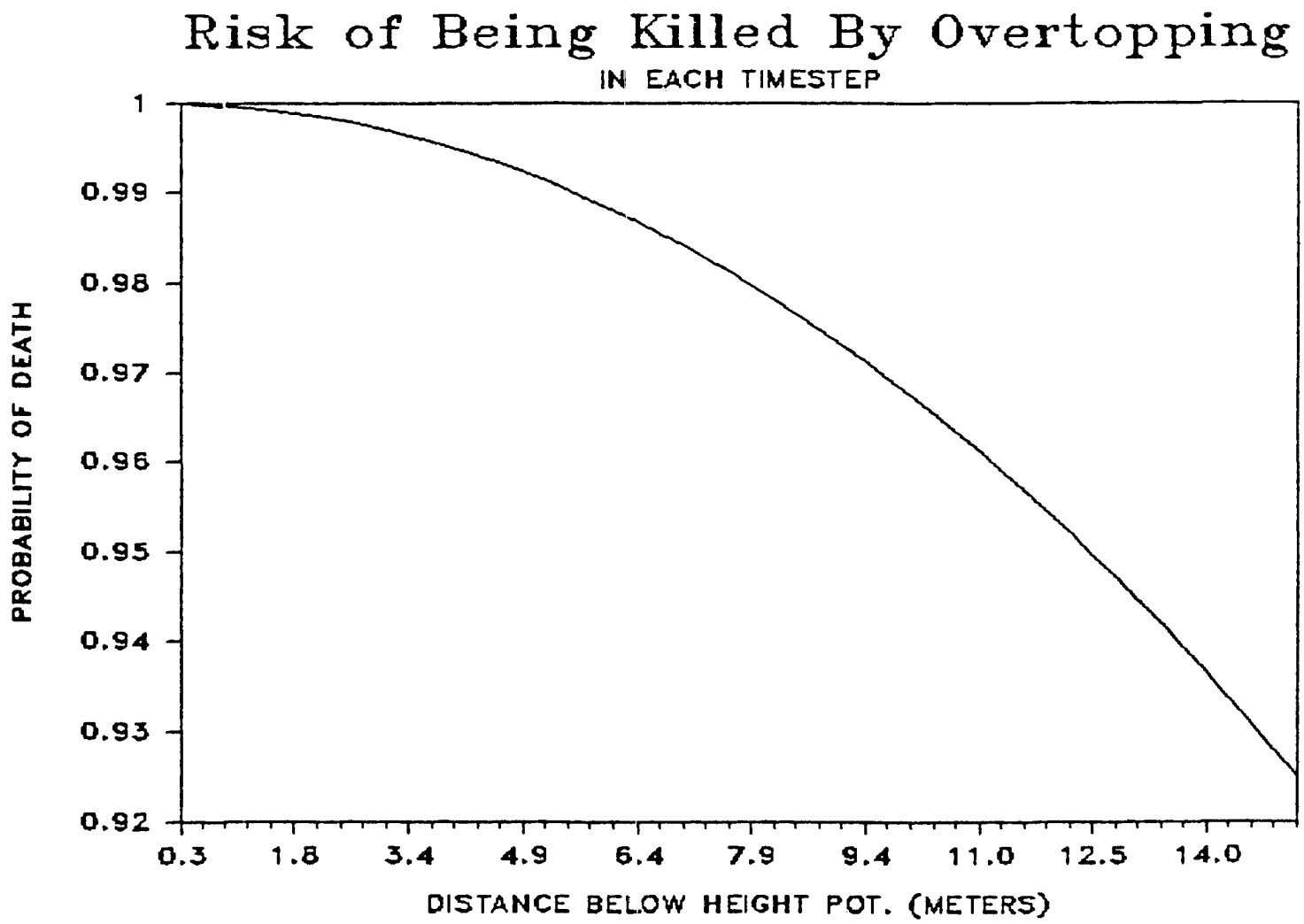

Risk of Being Killed By Overtopping
IN EACH TIMESTEP
PROBABILITY OF DEATH
1
0.99
0.98
0.97
0.96
0.95
0.94
0.93
0.92
0.3
1.8
3.4
4.9
6.4
7.9
9.4
11.0
12.5
14.0
DISTANCE BELOW HEIGHT POT. (METERS)

FIGURE 9

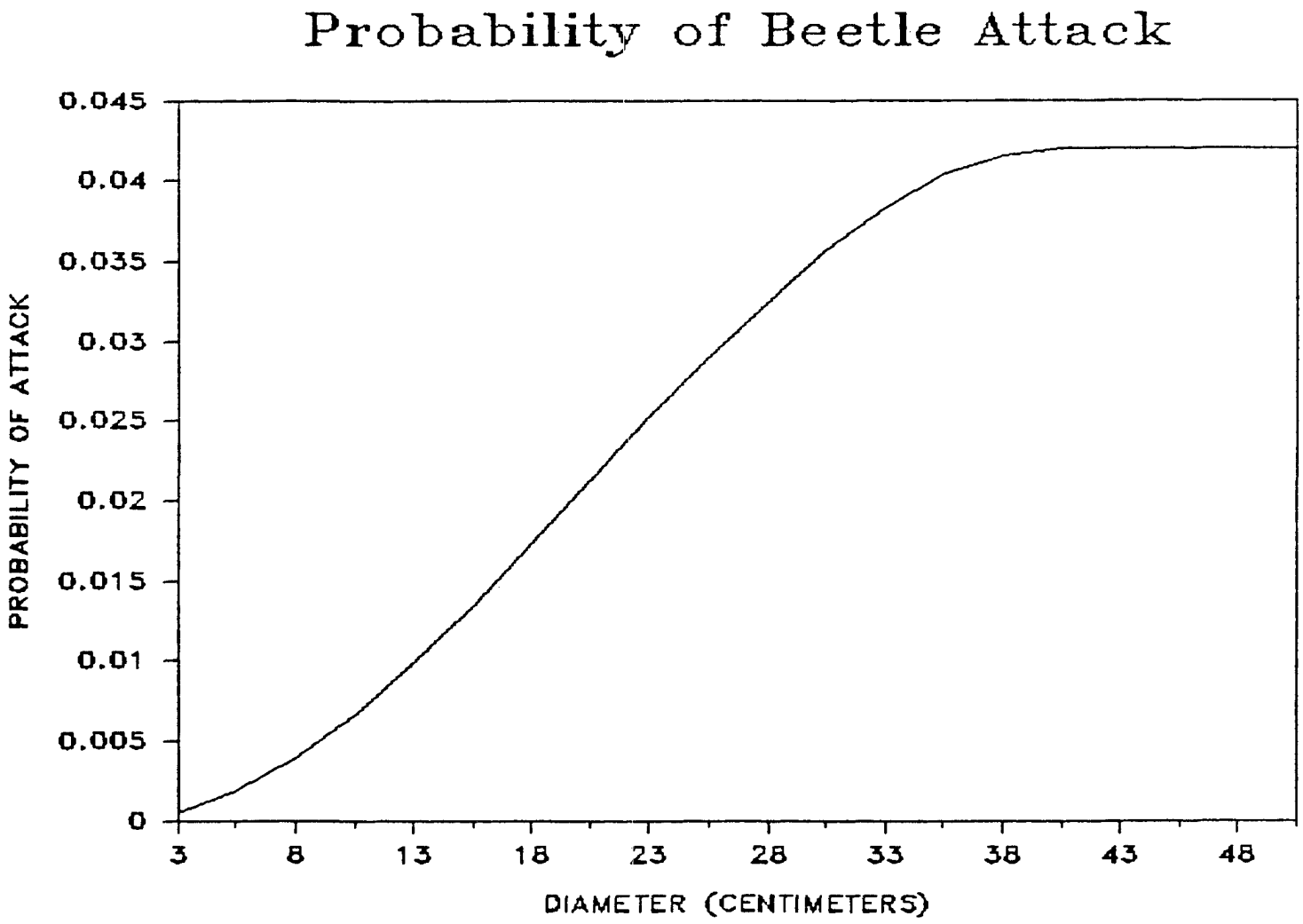

Probability of Beetle Attack
PROBABILITY OF ATTACK
0.045
0.04
0.035
0.03
0.025
0.02
0.015
0.01
0.005
0
3
8
13
18
23
28
33
38
43
48
DIAMETER (CENTIMETERS)

FIGURE 10

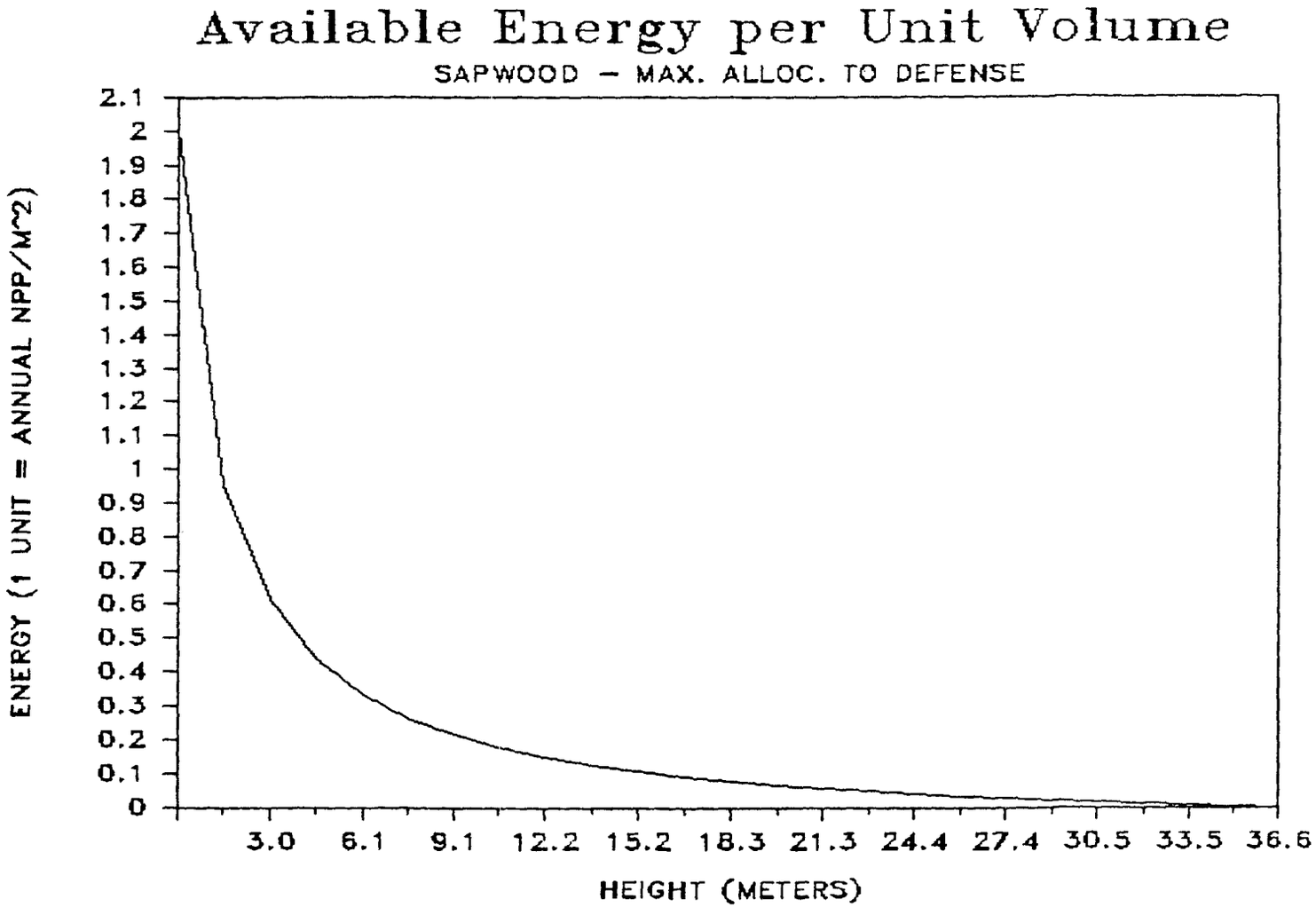

Available Energy per Unit Volume
SAPWOOD – MAX. ALLOC. TO DEFENSE
ENERGY (1 UNIT = ANNUAL NPP/M^2)
2.1
2
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
3.0
6.1
9.1
12.2
15.2
18.3
21.3
24.4
27.4
30.5
33.5
36.6
HEIGHT (METERS)

FIGURE 11

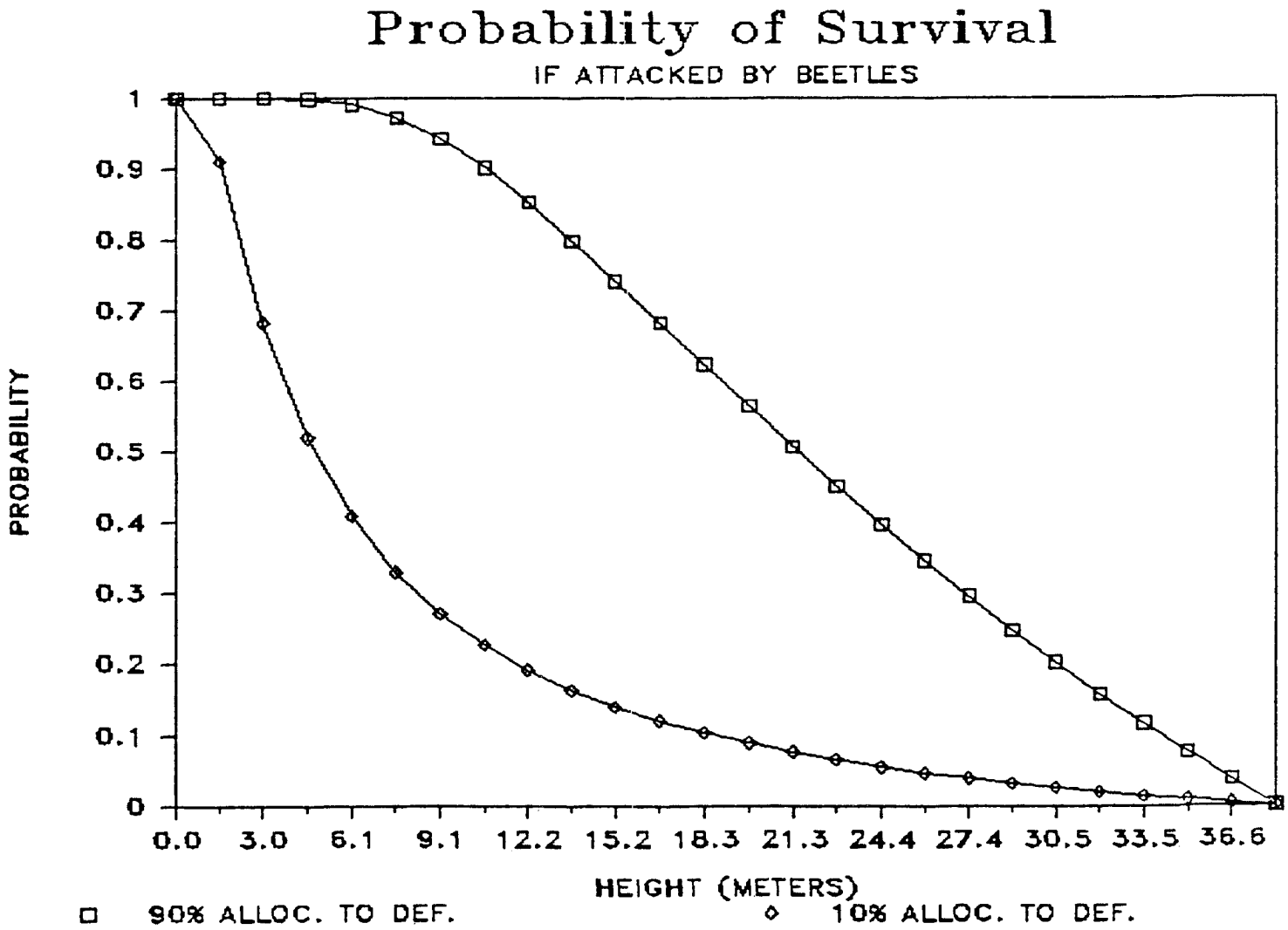

Probability of Survival
IF ATTACKED BY BEETLES
PROBABILITY
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0.0 3.0 6.1 9.1 12.2 15.2 18.3 21.3 24.4 27.4 30.5 33.5 36.6
HEIGHT (METERS)
90% ALLOC. TO DEF.
10% ALLOC. TO DEF.

FIGURE 12

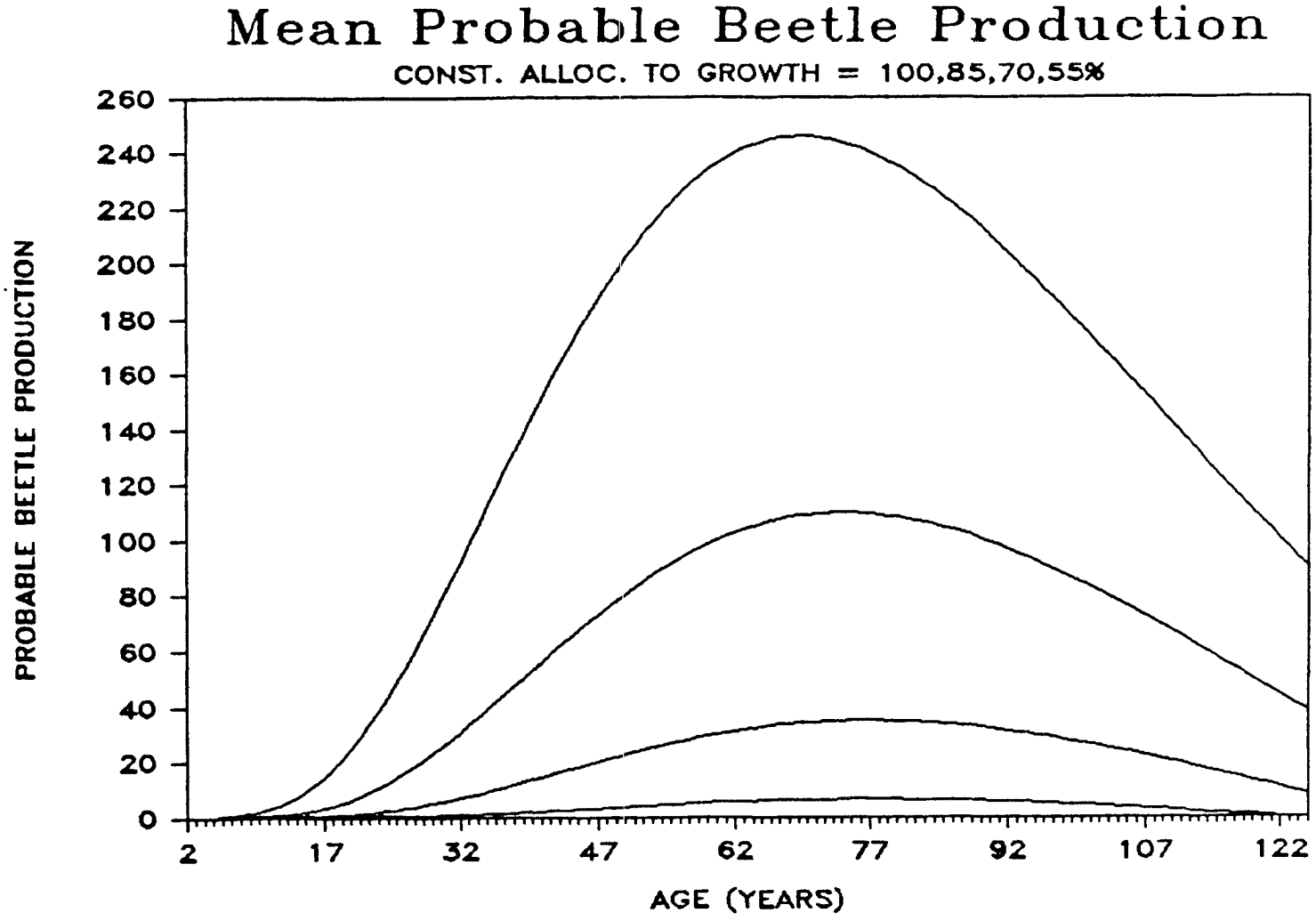

Mean Probable Beetle Production
CONST. ALLOC. TO GROWTH = 100,85,70,55%
PROBABLE BEETLE PRODUCTION
260
240
220
200
180
160
140
120
100
80
60
40
20
0
2
17
32
47
62
77
92
107
122
AGE (YEARS)

FIGURE 13

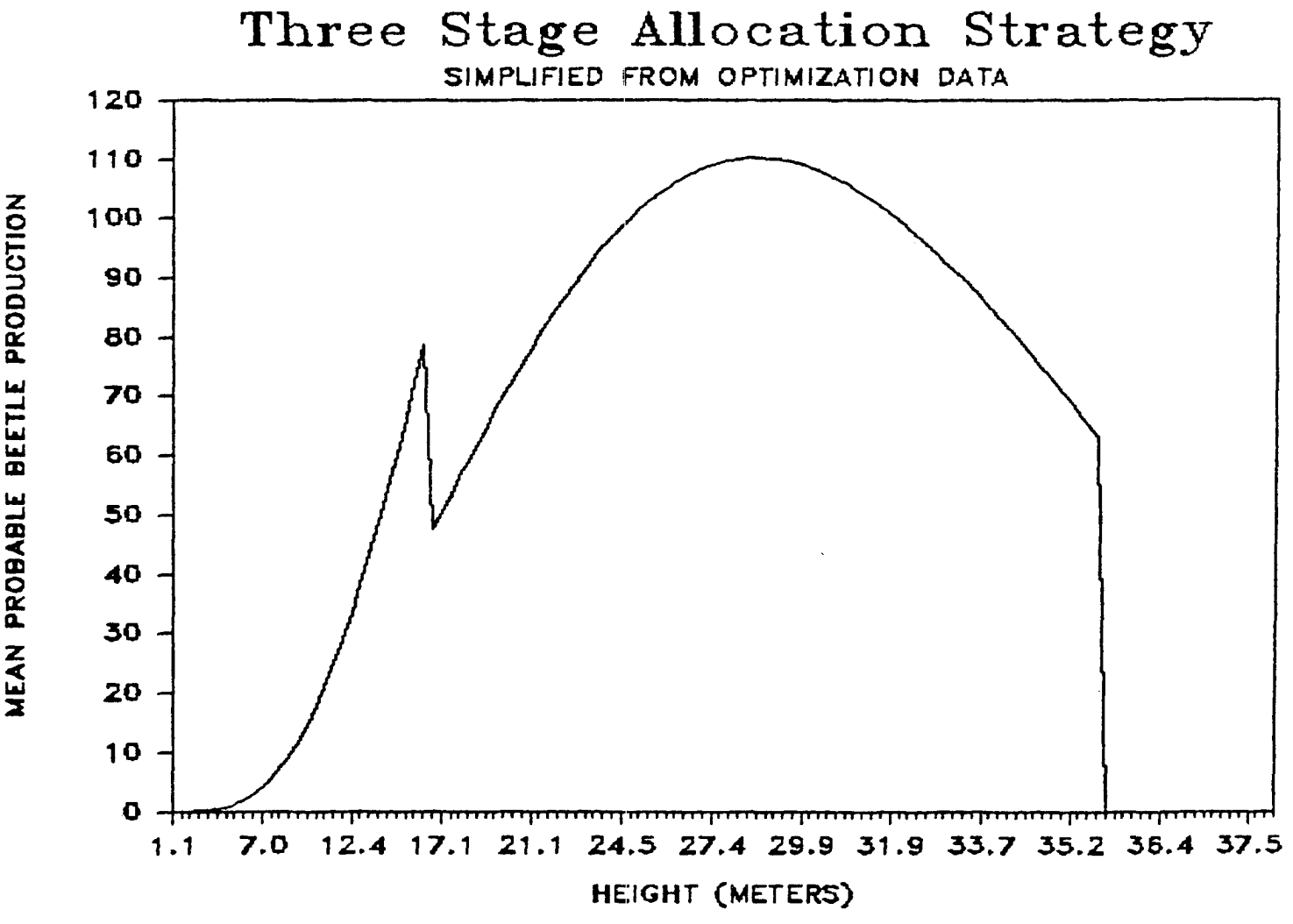
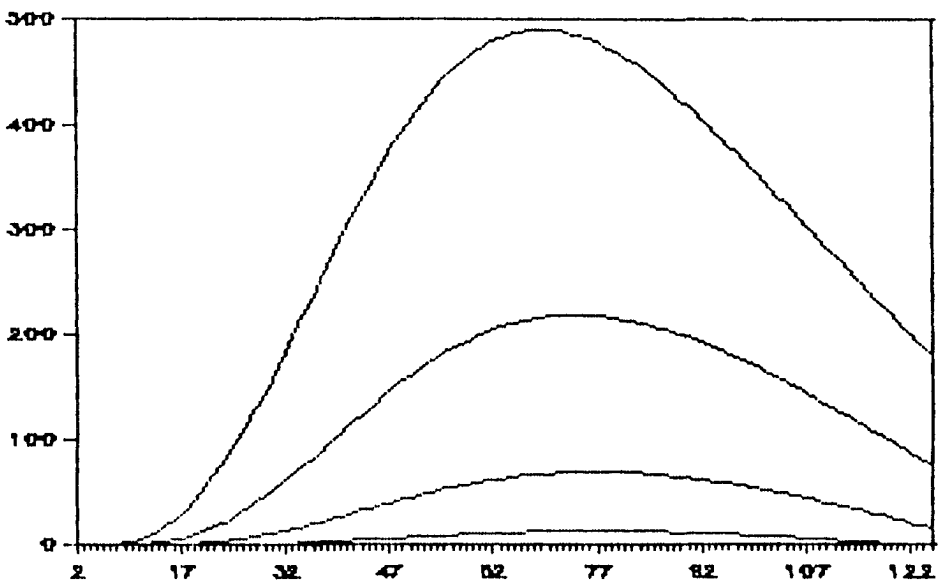

Three Stage Allocation Strategy
SIMPLIFIED FROM OPTIMIZATION DATA
MEAN PROBABLE BEETLE PRODUCTION
120
110
100
90
80
70
60
50
40
30
20
10
0
1.1
7.0
12.4
17.1
21.1
24.5
27.4
29.9
31.9
33.7
35.2
36.4
37.5
HEIGHT (METERS)

FIGURE 14

FIGURE 15

The graphs below plot mean probable beetle production as a function of age in years. Four energy allocation constants were used to generate the curves: 100, 85, 70 and 55% to growth.

In the top graph, probability of beetle attack is twice the standard value. In the bottom, the probability of beetle attack is one half the standard.



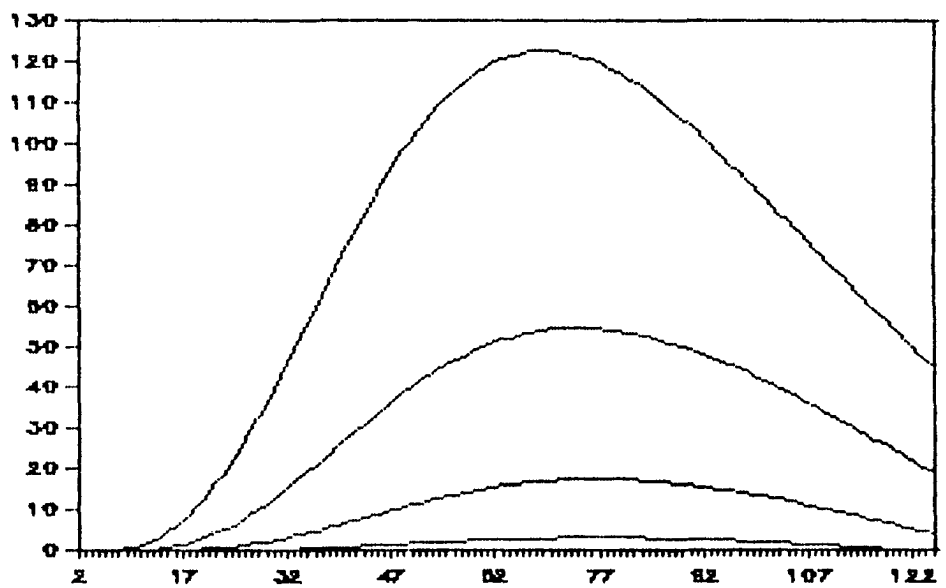
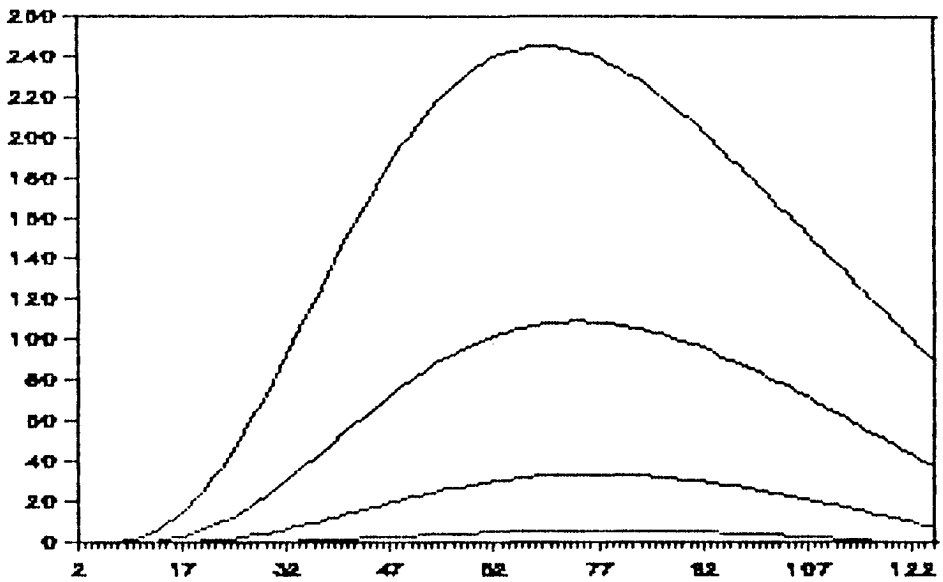


FIGURE 16

The graphs below plot mean probable beetle production as a function of age in years. Four energy allocation constants were used to generate the curves: 100, 85, 70 and 55% to growth.

In the top graph, the slope of the exponential function that sets the probability of overtopping is twice the standard value. In the bottom, the slope is one half the standard.



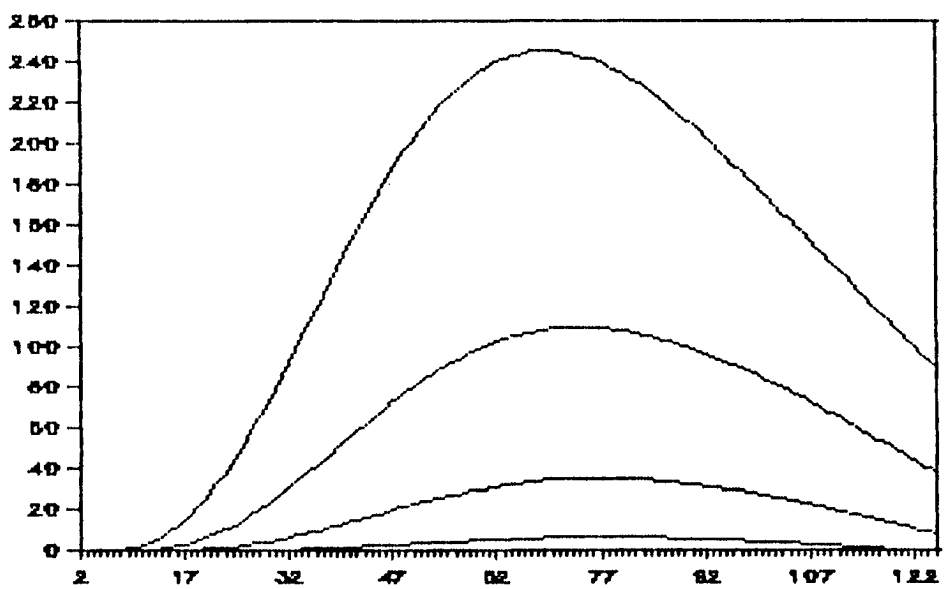
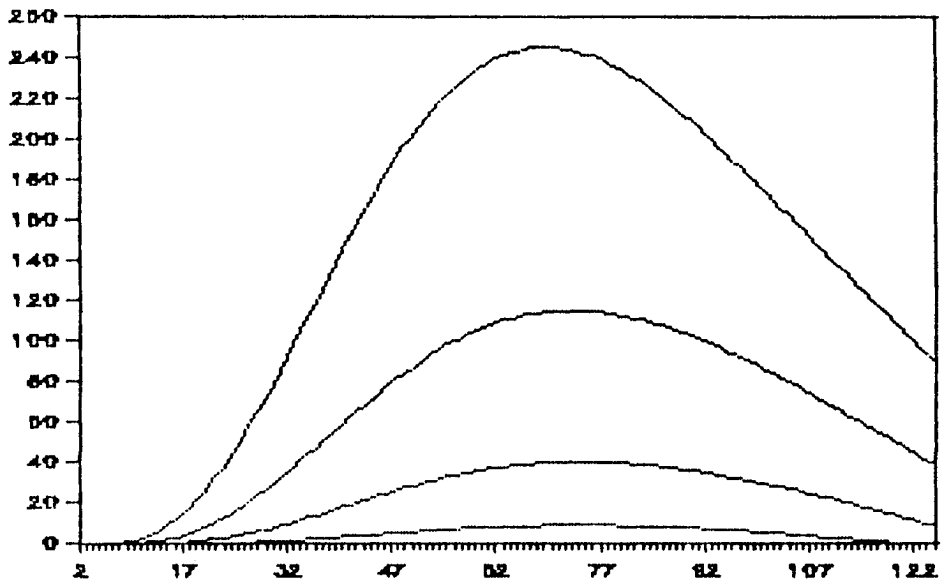


FIGURE 17

The graphs below plot mean probable beetle production as a function of age in years. Four energy allocation constants were used to generate the curves: 100, 85, 70 and 55% to growth.

In the top graph, the slope of the exponential function that sets the energy threshold for resistance to beetle attack is twice the standard value. In the bottom, the slope is one half the standard.



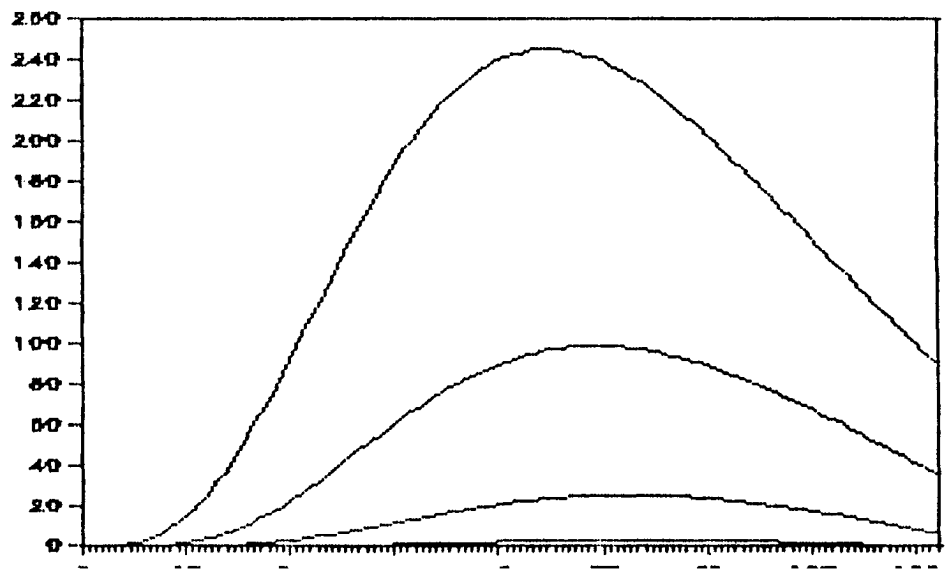
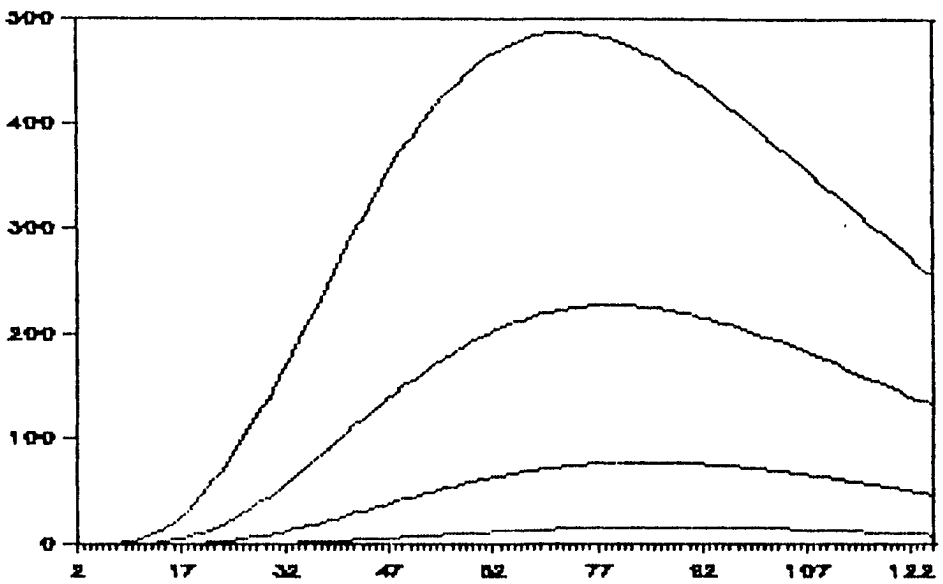


FIGURE 18

The graphs below plot mean probable beetle production as a function of age in years. Four energy allocation constants were used to generate the curves: 100, 85, 70 and 55% to growth.

In the top graph, phloem is retained for a greater period of time than the standard retention. In the bottom, phloem retention is less than the standard.



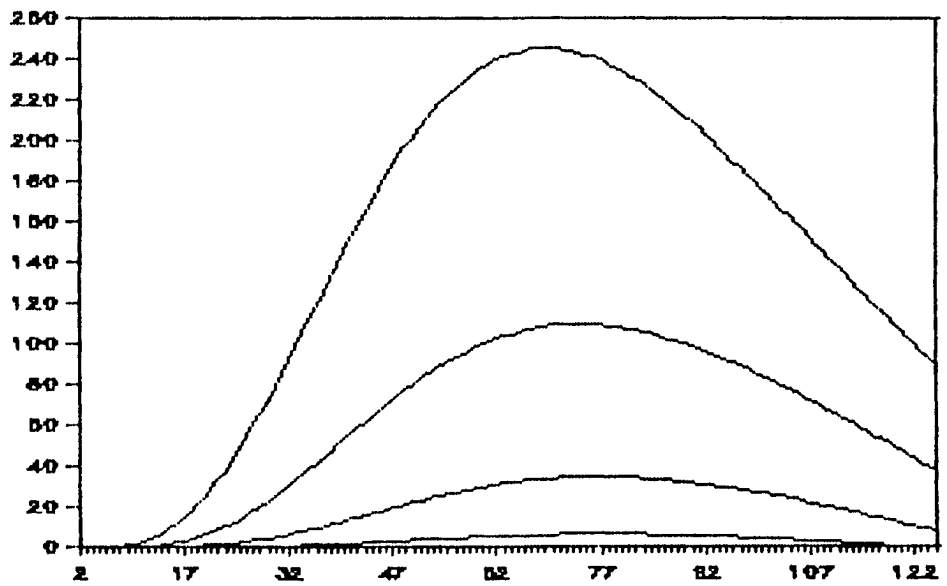
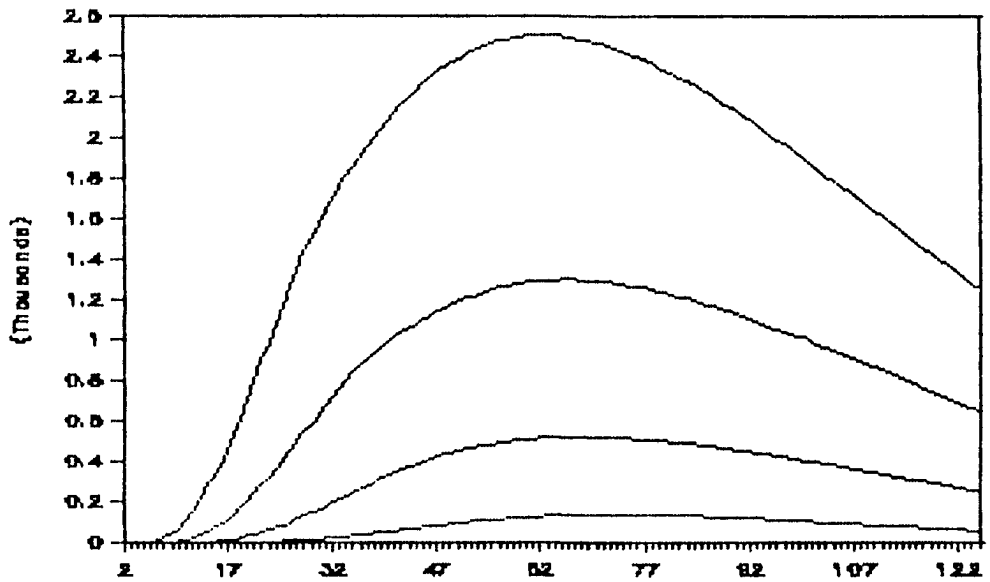


FIGURE 19

The graphs below plot mean probable beetle production as a function of age in years. Four energy allocation constants were used to generate the curves: 100, 85, 70 and 55% to growth.

In the top graph, the photosynthetic efficiency of a unit of leaf area is twice the standard. In the bottom, the efficiency is one half the standard.



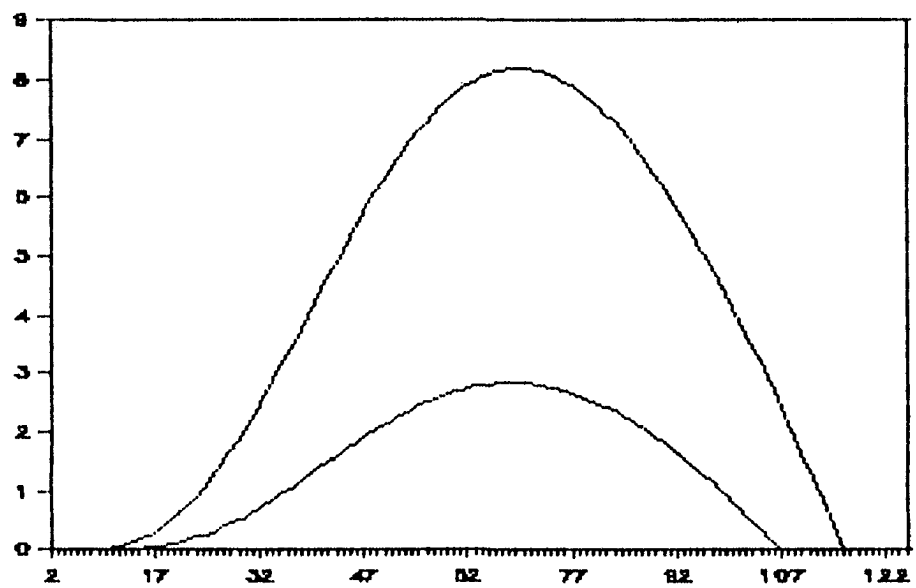
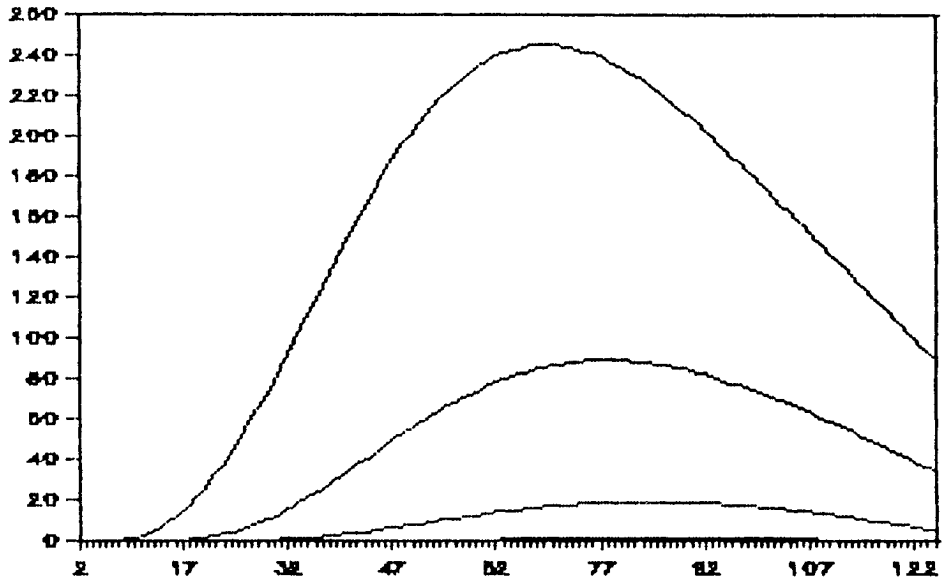
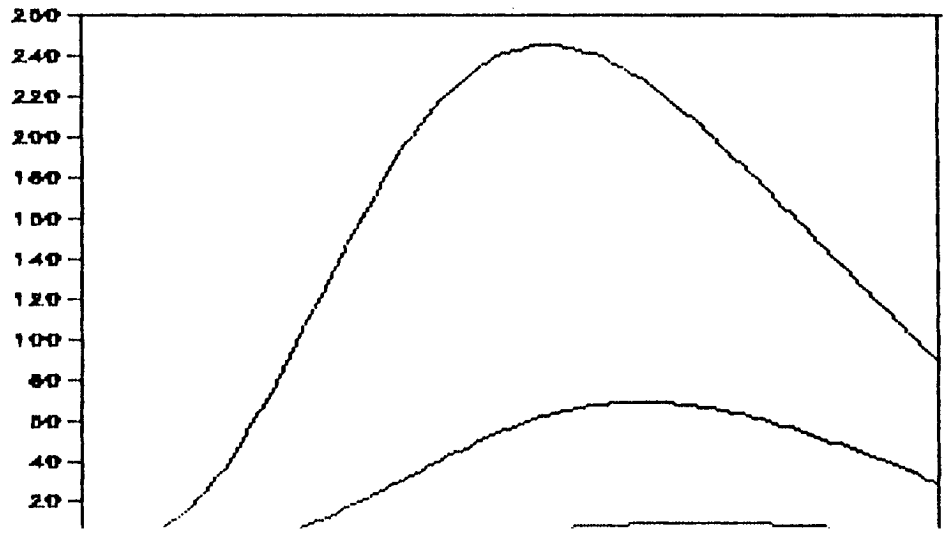


FIGURE 20

The graphs below plot mean probable beetle production as a function of age in years. Four energy allocation constants were used to generate the curves: 100, 85, 70 and 55% to growth.

These two graphs differ from the rest of the model output in that energy allocated to defense during a timestep is stored for later use. In the upper graph, the saved energy depreciates exponentially with time. In the lower, depreciation is linear.





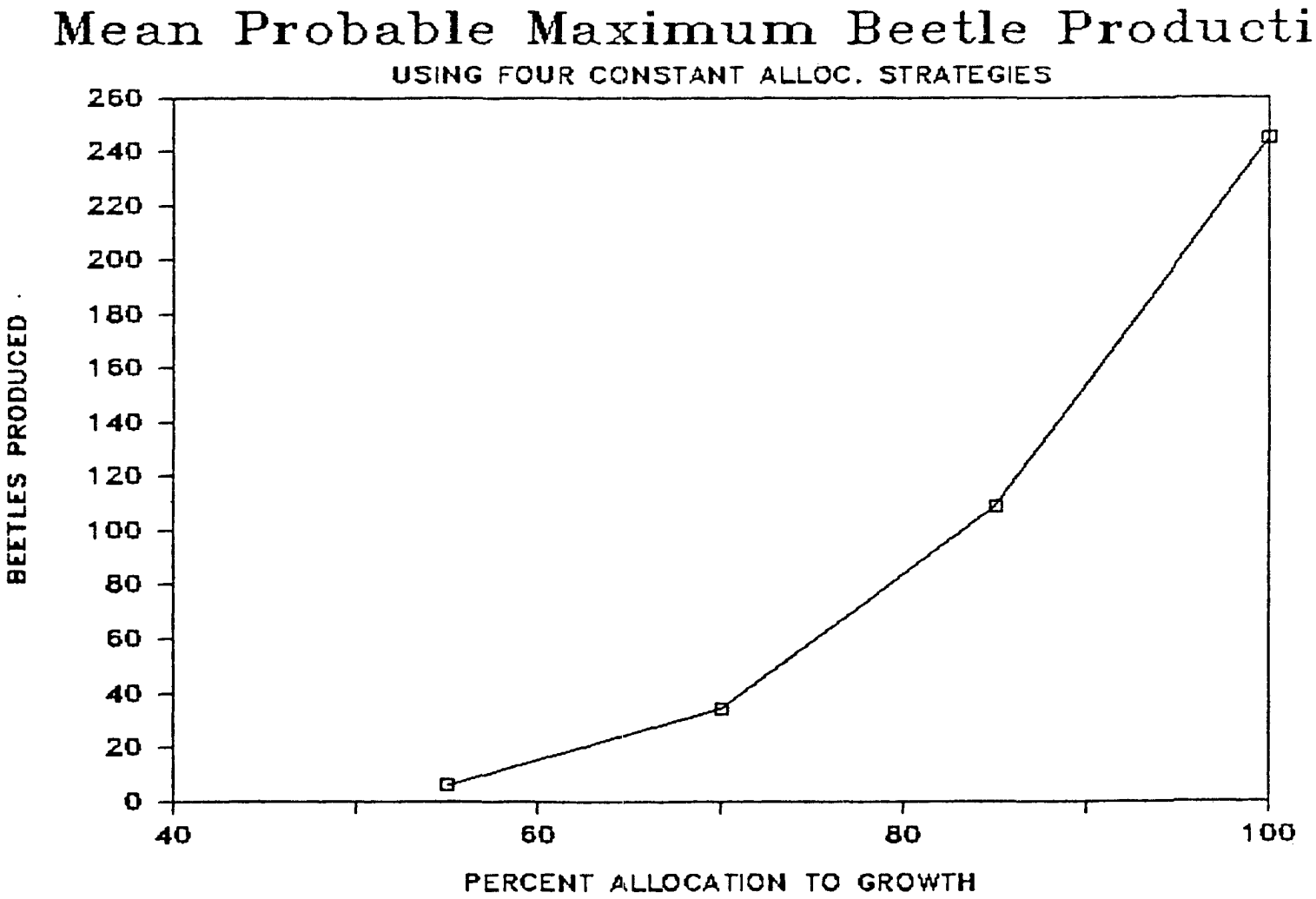
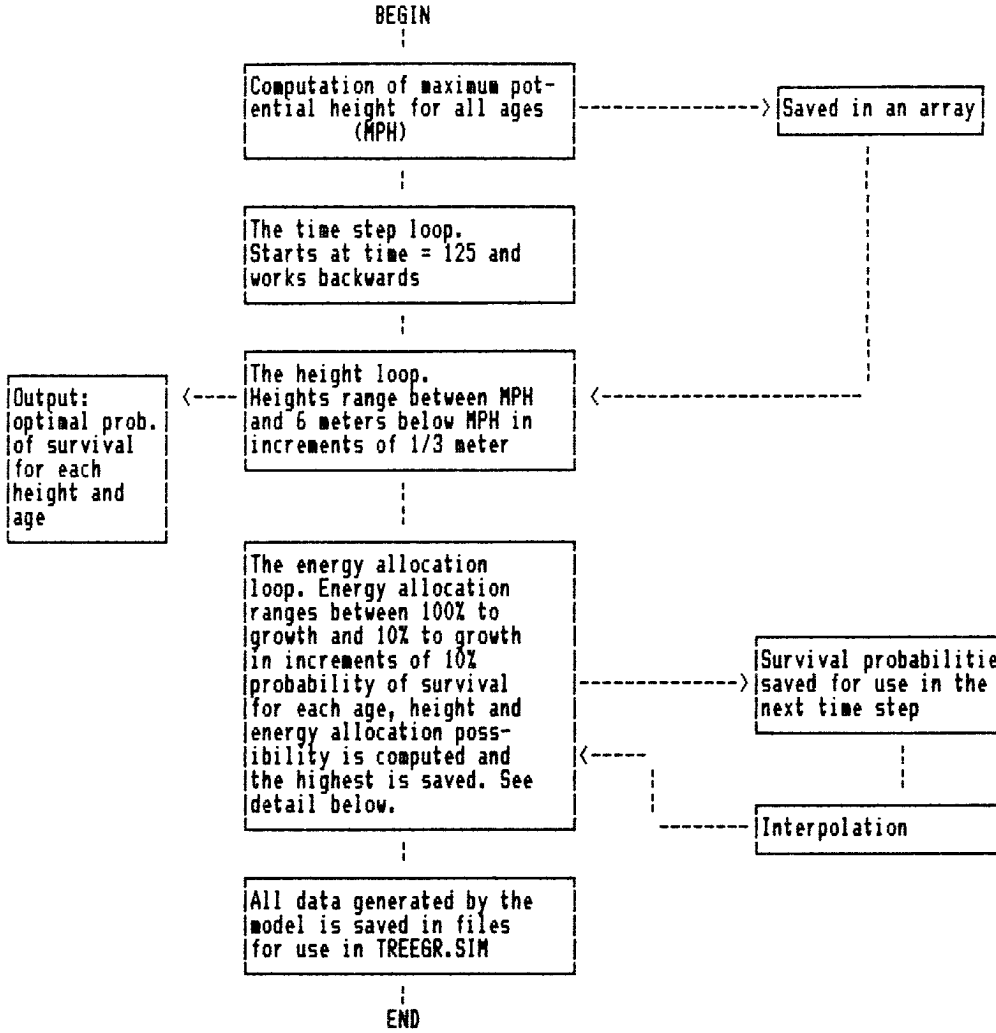

Mean Probable Maximum Beetle Production
USING FOUR CONSTANT ALLOC. STRATEGIES
BEETLES PRODUCED
260
240
220
200
180
160
140
120
100
80
60
40
20
0
40
60
80
100
PERCENT ALLOCATION TO GROWTH

FIGURE 21

Figure 22
A Flow Chart for TREEGR.FIL



THE OPTIMIZATION PROCESS

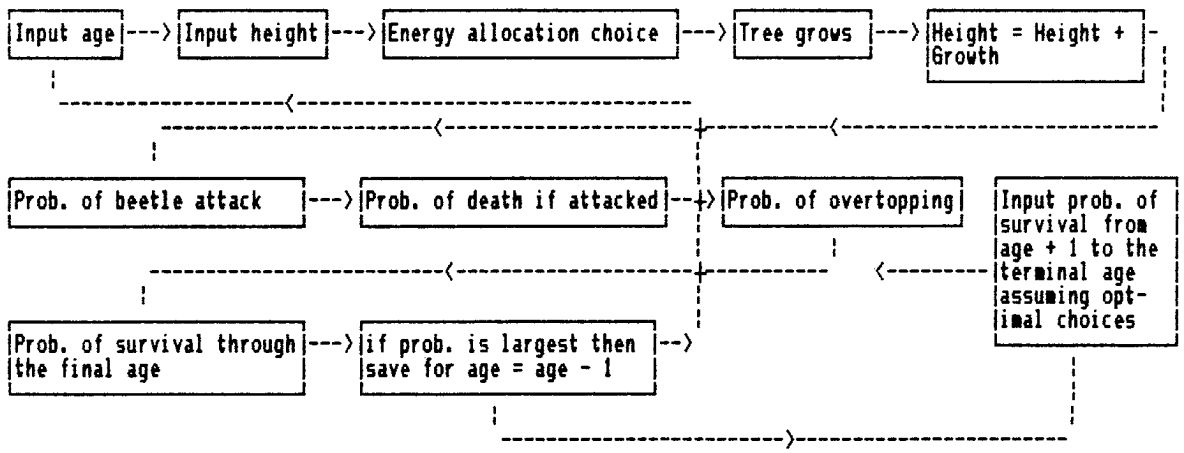


Figure 23
A Flow Chart for TREEGR.SIM

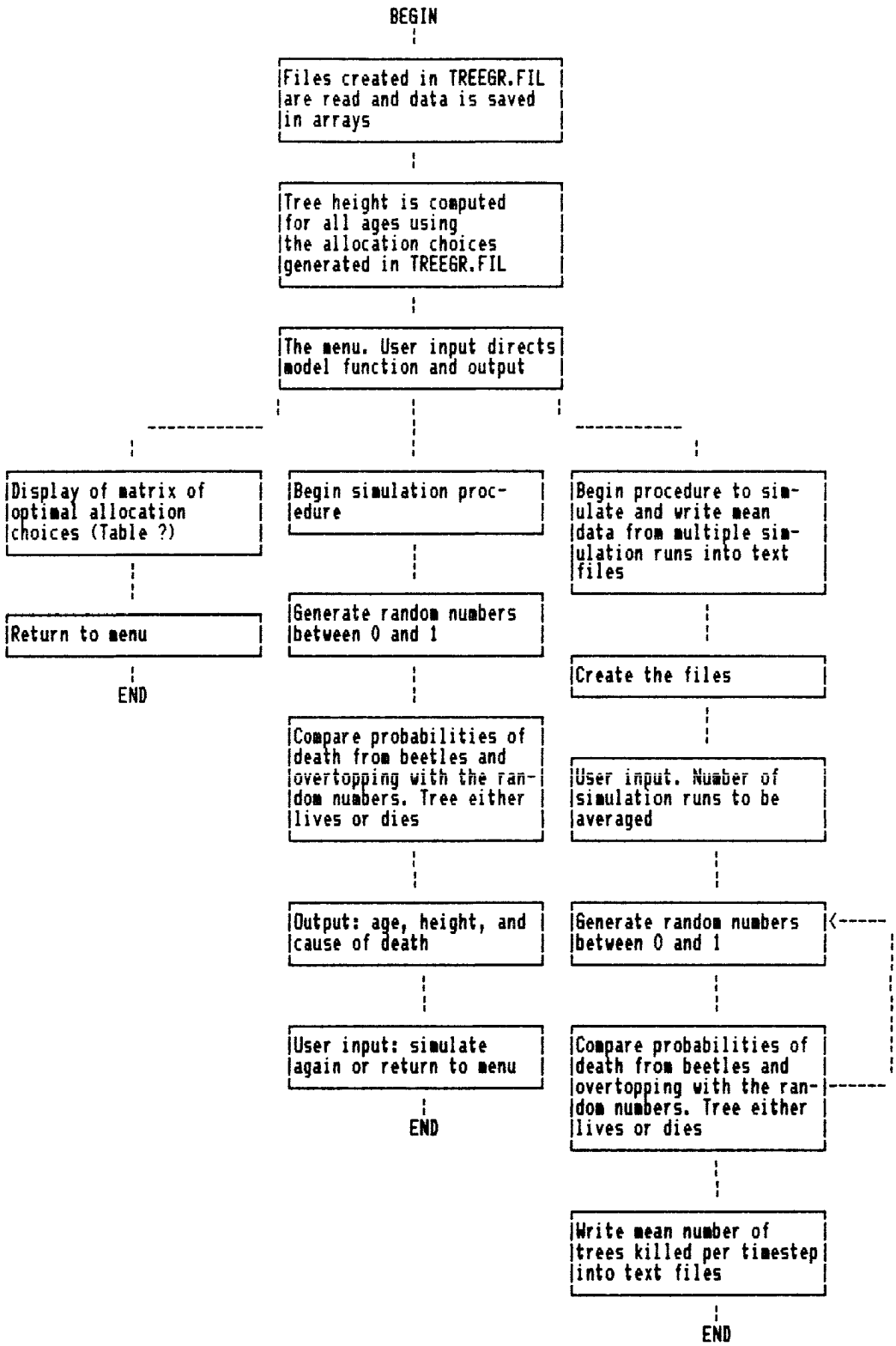


Figure 24
A Flow Chart for TREEGR.EQU

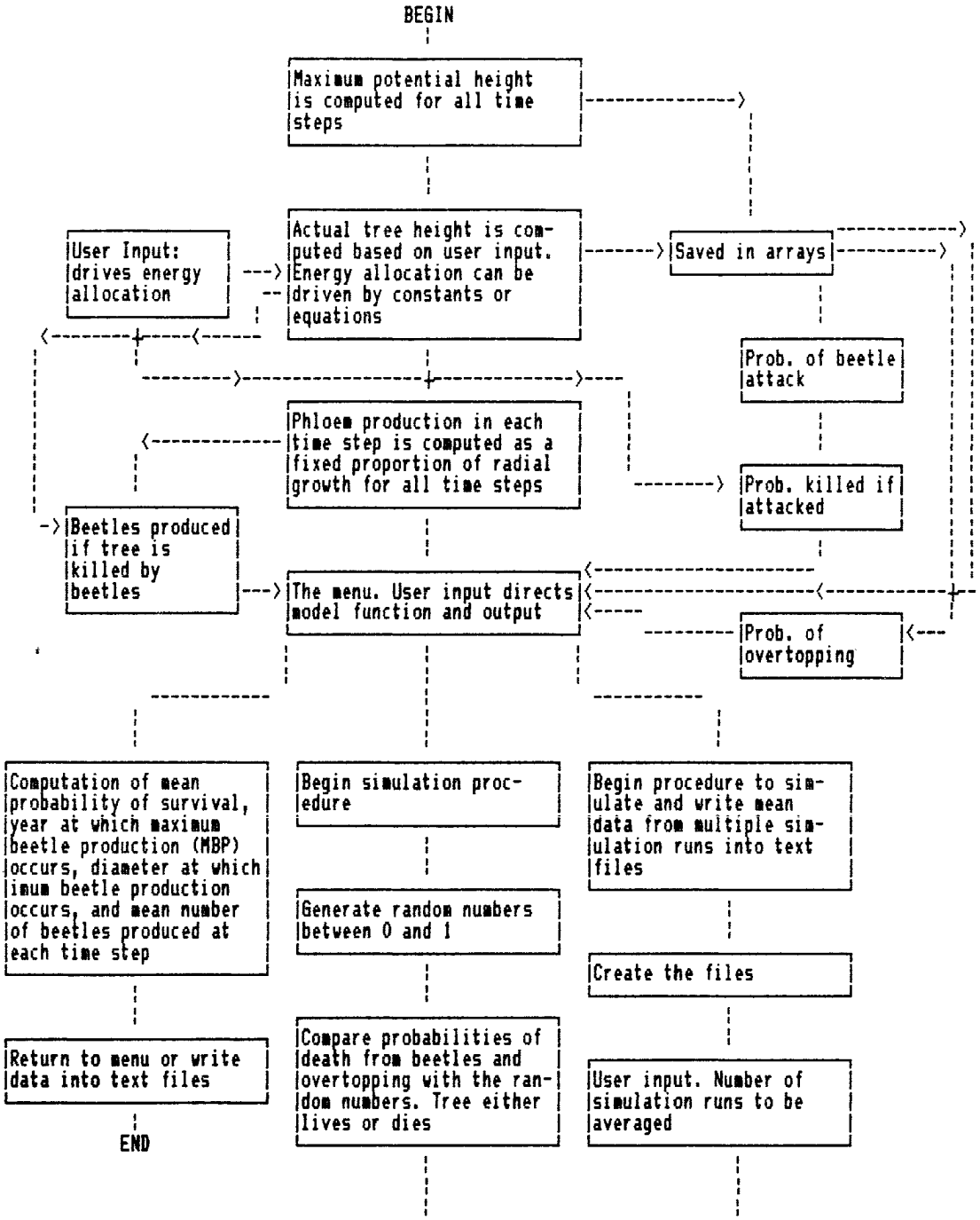
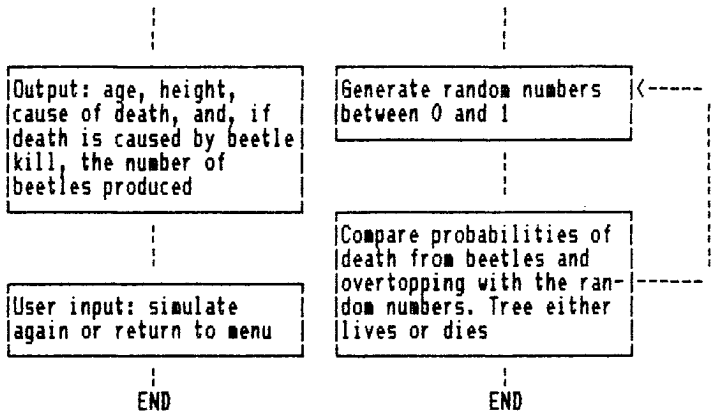


Figure 24 Continued



APPENDIX A

COMMENTED SOURCE CODE FOR

TREEGR.FIL

This program uses dynamic programming techniques to generate a matrix of optimal energy allocation choices based on the height and age of the tree.

```
program treegrowth_five_year_interval;
        type
            number = real;
        var
           h,ht            :    real;   {variable initialization}
           a,a1,a2,a3,
           b,b1,b2,b3      :    real;
           prob_T          :    real;
           best_prob       :    real;
           best_h          :    real;
           best_bp         :    real;
           best_over       :    real;
           count           :    integer;
           best_i          :    integer;
           T,k             :    integer;
           Hmax            :    array[1..25] of real;
           work_array      :    array[1..20] of real;
           bug,o,prob      :    array[1..25,1..20] of real;
           c               :    array[1..25,1..20] of integer;
procedure array_0;
          var
             kk,hh    : integer;              {setting all of the arrays to 0 to begin with}
          begin
               for kk := 1 to 25 do begin
                   for hh := 1 to 20 do begin
                       bug[kk,hh]  := 0;
                       o[kk,hh]    := 0;
                       prob[kk,hh] := 0;
                       c[kk,hh]    := 0;
                    end;
                 end;
end;
procedure htmax;                              {finding the height potential for all ages}
          var                                 {and saving it in an array for later use}
             htt,gro         : real;
             time            : integer;
          begin
               htt := 1;
               for time := 1 to 25 do begin
                   gro:= (5 * (sqr(htt)/1.8839 - sqr(htt)*htt*0.004))/((sqr(htt+1) *
                               (htt+1) - sqr(htt) * htt)/15);
                   htt      := htt + gro;
                   Hmax[time] := htt;
               end;
end;
procedure best_fit;                         {interpolation between time steps is  accomplished}
          var                                 {through the use of 4 least fit regression lines}
             x   : real;                      {this procedure assigns the interpolated values }
          begin                     {and assigns the appropriate line  based on distance from}
               x := hmax[t+1] - ht;           {height potential at time T + 1}
```

```
          if x <= 5 then
             prob_T := (a - b * 3) + b * x;
          if (x > 5) and (x <= 10) then
             prob_T := (a1 - b1 * 7.5) + b1 * x;
          if (x > 10) and (x <= 15) then
             prob_T := (a2 - b2 * 12.5) + b2 * x;
          if x > 15 then
             prob_T := (a3 - b3 * 17.5) + b3 * x;
end;
procedure intercept;            {finding the Y intercepts for the best fit regressions}
         var
            kk : integer;
         begin
              a := 0;
              a1 := 0;
              a2 := 0;
              a3 := 0;
              for kk := 1 to 20 do begin
                  if kk <= 5 then
                     a := a + work_array[kk];
                  if (kk >= 5) and (kk <= 10) then
                     a1 := a1 + work_array[kk];
                  if (kk >= 10) and (kk <= 15) then
                    a2 := a2 + work_array[kk];
                  if kk >= 15 then
                     a3 := a3 + work_array[kk];
              end;
              a := a/5;
              a1 := a1/6;
              a2 := a2/6;
              a3 := a3/6;
end;
procedure slopefind;                    {the slopefind procedures determine the least squares }
         var                            {regression lines based on the probabilities generated}
            x,xx,xy,sxx,sxy    : real;      {in the choice procedure at timestep t+ 1}
            kk                  : integer;
         begin
              sxx := 0;
              sxy := 0;
            for kk := 1 to 5 do begin
               x := kk - 3;
               xx := sqr(x);
               xy := x * work_array[kk];
               sxx := sxx + xx;
               sxy := sxy + xy;
            end;
            b := sxy/sxx;
end;
procedure slopefind1;
         var
```

```
            x,xx,xy,sxx,sxy    : real;
            kk                 : integer;
         begin
              sxx := 0;
              sxy := 0;
            for kk := 5 to 10 do begin
                x := kk - 7.5;
                xx := sqr(x);
                xy := x * work_array[kk];
                sxx := sxx + xx;
                sxy := sxy + xy;
            end;
            b1 := sxy/sxx;
end;
procedure slopefind2;
         var
            x,xx,xy,sxx,sxy    : real;
            kk                 : integer;
         begin
              sxx := 0;
              sxy := 0;
            for kk := 10 to 15 do begin
                x := kk - 12.5;
                xx := sqr(x);
                xy := x * work_array[kk];
                sxx := sxx + xx;
                sxy := sxy + xy;
            end;
            b2 := sxy/sxx;
end;
procedure slopefind3;
         var
            x,xx,xy,sxx,sxy    : real;
            kk                 : integer;
         begin
              sxx := 0;
              sxy := 0;
            for kk := 15 to 20 do begin
                x := kk - 17.5;
                xx := sqr(x);
                xy := x * work_array[kk];
                sxx := sxx + xx;
                sxy := sxy + xy;
            end;
            b3 := sxy/sxx;
end;
procedure array_fill;
         begin
              c[t,k] := best_i;
              bug[t,k] := best_bp;
```

```
            o[t,k] := best_over;
            prob[t,k] := best_prob;
end;
procedure choice;                                        {this is the heart of the program}
         var
           energy, energy_gro, energy_def, prob_no_sup,
           prob_bug, prob_sur, growth, bcount, energyb     : real;
           i                                               : integer;
         begin
             best_i := 0;
             best_prob := 0;
             bcount := 0;
             energy := 5 * (sqr(h)/1.88389 - (sqr(h) * h * 0.004));          {the available energy}
           for i := 1 to 10 do begin
             energy_gro := i * 0.1 * energy;                          { the allocation choice }
             energy_def := energy - energy_gro;
             growth     := energy_gro/((sqr(h+1)*(h+1) - sqr(h)*h)/15); {the growth obtained}
             ht         := h + growth;                                {from allocation}
           if count = 1 then
              prob_T := 1
           else
              best_fit;                                 {determining the prob. of  surviving}
             prob_bug   := (0.5 * sqr(0.16 * h) -                {through the last time step}
                           (0.021 * sqr(0.16 * h)*0.16*h))/200;  {prob. of attack by beetles}
             if prob_bug > bcount then
               bcount := prob_bug;
               energyb := energy_def/((sqr(h) * h * 0.004) * 5);{prob.of being killed by beetles}
             prob_bug   := (1-bcount) + bcount * (1 - exp(-energyb)); {prob.of surviving beetles}
             prob_no_sup   := (100 - (sqr(Hmax[t+1] - ht) * 0.03))/100;{prob.of being overtopped}
             prob_sur   := (prob_bug) * (prob_no_sup * prob_T);        {prob. of survival-total}
             if prob_sur >= best_prob then begin      {the optimization - picking the best choice}
               best_prob := prob_sur;
               best_i    := i;
               best_h    := ht;
               best_bp   := prob_bug;
               best_over := prob_no_sup;
               end;
           end;
           work_array[k] := best_prob;       {saving the probabilities of survival for processing}
           array_fill;                    {in the slopefind procedures and use in timestep T - 1}
end;
procedure height;                {generates heights from height potential to height potential - 19}
         begin
             for k := 1 to 20  do begin
                h := (Hmax[t] + 1) - k;
             if h<1 then h := 1;
                choice;
                writeln(5 * t:3,'     ',h * 0.3048:10,'     ',best_i:2,    {writing the results}
                          '     ', best_prob:12 );                         {of choice procedure}
             end;
```

```
end;
procedure age;              {generates the timesteps}
         begin
              count := 0;
              for t := 24 downto 3 do begin
                  count := count + 1;
                  height;
                  writeln('----------------------------------------');
                  intercept;              {calling the Y intercept and least squares procedures}
                  slopefind;
                  slopefind1;
                  slopefind2;
                  slopefind3;
              end;
end;
procedure file_fill;              {uses data from choice procedure to create binary files}
         var                      {for use by ARRCHK.PAS and TREEGR.SIM}
            hf,bf,ofil,pf         : file of real;
            cf                    : file of integer;
            kk,hh                 : integer;
         begin
              assign(hf,'hmax.dta');
              assign(cf,'count.dta');
              assign(bf,'bug.dta');
              assign(ofil,'overtop.dta');
              assign(pf,'bprob.dta');
              rewrite(hf);
              rewrite(cf);
              rewrite(bf);
              rewrite(ofil);
              rewrite(pf);
           for kk := 1 to 25 do
               write(hf,hmax[kk]);
           for kk := 3 to 24 do begin
               for hh := 1 to 20 do begin
                   write(cf,c[kk,hh]);
                   write(bf,bug[kk,hh]);
                   write(ofil,o[kk,hh]);
                   write(pf,prob[kk,hh]);
               end;
           end;
           close(hf);
           close(cf);
           close(bf);
           close(ofil);
           close(pf);
end;

{*****MAIN PROGRAM START*****}
```

```
begin                          (calls the procedures )
      clrscr;
      htmax;
      writeln('age    ','  height   ','  choice   ','prob. value');
      writeln('---------------------------------------');
      age;
      file_fill;
      end.
```

APPENDIX B

COMMENTED SOURCE CODE FOR

TREEGR.SIM

This program is a simulation and data display program that utilizes the optimal allocation choice data and probabilities of survival generated in TREEGR.FIL.

```
program Optimal_Allocation_Simulator;
        type                                    {variable initialization}
            number = real;
        var
            chr                                  : char;
            t                                    : integer;
            p_array,hmax,hpot                    : array[3..24] of real;
            bugrisk,overtop                      : array[3..24,1..20] of real;
            choice                               : array[3..24,1..20] of integer;

        function e( x:number; y :real ) : real;       {function creates the power function x^y}
                 var
                    z : real;
                 begin
                     if x = 0 then z := 0 else
                        z := exp(ln(abs(x)) * y);      {creating the function}
                     if x < 0 then begin          {special provisions if base is 0, <0, or power}
                        if frac(y) <> 0 then begin     {is a negative fraction}
                           writeln('error'); halt;
                        end;
                        if frac(y/2) <> 0 then
                           z:= -z;
                        end;
                     e := z;
        end;
        procedure randomize;                          {creates a random seed by calling the clock}
                  var
                     i,j     : integer;
                     rset    : record
                                  ax,bx,cx,dx,bp,si,ds,es,flags : integer;
                               end;
                     ch      : char;
                  begin
                       i := 0; j := 0;                    {getting a seed from the clock}
                       if (i=0) and (j=0) then begin
                          rset.ax := $2c00;
                          MSDos(rset);
                          i := rset.cx;
                          j := rset.dx;
                          delay(100);
                          MSDos(rset);
                       end;
                       MemW[DSeg:$129] := i;               {saving that seed in memory}
                       MemW[Dseg:$12B] := j;
        end;
        procedure file_read;                             {reading the files created in TREEGR.FIL}
                  var
                     hm,b,o          : file of real;
                     ch              : file of integer;
                     kk,hh           : integer;
```

```
          begin
               assign(hm,'hmax.dta');
               assign(ch,'count.dta');
               assign(b,'bug.dta');
               assign(o,'overtop.dta');
               reset(hm);
               reset(ch);
               reset(b);
               reset(o);
            for kk := 3 to 24 do
                read(hm,hpot[kk]);
            for kk := 3 to 24 do begin
                for hh := 1 to 20 do begin
                    read(ch,choice[kk,hh]);
                    read(b,bugrisk[kk,hh]);
                    read(o,overtop[kk,hh]);
                end;
            end;
            close(hm);
            close(ch);
            close(b);
            close(o);
     end;
     procedure ht_max;           {determines heights based on the allocation choices }
          var                    {that were read from the files}
             ht,growth,eh,x,z    : real;
             time,htdif          : integer;
          begin
               ht := hpot[3];
             for time := 3 to 24 do begin
                 htdif := round(hpot[time] - ht) + 1;
                   x := 0.1 * choice[time,htdif];
                  eh := ht;
{                  if ht > 45 then eh := 45;}      {device for limiting the crown area }
              growth := (5 * ((x * sqr(eh)/1.8839) - sqr(ht) * ht * 0.004))/{energy/marginal}
                        ((sqr(eh+1) * (eh+1) - sqr(eh) * eh)/15);       {cost of growth}
                        if growth < 0 then growth := 0;
                  ht := ht + growth;                  {summing the growth}
                  hmax[time] := ht;
              end;
    end;

     procedure cho_htsho;        {displays the choices taken and the heights derived from}
          var                    {those choices for all ages}
             ch      : char;
             time,x  : integer;
          begin
               clrscr;
               lowvideo;
               writeln('Age       Height       Choice');
```

```
            normvideo;
            for time := 4 to 24 do begin
                x := round((hpot[time] + 1) - hmax[time]);         {choices based on height }
                writeln ( time : 5:3,'      ', hmax[time] : 0.3048:8,'     ', {rounded to the}
                        choice[time,x]:2);                                    { nearest foot}
            end;
            lowvideo;
            writeln;
            write('Return to Menu?');
            normvideo;
            write(' Y/N');
            read(kbd,ch);
          if ch <> 'y' then halt;
end;
procedure chosho;     {displays all of  the best choices for all heights and }
var                   {ages in a block form}
   ch      : char;
   time,ht : integer;
begin
     clrscr;
     lowvideo;
     writeln('           Distance Below Height Maximum (meters)');
     writeln('     0.0  0.6  1.2  1.8  2.4  3.0  3.7  4.3  4.9  5.5 ');
     writeln('Age');
     normvideo;
     for time := 4 to 24 do begin
         write(time : 5:3,' ');
         write(' ');
         for ht := 1 to 20 do
         if frac(ht/2) <> 0 then
             write(choice[time,ht]:3,'  ');
             writeln;
     end;
     lowvideo;
     write('Return to Menu?  ');
     normvideo;
     write('Y/N');
     read(kbd,ch);
   if ch <> 'y' then halt;
end;
procedure lotus;{simulates the course of a tree's life with probabilities of survival based}
          label        {on the probabilities generated in TREEGR.FIL and generates .PRN}
               finished;{files for importation into Lotus 123 - tm. Lotus Development Corp.}
          var
             ch                      : char;
             x,height,
             over_dead, bug_dead,
             bug_tot                 : real;
             cho_ht,kk,n             : integer;
             time,d,od,bd,bp         : text;
```

```
          death,odeath,bdeath      : array[4..24] of integer;
          bprod_t                  : array[4..24] of real;
        begin
            clrscr;
            assign(time,'b:time.prn');  {creating the files}
            assign(d,'b:death.prn');
            assign(od,'b:ovdeath.prn');
            assign(bd,'b:bugdeath.prn');
            rewrite(time);
            rewrite(d);
            rewrite(od);
            rewrite(bd);
          randomize;                    {calling the random seeder}
        for kk := 4 to 24 do begin
          death[kk]   :=0;
          odeath[kk]  :=0;
          bdeath[kk]  :=0;
        end;
        lowvideo;
        writeln('How Many Times do You Want to Simulate?');
        normvideo;
        readln(n);
        for kk := 1 to n do begin
            if frac(kk/100) = 0 then randomize;   {re-seeding every 100 repetitions}
        for t := 4 to 24 do begin
            height := (hpot[t] - hmax[t]) + 1;
            cho_ht := round(height);
            over_dead := random;                      {comparing various probabilities }
          if over_dead >= overtop[t,cho_ht] then begin  {of overtopping and beetle kill}
             death[t] := death[t] + 1;               {with numbers created by the random}
             odeath[t] := odeath[t] + 1;                   {number generator}
             goto finished;
          end;
            bug_dead := random;
          if bug_dead >= bugrisk[t,cho_ht] then begin
             death[t] := death[t] + 1;
             bdeath[t] := bdeath[t] + 1;
             goto finished;
          end;
    end;
    finished:
end;
for kk := 4 to 24 do begin   {filling the files}
    writeln(time,kk*5);
    writeln(d,death[kk]/n);
    writeln(od,odeath[kk]/n);
    writeln(bd,bdeath[kk]/n);
end;
    close(d);
    close(od);
```

```
        close(bd);
        close(time);
        lowvideo;
        writeln('Ready for Lotus');
        halt;
      end;
      procedure simulate;    {see lotus - procedure is the same except that numbers are}
               label                {displayed on the screen rather than written into files}
                    finished;
               var
                  ch                     : char;
                  height,
                  over_dead, bug_dead    : real;
                  cho_ht                 : integer;
               begin
                    clrscr;
                    writeln;
                    lowvideo;
                    writeln('AGE       HEIGHT           ALLOCATION');
                    normvideo;
                 randomize;
               for t := 4 to 24 do begin
                  height := (hpot[t] - hmax[t]) + 1;
                  cho_ht := round(height);
                  over_dead := random;
                if over_dead >= overtop[t,cho_ht] then begin
                   writeln('killed by overtopping');
                   goto finished;
                end;
                  bug_dead := random;
                if bug_dead >= bugrisk[t,cho_ht] then begin
                   writeln('killed by beetles');
                   goto finished;
                end;
                    writeln(t:5:3,'        ',hmax[t] * 0.3048:8,'         ',
                           choice[t,cho_ht]:2);
        end;
        finished:
        writeln;
        lowvideo;
        write('Do You Want to Simulate?  ');
        normvideo;
        write('Y/N');
        read(kbd,ch);
       if ch = 'y' then
          simulate;
end;
procedure menu;                {creates the menu}
         var
            ch  : char;
```

```
          begin
               clrscr;
                  lowvideo;
               writeln('Pick the Option You Would Like to Execute by');
               writeln('Striking the Appropriate Letter (Highlighted)');
               writeln;
               writeln;
               write('View ');
                  normvideo;
               write('C');
                  lowvideo;
               writeln('hoice "Block"');
                  normvideo;
               write('V');
                  lowvideo;
               writeln('iew Choice/height route taken');
                  normvideo;
               write('S');
                  lowvideo;
               writeln('imulate');
               write('Generate Data for ');
                  normvideo;
               write('L');
                  lowvideo;
               writeln('otus');
                  normvideo;
               write('Q');
                  lowvideo;
               writeln('uit');
               writeln;
               writeln;
               writeln;
               write('Your Choice?  ');
                  normvideo;
               read(kbd,ch);
             if ch = 'c' then chosho;
             if ch = 'v' then cho_htsho;
             if ch = 's' then simulate;
             if ch = 'l' then lotus;
             if ch = 'q' then halt;
            menu;
end;
procedure wait;            {creates the please wait sign while the files are read}
         begin
               writeln;
               writeln;
               writeln;
               writeln;
               writeln;
               writeln;
```

```
            writeln;
            lowvideo;
            write('        ***********    ');
            normvideo;
            write('PLEASE         WAIT');
            lowvideo;
            writeln('    ***********');
end;

  {**********************MAIN PROGRAM BEGINS HERE*****************************}
       begin                    {calls the procedures}
            clrscr;
            wait;
            file_read;
            ht_max;
            menu;
       end.
```

APPENDIX C

COMMENTED SOURCE CODE FOR

TREEGR.EQU

This program is a simulation and data display program that drives optimal allocation choice production with equations, constants or groups of discontinuous data. This program also computes beetle production if the simulated tree is killed by beetles and generates mean beetle production data.

```
program simulator_with_equations;  {$r+}          {variable initialization}
        type
            number = real;
        var
            chr                                 : char;
            bug_dry,bug_pro,phlo_tot,ar         : real;
            t                                   : integer;
            hpot,hmax,attack,surv,overtop,cho   : array[1..125] of real;
            p_array,bugar                       : array[2..125] of real;

procedure instructions;              {prints directions while you wait for the arrays to fill}
     begin
          writeln;writeln;writeln;
          writeln('This program will generate tree survival data and beetle');
          writeln('production data using energy an energy allocation strategy');
          writeln('based on an equation.  The program will also generate text');
          writeln('files that can be imported into Lotus 123.  The Files gen-');
          writeln('erated using mean probabilities have the word "mean" in the');
          writeln('file name.');
          writeln;
        writeln;
          lowvideo;
          write('Adjust your ');
          normvideo;
          write('contrast ');
          lowvideo;
          writeln('so that this is readable');
     end;
        function e( x:number; y :real ) : real;   {creates the arithmetic function x^y}
                var
                   z : real;
                begin
                     if x = 0 then z := 0 else
                        z := exp(ln(abs(x)) * y);  {this is the function}
                     if x < 0 then begin
                        if frac(y) <> 0 then begin{special provisions for when the base = 0 or <0;}
                           writeln('error'); halt;    {or when the exponent is a negative fraction}
                        end;
                        if frac(y/2) <> 0 then
                           z:= -z;
                        end;
                     e := z;
        end;
        procedure randomize;   {creates a random seed by taking a time from the clock}
                  var
                     i,j     : integer;
                     rset    : record
                                  ax,bx,cx,dx,bp,si,ds,es,flags : integer;
```

```
                    end;
               ch      : char;
          begin
               i := 0; j := 0;
               if (i=0) and (j=0) then begin
                  rset.ax := $2c00;
                  MSDos(rset);                  {contacting the clock}
                  i := rset.cx;
                  j := rset.dx;
                  delay(100);
                  MSDos(rset);
               end;                             {storing the seed in memory}
               MemW[DSeg:$129] := i;
               MemW[Dseg:$12B] := j;
     end;
     procedure fileread;                   {this procedure is optional- if you want to input}
               var                         {complex discontinuous data setsthen you can import}
                  xfil    : file of real;          {them using this procedure}
                  k       : integer;
               begin
                    assign(xfil,'chopik.dta');
                    reset(xfil);
                    for k := 1 to 125 do
                        read(xfil,cho[k]);
                    close(xfil);
     end;
     {**********************the following procedures save their ******************}
     {**************************data in arrays for simulation*************************}

     procedure ht_pot;             {height if 100% of available energy was allocated to growth}
               var
                  ht,growth,eh        : real;
                  time                : integer;
               begin
                    ht := 1;
                    for time := 1 to 125 do begin
                        eh := ht;
{                      if ht > 45 then eh := 45;     }      {allows limitation of crown area}
                       growth := (sqr(eh)/1.8839  - sqr(ht) * ht * 0.004)/ {energy/marginal growth}
                           ((sqr(eh + 1) * (eh + 1) - sqr(eh) * eh)/12.7);
                      if growth < 0 then growth := 0;
                     ht := ht + growth;                {sum of growth}
                     hpot[time] := ht;
                     end;
end;
procedure ht_max;                          {height that the tree can obtain using the allocation}
               var                                  {strategy that has been chosen - choose it}
                  ht,growth,eh,x,z    : real;           {here!!!}
                  time,htdif          : integer;
               begin
```

```
                    ht := 1;
                   for time := 1 to 125 do begin
                     if time <= 30 then x := 1;
                     if (time > 30) and (time <= 40) then x := 0.85;
                     if (time > 40) and (time <= 85) then x := 0.85; {discontinuous functions can }
                     if (time > 85) and (time <= 105) then x := 0.85; {can be created }
                     if time  > 105 then x := 0.1;
                     x := 1;
                     cho[time] := x;
                   {  x := cho[time];}
                        eh := ht;
{                        if ht > 45 then eh := 45;}       {allows limitation of crown area}
                    growth :=  ((x * sqr(eh)/1.88389) - sqr(ht) * ht * 0.004)/     {energy/marginal}
                              ((sqr(eh+1) * (eh+1) - sqr(eh) * eh)/12.7);    {cost of growth}
                              if growth < 0 then growth := 0;
                        ht := ht + growth;                                    {sum of growth}
                        hmax[time] := ht;
                    end;
end;
procedure chance_attack;            {probability of attack based on diameter}
         var
            prob_attack,bug_count    : real;
            time                     : integer;
         begin
              bug_count := 0;
              for time := 1 to 125 do begin
                 prob_attack := ((0.5 * sqr(0.16 * hmax[time])) -
                                (0.021 * sqr(0.16 * hmax[time]) *
                                (0.16 * hmax[time])))/1000;
                 if bug_count < prob_attack then
                    bug_count := prob_attack;
                 attack[time] := bug_count;
               end;
end;
procedure surv_attack;    {probability of surviving an attack based on energy allocation per unit}
         label                  {volume of sapwood with or without the ability to store energy}
              finished;       {areas of code enclosed in brackets will cause storage if brackets}
         var                    {are removed}
            x,y,E_store     : real;
            time,k          : integer;
         begin
              for time := 1 to 125 do begin
                 E_store := 0;
                { for k := time downto (time - 10) do begin}  {sum of phloem for last 10 years}
                    {if k < 2 then goto finished;}
                    x := hmax[time];                  {replace time with k if you want storage}
                    y := (sqr(x)/1.8839)/(sqr(x) * x * 0.004) - 1; {allocation per unit area}
                    y := y * (1 - cho[time]) ;        {the allocation strategy chosen}
                   { y := y * 1/e(1.5,(time - k));}     {the depreciation}
                    E_store := E_store + y;
```

```
                { end;}
                 finished:
                 E_store := (1 - exp(-1 * E_store));
                 surv[time] := E_store;
              end;
end;

procedure overtop_risk;   {probability of surviving overtopping as a function of distance}
          var              {below height potential}
             y     : real;
             time  : integer;
          begin
               for time := 1 to 125 do begin
                   y := (100 - sqr(hpot[time] - hmax[time]) * 0.003)/100;
                   if y < 0 then y := 0;
                   overtop[time] := y;
              end;
end;


procedure phloem;                       {phloem creation in each time step as a linear}
                 var                    {function of diameter growth}
                    phlo_gro     : real;
                    time         : integer;
                 begin
                  for time := 2 to 125 do begin
                      phlo_gro := (Hmax[time] - Hmax[time-1]) * 0.0533;
                      p_array[time]  := phlo_gro;
                   end;
       end;
       procedure bug_production;        {beetle production as a function of phloem thickness}
                begin
                    bug_pro := -23.91 + 947.74 * phlo_tot;
                 if bug_pro < 0 then bug_pro := 0;
        end;
        procedure area;                 {area of the lower 1/3 of the tree bole at the time of }
                 begin
                      ar := pi * sqr(hmax[t])/150 - pi * sqr(hmax[t])/337.5;
        end;
        procedure dehydration;           {percent of beetle brood lost due to dessication}
                 begin                   {as a function of surface area/internal volume}
                      bug_dry := 210.84/(hmax[t] * 45);
                      if bug_dry > 1 then
                         bug_dry := 1;
        end;
        procedure phloem_total;   {total phloem available to the beetles as a sum of the}
                 label            {phloem produced over the past 10 years with a depreciation}
                      finish;     {to take into account the incorporation of phloem into the bark}
                 var
                    phlo_add   : real;
```

```
          c,cc       : integer;
        begin
             phlo_tot := 0;
             for c := t downto (t-10) do begin
               if c < 2 then goto finish;          {if there are not 10 years of phloem}
                 phlo_add := p_array[t] * 1/e(1.5,(t-c));    {the depreciation}
                 phlo_tot := phlo_add + phlo_tot;
             end;
             finish:
end;
procedure lotus2;                  {sets up the .PRN files for Lotus 123 - tm Lotus}
        var                        {development corp. that are created by the mean}
           age,dia,bug     : text;        {probabilities of survival, beetle kill, etc.}
           kk              : integer;
        begin
             assign(age,'b:meanage.prn');
             assign(dia,'b:meandia.prn');
             assign(bug,'b:meanbug.prn');
             rewrite(age);
             rewrite(dia);
             rewrite(bug);
          for kk := 2 to 125 do begin
              writeln(age,kk);
              writeln(dia,hmax[kk] * 0.4064);
              writeln(bug,bugar[kk]);
          end;
          close(age);
          close(dia);
          close(bug);
end;
procedure surv_prob;       {displays the probability of survival, maximum mean probable}
        var          {beetle production, the age at which it happens, and the diameter}
           ch                              :  char;
           surcount,surprob,bugsur,bugpro  :  real;
           beet_tot,beetmax                :  real;
           maxtime                         :  integer;

        begin
             clrscr;
             lowvideo;
             writeln;writeln;writeln;writeln;writeln;writeln;writeln;
             writeln('                              Please Wait');
             surprob := 1;
             beetmax := 0;
           for t := 2 to 125 do begin
               surcount := overtop[t] * (1 - attack[t]) +    {generating the prob. of }
                           overtop[t] * attack[t] * surv[t]; {survival}
               surprob := surprob * surcount;
               bugsur  := overtop[t] * attack[t] * (1 - surv[t]);
               phloem_total;
```

```
                bug_production;
                area;
                dehydration;
                beet_tot :=  bug_pro * ar;
                beet_tot := beet_tot - (beet_tot * bug_dry);        {beetle production}
                bugpro := beet_tot * bugsur;
               if bugpro >= beetmax then begin
                  beetmax := bugpro;
                  maxtime := t;
               end;
                 bugar[t] := bugpro;
            end;
            clrscr;
            writeln;writeln;writeln;writeln;writeln;writeln;
            writeln('The Probability of Survival Over 124 Timesteps is:');    {the display}
            normvideo;
            writeln('              ',surprob:10);
            writeln;writeln;
            lowvideo;
            writeln('The Maximum Beetle Production Occurs at');
            write('Age ');
            normvideo;
            write(maxtime:4);
            lowvideo;
            write(', a Diameter of ');
            normvideo;
            write(hmax[maxtime] * 0.4064:8);
            lowvideo;
            writeln(' Centimeters');
            write('and Equals ');
            normvideo;
            write(trunc(beetmax));
            lowvideo;
            writeln(' Beetles');
            writeln;writeln;writeln;writeln;
            write('Would You Like to Create Files for Lotus?');
            normvideo;
            write(' (Y/N)');
            read(kbd,ch);
            if ch = 'y' then lotus2;
end;
procedure lotus;        {simulates the life of the tree based on the probabilities of}
          label         {survival generated in the preceeding procedures and by comparing}
               finished;      {them with numbers generated by the random number generator}
          var                    {the mean data is then input into .PRN text files for }
            ch                      : char;    {importation into Lotus 123}
            x,height,
            over_dead, bug_dead,
            bug_tot                 : real;
            kk,n                    : integer;
```

```
    time,d,od,bd,bp,dia      : text;
    death,odeath,bdeath      : array[2..125] of integer;
    bprod,bprod_t            : array[2..125] of real;
 begin
      clrscr;
      assign(time,'b:time.prn');              {creating the files}
      assign(dia,'b:diam.prn');
      assign(d,'b:death.prn');
      assign(od,'b:ovdeath.prn');
      assign(bd,'b:bugdeath.prn');
      assign(bp,'b:bugprod.prn');
      rewrite(time);
      rewrite(dia);
      rewrite(d);
      rewrite(od);
      rewrite(bd);
      rewrite(bp);
   randomize;                        {creating a random seed}
 for kk := 2 to 125 do begin
    death[kk]   :=0;
    odeath[kk]  :=0;
    bdeath[kk]  :=0;
    bprod[kk]   :=0;
    bprod_t[kk] :=0;
 end;
 lowvideo;
 writeln('How Many Times do you Wish to Simulate?');
 normvideo;
 readln(n);
 lowvideo;
 writeln;writeln;writeln;writeln;writeln;
 writeln('                                  Please Wait');
 for kk := 1 to n do begin
if frac(kk/100) = 0 then randomize;         {re-randomizing every 100 repetitions}
 for t := 2 to 125 do begin
    over_dead := random;                   {comparing risk parameters with random}
  if over_dead >= overtop[t] then begin    {numbers if greater then the tree dies}
     death[t] := death[t] + 1;
     odeath[t] := odeath[t] + 1;
     goto finished;
  end;
    bug_dead := random;
 if bug_dead >= (1-attack[t]) + attack[t] * surv[t] then begin
     death[t] := death[t] + 1;
     bdeath[t] := bdeath[t] + 1;
   if bprod_t[t] = 0 then begin  {if the tree is killed by beetles, then}
     phloem_total;               {beetle production procedures are called}
     bug_production;
     area;
     dehydration;
```

```
            bug_tot := bug_pro * ar;
            bug_tot := bug_tot - (bug_tot * bug_dry);   {beetles produced}
            bprod_t[t] := bug_tot;
          end;
            bprod[t] := bprod[t] + bprod_t[t];
            goto finished;
         end;
   end;
   finished:
end;
for kk := 2 to 125 do begin         {input the mean data into .PRN text files}
    writeln(time,kk);
    writeln(dia,hmax[kk] * 0.4064);
    writeln(d,death[kk]/n);
    writeln(od,odeath[kk]/n);
    writeln(bd,bdeath[kk]/n);
    writeln(bp,bprod[kk]/n);
end;
    close(d);
    close(dia);
    close(od);
    close(bd);
    close(bp);
    close(time);
end;
procedure simulate;  {see procedure Lotus - process is identical except that the data is}
         label           {displayed on the screen instead of being written into files}
              finished;
         var
            ch                      : char;
            x,height,
            over_dead, bug_dead,
            bug_tot                 : real;
         begin
              clrscr;
              writeln;
              lowvideo;
              writeln('AGE          HEIGHT          ALLOCATION');
              normvideo;
           randomize;
        for t := 2 to 125 do begin
            over_dead := random;
          if over_dead >= overtop[t] then begin
            writeln('killed by overtopping');
            goto finished;
          end;
            bug_dead := random;
       if bug_dead >= (1 - attack[t]) + attack[t] * surv[t] then begin
              writeln('killed by beetles');
              phloem_total;
```

```
                bug_production;
                area;
                dehydration;
                bug_tot := bug_pro * ar;
                bug_tot := bug_tot - (bug_tot * bug_dry);
                writeln;
               writeln;
                writeln('beetle production = ', bug_tot);
                goto finished;
             end;
             if frac(t/5) = 0 then
                 writeln(t:3,'        ',(hmax[t] * 0.3048):8,'         ',
                       cho[t]:8);
      end;
      finished:
      writeln;
      lowvideo;
      write('Do You Want to Simulate? ');
      normvideo;
      write('(Y/N)');
      read(kbd,ch);
    if ch = 'y' then
       simulate;
end;
procedure menu;                    {creates the menu}
       var
          ch     : char;
       begin
            clrscr;
            lowvideo;
            writeln;writeln;
            writeln('Choose From The Menu by Striking');
            writeln('the Appropriate Highlighted Letter');
            writeln;writeln; writeln;
            normvideo;
            write('D');
            lowvideo;
            writeln('isplay Mean Results');
            normvideo;
            write('S');
            lowvideo;
            writeln('imulate');
            write('Generate Files for ');
            normvideo;
            write('L');
            lowvideo;
            writeln('otus Using Simulation Data');
            normvideo;
            write('Q');
            lowvideo;
```

```
            writeln('uit');
            writeln;writeln;writeln;
            write('Your Choice: ');
            read(kbd,ch);
          if ch = 'd' then surv_prob;
          if ch = 's' then simulate;
          if ch = 'l' then lotus;
          if ch = 'q' then begin
          clrscr;
          halt;
          end;
          menu;
    end;
{**********************MAIN PROGRAM BEGINS HERE*****************************}
    begin
         clrscr;                    {calls procedures}
         instructions;
         fileread;
         ht_pot;
         ht_max;
         chance_attack;
         surv_attack;
         overtop_risk;
         phloem;
         menu;
    end.
```

APPENDIX D

COMMENTED SOURCE CODE FOR

ARRCHK.PAS

This program is a data display program that allows quick access to all of the data produced by TREEGR.FIL

```
program array_checker;  {$c-,v-,i-}
        label                       {variable initialization}
             again,again1;
        var
           ch                :   char;
           bug,ov,prob       :   array[3..24,1..20] of real;
           ct                :   array[3..24,1..20] of integer;
           age,kk,hh         :   integer;
           b,o,p             :   file  of real;
           c                 :   file of integer;
procedure menu;
          begin                                          {creates the menu}
              lowvideo;
          writeln('Which Parameter Would You Like to Choose?');
          writeln('Enter the Highlighted Letter in the Menu Below');
          writeln;
          writeln;
          write('Allocation ');
                normvideo;
          write('C');
                lowvideo;
          writeln('hoice');
          write('Probability of ');
                normvideo;
          write('O');
                lowvideo;
          writeln('vertopping at Age ',age);
          write('Probability of ');
                normvideo;
          write('B');
                lowvideo;
          writeln('eetle Kill at Age ',age);
                normvideo;
          write('P');
                lowvideo;
          writeln('robability of survival through ',124-age,' Time Steps');
          writeln;
          writeln;
          write('Your Choice : ');
                normvideo;
          read(kbd,ch);
end;
        begin
            assign(c,'b:count.dta');      {reading the binary files set up in TREEGR.FIL}
            assign(b,'b:bug.dta');
            assign(o,'b:overtop.dta');
            assign(p,'b:bprob.dta');
            reset(c);
            reset(b);
            reset(o);
```

```
  reset(p);
for kk := 3 to 24 do begin
    for hh := 1 to 20 do begin
        read(c,ct[kk,hh]);
        read(b,bug[kk,hh]);
        read(o,ov[kk,hh]);
        read(p,prob[kk,hh]);
     end;
end;
   again:
   clrscr;
   lowvideo;
   writeln('       which age would you like to view?');
   write('enter an integer divisible by 5 between 15 to 120 : ');
   normvideo;
   read(age);
   clrscr;
   menu;
   again1:
   clrscr;

 if ch = 'c' then begin                        {displaying the various parameters}
   lowvideo;
   writeln('Choice           Age = ',age);
   writeln;
   normvideo;
for hh := 1 to 20 do
   writeln(ct[age div 5,hh]);
end;
 if ch = 'o' then begin
   lowvideo;
   writeln('Survival :  Overtop           Age = ',age);
   writeln;
   normvideo;
for hh := 1 to 20 do
   writeln(ov[age div 5,hh]);
end;
 if ch = 'b' then begin
   lowvideo;
   writeln('Survival :  Beetles           Age = ',age);
   writeln;
   normvideo;
for hh := 1 to 20 do
   writeln(bug[age div 5,hh]);
end;
 if ch = 'p' then begin
   lowvideo;
   writeln('Prob. of Survival           Age = ',age);
   writeln;
   normvideo;
```

```
          for hh := 1 to 20 do
             writeln(prob[age div 5,hh]);
          end;
             writeln;
             lowvideo;
             write('view another parameter? (y/n) : ');
             normvideo;
             read(kbd,ch);
             writeln;
           if ch = 'y' then begin
             clrscr;
             menu;                                    {return to menu}
             goto again1;
           end;
             lowvideo;
             write('view another age? (y/n) : ');
             normvideo;
             read(kbd,ch);
             writeln;
          if ch = 'y' then
             goto again;
end.
```

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