

ECOLOGICAL MODELLING
AND THE
STAND DYNAMICS OF
PINUS CARIBAEA IN MOUNTAIN PINE RIDGE,
BELIZE

by

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ABSTRACT

This study examines the stand dynamics of *Pinus caribaea* var. *hondurensis* in its native habitat in Central America. This species is currently the most important timber tree being planted in the lowland tropics, but knowledge of its autecology is extremely meagre. Data on the growth and population dynamics of the species were obtained in an intensive programme of field sampling and experimentation in the Mountain Pine Ridge area of Belize. These data served as input to a model (PINUS), which simulated the growth of mature stands of Caribbean pine. The model was used to explore the effects of forest management policies on the growth and dynamics of pine stands.

Fire protection of these pinelands in the last 30 years has initiated successional changes in the vegetation leading to reduced pine regeneration and invasion of broadleaved species into stands from which fire has been excluded. Field experiments clearly demonstrated that the overall small size of the pine seedling population was a result of seed-harvesting by the rodent, insect and avifauna of the area. There were however differentials in seedling establishment related to the successional status of individual stands. A further series of field and laboratory experiments monitored the effects of differential shading, seedbed conditions, competition, allelopathic interactions, and seed-predation on the germination

and survivorship of a population of 34,000 pine seeds in stands of varying age.

The differential seedling establishment of *P. caribaea* is considered to be mainly controlled by seedbed conditions. In stands which have been recently burnt the mineral-soil seedbed is subject to rapid desiccation, especially in open areas, and seeds suffer from lack of moisture. In areas where the litter depth exceeds 3.5 cms in thickness, the light pine seeds are perched above a moisture supply and germination is reduced. Those seeds that do germinate suffer severe mortality in the first year, as a result of limited root development.

The results obtained from these experiments are a source of data for the construction of the simulation model. The main simulation program requires three other items of input: number, diameter and age of seed-trees, age of the plot (usually set to zero) and the required thinning schedule.

The main simulation program was constructed from empirical data on the relationships between stem morphology, crown development, growth rate, and the light climate in the stand.

The model proceeds to update changes in population structure and individual-tree growth until maximum stand age of 50 years is reached. The main program performs the update by calling three workhorse subroutines. BIRTH recruits new seedlings into the

stand by multiplying fecundity coefficients by the numbers of trees in each age-class. This value is then derated by an equation which predicts germination based on incident radiation, litter depth, and stand basal-area. A second subroutine (MORT) calculates a probability of mortality based on the volume-increment of an individual in the previous year.

Subroutine GROW is a modified version of the JABOWA program of Botkin et alia (1970, 1972). The growth rate for individual trees is calculated using an optimum growth-rate equation derated by the effects of shading in the stand. Output from these three subroutines has been validated by comparing the development of actual stands of various ages with predicted growth and mortality rates over a seven-year period. No significant differences in stand growth or tree mortality were found in a series of paired tests.

The response of pine stands to two management regimes was explored using PINUS. The regeneration of stands with varying densities of seed-trees, and the effects of various thinning intensities and intervals on pine production were examined. Recommendations include the need for a minimum seed input after harvesting of 20,000 seeds/ha, a rotation-age for sawtimber of 60 years, and a restriction on thinning operations apart from in stands of exceptional stem density.

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CHAPTER ONE: INTRODUCTION TO THE STUDY

The decisions made by foresters in their management of forest resources often alter radically the potential uses of a forest ecosystem, yet the consequences of such decisions may not be apparent in the environment for several years. The nature of a decision is directly dependent upon the amount and quality of silvicultural and ecological information available to the forester, his experience in interpreting these, and the management goals in particular forest stands. The data base for making management decisions is usually derived from analogous situations elsewhere and from the results of field experimentation.

In many forest ecosystems in the tropics the silvicultural data-base is extremely meagre. Decisions which directly affect the forest resource and the potential yields of the constituent commercial species are made without foreknowledge of their consequences. Some tropical trees have become potentially important timber and pulp species in the last twenty years, but the commercial value of the species is not always matched by an adequate knowledge of its autecology.

An example of this situation is afforded by Caribbean pine (*Pinus caribaea*), an important member of the forest estate in many countries in Central America and the West Indies. In addition, the wide ecological tolerance of *P. caribaea* has

favoured its selection as a plantation species in other tropical and sub-tropical areas; it is currently the most important species being planted for timber in the lowland tropics.

This thesis attempts to rectify the predicament of a meagre data base for management of stands of P. caribaea, by examining the stand dynamics of the species in part of its natural range in Central America.

Apart from the economic justification for this study, the research is of interest for other reasons. Firstly the thesis deals in considerable detail with the population dynamics of a single tree species, and therefore adds to a surprisingly slim corpus of knowledge on the demography of plants. Secondly, it deals with a familiar genus in an unfamiliar environment, as almost all of the extant ecological research has dealt with the temperate congeners of Pinus caribaea. Thirdly, it considers and develops demographic theory and its relation to silvicultural problems. These tasks are practicable because of the comparative simplicity of these Caribbean pine communities compared to the great ecological diversity and more complex interactions of the neighbouring rainforests.

1.1: SILVICULTURE AS APPLIED PLANT DEMOGRAPHY

The objective of virtually all silvicultural research is to predict and optimize timber yield and the stem form of the individual trees that comprise the crop, either in the

short-term, or on a sustained-yield basis (Assmann, 1970). Silviculture is therefore akin to agriculture in manipulating the growth, size, form and genetic structure of plant populations in order to attain certain management goals.

Silviculture and agriculture comprise the applied arm of the science of plant demography, though this has seldom been explicitly stated. Demography deals with population flux, focussing on the birth and death characteristics, and the potential for numerical change, in a species population. As well as monitoring population change, plant demographers have addressed themselves to questions which are those of the silviculturalist in more general form:

- a) In what ways is recruitment to the population regulated?
- b) What factors determine the efficiency of resource utilization by the population? For example, what is the effect of increasing crop density on crop yield?
- c) What are the effects of competition between species on growth rate, fecundity, and yield?
- d) What factors control mortality rates in the population?

Silviculturalists have tended to ignore their kinship with plant demographers for several reasons. One is the almost total neglect of plant population dynamics by botanists and biogeographers alike in the first half of this century. Plant demography lapsed from a central position in Darwin's researches on plant ecology to a very subordinate position in later work,

until revived by Tamm (1948, 1956, 1972) Harper (1960, 1961, 1964a, 1964b, 1965, 1967) and de Wit (1960, 1961). Changes in natural, transplanted and sown populations of crop plants, weedy annuals, or perennial herbs have also been monitored by Sagar, (1959), Antonovics, (1966), Cavers and Harper, (1967), Putwain et al., (1968), Putwain and Harper, (1970), Williams, (1970), and Sarukhan and Gadgil, (1974), for various periods of time. Their emphasis on non-arborescent species is the second major reason for the neglect of plant demographic research by foresters.

A further reason for this neglect is that plant demography is distinct in a number of ways from its animal counterpart, and this uniqueness poses several problems for researchers. Individuals of a single species of plant are in general more morphologically variable, longer-lived, and have a wider variety of reproductive strategies available to them than do animal species. Individual trees may vary a million-fold in their biomass as a result of growing through various life-stages. Further morphological variation may result from genotypic and ecotypic plasticity in the species population, and from the effects of competition. Thus a demographic analysis of tree populations that dealt only with the numbers of plant individuals would have serious shortcomings, and be of little practical interest to forest managers. One way of surmounting this problem was suggested by Harper and White (1974), who

expanded on an idea outlined by Darwin (1839). Their proposal is that plants consist of subpopulations of functional units which are relatively non-plastic (e.g. shoots or leaves) which they term "ramets". Each of these modules has the genetic makeup of, and is engrafted onto, the individual plant or "genet". This method also overcomes the problem of vegetative reproduction by plants, as members of clonal populations can be enumerated in the ramet subpopulations. Harper and White insist that plant demography should deal not only with the number of genets, but also the number of ramets, and the interactions between the two. Although their paper represents the most coherent attempt to grapple with the inherent problems of plant demography, only one field study has employed this approach (Kays and Harper, 1974).

As virtually all of the species investigated in the resurgence of plant demography have been non-arborescent species with fairly short life-spans, the dynamics of the sample populations can be accurately monitored by field observation. Direct testing of hypotheses in the field by manipulation of the population or its environment is also possible. Field experimentation has focussed on the regulatory mechanisms of population change such as crop density, soil fertility, and inter- and intra-specific competition for environmental resources.

The silviculturalist who endeavours to place his research into a holistic demographic framework faces a number of problems. Forest stands are complex and highly variable phenomena. Any study of their dynamics must take into account the processes of generation, development, and demise, of either the stand viewed as a whole, or of the individual trees that comprise the stand. One of the principal problems results from the longevity of forest trees. Most tree species have attainable life-spans of 100 - 400 years (Harper and White, op.cit.), and even in commercial timber rotations of 50 years or so the observation or manipulation of field populations may only be practicable for short segments of the cohort life-span. Population turnover is greatest in the juvenile phase of the plant's existence (Darwin, op.cit.; Sukatshev, 1928; Harper and MacNaughton, 1962; Yoda, 1963). For this reason, most field research in forest demography has focussed on population flux in this phase.

1.2: DEMOGRAPHY OF SEEDLING POPULATIONS

There have been two distinct and parallel trends in research on the recruitment of seedlings to forest stands. The first of these is similar in methodology to the aforementioned research on herbaceous communities, and deals with the environmental and biological controls on seedling establishment. The principal determinant of seedling abundance of various tree species has been ascribed to seed-predation and predator avoidance (Watt, 1919; Smith and Aldous, 1947; Abbott, 1961; Gashwiler, 1967;

Shaw, 1968; Smith, 1970; Janzen, 1971, 1972; Hartshorn, 1972); seedling-predation (Vaartaja, 1962; Ross et al., 1970); competition (Korstian and Coile, 1938) and unsuitable seedling environments in terms of the light climate, moisture supply or seedbed conditions (Billings, 1938; Shirley, 1945; McDermott, 1954) or allelochemicals (Ooyama, 1954).

Attempts to model seedling establishment and seedling mortality represent the second mode of forest demographic research. The work carried out under the impetus of the late John T. Curtis at the University of Wisconsin by Auclair, Cottam, Hett, Loucks, Goff and K. Harper exemplifies this approach. Hett (1969), for instance, documented the age-structural dynamics of Tsuga canadensis and Abies balsamea, and tested the comparative utility of three simple models of population decay in seedling populations. Hett (1971) and Hett and Loucks (1971), used similar techniques to model mortality in seedling populations of sugar maple (Acer saccharum). The research described above is unique in its exploration of models of seedling demographic change.

An alternative modelling method is the life-table approach. Again, this technique has been extensively used for human and other animal populations, but has found few exponents in plant demography. Hawksworth (1965) was the first to employ the technique in plant population dynamics, calculating survivorship rates and life-expectancies for various developmental stages in

the life-cycle of dwarf mistletoe. Hett and Loucks (1968) also demonstrated the use of static life-tables in analysing mortality of three species of tree seedlings in Ontario, and Sharitz and McCormick (1973) derived life-tables to compare the competitive abilities of two annual plants in Georgia.

1.3: SIMULATION MODELS IN FOREST ECOLOGY

In addition to the models of seedling populations, models of the entire life-spans of tree species can be constructed. Because of the longevity of forest trees, direct observation of the dynamics of the species populations requires long periods of data collection to produce reliable results. Similarly, experiments designed to test alternative management strategies in forest stands have to be monitored over many years before conclusive results are obtained. Forests are spatially heterogeneous systems and consequently, a large number of observational or experimental plots need to be maintained in order to sample the forest universe.

Using simulation models, the forest ecologist or silviculturalist can observe processes or test alternatives which may be too time-consuming, too destructive, or too expensive to monitor in the field. High-speed digital computers can execute simulation model programs in very short time-periods relative to their real-time counterparts. This feature of time-compression is one of the major advantages of the method.

The constraints of simulation modelling are succinctly stated by Wiens and Dyer:

"Thus a simulation model is not a precise portrayal of reality and the conclusions which emerge from a modelling analysis must be regarded as preliminary, subject to the constraints imposed by the assumptions of the model. However, simulation models may play an important role in resource management by temporarily allowing the circumvention of inadequacies in field data to reach tentative conclusions and by directing field research efforts towards elucidating variables which appear especially critical."

Wiens and Dyer, 1975; p. 64.

C.S. Holling (1973), in an article on the role of models in ecology, noted that modelling efforts have ranged from the relatively general ("strategic" models) to the relatively specific ("tactical" models). Holling's terminology was a reformulation of Levins' (1968) triad of model attributes: generality, realism and precision. Strategic models attempt to maximise generality and realism; tactical models emphasise realism and precision. Most of the strategic models in ecology have dealt with such problems as species interactions and community stability, and have been developed by animal ecologists. In forestry and forest ecology, however, tactical modelling has held sway.

Mathematical description of forest stands dates back to the yield tables formulated by the German forester J.C. Paulsen in 1795. Tactical modelling, as opposed to mathematical

description, has been used by foresters at least since 1898 when de Liocourt represented the number of trees in successive dbh classes by the geometric series (Meyer *et alia*, 1961). Since that time mathematical models have been increasingly utilised in forest research. Prior to the advent of the digital computer, most work in stand projection centred on yield tables. For the most part they are based on previous mean yields for a limited range of stocking levels and site indices. More sophisticated models have grown out of these techniques in the last fifteen years, their variety stemming from the goals of individual researchers, which may vary from the desire to maximise economic returns in forestry enterprises to evaluations of the role of environmental stresses and of community succession on forest dynamics. These two disparate goals represent the extremes of a continuum of approaches to forest modelling.

1.31: Demographic Models

The origin of population models can be traced to the work of Lewis (1942) and Leslie (1945, 1948) in population mathematics. The basic approach utilised in this type of model is that of a projection matrix (Q) (Pielou, 1969; Keyfitz, 1968), which describes the population transition from one time-period to the next. The numbers of live births-per-individual in each age group are given in the top row elements and the principal subdiagonal elements contain the probabilities of surviving from one age-group to the next. The basic Leslie model can then be

written as: $Q.a = a + 1$ where a is the age-structure at time t and $t+1$. This model operates under two constraints, one is that the transition coefficients are constant in time, and the other is that the age-structure of the population must be known. Models in this class have been developed by biologists and have so far been neglected by foresters.

If the birth and death rates of the population are both age and density-dependent, then the first constraint can be overcome by calculating the transition coefficients in the manner proposed by Pennycuik et al. (1968). The second constraint was circumvented by the work of Lefkovich (1965), who considered that division of the population into stage or size-classes, rather than age-classes, might be more suitable for many organisms.

The projection-matrix approach has been fairly widely employed in animal ecology, but the only use of the technique in plant population dynamics has been that of Usher (1966, 1967, 1969, 1972, 1973); Sarukhan and Gadgil (1974); and Hartshorn (1975). The most innovative use of the technique in forest ecology was by Usher, who calculated the annual allowable cut in forests of Pinus sylvestris based on the magnitude of the dominant latent-root of the projection matrix. Hartshorn employed it to examine the short-term population stability of two tree species in the rainforest of Costa Rica. A similar model outlined by Bosch (1971), purported to show that redwood

(Sequoia) populations in California could expand indefinitely and support intensive exploitation, but was subsequently shown to be conceptually and mathematically invalid (Brussard et alia, 1971; Halbach, 1971).

Other types of projection matrix have been used in forest ecology. Waggoner and Stephens (1970) and Horn (1975) used a stationary Markov-chain process as a technique for modelling forest succession. The resultant projection-matrix describes the probabilities of replacement of an individual tree by members of the sapling population over a specified time-interval. This method allows estimation of the variability of possible successional sequences and "climax" states. The assumption of a stationary process allows the modeller to use developed theory, but the assumption may not be valid in most forest ecosystems. A deterministic variant on the above method was employed by Shugart, Crow and Hett (1973) to model forest succession in the Great Lakes area. They modified the Markovian approach so that transitional probabilities were represented by linear differential equations. The output from this model would be equivalent to the mean values generated by a series of runs on the Markov-chain model.

Somewhat similar modes of modelling forest succession are derived from compartment models of chemical kinetics (e.g. Rescigno and Segre, 1966). This source has provided the theoretical basis for most of the research on mineral and energy

fluxes in forest ecosystems (e.g. Olson, 1965), but the only application in the field of forest stand dynamics has been that of Bledsoe (1968) and Bledsoe and van Dyne (1969, 1971). They employed a compartmental model approach in which the biomass of each species or group of species is represented as a compartment, and the changes in biomass over successional time are visualised as fluxes between compartments, represented by first-order differential equations. The model provides a useful, though somewhat coarse method of simulating vegetation succession, as no demographic information is incorporated in the model.

Models of forest succession which are more firmly based on the behaviour of the tree populations are those developed by Leak (1970) and Botkin, Janak and Wallis (1970, 1972a,b). Leak utilised constant birth and death rates to simulate the changes in old stands judged to be approaching steady-state conditions, and density-dependent rates in 'dynamic' stands. The JABOWA model of Botkin et alia is a forest-growth simulator developed for the Hubbard Brook Ecosystem Study which mimics succession in stands at differing altitudes and with varying soil depth. The input of new trees to the model is generated by a subroutine which makes a random choice of 0, 1 or 2 saplings from each of nine tolerant species. Mortality is governed by the degree of canopy closure and is also a function of tree age. Both of the above models suffer from the severe drawback that seed and seedling dynamics are omitted from the model, and "births" are

the result of tapping sapling populations which are assumed to be infinite.

1.32: Forest Estate and Stand Models

Management of forest estates in which variables such as yields, harvesting schedules, thinning regimes, operational costs and lumber prices may be modified by the simulator in order to evaluate economic alternatives, were the subject of a series of modelling and gaming efforts (Gould and O'Regan, 1965; Clutter and Bamping, 1965; O'Regan, Arventis and Gould, 1966; Howard et al., 1966; Myers, 1968, 1971; Ware, 1969; Bare, 1969; 1970; and Sayers, 1971). An illustrative example of this approach is that of Sayers (op.cit.), who constructed a model of a private forest estate in Scotland. Tree growth is calculated from a stand yield table and the model requires input of an operational schedule for each year. The model prepares annual accounts based on these operations, some of which are mandatory.

Tree growth is predicted in greater detail in stand models than in the forest-estate models. Examples are afforded by the work of Mauge (1970), Myers (1973), Bruner and Moser (1973), Ek (1974). Mauge simulated changes in stand height, height of dominants and stand volumes in Pinus pinaster plantations as a function of stand age. Multiple and simple linear regressions equations are used to mimic these relationships, and the effects of thinning regimes and fertilization on yield and revenues are

simulated. The model outlined by Myers simulates the management of stands of even-aged P. ponderosa and P. contorta. It provides a variety of management alternatives and catastrophic possibilities, and calculates yields as a function of the age of the stand and site index. Ek developed a series of non-linear regression equations to simulate changes in stand diameter-increment and mortality for northern hardwoods, and Markovian methods have been employed to similar ends (Bruner and Moser, op.cit.)

All these models are deterministic in that their input consists solely of stand variables such as stand basal area and age, and they therefore fail to take into account stochastic variations in the growth process and in population fluctuation.

1.33: Individual-Tree Models

Models based on the birth, growth and death of individual trees in a stand are patently more realistic and flexible than models based on stand components, and provide many capabilities not available in stand models. Their chief asset is the ability to mimic the response of individual plants to environmental stress, either in terms of their growth rates or reproductive success. Against this they have two potential drawbacks. One is the danger of incorporating trivial detail in the model for the sake of completeness, and the second is the considerable increase in computer execution times and storage required by models of

this type. Dress (1968) discussed the theory of the individual-tree approach in forest stand modelling. The individual tree characteristics of diameter, height, crown length, crown radius, competition index, and location in the stand are included in his model.

One of the first individual-tree models to be developed was that of Newnham (1964) for Douglas fir (Pseudotsuga menziesii) plantations. The model computes diameter growth, crown width, diameter and height for each tree in the stand. The growth rate for a tree is calculated from regressions on open-grown trees, and growth is derated according to the amount of competition the tree receives from its neighbours. Competition is based on the relative magnitude of the crown radius for each tree, and the model calibrated against yield tables. Lee (1967) used Newnham's model to calculate yields and expected revenues in stands of Pinus contorta, and Bella (1971) used a similar method to model aspen (Populus tremuloides) stands. The model provides a variety of spatial arrangements (uniform, clumped, or random) for the trees, and calculates distance-dependent competition for each individual. Growth is calculated by an algorithm similar to that adopted by Newnham. A further development of this approach was made by Lin (1969) who successfully predicted dbh growth of a limited number of stands of Tsuga heterophylla.

The principal departure from Newnham's approach was that of Mitchell (1969) who modelled the growth of a white spruce stand.

In Mitchell's model the tree's competitive status is a function of radial branch-increment, and growth is calculated from allometric relationships between tree crown components. Arney (1971, 1973, 1974) simulated the stem radial-increment of individual Douglas fir trees, as well as stand growth, based on crown height and the radial increment of each branch whorl. Competition is assessed in a manner similar to that of Newnham (op. cit.). Arney's index of competitive stress is now fairly widely used by the Canadian Forestry Service (e.g. Ker, 1975).

Goulding (1972) constructed a distance-independent model of Douglas fir growth using multiple-regression equations to predict stand growth and mortality. The model is validated against plantation data and yield tables, and with the exception of some older stands, performs acceptably. An elegant model was developed by Hatch (1971) for Pinus resinosa plantations. Probability distributions are used to generate the initial stand, growth increments, and mortality schedules. Growth and mortality are both treated as stochastic variables, and stem growth rates are based on crown development.

1.4: OBJECTIVES OF THE STUDY

There are a variety of alternative methods available for the investigation of forest stand dynamics. The choice of research framework is mediated by factors such as the the detailed goals of the research project, logistical constraints and personal

preferences. The first objective of this study is to examine the germination, mortality and growth of P. caribaea populations, and to explore the mechanisms that regulate population size and dynamics. The second objective is to utilise these data to discuss the alternatives available to foresters in Central America in their management of the pine resource.

The first objective can be attained by monitoring the dynamics of seed and seedling populations in the field, and by testing the effects of biotic and environmental variables on the rate of seedling establishment. An individual-tree model of stand behaviour can then be constructed using the results of these experiments. The model incorporates information derived from increment and experimental plots and a priori principles in order to simulate the growth and development of mature trees. An individual-tree model has the advantages of being more realistic and flexible than the other types of simulators, and enables the modeller to relate differentials in tree establishment and growth to inter-tree competition and environmental influences.

The validated model can then be used to achieve the second objective by relating variations in stand yield to silvicultural practices, particularly the effects of various regeneration/harvesting strategies and thinning regimes.

In the succeeding chapters the taxonomy and biogeography of P. caribaea are discussed (Chapter Two), and the study area

(Chapter Three) and research stands (Chapter Four) described. The second part of the thesis develops and tests hypotheses on the effects of environmental and biotic influences on seedling establishment (Chapter Five), and proceeds to construct and validate a simulation model of stand behaviour (Chapter Six and Seven). Chapter Eight presents the results of silvicultural experiments performed on the verified model, and the final chapter summarise the conclusions of the study as a whole.

CHAPTER TWO: TAXONOMY, BIOGEOGRAPHY AND ECONOMIC STATUS OF CARIBBEAN PINE.

2.1: RANGE AND AFFINITIES OF CARIBBEAN PINE.

The natural pine forests of Central America cover some 45,000 sq. km. (Kemp, 1972), mostly in Honduras, Nicaragua and Guatemala, but with smaller areas occurring in Belize and El Salvador. Although the taxonomy of the pines of this area is still somewhat confused (Mirov, 1967), almost all pine populations below 1000 m. can be ascribed to two species: Pinus caribaea; and P. oocarpa. There is an altitudinal gradient in the species composition of the pine forest, with the latter species rarely ranging down below 600 m., whereas P. caribaea is restricted to the lowlands, only occasionally being found above 700 m. Outliers of Mexican highland pines (e.g. P. hartwegii; P. pseudostrabus) occur at altitudes above 1000 m., mainly in Guatemala.

In bioclimatic terms, P. caribaea is the most tropical of all pine species, ranging southwards along the Atlantic coastline of Central America from the Belize-Mexican border (18° 3' N.) to the vicinity of Bluefields in Nicaragua at 12° 13' N. (Fig. 2.1). On these coastal plains the stands of pine are very open, with scattered trees separated by grass and sedge savanna and perennial swamp. The rainfall at the southern end of this range is of the order of 400 mm. annually, and the pine savannas are seasonally inundated. Although the annual rainfall decreases

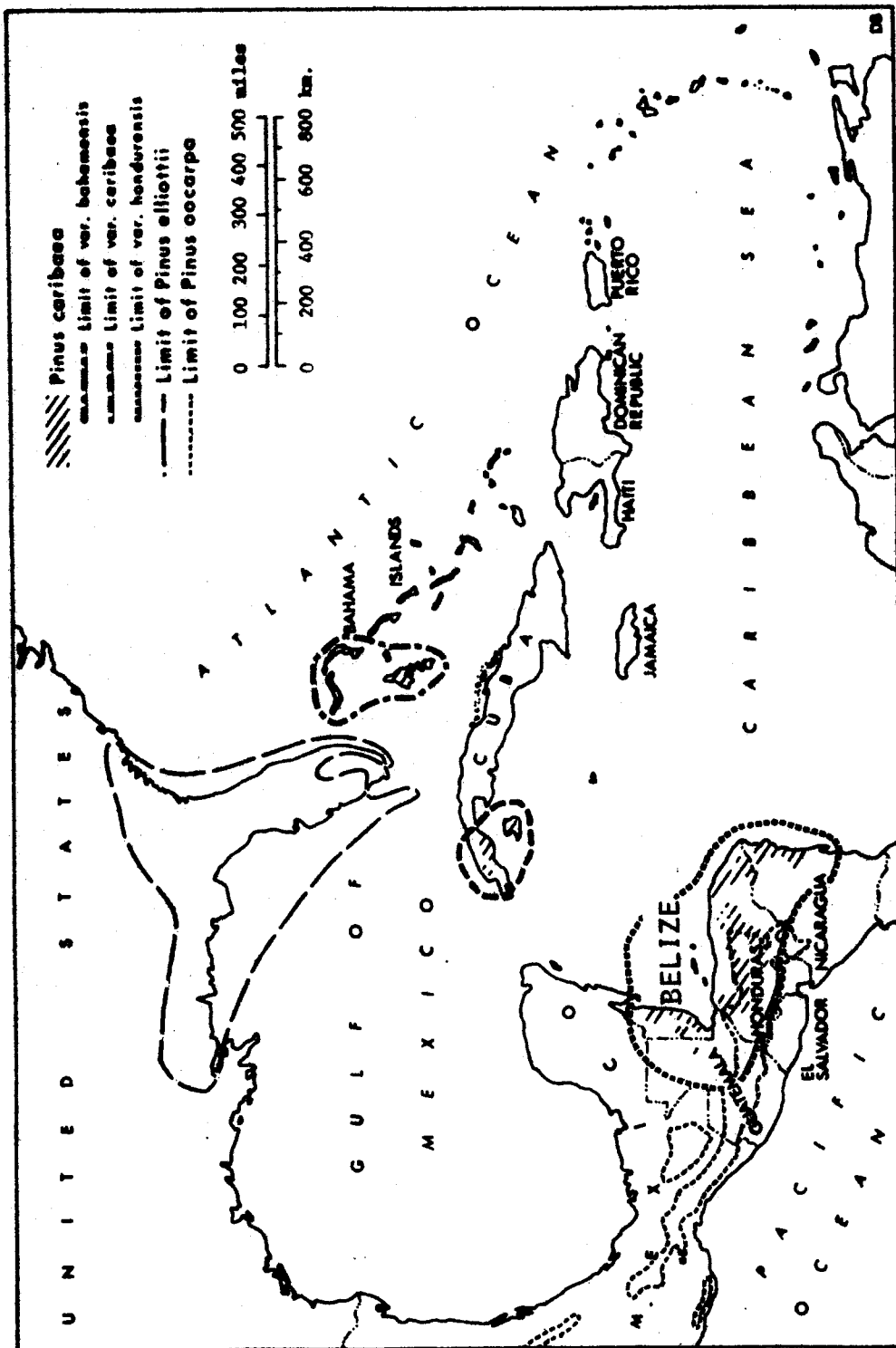


FIG. 2.1: DISTRIBUTION OF *P. CARIBAEA* AND ASSOCIATED PINE SPECIES

steadily northwards to 2600 mm. in northwest Honduras and to less than 2000 mm. in northern Belize, the low - lying, poorly-drained sediments of these coastal plains impose conditions of seasonal waterlogging, and the environment for pine growth is broadly similar throughout this six degrees of latitude.

Where the coastal pine savannas extend inland, they tend to occur on better-drained gravelly soils and environmental conditions are more similar to those in the interior populations of the species. These interior provenances consist of a very discontinuous but extensive series of population segregates in the foothills of eastern Honduras and Nicaragua, the Mountain Pine Ridge area of Belize, and some localised stands around Poptun in the Peten department of Guatemala. The climate in these inland areas is much more severe than that on the coast, with mean annual rainfall totals of 1600 mm. or less (<900 mm. in the Choluteca valley, Honduras) and prolonged dry seasons.

2.2: TAXONOMY OF CARIBBEAN PINE

The biosystematics of Caribbean pine, especially the status of the Central American populations, are still the subject of debate. After the slash pine (*P. elliottii*) populations of Florida were shown to be taxonomically distinct from *P. caribaea* (Loock, 1950; Little and Dorman, 1952; 1954), the remaining West Indian and Central American populations of the latter were surveyed by Barrett and Golfari (1962). They recognised three

distinct races of *P. caribaea*, two of which are restricted to the islands (var. *bahamensis* in the Bahamas and var. *caribaea* in Cuba). This thesis deals with the third subspecies, *P. caribaea* var. *hondurensis*, which is limited to the mainland of Central America. The distinguishing features of this variety are three-needled fascicles (occasionally 4 or 5, distinguishing it from the 2-3 needled Bahaman variety); seeds with articulate wings (distinguishing it from the Cuban variety, in which the seed wing remains attached); and larger cones (6-14 cm. long), those of the other varieties.

Hybridization of some Central American populations of *P. caribaea* with *P. oocarpa* var. *ochotenerai* causes taxonomic problems in this subspecies. Trees which are referable to neither species, and are presumed to be members of hybrid swarms, have been reported from the interior valleys of Honduras, and from the interior mountains of Belize (Williams, 1955; Mirov, 1967). The status of these population segregates is enigmatic. Loock (op. cit.), considered that the interior Belizean form was sufficiently different from other Central American pines referred to as *P. caribaea* to warrant elevation to specific status, and he suggested that the name revert to *P. hondurensis* (after Seneclauze), but Little and Dorman (1954) could establish no grounds for this differentiation. A more comprehensive review of these taxonomic problems and their relation to the historical biogeography of the pines of the Caribbean area can be found in Baldwin (1968).

2.3: MANAGEMENT AND EXPLOITATION OF FORESTS OF CARIBBEAN PINE

Over its entire range Caribbean pine has suffered from over-cutting, and regeneration has subsequently been poor. It is only within the last thirty years that any systematic efforts to conserve the pine resource have been made, and while in some countries these efforts have been successful, in other areas the protection afforded to the pine stands has been minimal. In the West Indies much former pine forest has been cut for timber and the land converted to sugar-cane farming, but in the years since the revolution in Cuba there have been attempts at re-forestation, (Lamb, 1973), and in the Bahamas the pinelands are now in a regeneration phase after fifty years of heavy exploitation (Henry, 1974).

In Central America small-scale exploitation of the coastal pine forest has been carried on since the eighteenth century (Parsons, 1955), but commercial lumbering only commenced in the 1920's when an American syndicate began cutting the pine in coastal Nicaragua (Anon., 1928; Fahnestock and Garrett, 1938). Exploitation was particularly heavy during and immediately following the Second World War (Harper, 1947), and when Taylor (1959; 1961; 1962; 1963) and Munro (1966) visited the area most of the pine stands had been cut, and regeneration was under way in areas where fire protection had been provided (Lamb, op.cit.). In the interior forests of Nicaragua the pinelands are being

cutover at the present time, and Denevan (1961) reported reduced areas under pine as a result of this exploitation. The Caribbean pine forests of the Honduras republic attracted considerable attention from lumber companies (e.g. Durland, 1927), but because the limited accessibility of the discontinuous coastal stands inhibited exploitation, only the interior forests (mainly of P. oocarpa), have been cutover. The depletion of the interior pinelands is only partly due to logging, the depredations of the bark beetle Dendroctonus mexicanus in the early 1960's also accounted for many trees in this area (UN/FAO, 1968).

The exploitation of the pine forests of Belize followed the Nicaraguan pattern. Because of the small domestic market, and the self-sufficiency of the lumber producers in the American south, the coastal pinelands were logged on a small-scale until 1938. Thereafter exploitation increased rapidly, and in the 1950's pine exports became one of the prime sources of foreign exchange for Belize, with pine supplanting mahogany as the chief forest product of the country. The interior pine forests came into production some years after the coastal stands, but because the total amount of exploitable timber was less than inventories had estimated (partially due to hurricane damage in 1961), levels of exploitation and export declined, and are currently back to their pre-war levels.

2.4: EXOTIC PLANTATIONS OF CARIBBEAN PINE.

Plantations of Caribbean pine, mainly derived from seed of a

Mountain Pine Ridge provenance, have become widespread in the tropics in the last twenty years. This is due to the wide ecological tolerance of the species, its rapid growth in humid tropical environments, and its low nutritional requirements (Cornforth, 1970; Lamb, 1973). P. caribaea was first planted as an exotic in a series of plot trials in South Africa in 1929 (Luckhoff, 1964). These and later plantations proved the adaptability of P. caribaea to a wide variety of environments, and led to its adoption as a plantation species elsewhere. At the present time P. caribaea is proving a successful exotic for both timber and pulp, and is currently being planted in areas where rainfall totals and annual temperatures are often quite different from those in its native range.

In the coastal lowlands of South and East Africa there are extensive plantations of Caribbean pine (see Appendix A), and further plantations have been established on the sub-tropical plateaux of Kenya and Uganda. In West and Equatorial Africa plantations are still in the process of being established, but the initial indications are that the species will prove successful in the moister parts of the savanna zones in these areas. (Lamb, op.cit.). In South America and the Caribbean some 15,000 ha. (37,000 ac.) of P. caribaea had been planted by 1970. Again the sub-humid lowlands and the moist savanna areas appear to have the greatest potential (Golfari, 1972). An intensive programme of plantings is currently developing plantations at the rate of 12,000 ha. (30,000 ac.) per annum

(Lamb, op.cit.).

In Asia and the Pacific, P. caribaea has been planted over a wide range of site conditions, from the lower foothills of the Himalayas (Seth, 1972), to the humid lowlands (Waring, 1971). The most successful trials of P. caribaea have been in Australia. In N. Queensland var. hondurensis has recorded very rapid growth, equivalent to that achieved by the best of the temperate pine species (cf. P. radiata in New Zealand).

In summary, P. caribaea, especially var. hondurensis, has proved to be capable of rapid growth in many different climatic and edaphic environments in the tropics and sub-tropics, and must be regarded as an important source of pulp and timber supplies for many Third World countries in the future. Before this future is assured, however, several critical areas of research and policy formulation exist. Data on the dynamics of Caribbean pine stands are required in order to conserve the pine resource through future cutting cycles. The recent overexploitation of the Caribbean and Central American stands cannot be allowed to re-occur. Research on the potential yields and tolerances of the various provenances of the species and on management strategies in exotic plantations of the species is required. For the Central American populations, the first of these research foci is an urgent necessity and provides the practical rationale for this thesis.

CHAPTER THREE: ENVIRONMENT OF THE STUDY AREA.

3.1: LOCATION

The area chosen for this research is part of the Mountain Pine Ridge Forest Reserve in Belize, Central America, which is located at 17 degrees north, 88 degrees west, some 11 km. south-west of Belize City and 20 km. from the border with Guatemala (Fig. 3.1). This area offers several advantages for research into the silvicultural ecology of P. caribaea.

Firstly, Mountain Pine Ridge has been gazetted as a forest reserve for the last three decades. Unlike virtually all other areas of pine woodland in Central America, it has therefore received some measure of protection from fire during this period, and records of fire extent and frequency are available for part of this time. Thus, Mountain Pine Ridge offers pine stands in various stages of successional development, and stand dynamics and history can be reconstructed. Secondly, because Mountain Pine Ridge has been the seed-source for most of the exotic plantations of P. caribaea in other tropical areas, information on the stand dynamics of this provenance of the species may well prove useful in the management of these plantations.

The vast secondary rainforest of the Yucatan Peninsula covers approximately ten percent of the Forest Reserve, encircling the pine savannas and cutting them off from the pinelands of coastal Belize. Although visits were made to all

Source: Lamb (1950)

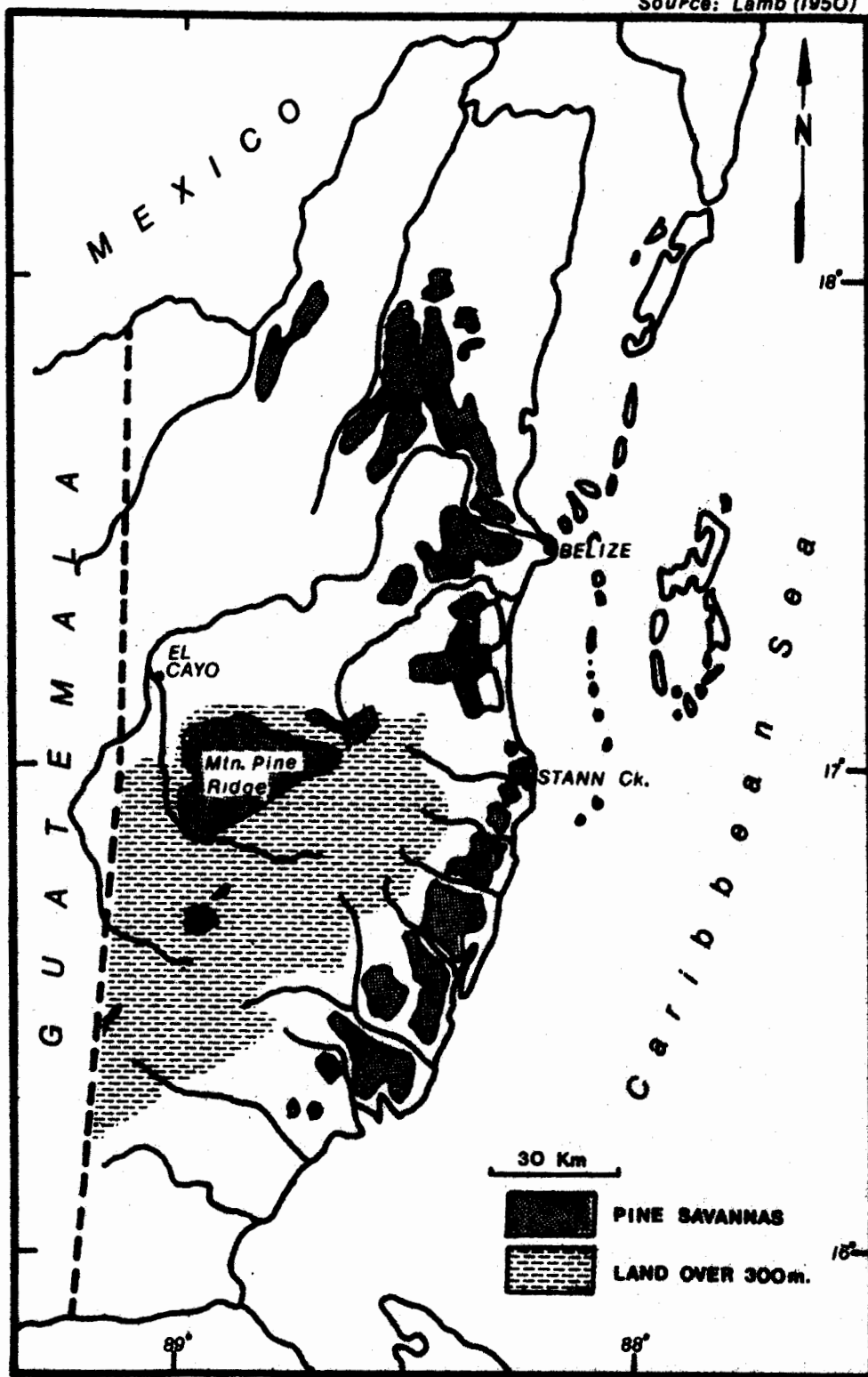


Fig. 3.1: The Pine Savannas of Belize

parts of the interior pinelands, field research was undertaken in the western part of the reserve, in the area known as the Granite Basin.

There is little altitudinal variation within the Granite Basin, and this factor, and the underlying granitic parent material, produce a fairly uniform soil type throughout the study area. The Granite Basin is also the most fertile and accessible area of Mountain Pine Ridge, and can therefore be expected to be of prime value in forest exploitation in the future. The range of *P. oocarpa* is limited in Mountain Pine Ridge to the hilly areas above 850 m. elevation to the south and east of the Granite Basin, and it is in these areas that *P. caribaea* x *P. oocarpa* hybrids occur. Confining the study to the Granite Basin, which is less than 700 m. throughout, therefore ensures a homogeneous genotype for field sampling.

3.2: GEOLOGY

Mountain Pine Ridge lies on the north-western flanks of the Maya Mountains, and topographically and geologically may be considered part of this massif. The bedrock geology of this upland area has been discussed in a number of papers (Sapper, 1899; Powers, 1918; Over, 1928; and Dixon 1956). The Maya Mountains massif is a horst block with fault-bounded scarps on its eastern and northern boundaries rising to elevations of 700-800 m. The dominant element of the lithology of the area is

the contrast between the intrusive and metasedimentary rocks of the Maya Mountain upland with the Mesozoic limestones which form the western and northern boundaries of Mountain Pine Ridge. This contrasting lithology is reflected, in part, by the distribution of soil and vegetation types in the area. The pinelands of the interior of Belize are restricted to, though not always coincident with, the outcrops of non-calcareous rocks.

Recent papers by Kesler *et alia* (1971) and Bateson and Hall (1971, 1974), have described the geological history of the area. The main mass of the Maya Mountains is composed of metasediments of late Palaeozoic age (the Santa Rosa group) which were intruded by granite batholiths during the Triassic. The mica-granites of one of these batholiths are now exposed over some 200 sq. kms. of Mountain Pine Ridge, forming a slightly dissected plateau at an elevation of 400-600 m. This is the area known as the Granite Basin, and the acidic rocks of this area now form the parent materials for the soils of all the sample sites (Fig. 3.2).

The Granite Basin is circumscribed to north and southeast by the arms of a crescent of hills, extending westwards from the main bulk of the Maya Mountains. The northern limb is composed of shales and fine-grained sandstones and the elevation of the area is congruent with that of the granite plateau. Conglomerates become more important in the sedimentary sequence to the east, while the southern limb consists mainly of shales and phyllites. Upfaulting of the rocks along the Cooma Cairn

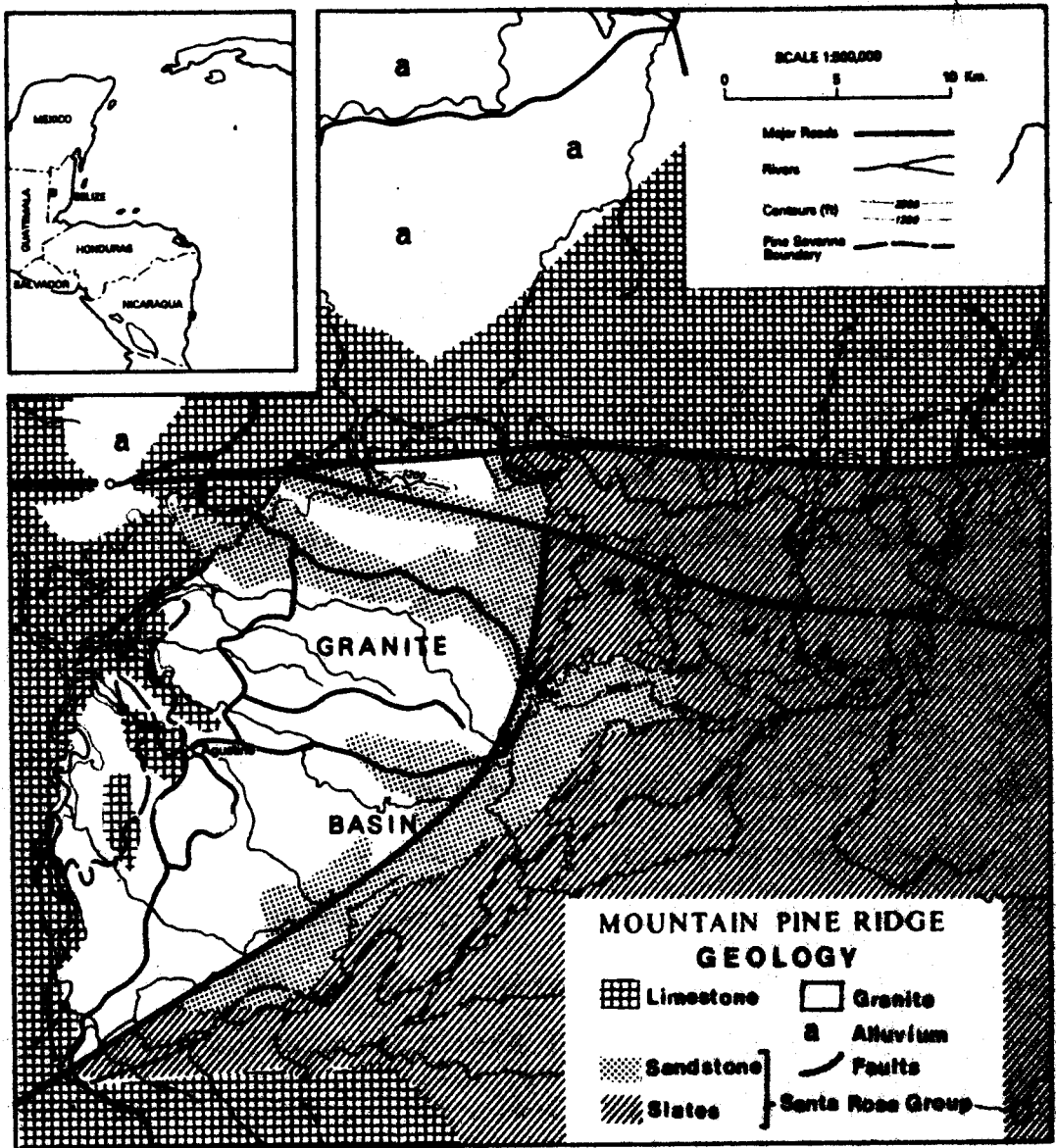


FIG. 3.2: GEOLOGY OF MOUNTAIN PINE RIDGE, BELIZE

fault has resulted in a range of hills (Forward Cairn, Granite Cairn, the Bald Hills), which rise above the Granite Basin to elevations of 850-950 m. These heavily dissected hilly areas display local relief of 200 m.

The limbs of the sedimentary rim which surrounds the Granite Basin are open to the southwest, where the granite shelves gently beneath Cretaceous limestones. These limestones are one of the basal members of a carbonate rock sequence which now outcrops across the entire peninsula of Yucatan. Marine carbonates were deposited over this area from the early Cretaceous to the Eocene with only short-lived periods of crustal disturbance to interrupt the sequence. Schuchert (1935) and Wright (1962) suggest that the Maya Mountain upland remained an island throughout this entire period of marine transgression. The influence of this extended period of exposure on soil development is discussed in the next section. The mantle of massive limestones now supports broadleaved forest and has weathered to "cone and tower" karst, dissected by streams draining the impermeable rocks of Mountain Pine Ridge to the east.

3.3: GEOMORPHOLOGY AND SOILS

On the granitic rocks of Mountain Pine Ridge a weathered regolith has developed to a depth in places of 15 m. As in other tropical regions, the joint patterns in the granite control the depth of the weathering profile and the distribution of tors and

ruwares (Thomas, 1973). Only in the westernmost parts of the Granite Basin are valleys entrenched; elsewhere shallow valleys and broad interfluves are found. In contrast, the valleys developed in the rocks of the Santa Rosa group are steep-sided with narrow interfluves. Regolith developed on the shales of this suite exhibits near-surface stonelines up to 15 cm. in thickness. On some slopes massive arcuate terraces have developed.

Several reconnaissance soil surveys have been made in this area. Charter (1941) divided the soils of Mountain Pine Ridge into the Blancaneau series, formed over granite, and the Chalillo series, developed over sedimentaries. These soils he noted as possessing good external drainage and low lime status.

Darcel (1952) and the British Honduras Land Survey team under the leadership of Romney (1959), were the first to describe the soils of Mountain Pine Ridge in any detail. All the soil types in Mountain Pine Ridge were placed in the Pinol soil set, which was then subdivided into soil types based on texture and lithology. The basis for the subdivision of each soil type was the degree of truncation of the soil profile.

Further research on the soil types of the area was reported by Furley (1968a, 1975a,b) from three transects in the Bald Hills. In each transect a dichotomous soil distribution was

encountered; moist valley-bottom soils, rich in organic matter, contrasted sharply with the eroded profiles on ridge-tops and side-slopes, with low base-status and only small amounts of organic matter. This same dichotomy is evident in the soils of the Granite Basin. Birchall (1973) describes the principal soil type of the Granite Basin as follows:

"The most widespread soil on granite parent material was found to be the Pinol coarse sandy clay loam as classified by Wright et al. This soil has developed over a thick mantle of weathered granite and has a complete range of pine densities growing on it. The soil consists of a shallow loamy sand to sandy loam topsoil containing much quartz sand and fine gravel, overlying mottled gritty clay loam and mottled gritty clay which grades gradually into weathered granite. Quartz sand and concretionary ironstone pebbles are sometimes found on the surface of this soil and the moderately leached topsoil is susceptible to sheet and gully erosion".

Birchall, *ibid.*, p. 12.

Darcel reported pH values of 4.0 - 5.3 and very low reserves of available phosphorus (3 - 8 ppm (Hunt, 1970)) and potassium for the soils derived from granite. Furley (1968b) reports similar results for the soils of the Bald Hills, with pH readings of 3.8 - 5.3 in the A horizon, available phosphorus reserves of 1 - 2 ppm and exchangeable potassium values of 22 - 352 ppm. Soils with very low reserves of potassium are restricted to the eroded sideslopes, with the high values being characteristic of valley-bottom soils.

The low base-status of these upland soils is probably due to a number of factors: a) intensive weathering of parent materials; b) the sandy texture of the majority of soils; c) low soil pH, linked to a high exchangeable aluminium content, which tends to block exchange sites, and d) a clay fraction dominated by 1:1 clay minerals.

Little research has been undertaken on the nutrient requirements of Caribbean pine. A series of experiments reported by Hanzah (1966, 1968) and Anthony (1971) are the sole source of information on this topic. Their results show that *P. caribaea* exhibits optimum growth at nitrogen, phosphorus and potassium levels of 50 - 125 ppm, but stress that good growth is maintained even on very infertile substrates, such as the soils of the coastal plain of Belize, which are equivalent in their nutrient status to the soils of Mountain Pine Ridge (Bazan, 1969).

The very low base-status and deep regoliths of the soils of the study area indicate their senility, and lend support to the opinion that this area has been exposed to the processes of sub-aerial weathering for long periods of geological time. These features, and others such as the highly mottled subsoils and textural B horizon, are all properties that have been reported for senile soils in other savanna environments in the Neotropics (Hardy, 1958, 1960, 1962; Ahmad and Jones, 1969; Hutchinson, 1970).

3.4: CLIMATE

The country of Belize experiences a tropical climate characterised by strongly seasonal fluctuations in rainfall and by slight annual variations in temperature. The Mountain Pine Ridge area, because of its altitude and position in the lee of the Maya Mountains, has a somewhat cooler climate than the rest of the country (Fig. 3.3). Climatic data for three stations in Mountain Pine Ridge are available (Augustine, Cooma Cairn and Mai Lookout) but only the first two have lengthy records. The data from Augustine can be taken as representative of the climate of the Granite Basin, and that of Cooma for the Bald Hills and the wetter eastern part of the Forest Reserve. Figure 3.4a shows the pattern of mean annual rainfall for these two stations. The contrast between wet (June- January) and dry seasons (Feb.-May) is the dominant feature of the local climate.

The dry season involves not only a relative decrease in rain-days and rainfall (Fig. 3.4b), but also an absolute water deficit in the months from February to May in Augustine and March and April at Cooma Cairn (Table III.1). The onset, intensity and length of the dry season are unpredictable phenomena. Contrary to the views of Romney et alia (1959), the calculated coefficients of variation for monthly precipitation (Table III.2) indicate that the amount of rainfall in the dry season months is more variable than that during the wet season. Rainfall in the month of May for instance may vary from <25 mm. (~15% of years) to 200 mm. (~8% of years).

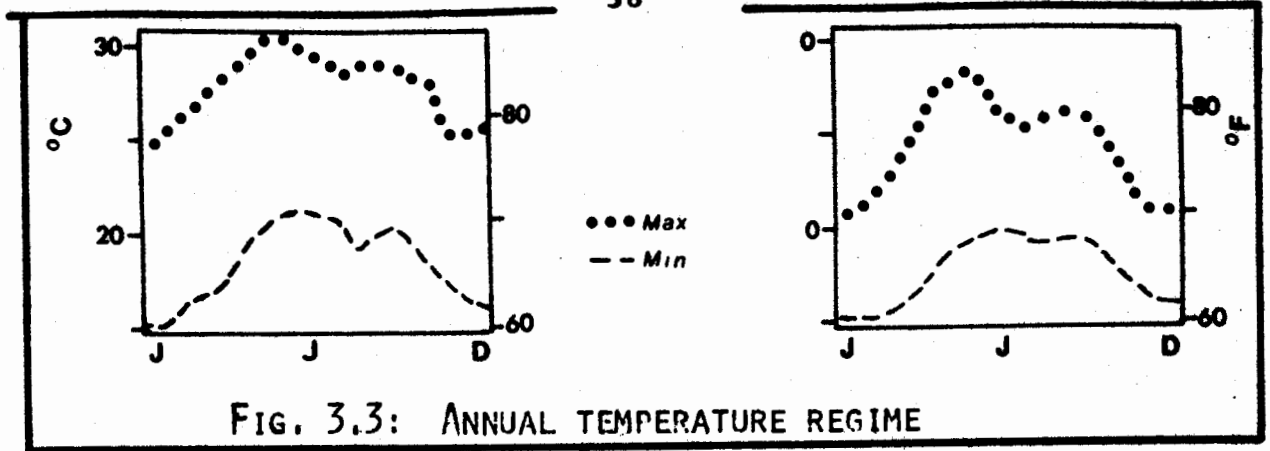
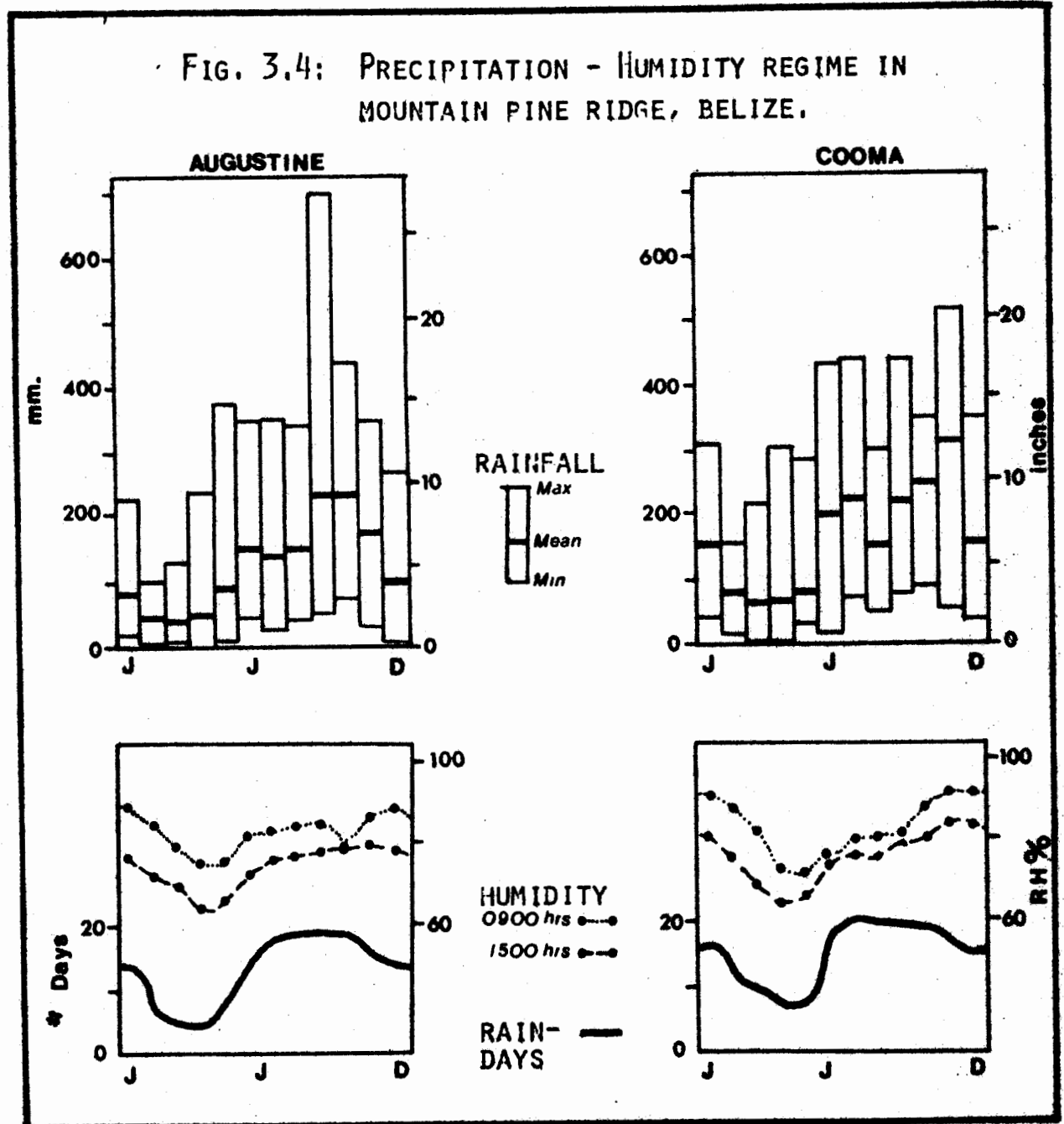


FIG. 3.3: ANNUAL TEMPERATURE REGIME



**TABLE III.1: WATER BALANCE COMPUTATIONS (Thorntwaite's Method),
FOR REPRESENTATIVE STATIONS IN THE STUDY AREA.**

It is assumed that soil depth at these stations is 1.5 m.
and the total water storage of the soil profile is 300mm.
All measurements are in mm.

| AUGUSTINE, BELIZE. | | | | | | | | | | | | | |
|--------------------|-------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|------|
| Variable | Month | | | | | | | | | | | | YR. |
| | J | F | M | A | M | J | J | A | S | O | N | D | |
| P.E.T. | 56 | 63 | 89 | 115 | 152 | 151 | 140 | 118 | 112 | 97 | 66 | 61 | 1221 |
| P. | 86 | 48 | 44 | 51 | 90 | 158 | 146 | 162 | 232 | 236 | 180 | 105 | 1539 |
| Storage | 300 | 286 | 245 | 198 | 160 | 167 | 173 | 217 | 300 | 300 | 300 | 300 | |
| A.E.T. | 56 | 62 | 85 | 98 | 128 | 151 | 140 | 118 | 112 | 97 | 66 | 61 | 1174 |
| Deficit | 0 | 1 | 5 | 17 | 24 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 47 |
| Surplus | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 38 | 139 | 114 | 44 | 365 |

| COONA CAIRN, BELIZE | | | | | | | | | | | | | |
|---------------------|-------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|------|
| Variable | Month | | | | | | | | | | | | YR. |
| | J | F | M | A | M | J | J | A | S | O | N | D | |
| P.E.T. | 51 | 52 | 78 | 105 | 127 | 118 | 115 | 111 | 100 | 86 | 56 | 50 | 1049 |
| P. | 161 | 82 | 70 | 74 | 83 | 202 | 231 | 161 | 225 | 253 | 318 | 168 | 2025 |
| Storage | 300 | 300 | 293 | 264 | 228 | 300 | 300 | 300 | 300 | 300 | 300 | 300 | |
| A.E.T. | 51 | 52 | 77 | 103 | 119 | 119 | 115 | 111 | 100 | 86 | 56 | 50 | 1039 |
| Deficit | 0 | 0 | 2 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 |
| Surplus | 30 | 0 | 0 | 0 | 11 | 116 | 50 | 125 | 167 | 262 | 118 | 110 | 989 |

P.E.T. = Potential Evapo-Transpiration
P. = Precipitation
A.E.T. = Actual Evapo-Transpiration

Portig (1965) considers that the rainy season in Belize is divisible into three distinct time periods. The first period, associated with the first zenithal passage of the sun, lasts from May to the end of June, and a second zenithal passage in July results in a secondary rainfall maximum in August and September. Outbreaks of "nortes", polar continental air from North America crossing the Gulf of Mexico, bring heavy rain and temporarily lowered temperatures to Belize from October to January.

Air temperatures at Augustine vary from monthly means of 20.3° C in January to 25.8° C in May and June. Monthly maxima are also highest at the end of the dry season, reaching 28.3° C in May, with monthly minima dropping to 15° C in January and February. Because of its elevation Cooma (900 m.) experiences temperatures generally 2° C less than those at Augustine (450 m.).

Climatic variables exert strong influences on the fecundity, mortality, phenology and growth of Pinus caribaea. The male strobili of P. caribaea begin to release pollen in November. Research on other gymnosperms (e.g. Allen, 1942; Lowry, 1966), indicates that the size of the resultant seed-crop is strongly controlled by the amount of rainfall during the period of pollen release as dessication causes the female strobili to abort.

The conelets, once fertilised, develop over a 19-month period, and seed is released from mid-June to the end of July in most years. The amount of rainfall and temporal distribution of

TABLE III.2: VARIABILITY OF THE ANNUAL AND MONTHLY PRECIPITATION IN THE STUDY AREA. THE COEFFICIENT OF VARIATION OF PRECIPITATION IS CALCULATED AS THE RATIO OF THE BEST ESTIMATE OF SAMPLE STANDARD DEVIATION TO SAMPLE MEAN.

| AUGUSTINE, BELIZE. | | | | | | | | | | | | | |
|--------------------|-------|----|----|-----|----|-----|-----|-----|-----|-----|-----|-----|------|
| Variable | Month | | | | | | | | | | | | YR. |
| | J | F | M | A | M | J | J | A | S | O | N | D | |
| P. | 86 | 48 | 44 | 51 | 90 | 158 | 146 | 162 | 232 | 236 | 180 | 105 | 1539 |
| Sample S.D. | 51 | 28 | 35 | 61 | 77 | 79 | 77 | 69 | 125 | 98 | 95 | 66 | 291 |
| Best Est. of S.D. | 52 | 28 | 36 | 63 | 79 | 81 | 79 | 70 | 128 | 100 | 97 | 68 | 297 |
| Coeff. of Var. (%) | 62 | 57 | 82 | 124 | 88 | 51 | 54 | 43 | 55 | 42 | 54 | 65 | 19 |

P. = Mean precipitation (mm.)
 Sample S.D. = Sample standard deviation
 Best Est. of S.D. = Best Estimate of Standard Deviation
 Coeff. of Var. = Coefficient of Variation as a percentage

storms at this period is critical for pine germination, which under optimal conditions takes 10 days. An extended period of dry weather in these early weeks of the rainy season will delay germination and allow ground-feeding seed-predators more time in which to locate seeds. Periods of alternating wet and dry weather may produce a large seedling crop which then suffers heavy mortality from subsequent dessication. Optimal conditions would appear to be a combination of continuous surface soil-moisture levels at or near field-capacity, with fairly high humidities and cloud cover to reduce evaporation from the soil surface.

Moisture stress induced by periods of low rainfall, high evapo-transpiration rates and the good external drainage of local soils, is one of the main controls on pine growth rates. Physiological drought, particularly during the long dry season, but also during shorter periods of moisture deficit, causes cambial cell division to slow, and latewood bands to be formed. Consequently each individual of P. caribaea, with the exception of those trees growing in moist valley-bottom soils, exhibits "rings" produced during these periods of moisture stress. As there may be several such periods each year the trees form several rings per year (2-3 are common) with the result that age-dating of trees by ring-counting becomes extremely difficult.

Hurricanes are a frequent but unpredictable element in the climate of Belize. High rainfall and localised flooding

associated with the passage of these tropical storms across the western Caribbean area in July - October are almost an annual occurrence. However the passage of a hurricane across Belize itself is fortunately much less frequent, generally occurring only once in a decade or so. Hurricane damage to forests resulting from high winds depends upon the distance from the storm centre and the intensity of the hurricane, but in most cases mechanical damage to trees is only severe for a distance up to 25 kilometres from the eye. The only recorded storm to strike Mountain Pine Ridge directly was Hurricane Hattie in 1961, when a great deal of pine was windthrown, particularly in those areas where logging had opened the tree canopy. Such catastrophic but irregular events represent an important factor that must exert considerable influence on the population dynamics of all forest types in Belize, including the pine savannas of the study area. At the moment the magnitude of this control is unknown, partly due to the low priority accorded to ecological research in the aftermath of a hurricane.

3.5: FIRES

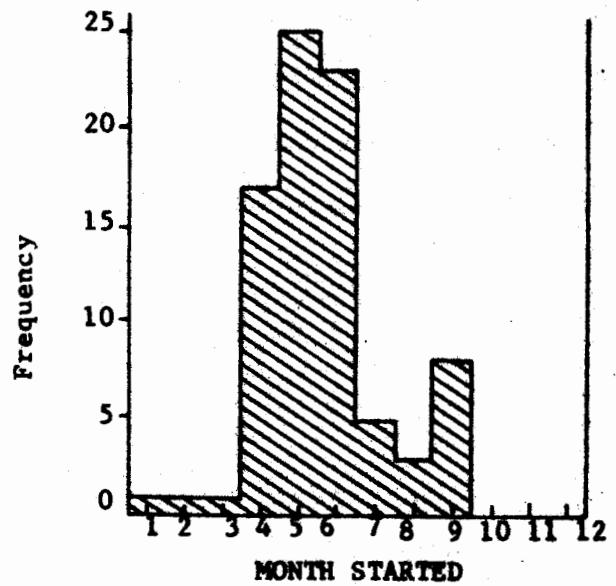
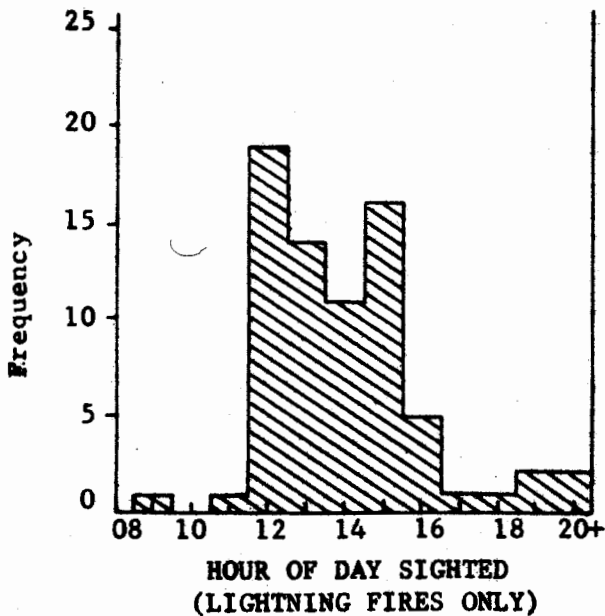
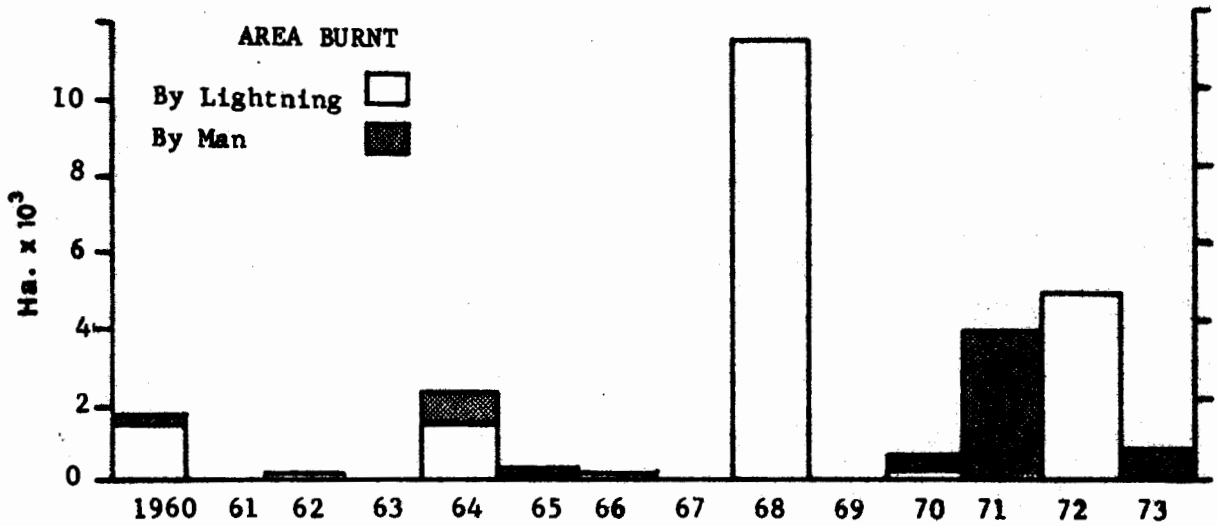
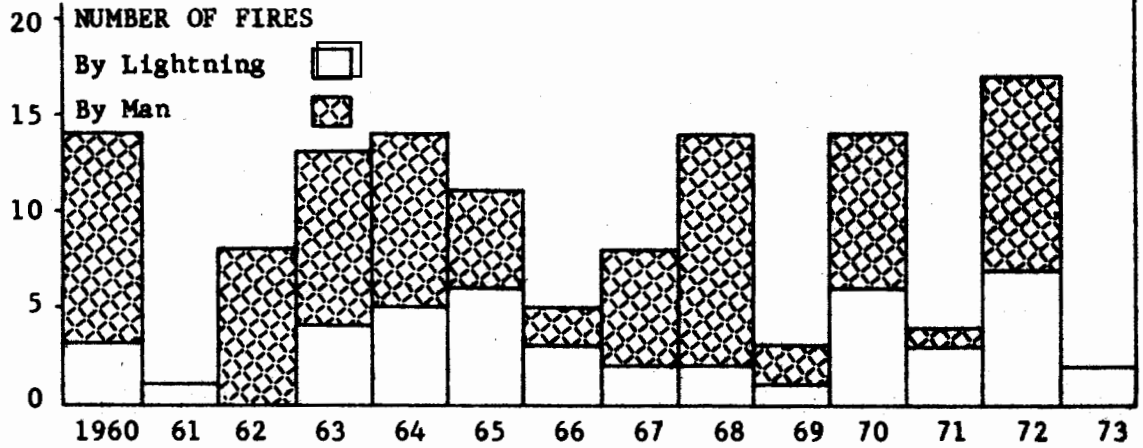
Mountain Pine Ridge, in common with other Neotropical savannas, has a history of frequent fires. The pinelands of Mountain Pine Ridge are currently divided into a protected or "control" area, roughly coincident with the extent of the Granite Basin, where fires are rigorously suppressed, and an outer area

(the Bald Hills and Macal watershed) where, because of limited accessibility, fire-fighting aims at containment rather than suppression. Within the last few years the encroachment of fires onto the protected area has led to systematic efforts to extend the control area over the entire pine savanna.

It is only in the last decade that records have been available from the Forestry Department of Belize on the frequency and extent of fires in Mountain Pine Ridge. The figures presented on fire incidence therefore represent the "controlled" situation and prior to 1960 fires must have been considerably more extensive in this area.

Fires are most common in the dry season, particularly in April and May, when a combination of low precipitation, high evaporation rates and low humidities dry out the grass and litter and produce a highly flammable fuel-bed. Towards the end of the dry season the fire hazard becomes extreme due to the frequency of storms which produce a great deal of lightning but no rain. Whilst lightning fires are frequent in the rainy season they are often extinguished by accompanying rain before being fought. Almost all lightning fires start during the day, particularly in the afternoons (Fig. 3.5c). Man-set fires may occur at almost any time of the year, but are most frequent in the dry season, some of them resulting from milpa fires in the rain-forest which escape into the pinelands. The effectiveness of fire protection within the control area is witnessed by the fact that the average

FIG. 3.5: FIRE INCIDENCE IN MOUNTAIN PINE RIDGE



fire covered only 54 ha. (133 ac.) in the period 1963-1973, compared to 180 ha. (400 ac.) for burns outside the control area. Forest Guards and Rangers who have lived and worked in Mountain Pine Ridge since the foundation of Augustine in the 1940's remember conditions in which burns were much more extensive and frequent than at the present-day.

Burns which overran almost the entire pine outcrop are known to have occurred as recently as 1945 and 1949, with other extensive fire events in 1953 and 1955, prior to the publishing of detailed fire reports. Some of the early photographs of Mountain Pine Ridge (e.g. Lundell, 1940), show large expanses of open pine savanna with very little regeneration of either pine or hardwoods, which confirm the oral evidence of destructive and frequent fires. The circumstance of fires overrunning the entire area of Mountain Pine Ridge is inconceivable at the present-day, and the data indicate that the recurrence interval for a fire at any point in the control area is now of the order of 100 years. The figure of 18 years recurrence interval for fires outside the control area at the present time is probably indicative of the regularity of fires over the entire pine savanna in the period prior to fire-protection.

Despite its obvious limitations, the data on fire occurrence present some interesting features. Previous research on the factors responsible for the genesis and maintenance of pine woodlands in tropical and subtropical environments has stressed

man's use of fire. In contrast, the role of lightning fires has been ignored or considered secondary, probably because most research has taken place in areas of medium or high population density. In the sparsely settled area of Mountain Pine Ridge, however, lightning fires accounted for 66% of the fires recorded between 1960 and 1973. Lightning fires are not only more frequent, but also more destructive than man-caused fires, averaging 237 ha. (585 ac.) as compared with 71 ha. (176 ac.) for fires started by human agency.

The relative importance of man-set fires may also have changed. The deliberate setting of fires by hunters or cattlemen to provide fresh grazing is still a major problem for foresters in the coastal pine savannas of coastal Belize, as well as the pinelands of Honduras and Nicaragua, but has been virtually eliminated in Mountain Pine Ridge. At the present time the man-set fires in the study area are due either to British Army personnel who conduct exercises in the area, or stem from carelessness by transients or permanent residents.

3.6: ORIGINS OF THE MOUNTAIN PINE RIDGE SAVANNA

The major point of contention in the controversy over the origin of Neotropical savannas concerns the role of fire, particularly fires set by man, as a factor in the genesis of savanna environments. Cook (1909), was probably the first to suggest that pine savannas in Central America were man-made. He

argued that the pines had invaded sites formerly occupied by broadleaf forest, succeeding on soils that had become progressively impoverished through shifting agricultural practices. Most research since has tended to support Cook's conclusions (see, for example: Durland, 1922; Holdridge, 1947; Allen, 1955; Budowski, 1959; Denevan, 1961; Taylor, 1962, 1963; Munro 1966), but almost all of this supportive research has been undertaken in the highland pine savannas of Nicaragua, Honduras, and Guatemala. In contrast, work on the coastal savannas has generated a countervailing theory (Charter, 1941; Beard, 1953; and Hardy, 1960). These authors contend that the pine savannas of the Atlantic coastal plain of Central America are all the result of edaphic factors, being limited in every instance to acidic, seasonally waterlogged soils. The recurring fires in these savannas are thought to be a maintaining, rather than a generative factor.

In the case of Mountain Pine Ridge there is a lack of prima facie evidence for either of these hypotheses. The available data indicate a total lack of coincidence between the geographical extent of Mayan settlement and the pinelands in Belize (Thompson, 1966; Prendergast, 1969, 1970). No house sites or agricultural earthworks are known from the area of acid soils in Mountain Pine Ridge (Bullard, 1963), although there is a plethora of such archaeological remains on the nearby river terraces and limestone plateaux of the Belize Valley, areas which

are still cultivated by shifting and permanent agriculturalists at the present time. This lack of geographical coincidence between savanna and cultural landscapes, both in the past and at the present, casts doubt on the validity of Cook's hypothesis.

Perhaps the most convincing refutation of Cook's theory however is contained in papers by Tsukada (1966), Tsukada and Deevey (1967) and Vaughan (1976). Their palynological investigations in the Peten led to the startling conclusion that savanna was at its most extensive during the period 4000 - 1000 B.P. (i.e. pre-Formative to late Classic Mayan Empire), when the pollen rain was dominated by grass, oak and pine genera. Since that time there has been a considerable increase in the proportion of rainforest species, with oak and pine pollen diminishing sharply. They conclude that the rainforest itself may to a large extent be a cultural artifact, rather than the savanna.

The historical continuity and antiquity of savanna communities in Central America is further demonstrated by the fact that the avifauna of the coastal savannas contains a number of endemic sub-species (Howell, 1971), and the finding by Kellman (1975) of charcoal fragments (carbon-dated at 11,220 B.P.), in a soil profile in the Bald Hills, substantiates the claim that fire, and, by extension, savanna vegetation, may be of considerable antiquity in the area. Indeed, the coastal savannas of Central America, like those of northern South America, may

well prove to have existed throughout the Plio-Pleistocene (Wijstra, 1969), their extent fluctuating with every change in climate and sea-level. If fire is to be retained as the prime generative or maintaining factor in savanna areas, these communities must result from recurrent lightning fires, exacerbated by man-set fires in the post-settlement period. In dry years lightning fires may erupt in the broadleaved forest in Belize, and within the last thirty years four such fires, each fairly severe, have been recorded in the rainforest of the Chiquibul Reserve immediately to the south of Mountain Pine Ridge. In the years following a hurricane the chances of such a fire starting, and the rate of spread of the burn, remain the same as in normal years, (Wolffsohn, 1967) but the amount of windblown material on the forest floor produces a very hot burn which causes severe damage. For example, the passage of Hurricane Hattie through southern Belize in 1961 created a considerable fire hazard (Wolffsohn, op.cit.). The damage from the fire may be so great that only a regrowth of bracken (Pteridium aquilinum) or "tiger-bush" (Dicranopteris pectinata) will persist in the burned area. These fern-dominated ecosystems carry fire much more readily than broadleaved forest, and so the frequency of burns may be increased.

Although the savannas of Mountain Pine Ridge are restricted to areas of acidic parent-materials and infertile soils, as required by the 'edaphic' theory, this is not a universal

condition in Belize. Other outcrops of granitic rocks occur to the south and east of Mountain Pine Ridge, but with the exception of some isolated ridgetops which support pines, these are otherwise covered with broadleaf forest. No climatological data are available for these other areas of granite to the south and east of Mountain Pine Ridge, but Romney *et alia* (1959) claim that much higher amounts of rainfall are received in these areas than in Mountain Pine Ridge, which lies in the rain-shadow of the Maya Mountains. Consequently the probability of fires in the dry season may be much reduced, and any pines that did occur would be limited to the drier sites such as ridgetops.

The reasons for the absence of pines from the limestone areas between the Maya Mountains and the coastal plain are obscure, but an explanation is provided by the possibility that the fungal symbionts of *P. caribaea* var *hondurensis* are acidophilic (Janos, pers. comm.). The absence of suitable mycorrhizal symbionts from the soil would effectively exclude pines from these areas, and the post-fire succession would be directed to broadleaved communities.

Until local palynological data become available, the vegetation history of the study area from the late Pleistocene to the present must remain a matter of speculation. However, in an area like Mountain Pine Ridge the infertile soils can only have supported at best a slow-growing broadleaved woodland.

Lightning fires in this type of ecosystem may initiate a positive feedback series tending to produce further impoverishment of the soil due to post-fire leaching and erosion, an open vegetation of still slower growth and biomass, soil desiccation in the dry season due to the reduced vegetation cover, and a consequent increase in the frequency of burns. This synergistic sequence should favour the establishment of a fire-resistant and tolerant vegetation type, in which, given an available seed source, pines will figure prominently. Once established, these pine-grass savannas may represent a homeostatic condition as long as fires are a persistent and frequent element in the environment.

Thus, the pine savannas of Mountain Pine Ridge can be considered to have developed in response to frequent lightning fires, which were on occasion exacerbated by the effects of hurricanes on a vegetation type rendered prone to fire by the long dry seasons, low rainfall amounts and infertile soils of the locality.

CHAPTER FOUR: VEGETATION OF MOUNTAIN PINE RIDGE

4.1: VEGETATION CLASSIFICATION

To the visitor from temperate lands, the vegetation of Mountain Pine Ridge has a surprisingly familiar look. Tourists and botanists alike have remarked on the superficial similarity with the pinelands of the southeastern U.S.A., the New Jersey Pine Barrens, or the Ponderosa pine grasslands of western North America. This apparent similarity stems from the visual dominance of P. caribaea interspersed with small trees and shrubs and an ecologically dominant stratum of grasses and sedges (Fig. 4.1). Certainly this and other pine savanna areas of Central America contrast greatly in species composition and diversity of both flora and fauna with the sea of tropical rainforest that surrounds them.

Botanical surveys of Mountain Pine Ridge were first made by teams from the University of Michigan and Carnegie Institution in the 1930's, and several papers were subsequently published on their collections (Bartlett, 1936; Standley and Record, 1939; Lundell, 1940). Bartlett was impressed at the time of the first expedition (1931) with the extensive systematic and vegetational knowledge of Mayan Indians, and he retained their descriptive terminology for his classification of the vegetation of Mountain Pine Ridge. The local nomenclature recognised three phases of pine savanna (= 'pine ridge')



FIG. 4.1: THE GRANITE BASIN IN MOUNTAIN PINE RIDGE. THIS AREA, WHICH WAS LAST BURNT IN 1964, IS LOCATED 8 KM. NORTH OF AUGUSTINE, AND IS TYPICAL OF THE OPEN PINE-SAVANNA LANDSCAPE OF MUCH OF THE STUDY AREA.



FIG. 4.2: A DETAILED VIEW OF THE ABOVE. SHRUBS SUCH AS CURATELLA AMERICANA (X), MICONIA ALDICANS (Y) AND BYRSONIMA CRASSIFOLIA FORM A SPARSE UNDERSTORY.

Pinar (Pinal) - 'pure' pine woodland

Encinal - oak woodland

Nanzal - Byrsonima woodland

In their survey of the vegetation of Belize Romney and Wright (op.cit.) classify the vegetation of Mountain Pine Ridge as "pine forest and orchard savanna without lime-loving species". Again three phases are recognised:

OAK - pine - florosul forest

OAK - pine - Clusia spp. forest with abundant silver pimento

SAVANNA grass with scattered pine, oak, Leucothoe sp., Clusia spp.

Hunt (1970) rightly criticises these classificatory schemes for being both misleading in terms of the suggested dominance of the tree stratum over the herbaceous layer, and also for the prominence they give to certain minor tree species. He notes (p. 7), that florosul (Tabebuia rosea) was never recorded in the pine savanna in his survey, nor was it observed by myself. A further criticism is that Clusia spp. are only infrequently found in the savannas, as small epiphytes on the roots of pines, or else as larger free-standing trees along watercourses. Hunt (op.cit.) adopts Beard's (1953) terminology for neotropical savannas in his own work on the vegetation of the study area. Whilst noting the ecological dominance of the herbaceous stratum, he states that the visual appearance of the savanna is controlled by the density and diversity of the arborescent layer.

He stresses also that the plant composition of the savannas reflects the moisture status of the stand as well as the history of disturbance. A somewhat idealised view of this relationship can be obtained by using a topographic sequence as a surrogate for moisture availability. In valley bottoms the ground layer is dominated by Mesosetum filifolium, Rhynchospora globosa, and, in areas where waterlogging is frequent, "cutting-grass" (Scleria bracteata) and Andropogon virgatus are common. Clumps of the palmetto Acoelorrhaphe wrightii are found.

On the sideslopes and interfluves the character of the vegetation changes considerably. Apart from the pines, which dominate the tree stratum in both height and total basal area, The following small trees and large shrubs are common:

Quercus oleoides

Quercus purulhana

Quercus hondurensis

Byrsonima crassifolia

Clethra hondurensis

Leucothoe mexicana

Psidium anglohondurensis

Schippia concolor

Enallagma latifolia

Ternstroemia tepezapote

Curatella americana

These and other members of the flora are indicative of the dual geographic origins of the savanna plants, with South American genera (Byrsonima, Psidium, Curatella) intermingling with elements from North America and Mexico (Pinus, Quercus, Myrica). The shrub and sub-shrub layer is also an important component of the pine savannas (Fig. 4.2), dominated by melastomes, particularly Miconia albicans and Clidemia rubra, with composites (Calea spp.), cycads (Zamia furfurata), legumes (Calliandra houstoniana, Cassia spp.) and vines (Davilla kunthii, Inga spp.) being fairly frequent.

The herbaceous layer on the sideslopes and interfluves is dominated by grasses, especially Trachypogon angustifolius, Paspalum pectinatum, and, in drier sites, Andropogon microstachyus. The density of these bunchgrasses is related to the dryness of the site, with more bare ground appearing in areas with thin or gravelly soils. Sparse populations of herbs such as Polygala adenophora, Burmannia capitata, or Bulbostylis paradoxa occur in these drier sites. A full listing of the flora collected in the study area is contained in Appendix B.

4.2: FIRE ECOLOGY OF THE VEGETATION

Pines, like other tree species, can be killed by fire in two ways, either through destruction of the terminal buds, or by heating of the cambium above a temperature of 65° C. The thick, platy bark of Caribbean pine serves as an insulating layer to

protect the cambium from excessive heating. Bark layers may be 1 cm. thick during the seedling stage and 2-3 cm. thick in mature trees. The terminal buds are protected from fire by their location in a skirt of heavy needle growth.

Whereas many of the hardwoods that occur within the pine savannas are capable of rapid regeneration following a fire, P. caribaea is not so adapted. Indeed, in comparison with some subtropical pine species, Caribbean pine appears vulnerable to fire. Longleaf pine (P. palustris), goes through a "grass-stage" where the terminal bud of the seedling lies on the soil surface protected by very heavy needle growth from fire damage, while P. oocarpa is capable of regenerating from its roots after a severe burn. P. caribaea has evolved neither of these strategies, instead it grows rapidly through the vulnerable seedling stage, and couples this with a propensity to abort the dead lower branches of the tree, which reduces the likelihood of a fire "crowning".

Data on pine mortality in burns in Mountain Pine Ridge is found in internal reports of the Forestry Dept., notably those of Moody (1964) and Hudson (1972a,b). Moody recorded 90% mortality for pines below 2 m. in height and 38% mortality for trees between 2 and 3 m. after a fire in 1964. Pine mortality from fires breaking out in 1972 was enumerated by Hudson at a number of stands, with a total sampled area of 1.2 ha. (3 ac.). Death rates were again highest in the seedling classes (Fig. 4.3), but

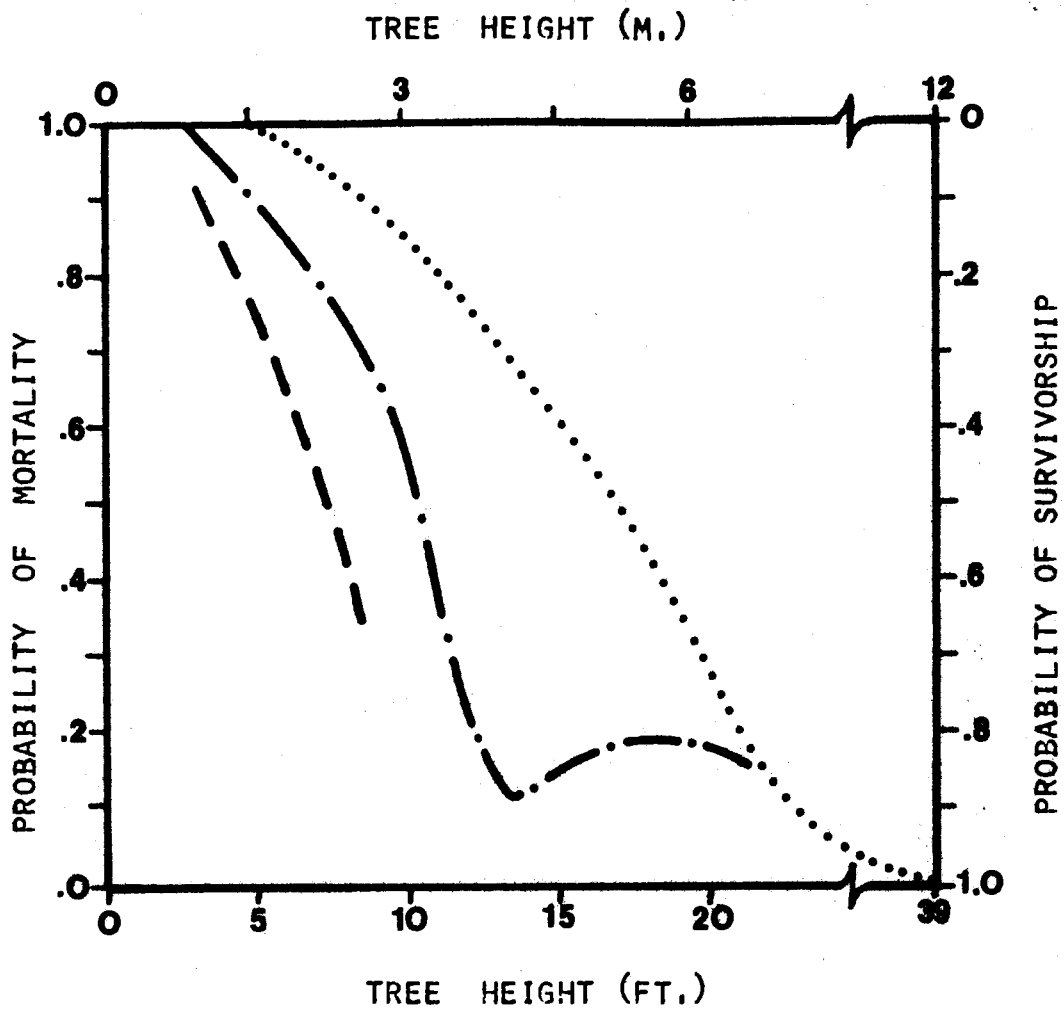


FIG. 4.3: PROBABILITY OF FIRE-INDUCED MORTALITY AS A FUNCTION OF TREE SIZE (*P. CARIBAEA*, MOUNTAIN PINE RIDGE).

DATA: — — — MOODY, 1964
 — — — HUDSON, 1972
 HUTCHINSON, UNPUB.

even the largest trees were susceptible, with trees over 6.5 m. suffering 12% mortality overall and 30% mortality in a 0.4 ha. (1 ac.) subplot.

Further comparisons may be made with a 1 ha. plot sampled from a burn that had taken place in 1971. None of the pine seedlings on the sampled plot survived while the probability of survivorship increased to 100 % for pine trees with basal areas >200 sq.cm. (\rightarrow 12 m. in height). More than 95 % of the hardwoods had survived and were regenerating, either from epicormic sprouts (Byrsionima) or from shoots produced around the root collar (Quercus spp., Clethra). The fire reports submitted by District Forest Officers responsible for the Mountain Pine Ridge contain further anecdotal information on fire-related mortality. The majority of reports classify the damage to pine stands as "nil" or "negligible". In some instances an estimate of mortality amongst regenerating pine is given. From an examination of these reports it would seem that the mortality in the fire reported by Moody (op.cit) is slightly less severe than most fires in Mountain Pine Ridge.

The rate of spread of a grass fire varies with wind-speed but in general burns travel at between 6 - 10 m. (20-33 ft.) per minute (Wolffsohn, 1965). Fires moving at rates greater than 13 m. (40 ft.) per minute are rare, and above this speed the burn travels by "spotting" ahead rather than "running". In windy conditions spotting may be occurring in a zone up to 0.8 km.

(0.5 mile) ahead of the main fire-line. Fires can start in the crowns of pines and palmettos (Accolgraphe wrightii), or occasionally in dead trees, but the low density of trees in these upland pine forests prohibits the transmission of fire from one pine crown to another and true crown fires therefore seldom occur. The main fuel source for burns is the grass and sedge stratum augmented by accumulations of grass, pine and hardwood litter. Grass regrowth after a fire is fairly rapid, particularly during the rainy season. After one such burn in 1973 the grass cover was observed to increase from 3% of ground area two months after the fire to 24% cover one year later. Wolffsohn (op.cit.), states that three months of grass regrowth is sufficient to support a burn in "High" fire hazard conditions, and after a year a fire will travel as rapidly in this young grass as in much older fuels.

Although the ground-cover of grass regrowth increases rapidly after fire, the grass biomass in these young stands is very small compared with that in older stands. The grass regrowth in the burn referred to above had attained a dry weight of only 0.2 kg./sq.m. by the end of two months and 0.24 kg/sq.m. after a year. Open pine stands of greater age (5 - 15 yrs.) may have a current grass crop of up to 0.6 kg/sq.m. Immediately following a burn scorched needles cover the ground to a depth of 1 - 2 cms., weighing 1.0 - 1.5 kg/sq.m.. These are fairly extreme figures, attained only in dense pine stands after severe

fires when much of the needle crop may be singed. More typical values would be in the range of 0.2 - 0.25 kg/sq.m., with a patchy distribution of needles on the ground surface. Wolffsohn's contention that the fuel-bed is sufficient to support a fire after a respite of three months would seem to be more plausible for pine litter fuels than for grass fuels.

No data on temperatures produced by these fires are currently available but comparisons may be made with other savanna areas. There is a generally recognised dichotomy in the literature on fire - research between "hot" and "cold" grass fires. Cold burns are characteristic of areas where fuel is restricted, either because of the nature of the vegetation, or the frequency of fire events. Pitot and Masson (1951) and Beadle (1940), working in W. Africa and New South Wales respectively, recorded surface temperatures of 80 - 200°C during the passage of a fire-front through short-grass savanna. Their results may be contrasted with those of Hopkins (1965) in Nigeria and Masson (quoted in Hopkins, *ibid*) in the Sudan. Maximal temperatures of 850° C were noted in these burns in long-grass savanna. There is no doubt, however, that burns in Mountain Pine Ridge vary considerably in their severity. As fire protection measures become more efficient the regular "cold" burns of the past are being reduced in frequency, and as fuel is progressively accumulated the fires of the future in Mountain Pine Ridge may well prove to be much more severe than those of the past.

4.3: VEGETATION SUCCESSION

The fire - protection policy in Mountain Pine Ridge, originally implemented in an attempt to encourage pine regeneration, has led, paradoxically, to successional changes in the pine savannas which have resulted in reduced pine establishment (Johnson and Chaffey, op. cit.). Where fire protection has been successful, stands are undergoing changes which include: closure of the tree canopy as the initial flush of pine regeneration converts pine savanna into pine forest, revitalised growth of fire-tolerant hardwoods, especially the oaks, and, in the savanna-rainforest ecotones, the invasion of fire-sensitive species which were formerly excluded from the pinelands.

This situation is equivalent to the successional changes reported from other areas of Caribbean pine (Parsons, 1955; Munro, 1966), and analagous to those in the longleaf and slash pine stands of Florida, and the shortleaf and loblolly pine stands of the Piedmont of the U.S.A. (Billings, 1938; Heyward, 1939; McQuilkin, 1940; Bard, 1952; Clewell, 1970).

In each of these cases the pines are gradually excluded from the community by conditions which inhibit their regeneration, and the pine populations consequently undergo a rapid transition from an expanding to a declining population structure within a few decades. There is no universal explanation for the decline of

the pine populations in the studies reviewed above. In each case the controls on population recruitment appear to be species-specific. The trigger for this demographic decline is reduced establishment of seedlings, either because of increased seedling mortality, or through declining germination. The data presented by Johnson and Chaffey on size-class structures of pine in savanna, open woodland and pine forest environments (Fig. 4.4), are indicative of the extent of the decline in Caribbean pine populations with fire exclusion.

As a first step in analysing the dynamics of P. caribaea populations a range of stands of various ages and densities were sampled in the study area in order to formulate some preliminary hypotheses about the relationships among stand history, pine-population structure and dynamics, and stand environment.

4.31: Selection of Stands for Vegetation Sampling

Sample stands were selected on the basis of several criteria. Firstly, each stand had to be fairly homogeneous in its age-structure and species-composition, buffered by a more extensive area of similar structure. Secondly, the age of the stand must be estimable. Stand ages were derived either from fire-history data or from an analysis of the age-structure of the trees on the plot.

Virtually all of Mountain Pine Ridge was burnt over in the fire of 1949, and this was taken as a base-year for estimating

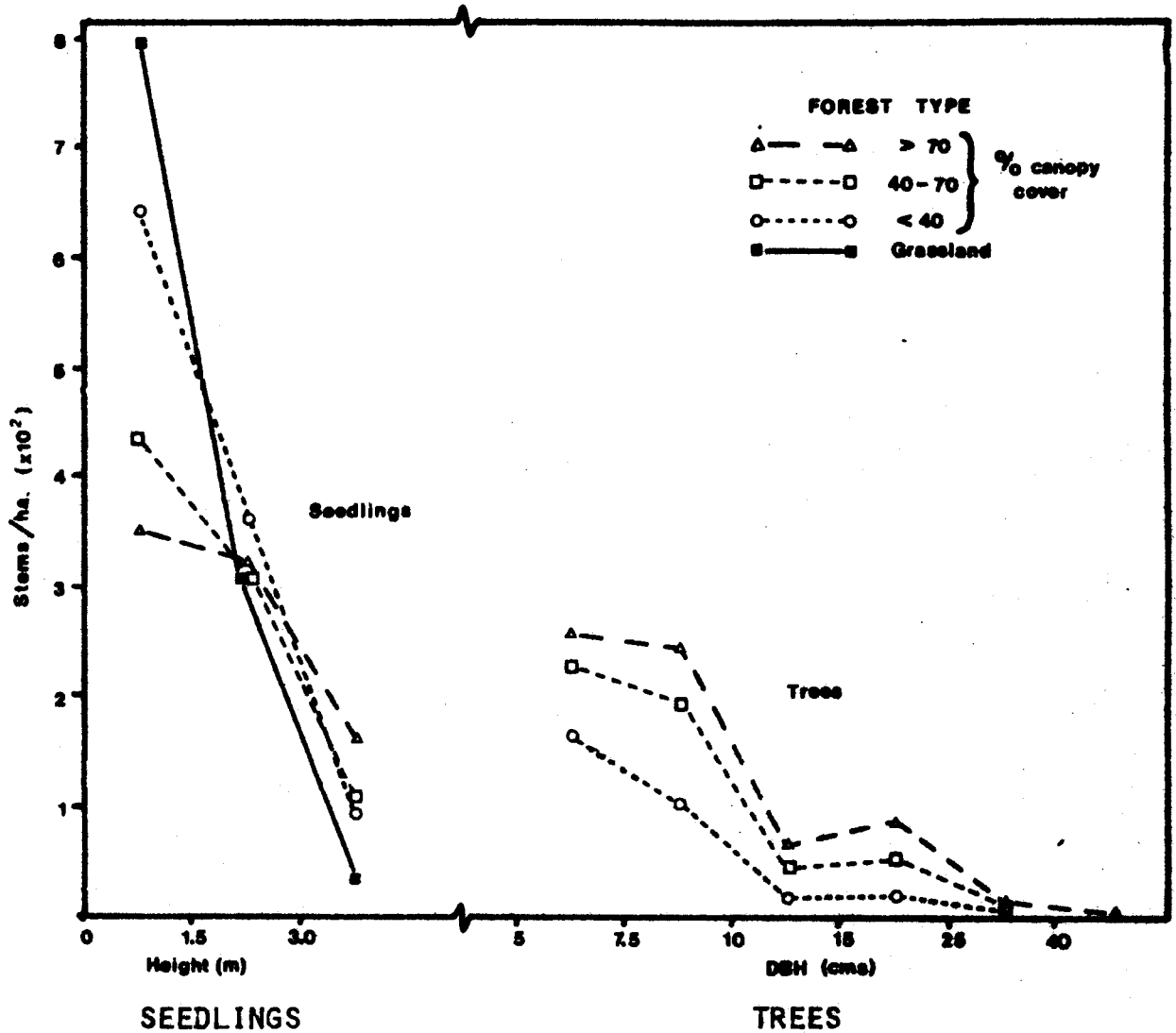


FIG. 4.4: SIZE-CLASS DISTRIBUTIONS OF *P. CARIBAEA* IN VARIOUS TYPES OF WOODLAND IN MOUNTAIN PINE RIDGE. DATA FROM JOHNSON AND CHAFFEY (1973).

the maximum "age" of stands. The choice of sample stands and the delineation of their recent history proved to be the single most intractable problem encountered in the research programme. The tree-size distribution and species composition of a stand of P. caribaea is a palimpsest, recording the effects of a host of past and recent influences. Lamb (1950), contends that the major influence on virtually all the stands in the study area is the fire history of the stand. This includes not only the date and intensity of the last fire event, but also the frequency and intensity of previous fires. As mentioned in Chapter Three, fire records only exist for the period from 1961 to the present for Mountain Pine Ridge, and the extent and intensity of prior fires is known only from oral evidence and scattered comments in the Annual Reports of the Forestry Department.

Superimposed on the effects of fire are the compound effects of logging, thinning and clearing of "weed" tree species. These processes have touched all the stands in the Granite Basin at some time or another in the last twenty years. To some extent these latter processes are akin to fire in the effects that they have on the stand, particularly as, until 1960, control burning of logged stands was an accepted practice in Mountain Pine Ridge.

Unfortunately no records exist of the dates at which certain areas were cutover, and the data on thinning regimes are equally sparse. Consequently the reconstruction of the history of a stand, and the intensity of disturbance that it has suffered, can

be achieved in many cases only by analysis of the age-distribution of the pine populations forming the stand.

The task of delineating stand history is further complicated by the fact that the multiple growth flushes of *P. caribaea* in a single year, presumably in response to moisture availability (Hughes, 1970), are reflected in multiple latewood bands in the stem. Stem age can therefore only be determined by an attempt to discriminate between "false" rings, laid down during short periods of water deficit, and "annual" rings, produced during the long annual dry season. Often the "annual" ring may consist of a coalescent series of "false" rings which seem to represent a single drought event. Fortunately, the problem is least acute in the Granite Basin. Hughes (op. cit., p. 339) states: "samples (from the Granite Basin) showed a clearly defined "annual" ring with few "false" rings, a pattern which reflects site conditions where there is adequate rainfall and good rooting depth". Kellman (1976) notes that these "false" rings cannot be distinguished from "annual" rings on the basis of X-ray densitometry, and suggests a technique of calibration using core samples from plantation trees of known age. This technique was independently employed in the present study.

A further criterion for stand selection was that all stands had to be on topographically similar sites, namely, flat interfluves. Finally, the sample stands were chosen so as to give a wide range of pine densities in each stand age-class. A

total of 17 stands in the Granite Basin area were ultimately selected. The distribution of the sample stands is shown in Fig. 4.5 and the data for each stand are summarised in Appendices C and D.

4.32: Stand Description: Vegetation

Within each stand a sample plot of 20 m. x 20 m. was laid out at random, and data were collected on the basal area (by species) of all trees within the plot. A 10 % sample of pine trees (i.e. every tenth tree sampled) were cored with an increment borer, and the age of each tree was estimated. In addition the height of all pine seedlings (trees < 2 m. in height) was recorded, and the percentage ground cover of all trees and shrubs with stem basal areas of < 15 sq. cm. was estimated. The vegetation data for each stand are presented in Appendix C.

In forest stands in which active regeneration of the canopy species is occurring, the size-class or age-class distribution of the species population assumes a reverse J - shape, and can often be represented by a negative power function (Hett and Loucks, 1971). Where the population is not regenerating, and population size is declining with time, the age-class or size-class distribution departs from this model.

The data from the field sample stands (Fig. 4.6) indicate that the applicability of this model to these sites is dubious.

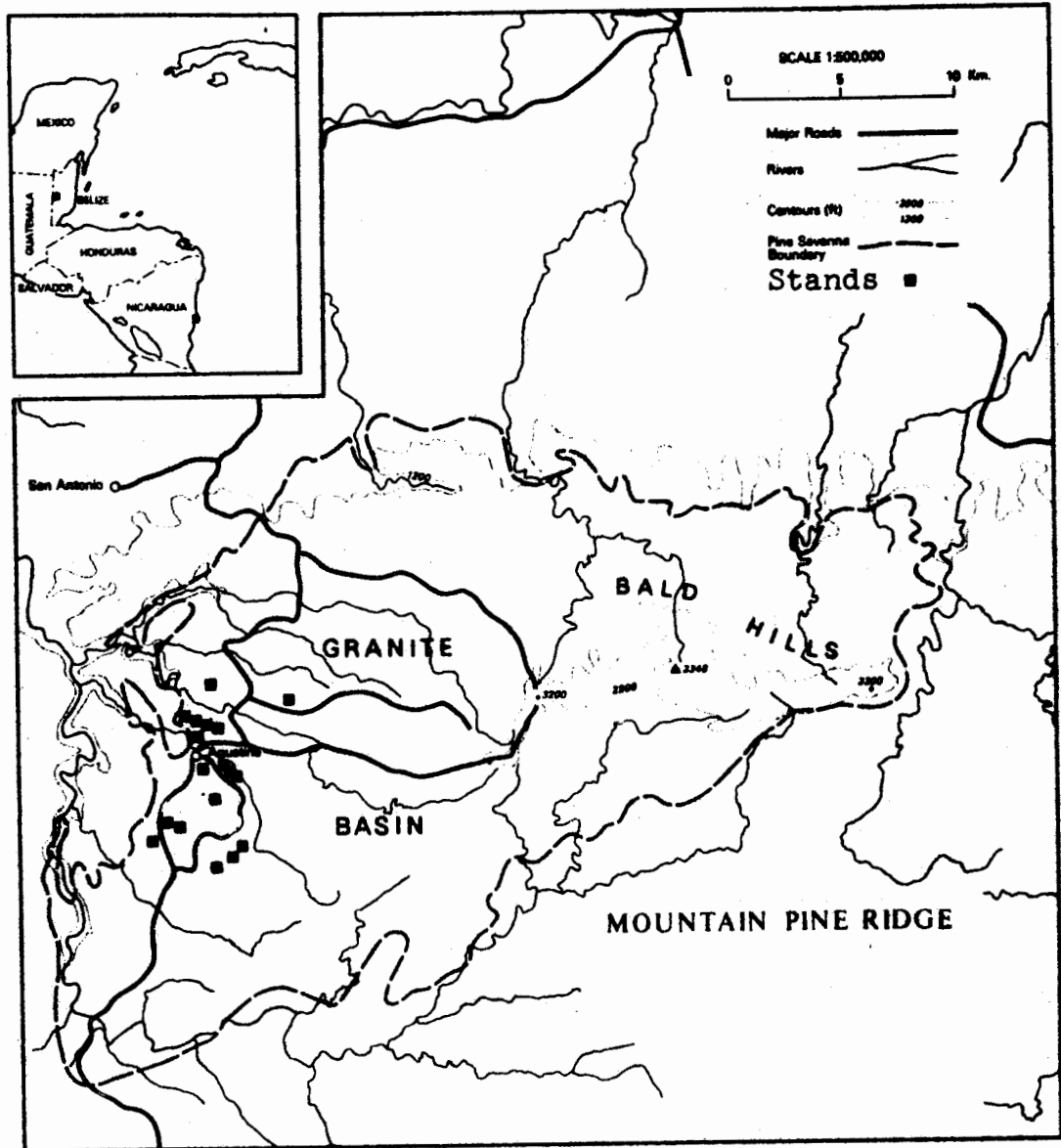


FIG. 4.5: LOCATION OF THE SAMPLE STANDS IN THE STUDY AREA

It is apparent that in most of the older stands (#2,5,6,10,11 and 15) the pines are failing to regenerate themselves, as there is an almost total lack of seedlings in the population distribution. In only two of the older stands (#13 and #14) is regeneration occurring, and these anomalous stands are ones in which selective logging has taken place fairly recently. These data confirm and supplement the preliminary conclusions derived from the tables of Johnson and Chaffey (op. cit.) presented above. The next chapter will return to this theme and discuss in detail the dynamics of the seedling populations.

Although the numbers of pine individuals decline with advancing stand age, Caribbean pine still remains the dominant tree species in all the stands sampled (Fig. 4.7). There is an increase in the total basal area of hardwoods with stand age, but in the sample stands they account for only 8% of the the total stem basal area on average. In only one stand (#12) did the hardwoods attain > 20 % of this value. The histograms of hardwood basal area per stand (Fig. 4.8) demonstrate the dominance of three genera in the hardwoods flora: Byrsonima crassifolia, Clethra hondurensis and the two common species of oak (Quercus oleoides and Q. purulhana), accounting for some 80 % of the total hardwoods basal area.

Shrub cover averages 21 % of ground area in the sample stands, and like the hardwood tree cover, tends to increase with

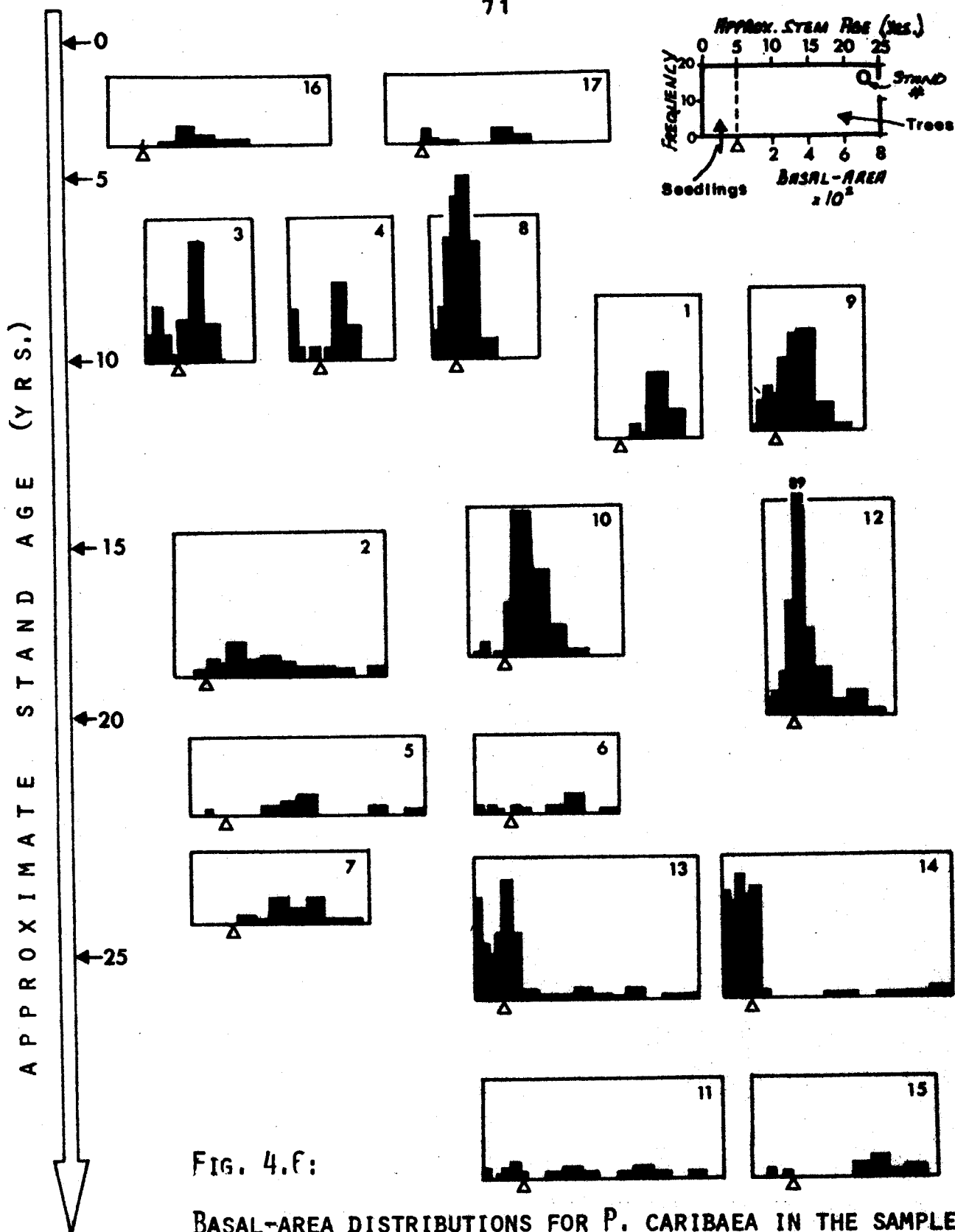
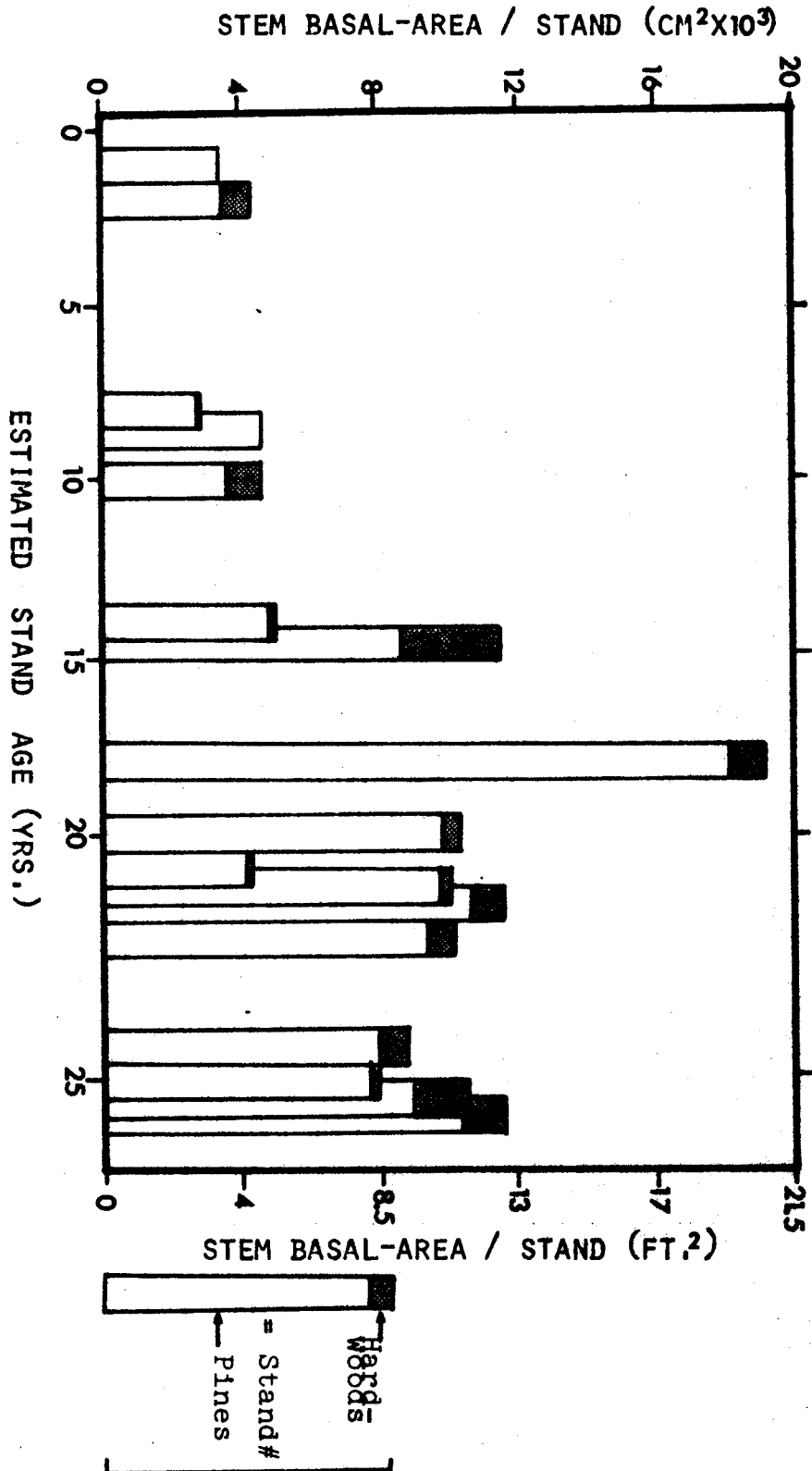


FIG. 4.f:

BASAL-AREA DISTRIBUTIONS FOR *P. CARIBAEA* IN THE SAMPLE STANDS. THE FREQUENCY OF SEEDLINGS (STEMS 2M.) AND TREES IS PLOTTED AS A FUNCTION OF STEM SIZE. SEEDLINGS ARE GROUPED INTO FOUR 0.5M. CLASSES, TREES INTO BASAL-AREA CLASSES OF 100 SQ. CMS.

Fig. 4.7: STANDING CROP OF PINES AND HARDWOODS IN THE SAMPLE STANDS AS A FUNCTION OF STAND AGE.



Mean values for all stands.

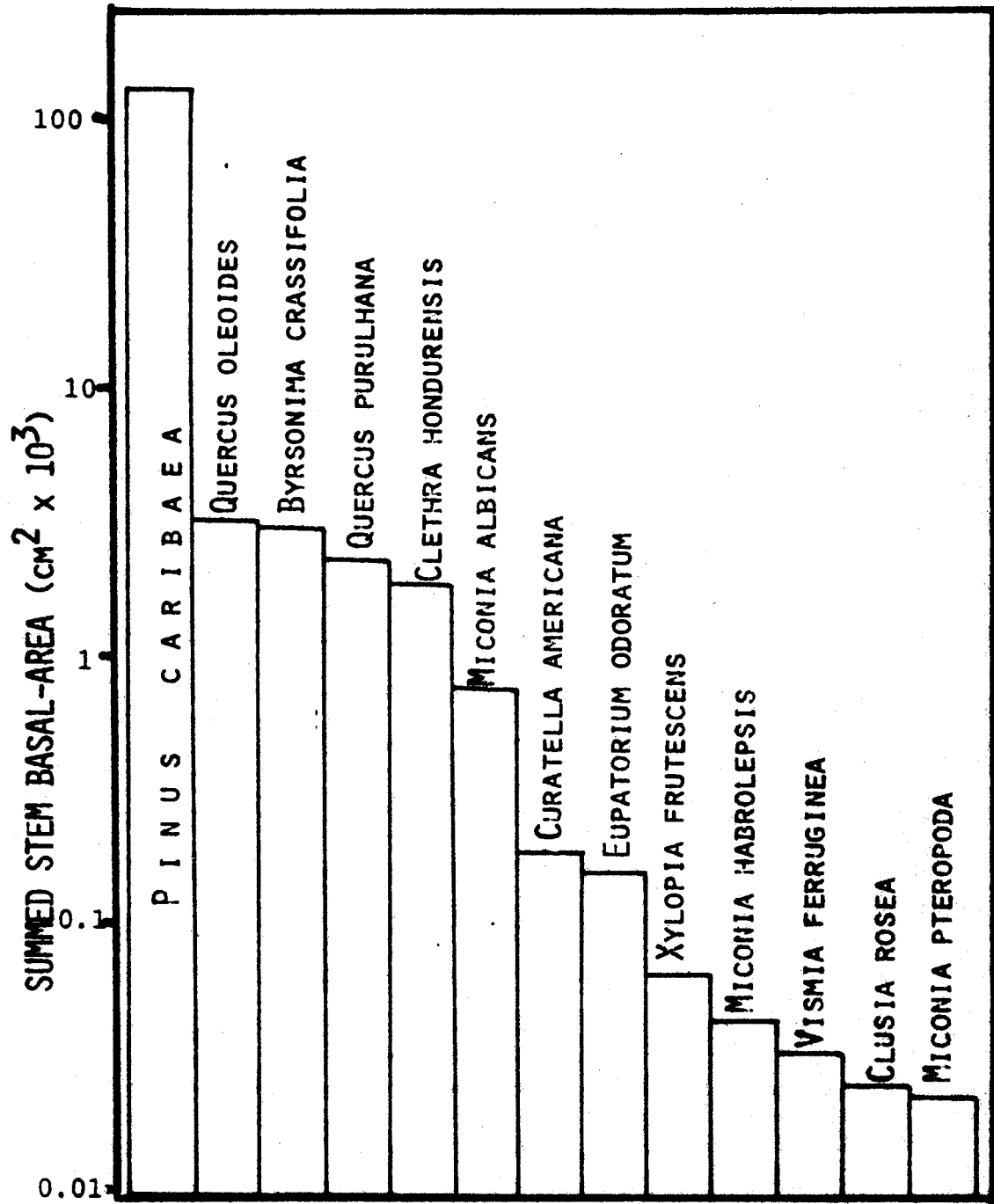


FIG. 48: RELATIVE BASAL-AREAS OF THE MAJOR TREE SPECIES IN THE SAMPLE STANDS.

stand age. The shrub layer is dominated by members of the Melastomataceae (9 spp. recorded), particularly Miconia albicans and the sub-shrub Clidemia rubra. Seedlings and small stems of the prominent tree species are also common members of the shrub layer.

Grass biomass was also measured in each stand and data were recorded in two forms. The grass biomass in a stand was determined by clipping eight random 0.25 sq. m. quadrats. Grass cover was estimated from a further 12 random quadrats of 0.25 sq. m. in each stand. A wooden frame was positioned over each quadrat and the grass cover of each 0.1 sq. m. subquadrat estimated. Grass growth in the sample stands is very patchy, and varies with the age of the stand and the degree of canopy closure. Grass biomass reaches mean values of 0.6 kg/ sq.m. in stands between 5 and 15 years of age, and declines somewhat thereafter, although some older stands may retain fairly heavy grass growth (Fig. 4.9). The grass cover variable shows a similar pattern of a rapid increase after a fire, a long period of stability, and slow decline as the stand ages. Two years after a fire some 25 % of the ground may be covered by the sparse herbage of wiregrasses. Over the next decade these grass clumps expand vertically and laterally until some 40 % of the stand will be covered. The clumps become masses of entangled dead and current leaves growing to a height of some .5 m. In dense stands of pine which have been undisturbed for 20 - 25 years the grass

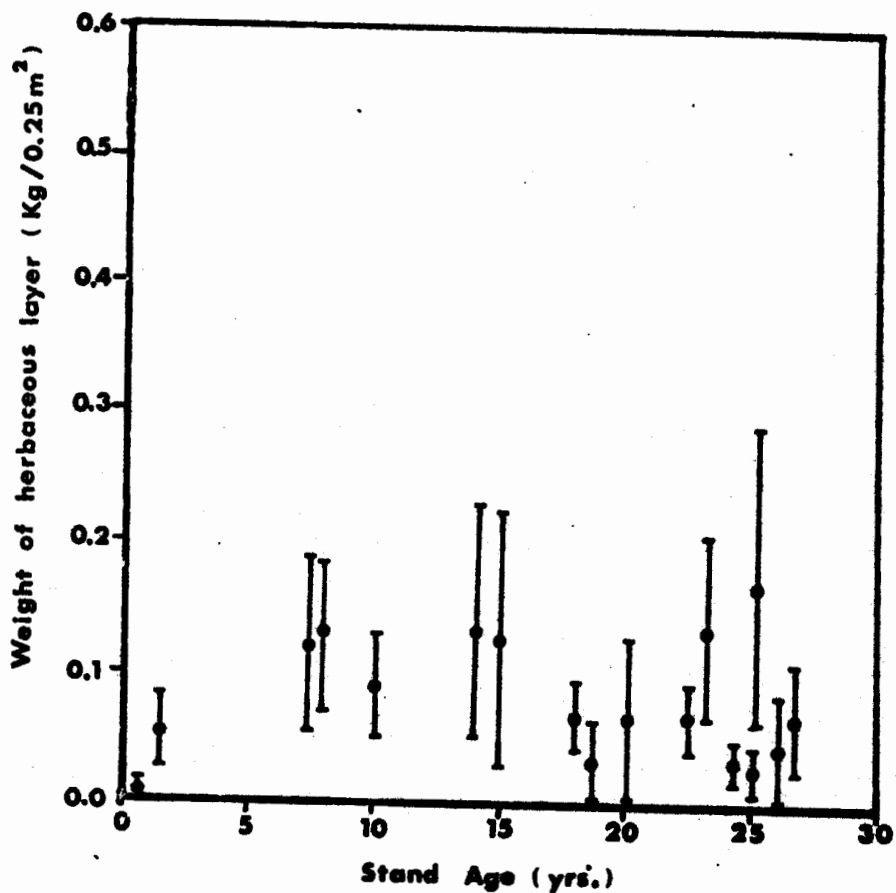


FIG. 4.9: GRASS BIOMASS AS A FUNCTION OF STAND AGE IN THE SAMPLE STANDS.

cover declines, and only 5 - 10 % of the ground area may be covered.

4.33: Stand Description: Environment

The following environmental data were collected in each sample stand: litter depth, litter weight, radiation intensity and light intensity. The forest-floor litter-layer was measured in two ways. Litter depth was measured at 40 points one-half metre apart along a random transect through the sample stand. Litter depth was recorded by gently inserting a ruled stake into the litter until the soil surface was reached, and then measuring litter depth to the nearest 0.5 cm. In addition, the surface litter layer was collected in each stand from four 0.25 sq. m. quadrats scattered randomly over the sample stand, air-dried, and weighed.

Data collected by this procedure are presented in Appendix D and Fig. 4.10. The mass of litter varies considerably within and between stands of similar ages, but the general trend is a linear increase in litter mass on the forest floor over the first 25 years following a fire. Litter depth also increases linearly over successional time. Undoubtedly as the stand ages a dynamic equilibrium between litter production and decomposition develops, and the mass and depth of litter reaches an asymptote.

Incoming radiation and illumination were recorded at each experimental stand at 25 points spaced one metre apart along a

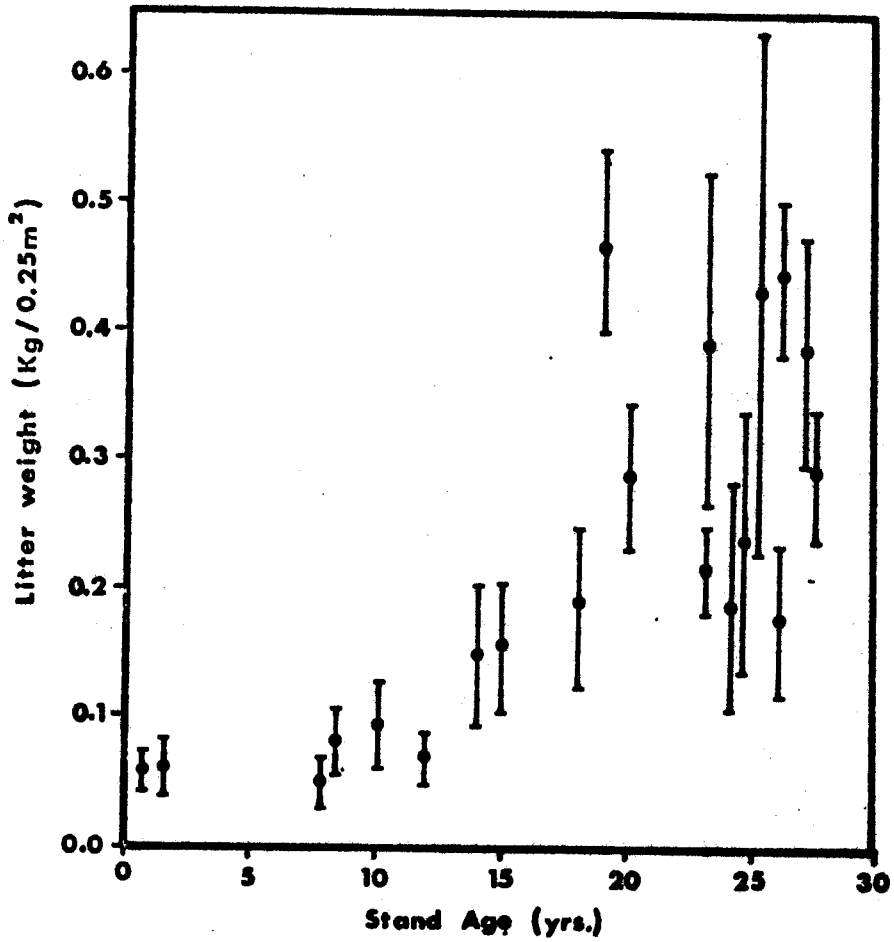


FIG. 4.10: LITTER MASS AS A FUNCTION OF STAND AGE IN THE SAMPLE STANDS.

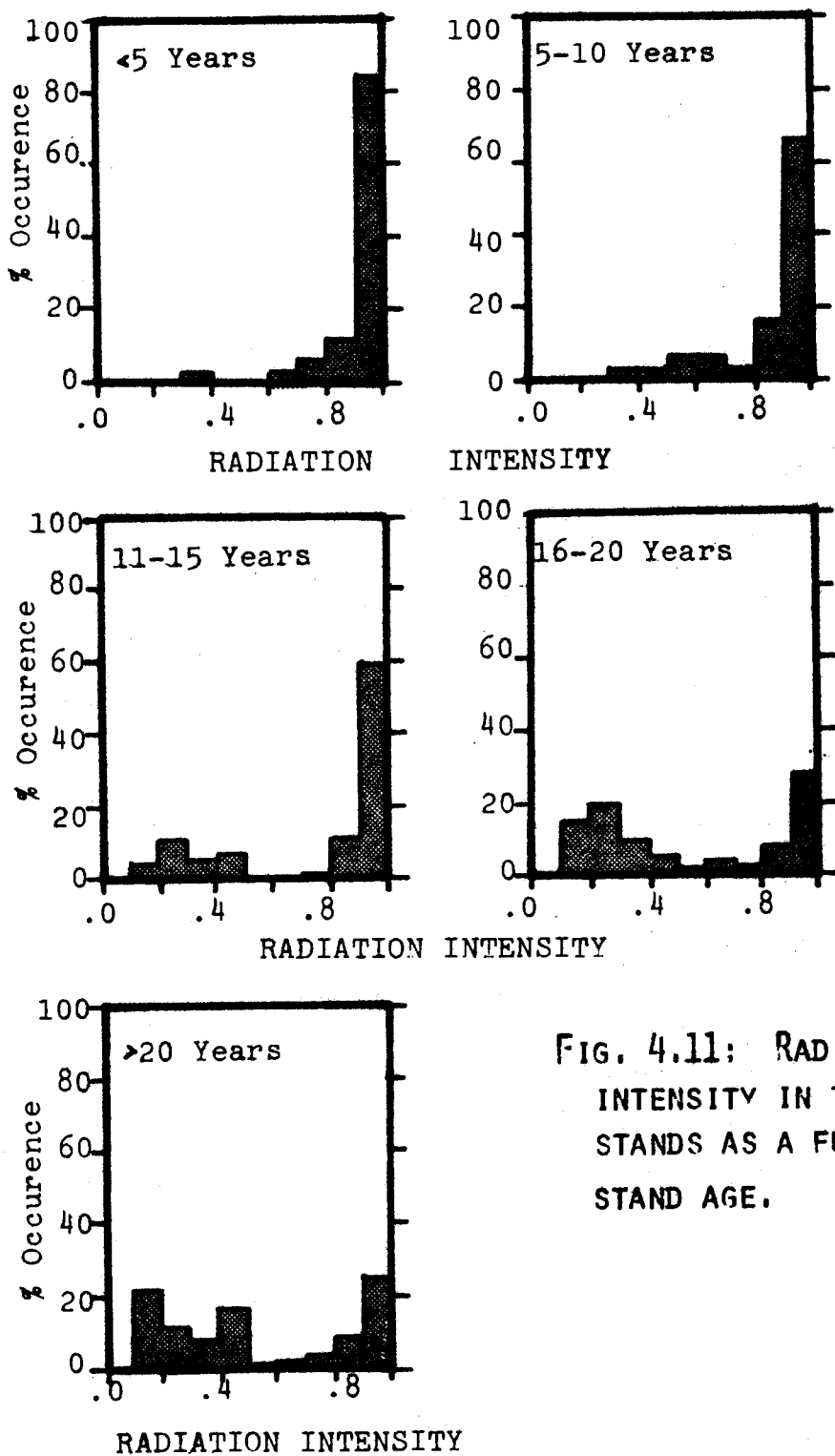


FIG. 4.11: RADIATION INTENSITY IN THE SAMPLE STANDS AS A FUNCTION OF STAND AGE.

diagonal transect. Solar radiation measurements were made using a Middleton CN7 solarimeter when the sun was close to solar noon (1000 - 1400 hours), in periods when the sun's disc was visible, with the instrument positioned horizontally, 0.5 m. above ground level. Visible light readings were taken at the same time using a Nikon FTN camera fitted with a centre-weighted light meter, and these were converted to foot-candles using the chart in Appendix E. Both sets of readings were standardised by reference to values taken in the open at the beginning and end of each transect. Readings were taken during a period towards the end of the dry season (May 1973), and weather conditions were fairly constant, with light cumulus cloud conditions (~ 20 % cover) prevailing.

In the youngest stands, particularly those where logging had left only a few seedtrees, the reduction in radiation intensity at ground level is slight, with median values of circa 90 - 95% of those in the open. As canopies progressively close so the median radiation values gradually become reduced (Fig. 4.11). The distribution of radiation values also changes over successional time. In the youngest stands the radiation values exhibit a unimodal distribution skewed towards the maximum possible values. In stands over 15 years of age the distribution becomes markedly bimodal. The higher mode represents measurements taken beneath holes in the canopy, and the lower mode represents beneath-canopy measurements. Consequently, in

the oldest stands, median radiation levels on the forest floor may be only 20 - 30 % of those in the open. A similar reduction in light intensity occurred over successional time.

CHAPTER FIVE: REGULATION AND FLUX OF PINUS CARIBAEA SEED AND SEEDLING POPULATIONS.

5.1: INTRODUCTION

Research on the dynamics of stands of *P. caribaea* focussed on the demography of the seed and seedling populations, as these were not only the most amenable to field observation and examination, but also represent the most active phase of the plant's lifecycle in terms of population turnover. Two aspects of the population dynamics of the species were examined: the regulatory mechanisms, fluxes and size of the overall seed and seedling (stems less than 2 m. tall) populations; the variations in the rate of seedling establishment with stand age, and the environmental determinants of this differential establishment.

5.2: DYNAMICS OF OVERALL SEED AND SEEDLING POPULATIONS

5.2.1: Life-Table Analysis

Life-tables are employed in demographic research as a means of pinpointing significant phases in the dynamics of a species population. Two types of life-table are generally recognised. A cohort life-table is constructed by censusing the survivorship of a large sample of a single population cohort throughout its life-cycle. A static life-table on the other hand is derived from an analysis of a cross-section of the population at a specific time. The static life-table assumes that mortality rates in each age-class, and recruitment to the species

population, are relatively constant over time. Although these assumptions may not be valid for many plant populations, static life-tables are considerably easier to construct for long-lived organisms such as trees, and have therefore previously been utilised by forest ecologists to monitor stand dynamics (Hett and Loucks, 1968; van Valen, 1975). The static life-table outlined here was used only as an indicator of the life-stages at which population turnover was highest, in order to direct further research efforts to these stages.

Five items of census data are required in order to produce a life-table:

1) Life-table stage, x , the age-class of the population, or period at which some significant development takes place. In *P. caribaea* seedling populations six such stages were recognised: a) Seed-production, b-f) Established seedlings from one to five years of age.

2) Age, Ax , of the population. The population can be considered to come into existence with seed maturation 2-3 months before dispersal.

3) Survivorship, l_x , number of individuals in each age-class.

4) Senescence, dx , the number dying during the age-interval x to $x+1$

5) Mortality rate, q_x , ($q_x = dx/l_x$)

5.211: Data Collection: Census of Seed Production

Seed production can be computed by censusing the current seed-crop from a cone count. A complete tally of all green cones in their second year of development in the sample

stands was made in May 1973, using binoculars. Seed production per cone was then estimated by counting the numbers of seed impressions in 300 fallen cones (20 from each of the stands in which the current cone crop was undamaged by fire). Stands which had been burnt in the last two years had virtually no extant cones and so these sites were omitted from the sampling scheme. The drawback to this censusing method is the tacit assumption that seedfall in a stand is wholly from trees within the stand boundaries, and ignores seeds arriving from outside.

Data on seeds-per-cone ratios, and the relationship of this variable to stand age are presented in Fig. 5.1. Although both the number of seeds-per-cone and the cone yield of pines may vary widely from year to year (McLemore, 1975), there is a close correlation between tree size and seed yield (Fig. 5.2). The field data on cone crops and seeds-per-cone ratios indicate that the number of cones and seeds per tree can be represented as a function of tree basal area:

where BA is the tree basal area in sq. cms.

Precocious seeding may begin when the tree reaches 25 - 30 sq. cms., but the few cones borne on trees of this size are very small. Trees begin to bear seeds in significant numbers (> 10 seeds/tree) when a basal area of 200 sq. cms., equivalent to a tree of some 15 years of age, is reached. However, only 50 % of

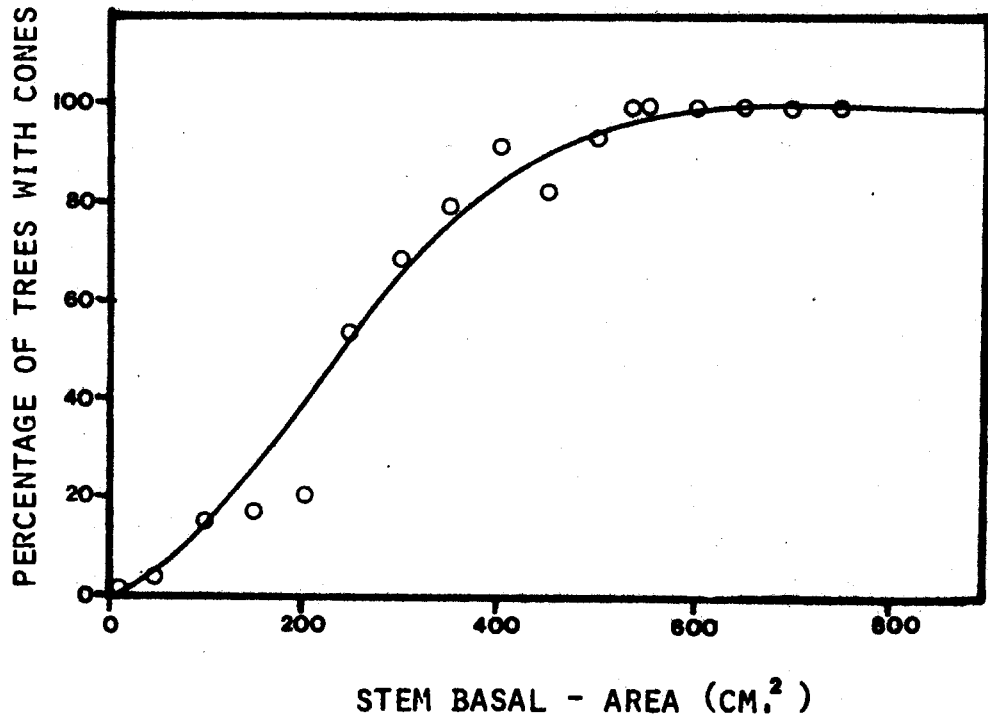
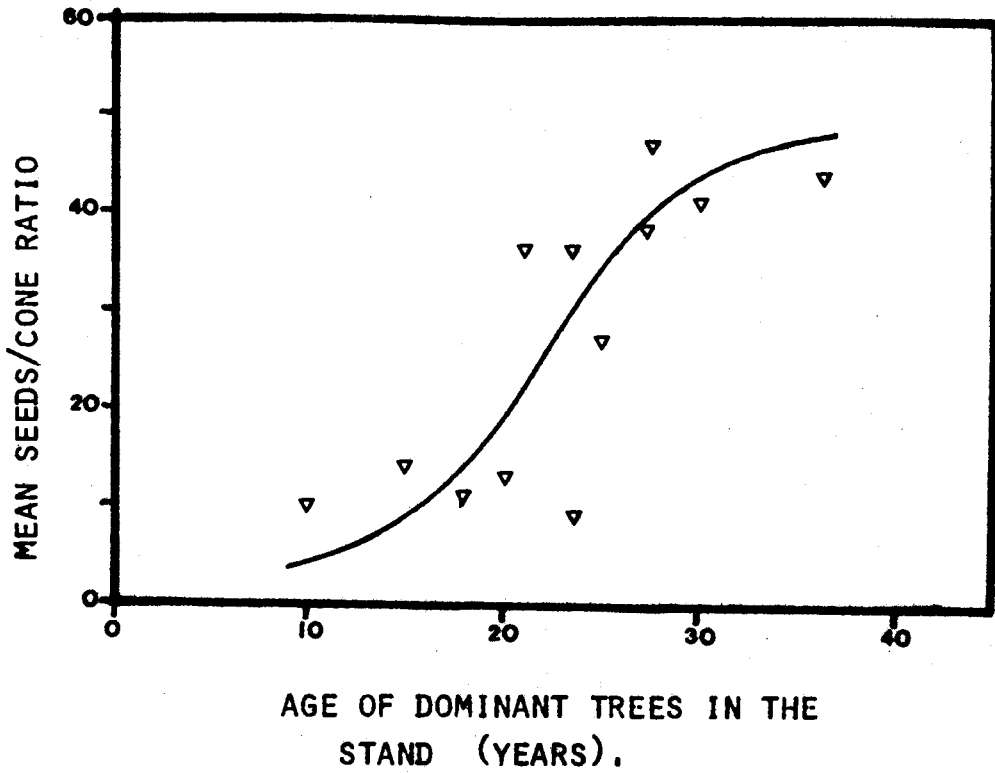


FIG. 5.1: FECUNDITY OF *P. CARIBAEA*

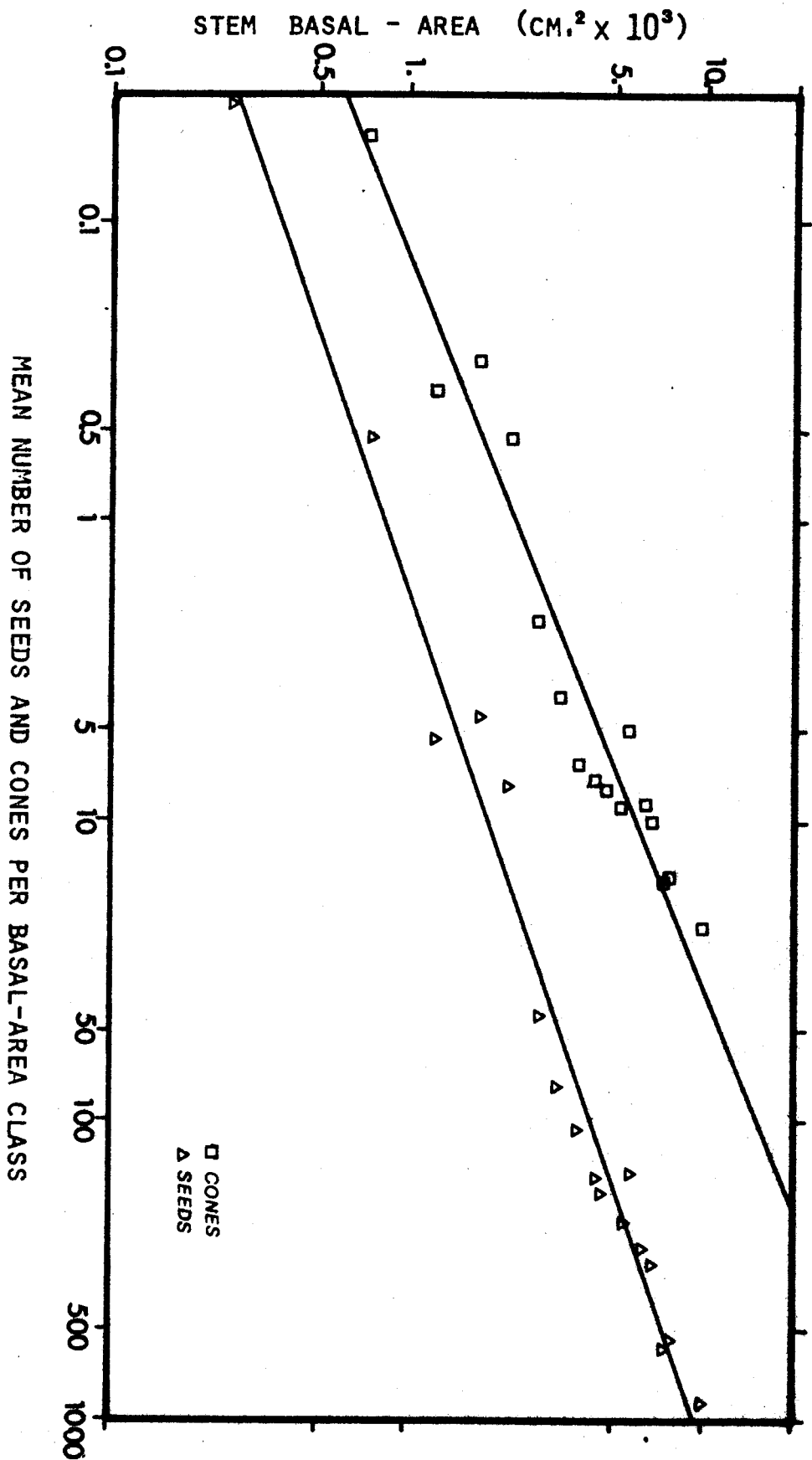


FIG. 5.2: FECUNDITY OF *P. CARIBAEA*: SEED YIELD AS A FUNCTION OF TREE SIZE

the trees of this size may bear cones in any one year, and it is not until a basal area of 400 sq. cms. is attained that all trees become cone-bearers. Almost all the seed in a stand is derived from trees over 1000 sq. cms. basal area. Trees in this size class may bear anywhere from 10 - 1000 cones per season, with the more fruitful trees each yielding 4000 - 5000 seeds. In comparison with some of the pines from the southeastern U.S.A. (Fowells, 1965), *P. caribaea* is not a heavy seed-bearer, which may be a result of the low fertility of soils in the study area.

The field data obtained by this method indicates that seed production in *P. caribaea* stands may vary from 2,000 - 200,000 seeds/ha. depending on tree age and stand density, with a mean value of 63,000 seeds/ha.

5.212: Data Collection: Census of Seedling Populations

Data on seedling height and age relationships were collected from a random sample of 100 seedlings in the sample stands. Age was censused by ring-counts through the base of each seedling, and seedling height was recorded in metres. The relationship between the two censused variables is presented in Fig. 5.3. It is apparent from this graph that the heights of the seedling population can be utilised as a surrogate for age, with each of the age-groups corresponding roughly to:

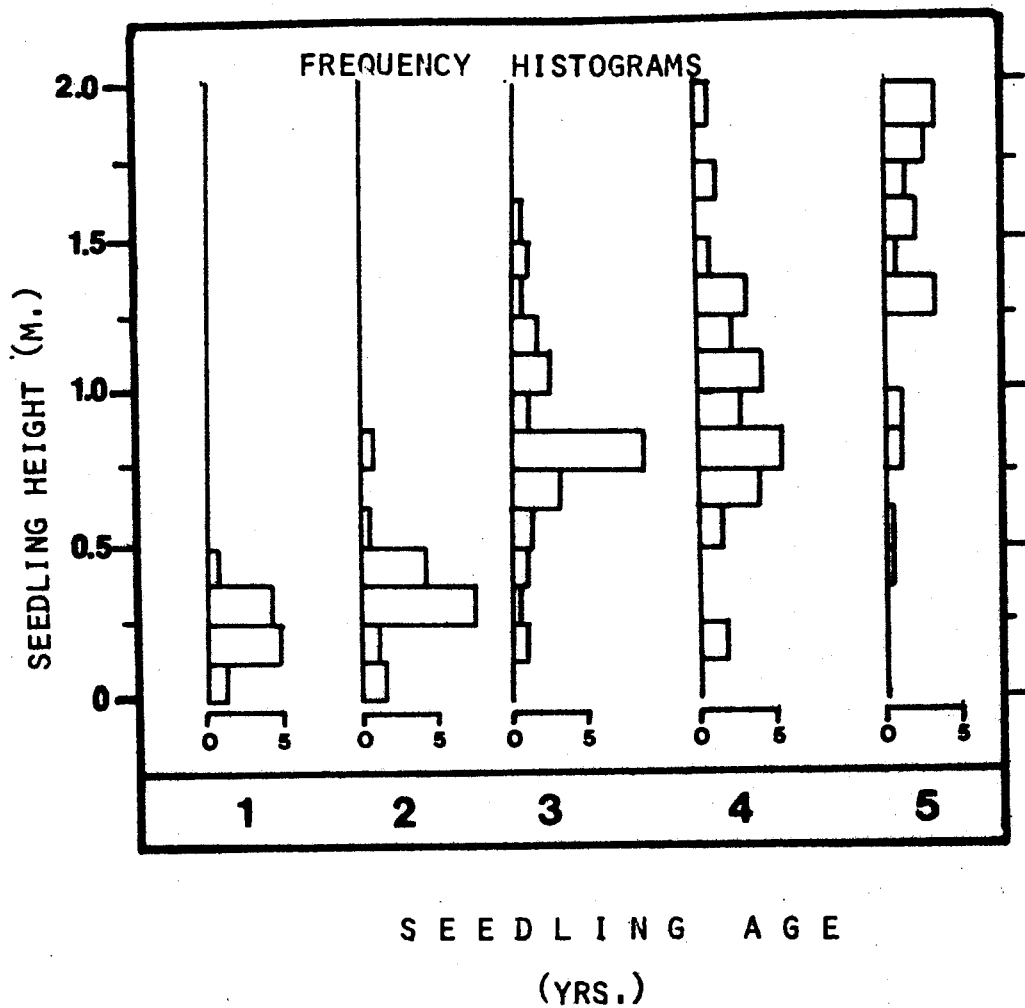


FIG. 5.3: AGE-HEIGHT RELATIONSHIP FOR *P. CARIBAEA* SEEDLINGS. THE RECORDED HEIGHT-DISTRIBUTIONS OF SEEDLINGS IN EACH OF THE 1 - 5 YEAR AGE-CLASSES ARE PLOTTED.

| Age (yrs.) | Height (m.) |
|------------|-------------|
| 1 | 0.00 - 0.25 |
| 2 | 0.25 - 0.5 |
| 3 | 0.50 - 1.00 |
| 4 | 1.00 - 1.5 |
| 5 | 1.50 - 2.00 |

Using this relationship, the ages of all seedlings in the sample stands were estimated.

5.213: Results

The summed values for all sample stands are used to construct the static life-table (Table V.1). The nature of static life-tables precludes an exact calculation of survivorship from year to year, due to possible variations in the magnitude of seed inputs, but provides an overview of stand dynamics.

Seed production amounted to 63,000 seeds/ha. in sampled stands, but first-year seedling populations were only of the order of 280 individuals per hectare. In more traditional life-table terms, a cohort of 1000 seeds gave rise to less than 5 seedlings. In contrast, the numbers in each seedling age-class remain fairly constant (280 - 150 seedlings/ha.) over time. The life-table categorically demonstrates therefore that the period of greatest risk of mortality is not in the early years of the seedling's existence, but occurs during the transition from seed to established seedling. Several explanations can be postulated for this massive decline in numbers in this transition phase.

TABLE V.1: STATIC LIFE-TABLE FOR POPULATIONS OF P_2 CARIBAEA SEEDLINGS IN SAMPLED STANDS.

| (x) | (Dx) | (Ax) | (nx) | (lx) | (dx) | (qx) |
|-----------------|------|------------|-------|------|------|------|
| Seeds produced | 0.25 | 0.0 - 0.25 | 62687 | 1000 | 111 | 0.11 |
| Seeds available | 0.10 | 0.25-0.35 | 55697 | 889 | 884 | 0.99 |
| S 1st yr. | 1.00 | 0.35-1.35 | 280 | 4.5 | 1.8 | 0.39 |
| e 2nd yr. | 1.00 | 1.35-2.35 | 166 | 2.7 | 0.2 | 0.07 |
| d 3rd yr. | 1.00 | 2.35-3.35 | 153 | 2.5 | - | - |
| l 4th yr. | 1.00 | 3.35-4.35 | 208 | 3.3 | - | - |
| i 5th yr. | 1.00 | 4.35-5.35 | 240 | 3.8 | - | - |

x = Life-stage

Dx = Length of life-stage in years

Ax = Age of individuals

nx = # of individuals observed

lx = Survivorship

dx = # dying

qx = Mortality rate

Research within the last decade within the tropics, particularly in Central America by Janzen (1969, 1971, 1972), has shown the importance of seed-predation as a control on the size of the seedling population and the spatial distribution of tree regeneration. Such predation may either precede or succeed seed dispersal. As P. caribaea attains densities considerably greater than those of tree species in the neighbouring rainforest, it might be expected therefore that its seeds would also experience heavy predator pressure. Alternatively, the population decline may result from germination failure or high seedling mortality in the first year of existence. Each of these factors will be examined in turn.

5.22: Pre-dispersal predation of Pinus caribaea seed.

Etheridge (1968), reports that in 1965, 8 % of the cone crop of P. caribaea in Mountain Pine Ridge was infected by the cone-rust Cronartium conigenum. This pathogen completely mummifies the cones it infects, turning them into bulbous masses of yellow aeciospores. After infection, insects invade and consume the cone tissue. The incidence of infection varies in time and space in the study area, but of 1272 cones in the 1973 cone crop, 65 (5.1 %), showed evidence of infection, with some stands having 20 % of their cones destroyed by this parasite (Table V.2).

TABLE V.2: CONE INFECTION BY CRONARTIUM CONIGENUM IN SAMPLED STANDS - 1973 DATA

| Stand # | Current Cone Crop | # infected | % infected | # sound seeds |
|---------|------------------------------------|------------|------------|---------------|
| 1 | 31 | 0 | 0.0 | 453 |
| 2 | 191 | 5 | 2.6 | 1729 |
| 3 | 7 | 1 | 14.3 | 64 |
| 4 | 3 | 0 | 0.0 | 32 |
| 5 | 94 | 1 | 1.1 | 2438 |
| 6 | 96 | 5 | 5.2 | 3312 |
| 7 | 90 | 18 | 20.0 | 3136 |
| 8 | 2 | 0 | 0.0 | 21 |
| 9 | 8 | 0 | 0.0 | 89 |
| 10 | 84 | 4 | 4.8 | 1040 |
| 11 | 199 | 12 | 6.0 | 8698 |
| 12 | 59 | 3 | 5.1 | 571 |
| 13 | 152 | 6 | 3.9 | 5565 |
| 14 | 143 | 10 | 7.0 | 5772 |
| 15 | 115 | 0 | 0.0 | 4692 |
| 16 | Cone crop destroyed by recent fire | | | |
| 17 | | | | |

Total # cones examined = 1272

Total # cones infected = 65

Incidence of infection = 5.11 %

Range of % infection/stand = 0.0 - 20.0 %

The susceptibility of P. caribaea cones to further pre-dispersal seed loss was censused by examining freshly-fallen cones for evidence of scale removal by squirrels or birds, and for the presence of larval galleries of insects in scales or cone axes. Of 300 cones examined, containing a mean of 27 seed impressions per cone, almost all were free of damage (Table V.3). Somewhat surprisingly, there was no evidence of squirrel or parrot feeding, although both animals are known to open cones of P. caribaea. Three squirrels of the genus Sciurus are known from Belize (Kirkpatrick and Cartwright, 1975), but all are rainforest species and only rarely venture into the pinelands. A total of six squirrels was seen by the author in Mountain Pine Ridge in the course of two years residence, and all were within 100 m. of the forest edge. The only cone-damage by squirrels occurred in this transitional zone.

In contrast, parrots are fairly common in the pinelands (especially Amazona autumnalis L., the red-lored parrot), but the cone scales of P. caribaea are sufficiently thickened to inhibit anything more than casual feeding by these birds. Another avian pine seed predator is the red crossbill (Loxia curvirostra L.), reported by Russell (1964) as occurring in Mountain Pine Ridge, but being so rare as to go unnoticed by Austin (1929) and myself.

Insect predation of seeds in the sampled cones was also on a small scale, with only 1.25% of the cones exhibiting larval galleries in and around the cone axis. It was estimated from the

TABLE V.3: PRE-DISPERSAL SEEDLOSS FROM SAMPLE STANDS OF
P. CARIBAEA.

| Stand # | # Seed impressions | Seedloss attributable to these agents: | | | |
|---------|--------------------|--|-----------|---------|----------|
| | | parrots | squirrels | insects | attached |
| 1 | 292 | 0 | 0 | 0 | 25 |
| 2 | 186 | 0 | 0 | 0 | 6 |
| 5 | 524 | 0 | 0 | 0 | 38 |
| 6 | 728 | 0 | 0 | 10 | 34 |
| 7 | 1089 | 0 | 0 | 4 | 34 |
| 8 | 428 | 0 | 0 | 24 | 7 |
| 9 | 333 | 0 | 0 | 0 | 18 |
| 10 | 260 | 0 | 0 | 2 | 17 |
| 11 | 1395 | 0 | 0 | 0 | 46 |
| 12 | 306 | 0 | 0 | 0 | 53 |
| 13 | 840 | 0 | 0 | 0 | 58 |
| 14 | 868 | 0 | 0 | 0 | 89 |
| 15 | 816 | 0 | 0 | 0 | 9 |

Total # cones examined = 300
 Total # seed impressions = 8067
 Mean seeds/cone ratio = 26.89 %

Total # seeds lost to parrots = 0
 Total # seeds lost to squirrels = 0
 Total # seeds lost to insects = 40
 Total # seeds attached to cone-scales = 451

% Loss to parrots and squirrels = 0.0 %
 % Loss to insects = 0.45 %
 % Remaining attached to cone-scales = 5.59 %

Incidence of *Crocartium* infection = 5.11 %
 (from Table V.2)

Total pre-dispersal seedloss = 11.15 %

number of holes in cone scales that some 40 % of the seeds in the host cones had been destroyed, indicating a predation rate on the seed population as a whole of 0.5 %. The insect pests responsible for this damage were not identified, but coneworms (Dioryctia spp.), are suspected, as they are known to attack rust cones in Mountain Pine Ridge (Billings, 1973), and larvae can spread from rust cones to green cones in some circumstances (Merkel, 1958).

The major source of seedloss in the fallen cones was not attributable to predation by animals, but to non-dispersion of the seeds. Some 5.6 % of the seeds remained in the cones after cone abscission, glued to the cone-scales by resin exuding from the cone axis. Thus the total pre-dispersal seedloss amounted to 11 % of the population, the same figure as reported by de Barr and Barber (1975) for P. elliottii in Florida. Most of the loss occurred as a result of rust infection and retention of seeds in the cone. In terms of the initial cohort of 1000 seeds, pre-dispersal loss would result in a reduction of the population to 889 individuals. Pre-dispersal loss can therefore be accorded only a minor role in the decline of pine populations during the transition from seed to seedling.

5.23: Post-dispersal predation of P. caribaea seed

To measure the intensity of predation during the period prior to germination and after seed-dispersal, a series of piles

of P. caribaea seeds were laid out at 25 cm. intervals in a 15 year old pine stand with a light grass and litter cover. One line of seeds was covered with 0.68 cm. mesh chicken-wire to exclude rodent and bird predators. The other line was left uncovered, and the seeds were freely available to insects, birds, and rodents.

The number of seeds removed from the piles was recorded daily for a week (Fig. 5.4). The experiment was abandoned because of heavy rains which repeatedly dispersed the seed-piles after this time-period. At the termination of the experiment 22 % of the seed had been taken from the piles in the wire-mesh plot, and 50 % of the seeds had been removed from the open plot. This indicates that "micro-predators" (insects) and "macro-predators" (rodents and birds), have an approximately equal effect as seed-harvesters in Caribbean pine stands. In the period prior to the onset germination some 65 % of the available seed may be lost to these animals, with a further 30 % loss over the 30 day germination period.

No rodents or birds were seen to take seeds from these piles, but general knowledge of the feeding habits of the fauna of the pinelands indicates two rodents (particularly the cotton rat, Sigmodon hispidus), several species of birds, and four genera of insects as prime suspects. Disney (1968), reports that the cotton rat is very common in Mountain Pine Ridge, as 98 % of his trap records were referable to this species, with a spiny

pocket mouse (Heteromys desmarestianus) the only other rodent recorded. The birds most likely to be major predators of pine seed are the white-collared seedeater (Sporophila torqueola), the rusty sparrow (Aimophila rufescens), and the melodius blackbird (Dives dives). Less common are the yellow-backed oriole (Icterus chrysater), and the hepatic tanager (Piranga flava). Seeds of P. caribaea probably form only a small proportion of the diet of these latter three species. In his monograph on P. caribaea, Lamb (1973; p.91), mentions the depredations of ants on pine seed planted in nurseries in Belize. Insects feeding on the seed piles included fire ants (Solenopsis spp.; see: Campbell 1974), harvester ants (Pheidole spp.), carpenter ants (Campanotus spp.) and crickets (Gryllidae). A full listing of the seed-predator species is given in Table V.4.

The results of this experiment indicate that the population decline during the seed to seedling transition may be primarily due to post-dispersal predation. The next section examines the consequences of heavy post-dispersal predation.

5.24: Seedling recruitment: Predation, germination, and first-year mortality.

A further series of experimental plots were established in the field to monitor (a) the magnitude of seed predation, (b) the rate of germination of seeds which escape predation, and (c) the survivorship of these seedlings during their first year of existence. Within each of the 17 sample stands two 1 sq. m.

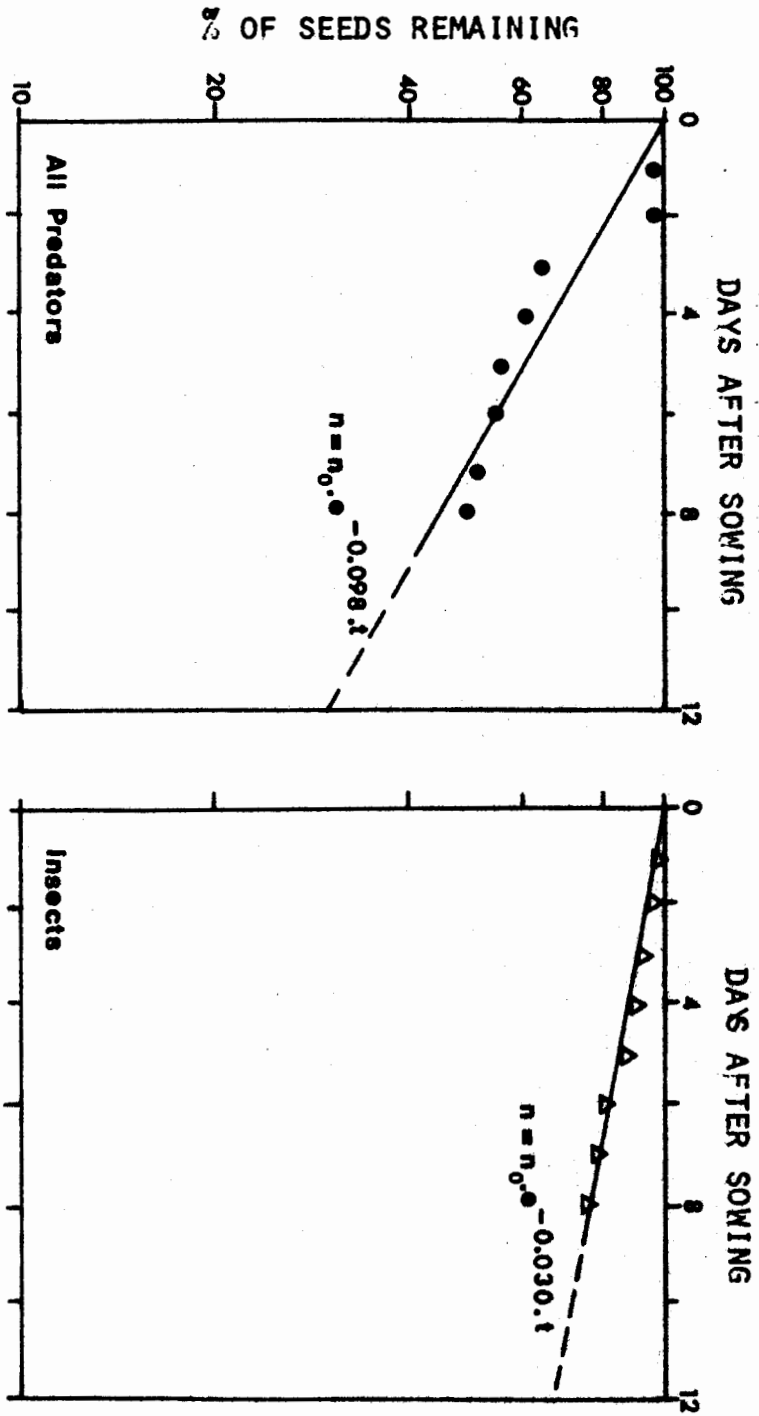


FIG. 5.4: PREDATION RATES OF *P. CARIBAEA* SEED FROM PILES IN OPEN (●) AND EXCLOSURE TREATMENTS (▲).

plots were laid out at opposite corners of a 10 m. x 10 m. square. These served as control plots. The remaining two corners of the square were occupied by exclosure plots, each .25 sq. m. in area, surrounded by a cage (0.25 m. high), of 1.25 cm. mesh chicken-wire. These plots were designed to provide data on germination and survivorship in the absence of "macropredators". The smaller size of the exclosure plots was necessitated by the limited supply of chicken-wire in Belize.

Pinus caribaea seed was sown evenly by hand over these plots at a density of 400 seeds/sq. m. The plots were sown in the first week of July 1974, coincident with the first flush of natural seeding. The seeds were a batch of the current crop obtained through the Forestry Department in Augustine. Cones had been collected three weeks previously and dried in the sun to release their seeds, and then de-winged by hand-rubbing in sacks. Some 8% of the seed purchased turned out to be broken, empty, or filled with granular frass as a result of insect predation; and these were discarded. Radicle emergence takes a minimum of 10 days, and the first count of germination was made after 14 days had elapsed. Subsequent tallies were made at one-month intervals, and at each census the number of both live and dead pine seedlings was counted. The results are presented in Fig. 5.5.

Initial germination rates in the control plots were surprisingly low, and the mean maximum germination rates for the

TABLE V.4: PREDATORS OF *P. CARIBAEA* SEEDPre-Dispersal Predators

| | | | |
|----------------------|-----------------------------|---|---|
| Fungi: | | | |
| | <i>Cronartium conigenum</i> | + | * |
| Insecta: Lepidoptera | | | |
| | <i>Dioryctia</i> spp. | + | |
| Aves: Psittacidae | | | |
| | <i>Aratinga astec</i> | | |
| | <i>Amazona albifrons</i> | | |
| | <i>Amazona autumnalis</i> | | * |
| | : Fringillidae | | |
| | <i>Loxia curvirostra</i> | + | |
| Mammalia: Rodentia | | | |
| | <i>Sciurus yucatenensis</i> | | |
| | <i>Sciurus deppei</i> | | |

Post-dispersal Predators

| | | | |
|--------------------|-----------------------------|--|---|
| Fungi: | | | |
| | Unknown | | |
| Insecta: Gryllidae | | | |
| | <i>Gryllus</i> spp. | | * |
| | : Hymenoptera | | |
| | <i>Solenopsis</i> spp. | | * |
| | <i>Campanotus</i> spp. | | * |
| | <i>Pheidole</i> spp. | | * |
| Aves: Icteridae | | | |
| | <i>Dives dives</i> | | * |
| | <i>Icterus chrysater</i> | | * |
| | : Thraupidae | | |
| | <i>Piranga flava</i> | | * |
| | : Fringillidae | | |
| | <i>Sporophila torqueola</i> | | * |
| | <i>Aimophila rufescens</i> | | * |
| | <i>Spizella passerina</i> | | * |
| | <i>Spinus nctatus</i> | | * |
| Mammalia: Rodentia | | | |
| | <i>Sigmodon hispidus</i> | | * |

+ = Pine seeds form large part of 'diet'
 * = Occurs frequently in the study area

control plots in all the sample stands reached only 0.89 % of the 13,600 seeds sown. This is in sharp contrast to the germination rates recorded under ideal conditions in nurseries, which are usually in the 90 - 95 % range with fresh seed.

Maximum germination rates in the control plots were attained 15-40 days after sowing, and the numbers of live seedlings thereafter declined. The initial rate of population decay was very rapid. Six months after sowing 30 % of the initial seedling population survived, but after this the rate of mortality slowed. At the end of the first year only 23 % of the initial population survived. The rate of seedling loss can be represented as a power function (Fig. 5.6).

$$N = 380. T_S^{-0.44}$$

where T_S is the number of days after sowing.

These results confirm the conclusion drawn from the static life-table, namely, that the major decline in *P. caribaea* populations occurs during the transition between the seed and seedling stage, as less than 1 % of the available seeds enter the seedling population. In addition, almost 80 % of these seedlings die in their first year of existence.

The results from the enclosure plots contrast sharply with those of the controls (Fig. 5.7). Thirty-nine days after sowing 5 % of the seeds in the enclosure plots had germinated, compared

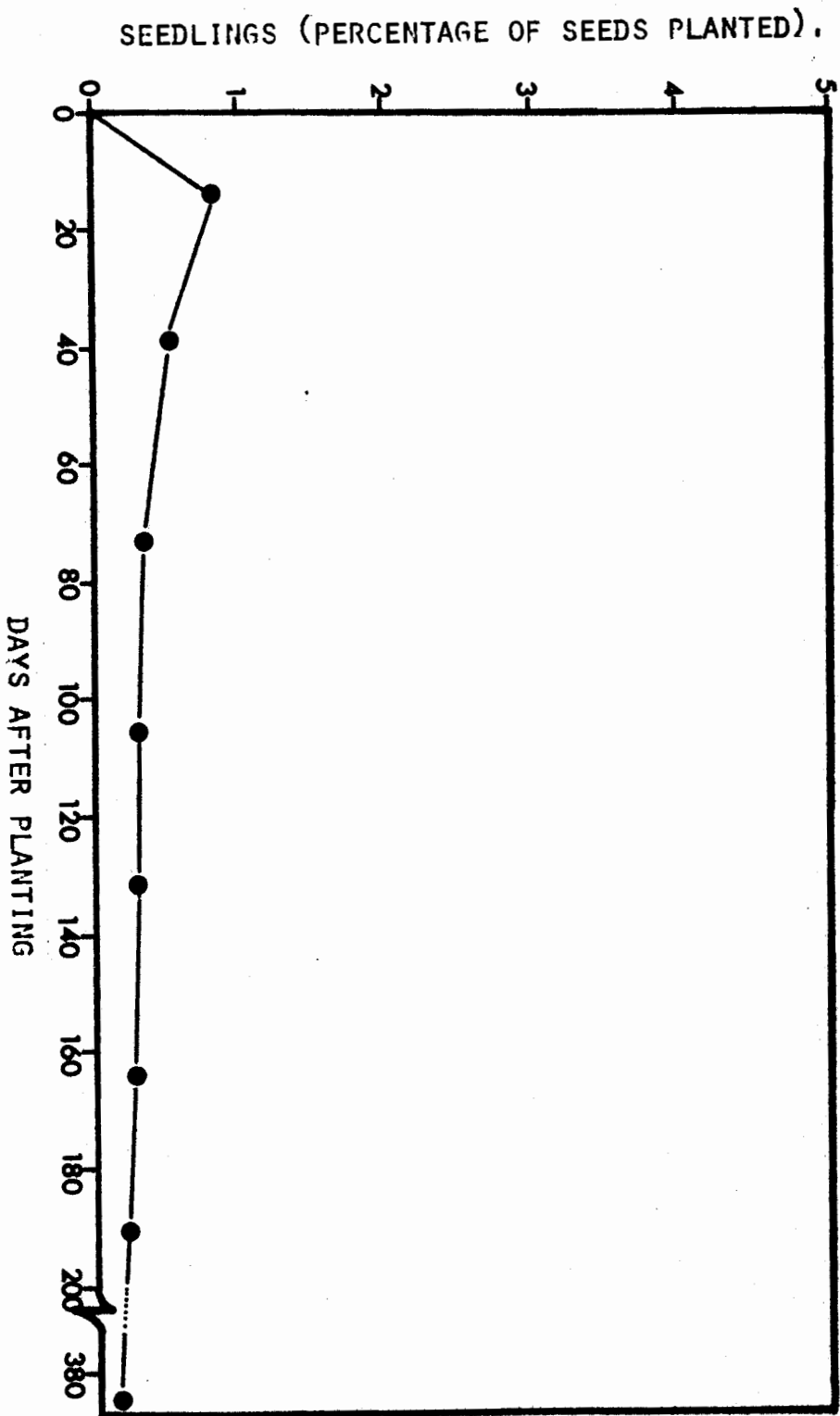


FIG. 5.5: SEEDLING ESTABLISHMENT AND SURVIVAL IN THE CONTROL PLOTS

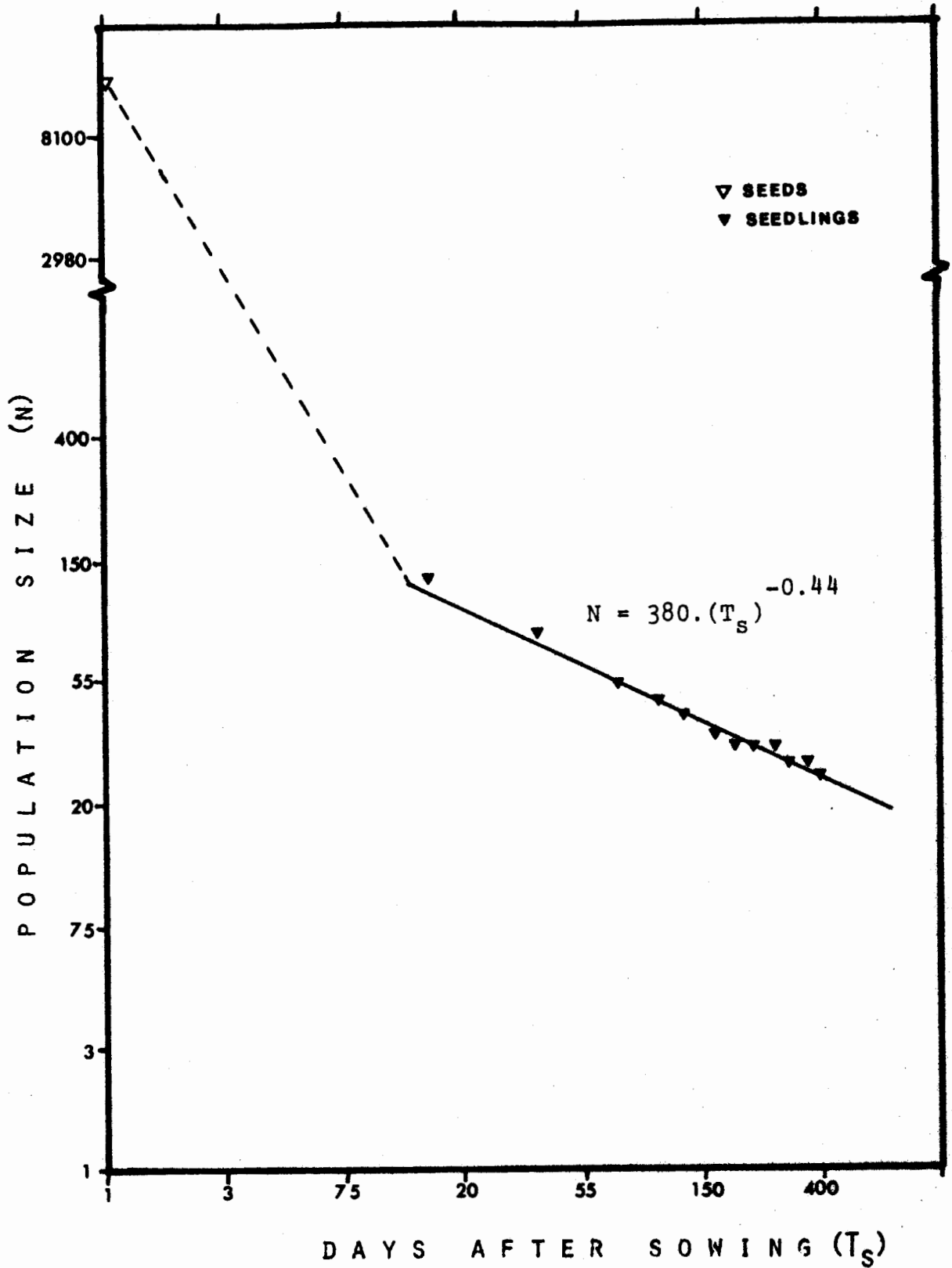


FIG. 5.6: POPULATION DECLINE OF SEEDLINGS IN THE CONTROL PLOTS EXPRESSED AS A POWER FUNCTION.

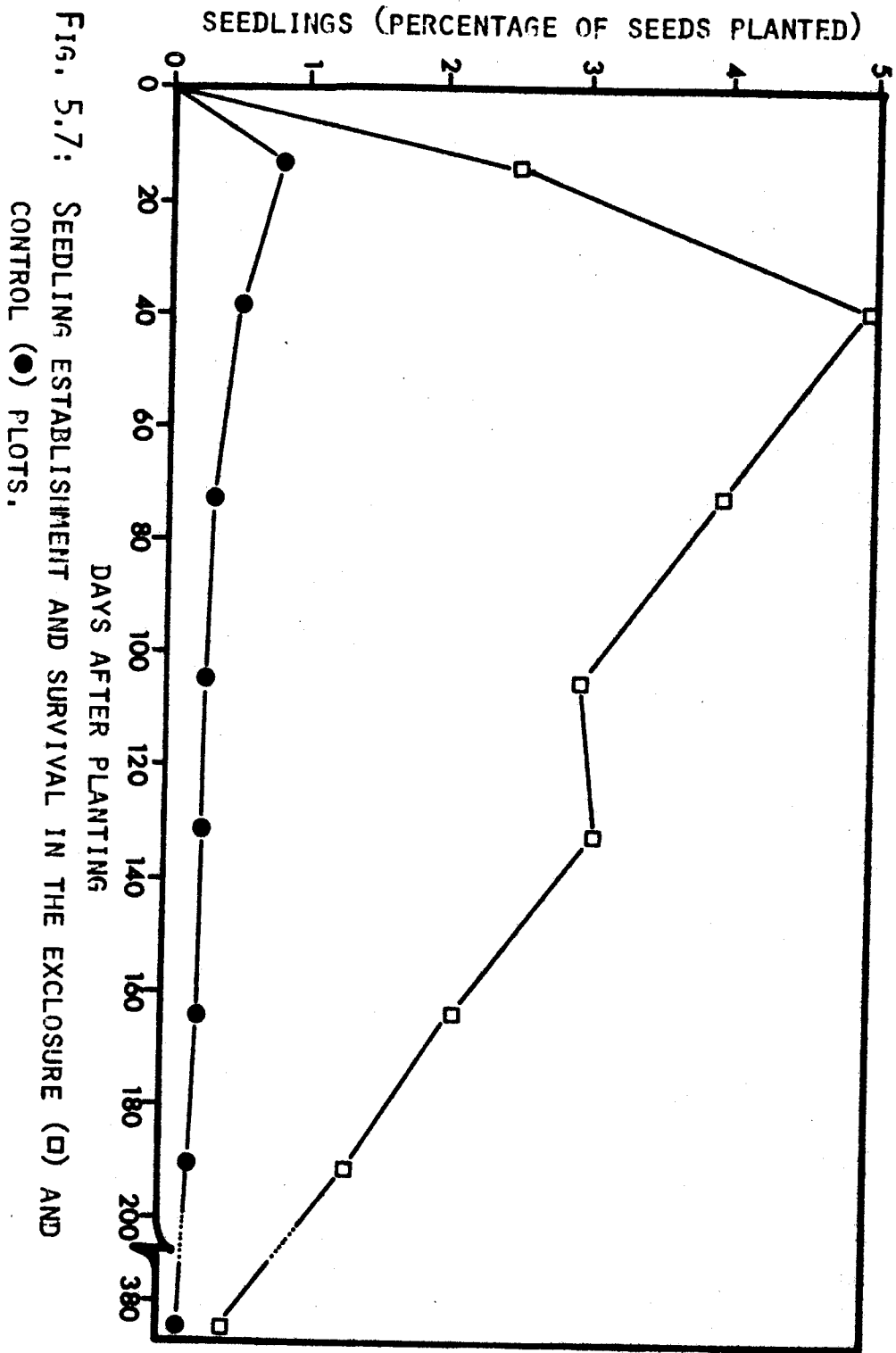
to less than 1 % in the controls. Because of this initial differential, the size of the resultant seedling populations remains significantly higher in the exclosure plots than the control throughout the year, although almost 90 % of the seedlings in the exclosure plots died in the interval.

The disparity in numbers of germinating seedlings between the exclosure and control plots therefore confirms the claim that the intensity of post-dispersal predation is the principal control on the size of the resultant seedling population.

5.3: STAND AGE AND SEEDLING RECRUITMENT.

It has been demonstrated in the previous section that there is a massive decline in the pine population cohorts during their first year of existence. The extent of this decline is not constant in all stands, but varies with successional time. As the stand ages there is a drop-off in pine seedling recruitment (Fig. 4.4), until, in stands which have been undisturbed for 20 - 25 years, very few pine seedlings become established. Data from the control plots in the sample stands confirm this differential recruitment (Fig. 5.8). When seedling establishment rates are graphed as a function of stand age it becomes apparent that:

- a) Maximum recruitment rates are attained in stands of intermediate age (5-15 years) where germination and seedling survival are highest.



- b) Low recruitment rates in younger stands (< 5 years) are a result of pre-germination predation or germination failure.
- c) Low recruitment rates in older stands (> 15 years) are primarily due to high mortality of germinated seedlings, although germination rates in these older stands were somewhat lower than in stands of the 5 - 15 year age-class.

Any attempt to link seedling dynamics to environmental controls must explain these three elements.

The mechanisms that regulate seed germination and seedling survival are a combination of the internal biochemical and physical reactions, and the external environment of the propagule. The external controls include moisture supply, soil compaction and pH, concentration of solutes, oxygen supply, the presence and absence of pathogens, predators, or inhibitory chemicals, and the radiation and light environment of the seed (Toole et al., 1956; Mayer and Poljakoff-Mayber, 1963). In the field these factors interact in a complex and often inextricable fashion. As Harper (1960) points out, sites in which the factors co-occur in the right combinations are not ubiquitous in nature. At the size scale of the seed, the soil surface presents a very complicated pattern of suitable and unsuitable microsites. Moreover, "sites which are temporarily suited for germination of a seed.... may quickly become unsuitable for the establishment of a self-supporting seedling..." (Harper, *ibid.*, p.124).

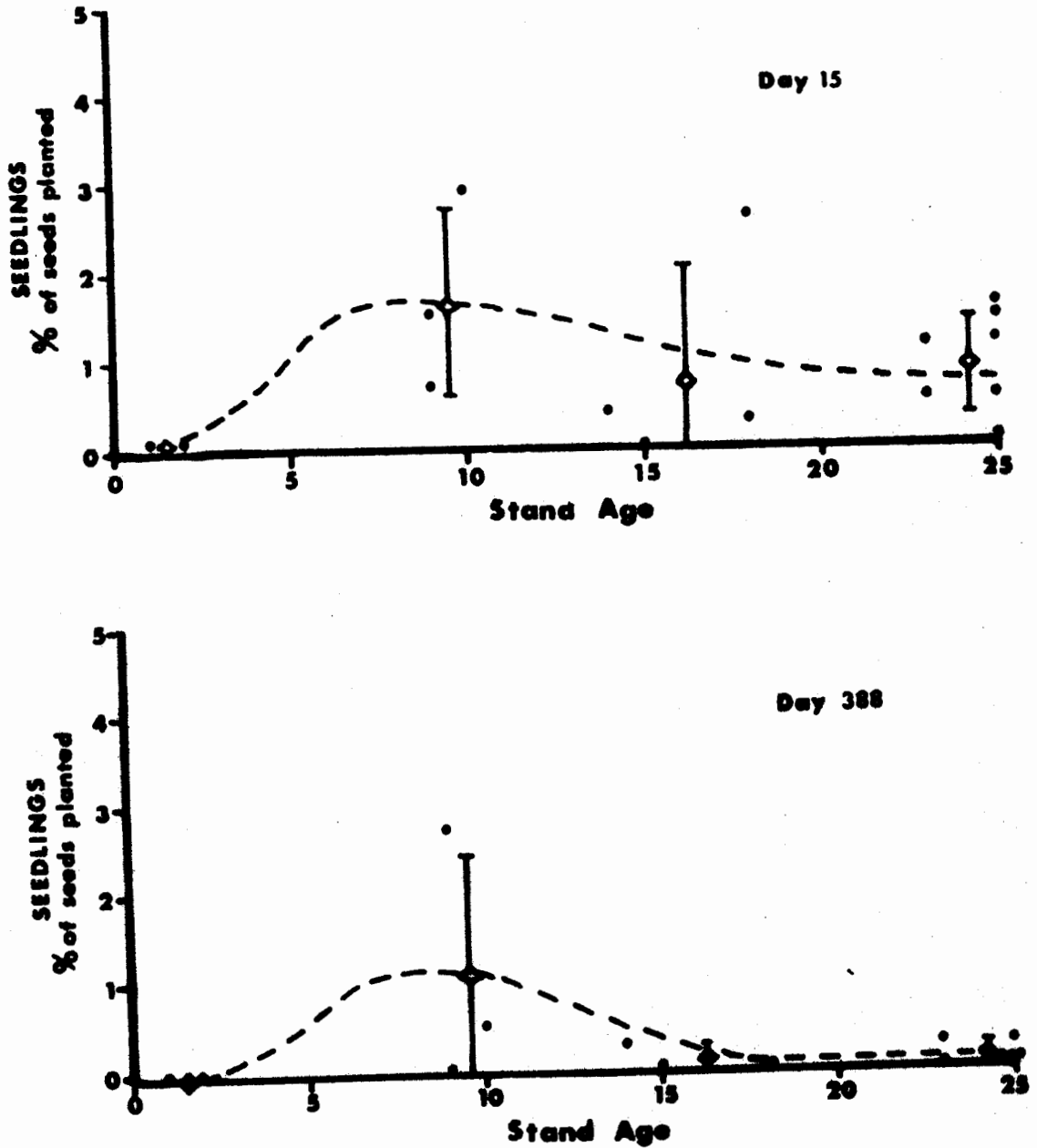


FIG. 5.8: SEEDLING ESTABLISHMENT AS A FUNCTION OF STAND AGE IN THE CONTROL PLOTS. DATA FROM THE FIRST AND LAST CENSUS.

The maximum rates of seedling establishment in stands of intermediate age must therefore represent a situation in which favourable microsites are also maximised. This favourable germination-survivorship time-frame may be causally linked to the co-occurrence of a peak (Fig. 5.9a), plateau (Fig. 5.9b) window (Fig. 5.9c) or trough (Fig. 5.9d) in a state variable. However, as the 'tails' on either side of the favourable time period result from a recruitment failure in the very young stands, and a failure to survive in the oldest stands, it would seem more reasonable to assume that the peak in seedling establishment represents the unilateral or interactive effects of two or more regulatory mechanisms (e.g. Fig. 5.9e).

Five environmental factors in particular may be expected to co-vary as a consequence of autogenic changes accompanying vegetational succession. These are: predator pressure, light and radiation intensity, the nature of the seedbed, root competition, and the intensity of allelopathic interactions between species.

In the following sections the role of these five factors is examined by means of field and laboratory experimentation. The isolation of the field area, constraints of time, and a limited supply of some materials, precluded using a full factorial experimental design to test the effects of these environmental variables.

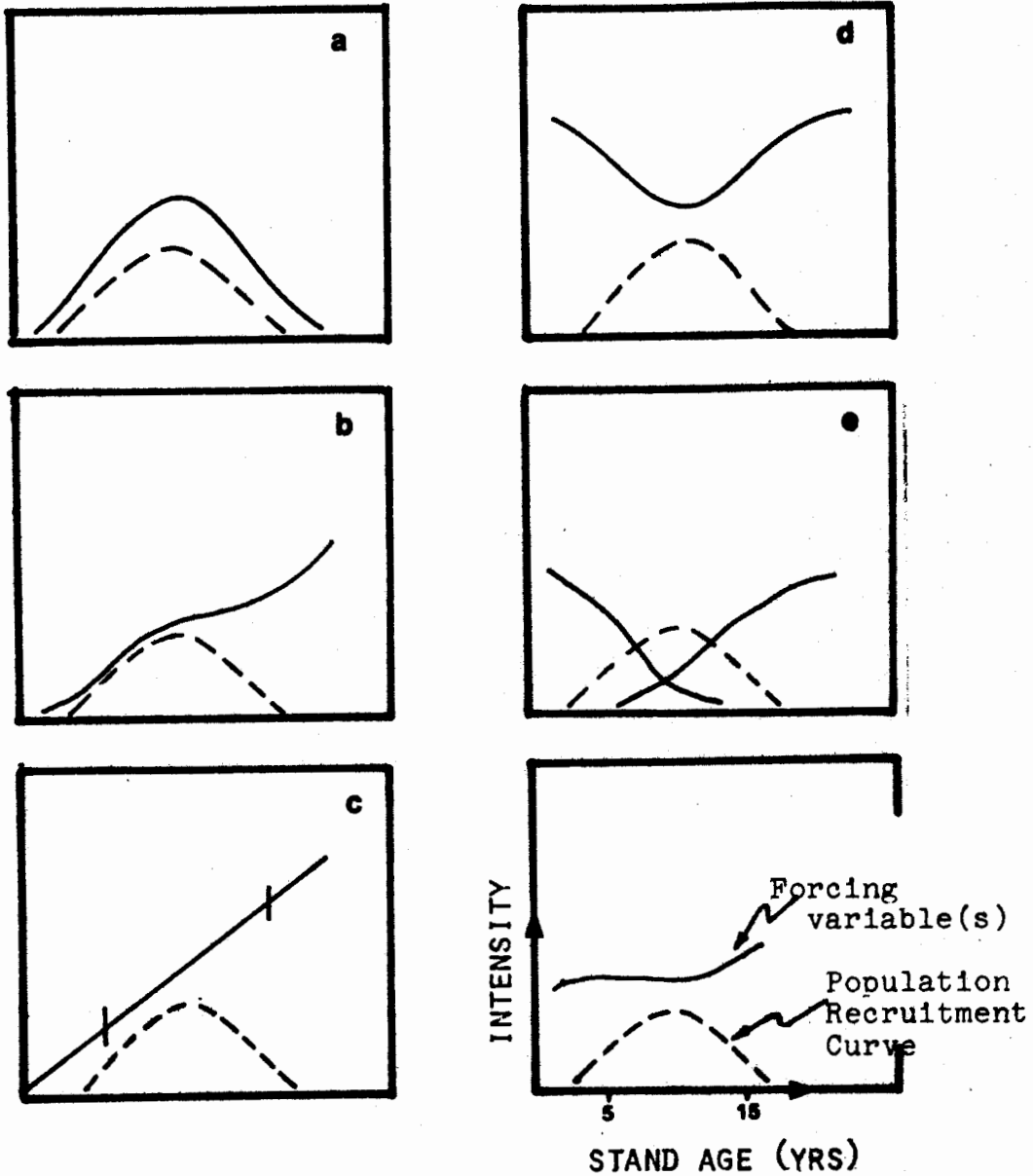


FIG. 5.9: THEORETICAL STATE VARIABLES AND THE RECRUITMENT OF PINE SEEDLINGS - SOME POSSIBLE RELATIONSHIPS.

5.31: Predator Pressure

As post-dispersal seed-harvesting by rodents, birds and insects is known to be the primary regulator of the overall pine seedling population, it was hypothesised that the regeneration failure in the youngest stands was caused by severe seed-predation rates. This postulate requires that the re-occupation of a burnt area by the seed-harvesting fauna is fairly rapid. Although the rapidity of re-invasion depends to a large extent on the area of the burn, data from logged and burned areas of North American forests show that granivorous mammal populations may decline by 50 % immediately after the disturbance (Spencer, 1956), but pre-disturbance population levels are attained or passed a few months later (Tevis, 1956; James, 1956; Gashwiler, 1970).

It is known from laboratory experiments that predator pressure on prey is reduced as the environment searched for prey becomes more complex (Gause, 1934; Huffaker, 1958). In recently burned stands with a bare mineral soil substrate the probability of a seed being found is extremely high. Litterfall and grass regrowth cover this exposed surface and the area to be searched by seed-harvesters becomes much more patchy, so the probability of a seed being found decreases. Consequently, in stands of intermediate age, there may be a higher rate of seedling establishment than in younger stands.

In the oldest stands the reduced germination of pine seed may also result from an increase in the predation rate. One of the consequences of increased shading on the forest floor is a reduction in grass cover in older stands. The loose litter layer in these stands may comprise a more-readily searched environment than that of stands with greater grass biomass. Alternatively, the suite of seed-harvesting organisms themselves may change over successional time, bringing more pressure to bear on the seed resource in the oldest stands.

Two tests of this predation hypothesis were made. If predator pressure is the prime determinant of the differential seedling recruitment in stands of varying age, then seeds protected from macro-predators should exhibit age-invariant germination rates. However, the numbers of seedlings germinating in the exclosure plots show the same age-dependent characteristics as do seedlings in the control plots (Fig. 5.10). To test whether predation is independent of stand age, a G-test of association (Sokal and Rohlf, 1969) was conducted on these germination data. The resultant analysis (Table V.5), indicated that predation rate is independent of stand age. Consequently the seed-predation hypothesis can be dismissed as a cause of differential seedling establishment.

In addition to the pine seeds, the emergent seedlings also represent a food source for herbivores, and it is conceivable that the high mortality rates in the oldest stands are attributable to

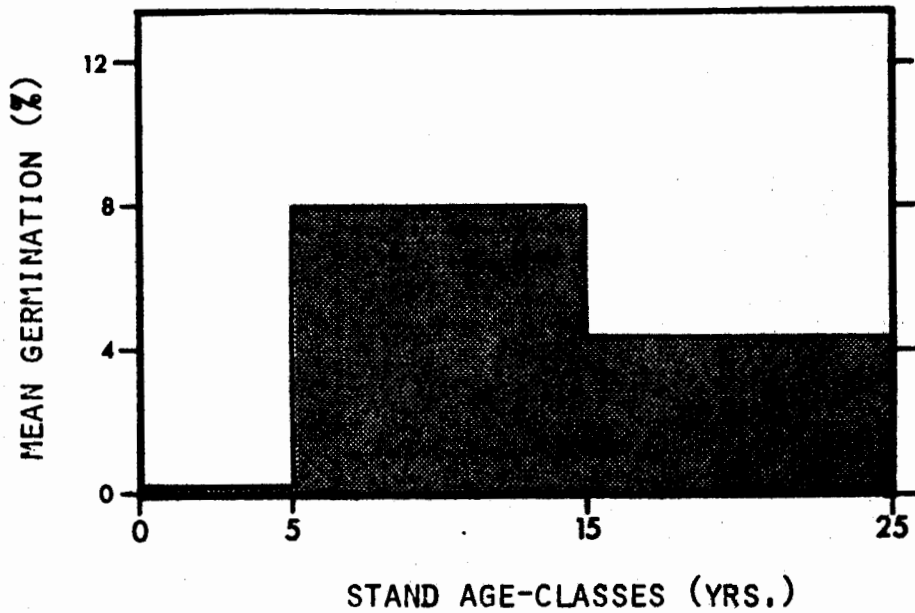


FIG. 5.10: GERMINATION RATES IN EXCLOSURE PLOTS AS A FUNCTION OF STAND AGE. DATA DERIVED FROM A CENSUS OF THE EXCLOSURE PLOTS 39 DAYS AFTER SOWING, THE DAY OF MAXIMUM SEEDLING EMERGENCE IN THE EXCLOSURE PLOTS.

TABLE V.5: G-TEST OF ASSOCIATION BETWEEN THE INTENSITY OF SEED-PREDATION AND STAND AGE.

H₀: That there is no difference in seed-predation rates (and therefore the proportionate germination in control and exclosure plots), with stand age.

Treatments (a=2)
Categories (b=3)

| Stand Age | Control Plots | Exclosure Plots | Row Sum | Control/Total |
|-------------|---------------|-----------------|---------|---------------|
| < 5 Yrs. | 1 | 2 | 3 | 0.33 |
| 5 - 15 Yrs. | 85 | 78 | 163 | 0.52 |
| > 15 Yrs. | 111 | 88 | 199 | 0.56 |
| Column Sum | 197 | 168 | 365 | 0.54 |

$$G = 2 \left[\sum_{i=1}^b \sum_{j=1}^a f_{ij} \ln f_{ij} - \left(\sum_{j=1}^b \left(\sum_{i=1}^a f_{ij} \right) \ln \left(\sum_{i=1}^a f_{ij} \right) \right) - \left(\sum_{i=1}^a \left(\sum_{j=1}^b f_{ij} \right) \ln \left(\sum_{j=1}^b f_{ij} \right) \right) + n \ln n \right]$$

$$= 2 [1635.598 - 1886.945 - 1901.617 + 2153.463]$$

$$= 2 [0.499]$$

$$= 0.998$$

$$df = (a-1)(b-1) = 2$$

Since $\chi^2_{0.05}(2) = 5.991$, the G value is not significant,

and the null hypothesis (H₀) is accepted.

this cause. A census of recently-emerged seedlings (15 days after sowing), showed that some 13 % exhibited herbivore damage. This took the form of severance of the stem immediately above the ground or at the base of the cotyledons. Cutworms (Noctuidae), and leaf-cutting ants (Atta spp.), feed in this fashion on planted pine seedlings elsewhere (Wormald, 1975; Weber, 1972), but I never observed either to feed on pine in Belize. This type of damage may also be caused by molecrickets (Gryllotalpinae), and Lamb (1973), notes the necessity of protecting pine nursery beds from these insects in Belize.

Although these predators are all generalists, and presumably fairly ubiquitous in the pinelands, the seedlings in the oldest stands exhibited predation rates which were almost twice as great as those in stands between 5 and 15 years of age. This difference proved to be statistically significant (Table V.6), and may be the primary reason for the low seedling survivorship in the older stands. There is, however, no evidence to indict larger herbivores such as deer (Odocoileus truei) or cattle as predators of pine seedlings, as mortality rates of seedlings were somewhat greater in the enclosure plots than in the control plots (Fig. 5.7).

5.32: Allelopathic Interactions

The suppression of higher plants by substances released from the live or dead tissues of other species has been reported for

TABLE V.6: BINOMIAL TEST ON THE DIFFERENCES BETWEEN NUMBERS OF SEEDLINGS DAMAGED BY HERBIVOROUS INSECTS IN INTERMEDIATE-AGED AND OLD STANDS.

Ho: That there is no significant increase in herbivory rates with increasing stand age. (1-tailed test).

| Stand Age | # Seedlings Alive (N) | # Seedlings eaten (A) | % eaten (p) |
|-----------|-----------------------|-----------------------|--------------------|
| 5-15 Yrs. | 131 | 11 | 8.40 |
| >15 Yrs. | 224 ^o | 34 ^o | 15.17 ^o |

$$\text{Pooled } p = (A + A') / (N + N') = 45/355 = 12.676 \%$$

$$\text{Pooled } s^2 = 12.676 (87.324) = 1106.92$$

$$s_p^2 = 1106.92/131 = 8.45$$

$$s_{p'}^2 = 1106.92/224 = 4.94$$

$$s_d^2 = 8.45 + 4.94 = 13.39$$

$$s_d = 3.66$$

$$x^* = 1.84$$

Since $x_{0.05}^* = 1.64$, the difference in herbivory rates is significant, and the null hypothesis (Ho) rejected.

cultivated and wild species in various communities (e.g. Muller, 1965; Cannon et al., 1967; del Moral and Muller, 1969). Germination of two species of pine, *P. banksiana* (Brown, 1967) and *P. densiflora* (Ooyama, 1954), is known to be inhibited by allelochemic suppression by associated species and by autotoxicity. In successional communities an invader may suppress a competitor, and delay its own replacement, by means of allelochemicals (Rice, 1969). It is proposed therefore as a working hypothesis that species occurring with *P. caribaea*, particularly arborescent species (including *P. caribaea* itself), exclude young pine from the stands older than 15 years by allelopathic inhibition. In the youngest stands the potential allelopathic species are too infrequent and small to affect the germination or survivorship of young pine. (Fig. 4.7). This section therefore deals only with the relative importance of allelopathy in stands in the two older age-classes. The hypothesis can be examined by growing pine seeds on media supplied with aqueous extracts of tissues (in this case of the leaves) of selected species, and testing for the presence of allelochemicals. No test was made for the presence of volatile inhibitors.

A total of twelve species were chosen for testing, representing not only the most frequent species in the pinelands, but also a cross-section of the plant families which are important members, or potential invaders, of the pinelands. The

species used are listed below:

- Byrsonima crassifolia (Malpighiaceae)
- Miconia albicans (Melastomataceae)
- Clidemia rubra (Melastomataceae)
- Vismia ferruginea (Hypericaceae)
- Miconia belizensis (Melastomataceae)
- Eupatorium odoratum (Compositae)
- Quercus purulhana (Fagaceae)
- Pinus caribaea (Pinaceae)
- Xylopia frutescens (Anonaceae)
- Clethra hondurensis (Clethraceae)
- Davilla kunthii (Dilleniaceae)
- Quercus oleoides (Fagaceae)
- Calliandra houstoniana (Leg: Mimosidae)

5.321: Experiment 1. Sponge bioassay

Fifty grams of air-dried leaves of each species were soaked in 100 gms. of distilled water at 20° C. The solution was then mechanically shaken for 20 minutes and left to soak for 24 hours. The leachates were then collected using Buchner funnels. The osmotic potential of each was determined by the method of freezing-point depression using a Precision Systems Osmette. These readings were repeated until the difference between successive readings was less than 2 milliosmos. The final values obtained for each extract are included in Table V.7. Control solutions of mannitol were prepared with osmotic potentials of

TABLE V.7: GERMINATION AND RADICLE EXTENSION IN LABORATORY ALLELOPATHY EXPERIMENT.

| Treatment | a | b | c | d | e |
|-------------------------------|----|----|---------|--------|-----|
| <i>Byrsonima crassifolia</i> | 2 | 0 | 4.4 ** | 8.63 | 35 |
| <i>Pinus caribaea</i> | 12 | 21 | 50.0 | 12.48 | 2 |
| <i>Miconia albicans</i> | 14 | 21 | 58.3 | 19.85 | 3 |
| <i>Xylopia frutescens</i> | 6 | 0 | 13.3 ** | 8.50 | 30 |
| <i>Clidemia rubra</i> | 13 | 32 | 100.0 | 18.07 | 75 |
| <i>Clethra hondurensis</i> | 3 | 0 | 6.6 ** | 7.25 | 50 |
| <i>Vismia ferruginea</i> | 7 | 0 | 15.5 ** | 10.84 | 17 |
| <i>Davilla kunthii</i> | 6 | 1 | 13.6 ** | 6.46 | 74 |
| <i>Miconia belizensis</i> | 20 | 17 | 71.4 | 21.88 | 54 |
| <i>Quercus oleoides</i> | 3 | 4 | 7.3 ** | 15.98 | 23 |
| <i>Eupatorium odoratum</i> | 1 | 0 | 2.2 ** | 5.40 | 2 |
| <i>Calliandra houstoniana</i> | 5 | 5 | 12.5 ** | 7.53 | 120 |
| <i>Quercus purulhana</i> | 2 | 0 | 4.4 ** | 1.99 * | 25 |
| Mannitol #1 | 8 | 28 | 47.1 | 9.26 | 0 |
| Mannitol #2 | 4 | 33 | 33.3 | 6.75 | 10 |
| Mannitol #3 | 4 | 36 | 44.4 | 5.40 | 50 |
| Mannitol #4 | 2 | 40 | 44.0 | 8.50 | 100 |

a = # seedlings germinated

b = # seeds infected by fungus

$c = (a / (n - b)) \cdot 100$
 where n = # seeds planted

d = mean radicle length (mm.)

e = osmotic potential of extracts (milliosmos)

** = significant inhibition of germination (p=0.01)

* = significant inhibition of growth (p = 0.05)

10, 50, and 100 milliosmcs respectively (see del Moral and Cates, 1971).

Cellulose sponges soaked in 40 ml of either the mannitol control or the leachate were placed in Petri dishes. Each experimental treatment was planted with 15 sound seeds of P. caribaea per dish, with 3 replicates per treatment, and the dishes were placed at random under an array of Coolwhite fluorescent lamps set on a 12-hour photoperiod at an intensity of 3000 ft-c. Germination and radicle extension of the seeds were then recorded over a three-week period.

Because of the high relative humidities in each of the Petri plates many seeds were infected by fungal pathogens, which were presumably dormant in the seedcoat. The mannitol controls and the three extracts from Melastomataceae were particularly susceptible to attack. Germination was measured on day 18 and again on day 23 when the experiment terminated. Hypocotyl extension was estimated at the end of the experiment. The results of the experiment are recorded in Table V.7. There is a positive correlation between the number of uninfected seedlings that germinate, and the number of seeds infected with fungus in the extract treatments, strong circumstantial evidence of the presence of antibiotic substances in some leachates.

The hypothesis that there is no difference in germination rates between treatments and controls can be tested using

Chebyshev's inequality (Dixon and Massey, 1957). This states that the maximum area under any symmetric, unimodal distribution curve which is $> k$ standard deviations from the mean is $< (2/3k)$. As there is no apparent decline in the germination rates of uninfected seed in the controls, these values were pooled. This produced a distribution for the control with mean germination rates of 41.9 % and a standard deviation of 6.1 %. Taking a rejection region of $p=0.05$ the critical value for k is then 3.0 ($p=0.0494$), which is equivalent to a germination rate of 24.1 %. Consequently any treatment having a germination rate < 24.1 % is significantly different from the controls. Nine of the tested species showed significant inhibitory effects (Table V.7). These were:

Xylopia frutescens
Quercus oleoides
Quercus purulhana
Byrsonima crassifolia
Clethra hondurensis
Calliandra houstoniana
Vismia ferruginea
Eupatorium oderatum
Davilla kunthii

To test the hypothesis that the leaf extracts inhibit radicle extension, the sample means of the control and experimental populations can be compared using the

t-distribution. Tests between the mannitol controls utilising log-normalised data indicated no significant decrease in hypocotyl length with increased osmotic potential ($t_{max}=1.86$, $df=6$; n.s. at $p=0.05$). The control results were therefore pooled. Examination of the relationship between osmotic potential and radicle elongation reveals little correlation between the two variables (Fig. 5.11). Eight of the test species recorded mean radicle extension less than the controls, and these were tested in turn. Of the eight, only one (Quercus purulhana, the deciduous oak) was found to produce significant inhibition of pine seedling growth at a $p=0.05$ level (Table V.7).

5.322: Experiment 2: Field bioassay

Because of the marked fungal infection of the laboratory cultures, the experiment was repeated in the field at a later date, using the same species with the exception of Miconia belizensis. In this second experiment 1.35 kg of air-dried leaves of each species were soaked in a 1:5 solution of tap-water for 24 hours. Clean sand from the local river was spread to a depth of 4.5 cms in aluminium seedpans and 33 seeds were planted in each pot with three replicates for each treatment (#3 with 34 seeds).

The experiment was initially established on the ground, but mice and insects removed many of the seeds, and rain periodically flooded the pans, so it was re-established under cover of the

MEAN RADICLE EXTENSION PER TREATMENT (MM.)

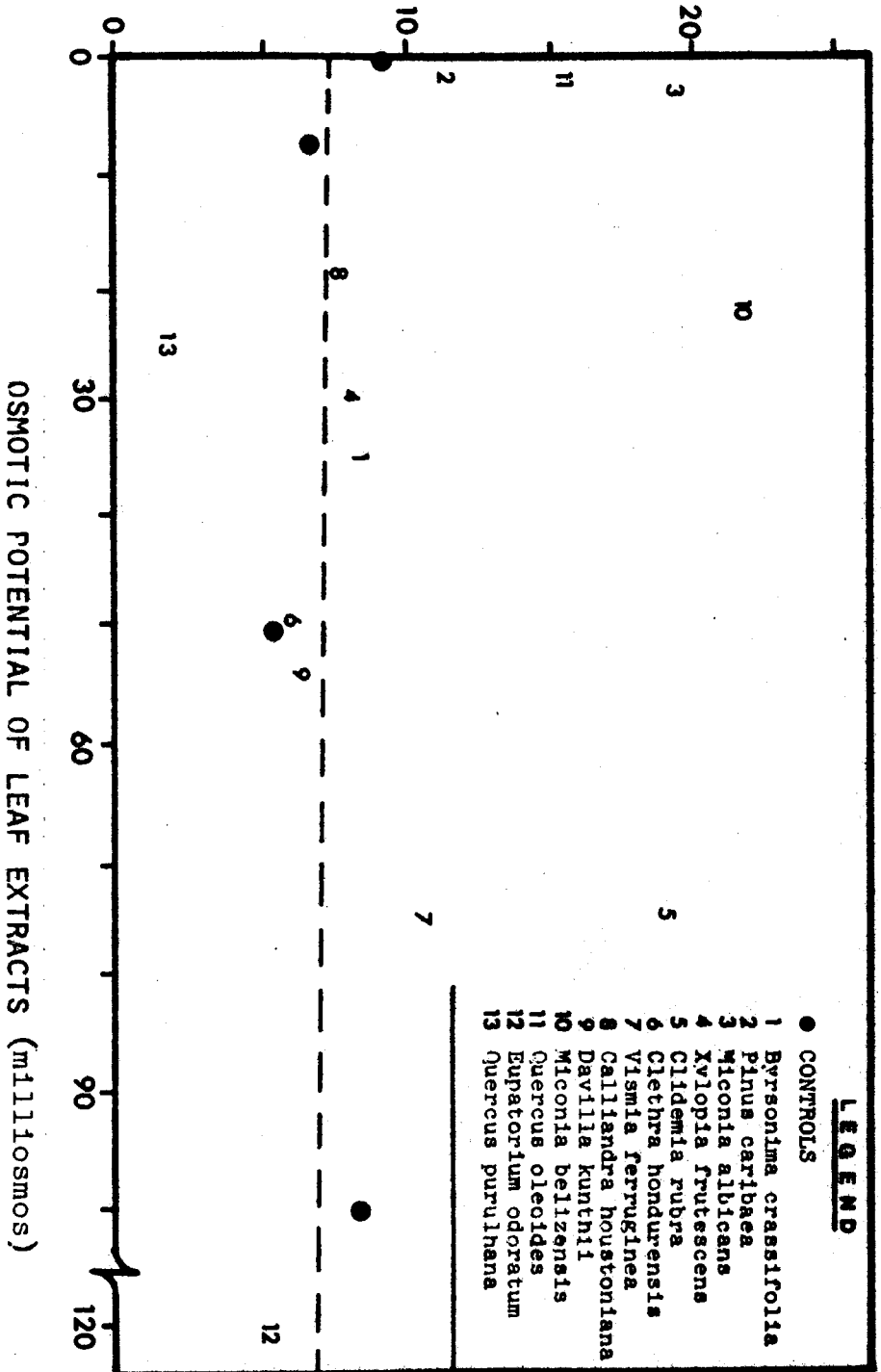


FIG. 5.11: ALLELOPATHIC POTENTIAL OF TREES AND SHRUBS IN THE FLORA OF MOUNTAIN PINE RIDGE.

seed-drying sheds of the Forestry Department at Augustine. These protected the seeds from predators and rain, and provided some shade (midday light intensity ~ 3000 ft.-c.). The pans were watered with 250 ml of the extract at two-day intervals, and the course of germination was followed for a one-month period.

Germination began on day 9 and the total number of seedlings reached maximum levels some 4 to 14 days later, with almost all treatments peaking on day 15. The number of live seedlings declined steadily from this point onwards (Fig. 5.12). No fungal infection of the seedcoats was recorded. The hypothesis of no significant difference ($p=0.05$) between the control and treatment populations was tested using the t-distribution (Table V.8). Of the species tested, one (Eupatorium odoratum), produced significant inhibition, and two (Xylopia frutescens and Vismia ferruginea) were mildly inhibitory, with t-values on the verge of statistical significance. All three of these species were also significant inhibitors in the laboratory experiment. This second experiment does not support the claim of significant inhibition of germination by Byrsonima, Clethra, Davilla, Calliandra or the two oak species. Because of these ambiguous results only Eupatorium, Xylopia, Vismia and O. purulhana, which inhibited seedling growth in the laboratory experiment, can be considered as potential allelochemic species.

Although all four potential allelopathic species increase in size and density with successional time, the increase from the

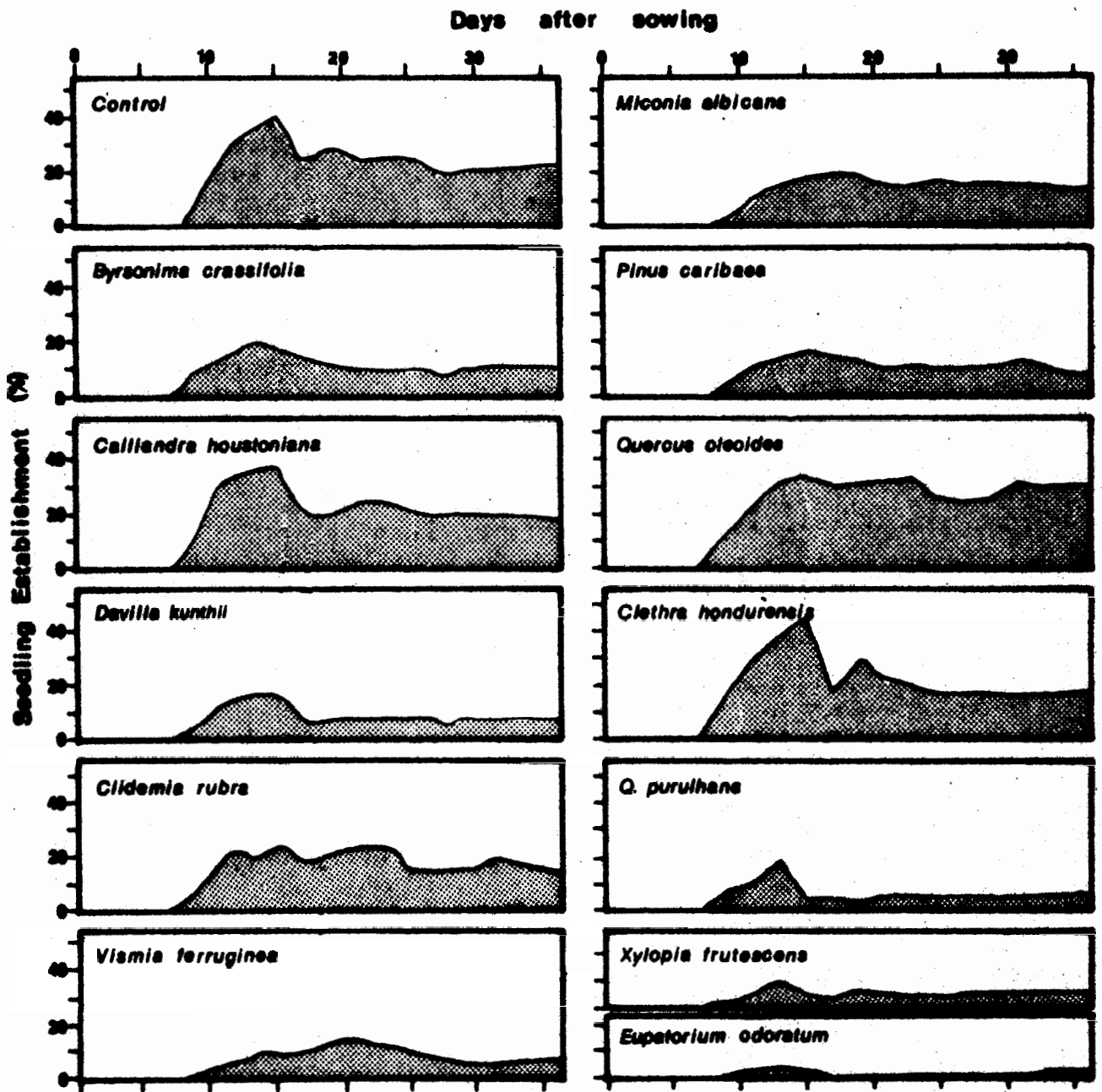


FIG. 5.12: COURSE OF SEEDLING ESTABLISHMENT AND SURVIVAL IN THE ALLELOPATHY EXPERIMENT IN THE FIELD.

TABLE V.8: "T"-TEST ON THE RESULTS OF THE FIELD ALLELOPATHY EXPERIMENT (Augustine, 27/7/74 - 31/8/74).

Day 15: # seeds germinated

| Treatment | # Germinated /Replicate | Mean | Var. | "t"-value |
|------------------------|-------------------------|------|------|-----------|
| Byrsonima crassifolia | 6 10 2 | 6.0 | 16.0 | 1.62 |
| Pinus caribaea | 11 4 3 | 6.0 | 19.0 | 1.59 |
| Miconia albicans | 11 4 3 | 6.0 | 19.0 | 1.59 |
| Xylopia frutescens | 3 4 0 | 2.3 | 4.3 | 2.73 * |
| Clidemia rubra | 4 13 6 | 7.7 | 22.3 | 1.18 |
| Clethra hondurensis | 12 19 13 | 14.7 | | |
| Vismia ferruginea | 3 3 3 | 3.0 | 0.0 | 2.68 * |
| Davilla kunthii | 2 8 3 | 4.3 | 10.3 | 2.10 |
| Quercus oleoides | 8 13 12 | 11.0 | 7.0 | 0.29 |
| Eupatorium odoratum | 2 2 0 | 1.3 | 1.3 | 3.08 ** |
| Calliandra houstoniana | 15 13 9 | 12.3 | 9.3 | 0.24 |
| Quercus purulhana | 2 8 8 | 6.0 | 8.0 | 1.75 |
| Control | 6 15 19 | 13.3 | 44.3 | |

** = significant at $p=0.05$ level

* = marginally significant

intermediate age stands to the oldest stands is not statistically significant (Table V.9), when analysed by the Mann-Whitney U-test. Consequently the hypothesis of allelopathic inhibition can be dismissed. However, it should be noted that all of these allelopathic species may have an inhibitory effect on pine establishment in the savanna - forest ecotone, where they are particularly common.

5.33: Shading

The availability of light to pine seeds and seedlings in stands of differing age depends upon the amount of shading by opaque elements such as branches, and selective transmission by the foliage, which includes all the various canopy strata, from that of hardwoods and pines, down to the shrub and herbaceous layers. Whereas plants have evolved various geometries and photosynthetic strategies to deal with the ambient light environment, seeds and young seedlings are entirely at the mercy of the light conditions in their submicroenvironment.

It is postulated that the differential seedling establishment of *Pinus caribaea*, both the failure to germinate in recently-burned stands, and failure to survive in the old stands, derives from changes in the light climate over successional time. Kozlowski (1971), reports that seeds of *Pinus* spp. will germinate at light intensities above 5 lux (0.5 foot-candles). The illumination in the open in the study area usually attains

TABLE V.9: MANN-WHITNEY U-TEST ON THE ASSOCIATION BETWEEN THE RELATIVE IMPORTANCE OF POTENTIALLY ALLELOPATHIC SPECIES AND STAND AGE.

H₀: That there is a significant increase in the basal-area or % cover of potentially allelopathic species with stand age (1-tailed test).

| Species Name | Eupatorium odoratum (shrub) | | Vismia ferruginea (shrub) | | Davilla kunthii (vine) | | Quercus purulhana (shrub) | | Quercus purulhana (tree) | |
|---------------|-----------------------------|---------|---------------------------|---------|------------------------|---------|---------------------------|---------|--------------------------|---------|
| | 5-15 yrs | >15 yrs | 5-15 yrs | >15 yrs | 5-15 yrs | >15 yrs | 5-15 yrs | >15 yrs | 5-15 yrs | >15 yrs |
| Ranked | 7 | 7 | 6.5 | 6.5 | 6 | 6 | 4 | 4 | 4 | 4 |
| Cover | 7 | 7 | 6.5 | 6.5 | 6 | 6 | 4 | 4 | 4 | 4 |
| or | 7 | 7 | 6.5 | 6.5 | 6 | 6 | 4 | 8 | 4 | 8 |
| Basal-area | 7 | 7 | 6.5 | 6.5 | 6 | 6 | 12 | 9 | 11 | 9 |
| | | 7 | | 6.5 | | 6 | | 10 | | 10 |
| | | 7 | | 6.5 | | 12 | | 11 | | 12 |
| | | 7 | | 13 | | 13 | | 13 | | 13 |
| | | 14 | | 14 | | 14 | | 14 | | 14 |
| | | 15 | | 15 | | 15 | | 15 | | 15 |
| R1 | 35 | | 32.5 | | 30 | | 28 | | 27 | |
| R2 | 85 | | 87.5 | | 90 | | 92 | | 93 | |
| U-value | 20 | | 17.5 | | 15 | | 13 | | 12 | |
| Signif. Level | N.S. | | N.S. | | N.S. | | N.S. | | N.S. | |

$$U = (n_1)(n_2) + n_2(n_2+1)/2 - R_2; \quad n_1 = 5, n_2=10$$

Since $U_{.05} \leq 11$ for $n_1=5, n_2=10$, all computed values are not significant, and the null hypothesis (H₀), is rejected.

intensities $> 100,000$ lux ($\sim 10,000$ foot-candles) at solar-noon, and it is conceivable that the seeds of P. caribaea may be inhibited by long periods of exposure to such high intensities of blue and far-red light. It is hypothesised therefore that the high light levels are detrimental to the germination success of P. caribaea in the youngest stands. The closure of the pine canopy results in increased shade on the forest floor in older stands. It is therefore further postulated that seedlings of P. caribaea are shade intolerant and that increased shade is the cause of the high seedling mortality in the oldest stands.

The light climate on the forest floor is highly variable in time and space, and it is consequently extremely difficult to quantify precisely the light environment of a seed or seedling population, except in very general terms. As well as fluctuating in quantity, the woodland light environment also changes in quality. Not only is the light under a forest canopy depleted in blue and red wavelengths, but the red - far-red ratio is also modified, which directly influences the germinative ability of the seed (Koller et alia, 1962).

5.331: Experiment 1. Light Intensity as a function of Stand Age.

The contention that germination failure in the youngest stands is a product of high light intensity requires as a first condition that light levels are significantly higher in these stands than in stands between 5 and 15 years of age. The

measurement of stand light climate was described in Chapter Four. A comparison of the relative light levels in these stand age-classes by the Kolmogorov-Smirnov two-sample test (Table V.10), revealed that the differences were not statistically significant. This hypothesis can therefore be dismissed. However, a comparison of light levels in stands of intermediate age with those in older (> 15 years) stands by the same technique (Table V.11) demonstrated a significant difference between the two groups. Consequently two further experiments were performed to attempt to disprove the shading hypothesis, one in the field, the other in the laboratory.

5.332: Experiment 2. The Light Climate of Established Seedling Populations.

The light levels (in foot-candles), above each seedling < 2 m. in height (up to a maximum of 25 seedlings per site) were measured and compared to the overall stand light conditions. If light levels become limiting for seedling establishment as the stand ages, then there should be a gradual divergence in the light environment of the established seedling population and that of the stand in general. In other words, the seedling population will become limited in its spatial distribution to a few favourable microsites in which light levels are sufficiently above some threshold value (the compensation point) to promote vigorous growth. These favourable microsites will presumably consist of those patches of the forest floor beneath holes in the

TABLE V.10: KOLMOGOROV-SMIRNOV TEST ON LIGHT LEVELS IN STANDS OF < 5 YEARS OF AGE COMPARED TO STANDS OF 5 - 15 YEARS OF AGE.

Ho: That light levels in stands of less than 5 years are not significantly greater than those in stands of 5 - 15 years (1-tailed test).

| Cumulative Frequency Data | | | | | |
|---------------------------|----------------|--------|--------|--------|-----|
| Stand Age | Foot - Candles | | | | |
| | < 500 | < 2000 | < 4000 | < 8000 | |
| < 5 yrs. | 0 | 0 | 0 | 0 | 50 |
| 5-15 yrs. | 0 | 0 | 1 | 10 | 125 |
| Sn1(x) - Sn2(x) | 0 | 0 | -0.008 | -0.080 | 0 |

$$D = \max [S_{n1}(x) - S_{n2}(x)] = 0.080$$

$$\chi^2 = 4 \cdot D^2 \cdot ((n1)(n2) / (n1 + n2))$$

$$= 4 (0.08)^2 \cdot (35.714)$$

$$= 0.914$$

$$df = 2$$

Since $\chi^2_{0.05(2)} = 5.99$, the D value is not significant, and the null hypothesis (Ho) is accepted.

TABLE V.11: KOLMOGOROV-SHIRNOV TEST ON LIGHT LEVELS IN STANDS OF > 15 YEARS OF AGE COMPARED TO STANDS OF 5 - 15 YEARS OF AGE.

Ho: That light levels in stands of more than 15 years are not significantly less than those in stands of 5 - 15 years (1-tailed test).

Cumulative Frequency Data

| Stand Age | Foot - Candles | | | | |
|-----------------|----------------|--------|--------|--------|-----|
| | < 500 | < 2000 | < 4000 | < 8000 | |
| 5-15 yrs | 0 | 0 | 1 | 10 | 125 |
| > 15 yrs. | 3 | 22 | 43 | 87 | 250 |
| Sn1(x) - Sn2(x) | -0.012 | -0.088 | -0.164 | -0.268 | 0 |

D = max [sn1(x) - Sn2(x)] = 0.268

= 4 D ((n1) (n2) / (n1 + n2))

= 4 (0.268) (83.333)

= 23.941

df = 2

Since = 13.82, the D value is significant, and the null hypothesis (Ho) is rejected:

canopy, and which form the higher mode of radiation intensities graphed in Fig. 4.11. Furthermore, as the stand ages, the number of such favourable microsites should decline, and so will the seedling population.

If the data from all the stands in each age-category are accumulated the Kolmogorov-Smirnov two-sample test can be employed to compare the magnitude of the differences between the randomly sampled light population, and the light climate above seedlings. The results of the tests are presented in Tables V.12 and V.13. No significant differences in these data could be detected in either the 5 - 15 year age-group or the older stands. Consequently the light climate in these stands does not limit pine seedling establishment. A laboratory experiment was undertaken to confirm these results, and to determine the exact form of the relationship between germination, seedling performance and low light intensities.

5.333: Experiment 3. Germination and Mortality of P. caribaea populations as a function of Light Intensity.

The experiment was set up using two PS Model 802 incubators equipped with a series of cool-white fluorescent lamps. The seedbeds for the experiment were prepared by half filling plastic pots of 7.5 cm. depth and 58 sq. cm. surface area with vermiculite, and then adding an equal amount of bulked and sterilized surface soil from the study area to each pot. The soil in each pot was kept moist by bottom-watering. Vertical

TABLE V.12: KOLMOGOROV-SMIRNOV TEST ON LIGHT LEVELS IN STANDS OF 5-15 YEARS OF AGE COMPARED TO LIGHT LEVELS ABOVE SEEDLINGS.

H_0 : That light levels in stands of 5 - 15 years of age are not significantly less than those above seedlings in the same stands (1-tailed test).

| Cumulative Frequency Data | | | | | |
|---------------------------|----------------|--------|--------|--------|-----|
| | Foot - Candles | | | | |
| | < 500 | < 2000 | < 4000 | < 8000 | |
| Stand Sample | 0 | 0 | 1 | 10 | 125 |
| Seedling Sample | 0 | 0 | 1 | 9 | 121 |
| $S_{n1}(x) - S_{n2}(x)$ | 0 | 0 | 0 | 0.006 | 0 |

$$D = \max [S_{n1}(x) - S_{n2}(x)] = 0.006$$

$$\chi^2 = 4 \cdot D^2 \cdot ((n1)(n2)/(n1 + n2))$$

$$= 4 \cdot (0.006)^2 \cdot (61.484)$$

$$= 0.009$$

$$df = 2$$

Since $\chi^2_{0.05[2]} = 5.99$, the D value is not significant, and the null hypothesis (H_0) is accepted.

TABLE V.13: KOLMOGOROV-SMIRNOV TEST ON LIGHT LEVELS IN STANDS OF > 15 YEARS OF AGE COMPARED TO LIGHT LEVELS ABOVE SEEDLINGS IN THE SAME STANDS.

H₀: That light levels in stands of > 15 years of age are not significantly less than those above seedlings in the same stands (1-tailed test).

Cumulative Frequency Data

| | Foot - Candles | | | | |
|-----------------|----------------|--------|--------|--------|-----|
| | < 500 | < 2000 | < 4000 | < 8000 | |
| Stand Sample | 3 | 22 | 43 | 87 | 250 |
| Seedling Sample | 1 | 2 | 6 | 29 | 131 |
| Sn1(x) - Sn2(x) | 0.004 | 0.073 | 0.126 | 0.127 | 0 |

$$D = \max [S_{n1}(x) - S_{n2}(x)] = 0.127$$

$$\chi^2 = 4 \cdot D^2 \cdot ((n1)(n2)/(n1 + n2))$$

$$= 4 \cdot (0.127)^2 \cdot (85.958)$$

$$= 5.55$$

$$df = 2$$

Since $\chi^2_{0.05[2]} = 5.99$, the D value is not significant, and the null hypothesis (H₀) is accepted.

placement of the experimental pots produced stratified light levels in the incubators with values from top to bottom of:

Incubator 1. 2000 ft-c.
1000 ft-c.

Incubator 2. 500 ft.c.
250 ft-c.

The incubators were programmed for a 12 hour photoperiod (0600 - 1800 hours), a daytime (0800 - 1730 hours) temperature of 30°C and a nighttime temperature of 20°C. These values are based on the diurnal regime encountered in the study area in the early part of the wet season. After soaking in distilled water for 18 hours, five seeds were planted in each pot, with six replicates per treatment.

Germination commenced on the tenth day after sowing, and was most rapid in the low light treatments. The number of germinated seedlings stabilised at some 40 - 45 % of the original seed population after 20 - 25 days in the 250 and 500 ft-c. treatments, with the higher light intensity treatments stabilising at the same level some 5 - 10 days later (Fig. 5.13). Cotyledons were exposed three to four days after germination commenced, and the seed-coat was shed after another three day interval, with primary needle elongation commencing on or about the seventeenth day.

No mortality was recorded at light intensities above 500 ft-c., but 12.75 % of the seedlings that germinated died in the

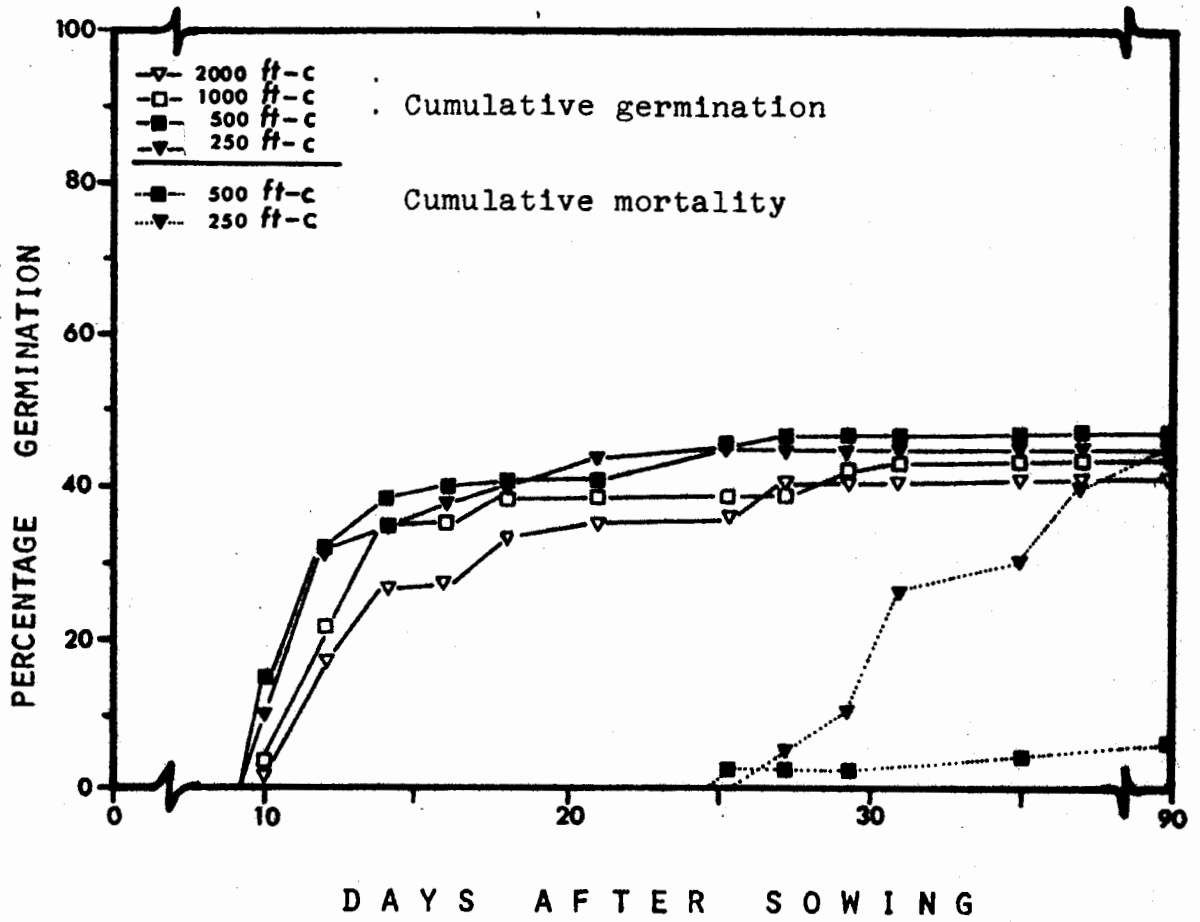


FIG. 5.13: SEEDLING ESTABLISHMENT AND MORTALITY AS A FUNCTION OF LIGHT INTENSITY.

500 ft-c. treatment over the course of the three-month experimental period, and all the seedlings at the 250 ft-c. level died. Vigorous seedlings began to develop primary needles some 17 days after germination, and the seedlings had by then passed from an independent existence where their food supply came from seed reserves, to an autotrophic state. In the 250 ft-c. treatment the cotyledons and the few primary needles that appeared showed signs of wilting at this time, even though the soil surface remained moist throughout the experiment. Over the next week signs of wilting and etiolation became more pronounced, and most seedlings died in this period.

Germination was uniform in all four treatments in the experiment. Therefore we can conclude that light intensity per se does not control the level of germination. However at light intensities below 1000 ft.-c. there is an increasing probability of seedling mortality. Of the 250 light readings taken in the field in the oldest stands, less than 2 % fell below this threshold, and therefore shading can only play a very minor role in the dynamics of the first-year seedling population in stands up to 25 years of age. This is further borne out by the results of the analysis to test the homogeneity of the general light climate in the woodlands with that of the seedling population. Older seedlings may react somewhat differently from first-year seedlings because of self-shading of secondary needle clusters. This may result in lowered growth and survivorship rates at light levels at or above 1000 ft-c.

We can therefore dismiss the hypothesis that shading in stands up to 25 years of age controls the level of seedling establishment.

5.34: Seed and Seedling Dessication

The moisture balance in the micro-environment of the seed in the field is controlled by several factors; macro-meteorological variables such as the amount of precipitation and direct solar radiation, and micro-meteorological factors such as soil field capacity, shading of the soil surface and the soil albedo. In soils with sandy surface horizons, such as those of the study area, most of the suspended water is retained as isolated shards of water between soil particles ("pendular" water (Rode, 1969)). This pendular water is immobile in the liquid state and will not move to the soil surface to evaporate under drying conditions, with the result that the drying point gradually moves downward in the soil. Consequently seeds exposed on a bare mineral soil substrate are subject to rapid wetting by a precipitation event and subsequent dessication caused by rapid evaporative water loss from the surface soil. It seems likely that only seeds in favourable microtopographic positions will germinate in these conditions. Any environmental factor that reduces the rate of evaporative heat exchange and water loss from the soil surface should therefore reduce dessication and stimulate germination.

Reduced moisture stress can result from lowered radiation-levels on the forest floor or changing substrate conditions. The relationship between radiation-levels and moisture-levels at the soil surface is probably inversely linear; any increase in the canopy cover of trees or shrubs, or ground cover, should therefore result in a concomitant increase in moisture availability to the seed. In contrast, the relationship between substrate conditions and moisture stress is not as straightforward. Litter layers act as a surface mulch, and depress the evaporation rate from the soil surface, but as the litter layer increases in thickness it is increasingly difficult for light seeds such as those of *P. caribaea* to penetrate the litter mat to contact moist soil underneath. Hence there is a "window" of intermediate litter-thicknesses in which the probability of seed desiccation is minimized.

Seedling survival may also be controlled by a similar suite of environmental variables. In open stands with high radiation-intensities and thin litter-layers, seedling survival may be reduced due to soil desiccation or very high soil-surface temperatures. Seedlings may also suffer from moisture stress in stands in which competition for moisture with members of the tree, shrub, or ground flora is intense.

Because it is virtually impossible to measure the moisture supply in the microenvironment of a large seed and seedling population in the field, the influence of intermediate variables

(radiation, litter, competition, etc.), will be examined as surrogates for moisture availability.

5.341: Radiation levels and seed germination

It has been postulated that seed-germination levels should be inversely related to the radiation intensity on the forest floor because of the increased dessication of the surface soil as crown and shrub cover decreases. A plot of the median radiation-intensity against initial seedling-emergence (Fig. 5.14), demonstrated that the relationship was more complex than had been hypothesised. The predicted inverse relationship holds true for stands in which the median radiation-intensity is greater than 75 % of that in the open. However, at intensities below this threshold, seedling emergence rates level off, and decline below 50 % of full radiation. The marked departure of the field data from the predicted values is presumably a response to the influence of changing substrate conditions.

If the radiation-levels in the youngest group of stands are significantly greater than the levels in intermediate-aged stands, then the low germination rates in young stands may be attributable to dessication brought about by high radiation intensities. A comparison of the measured radiation-levels in these two groups of stands by the Kolmogorov-Smirnov two-sample test (Table V.14), indicated that radiation-levels were indeed significantly greater in the youngest stands. Thus the failure

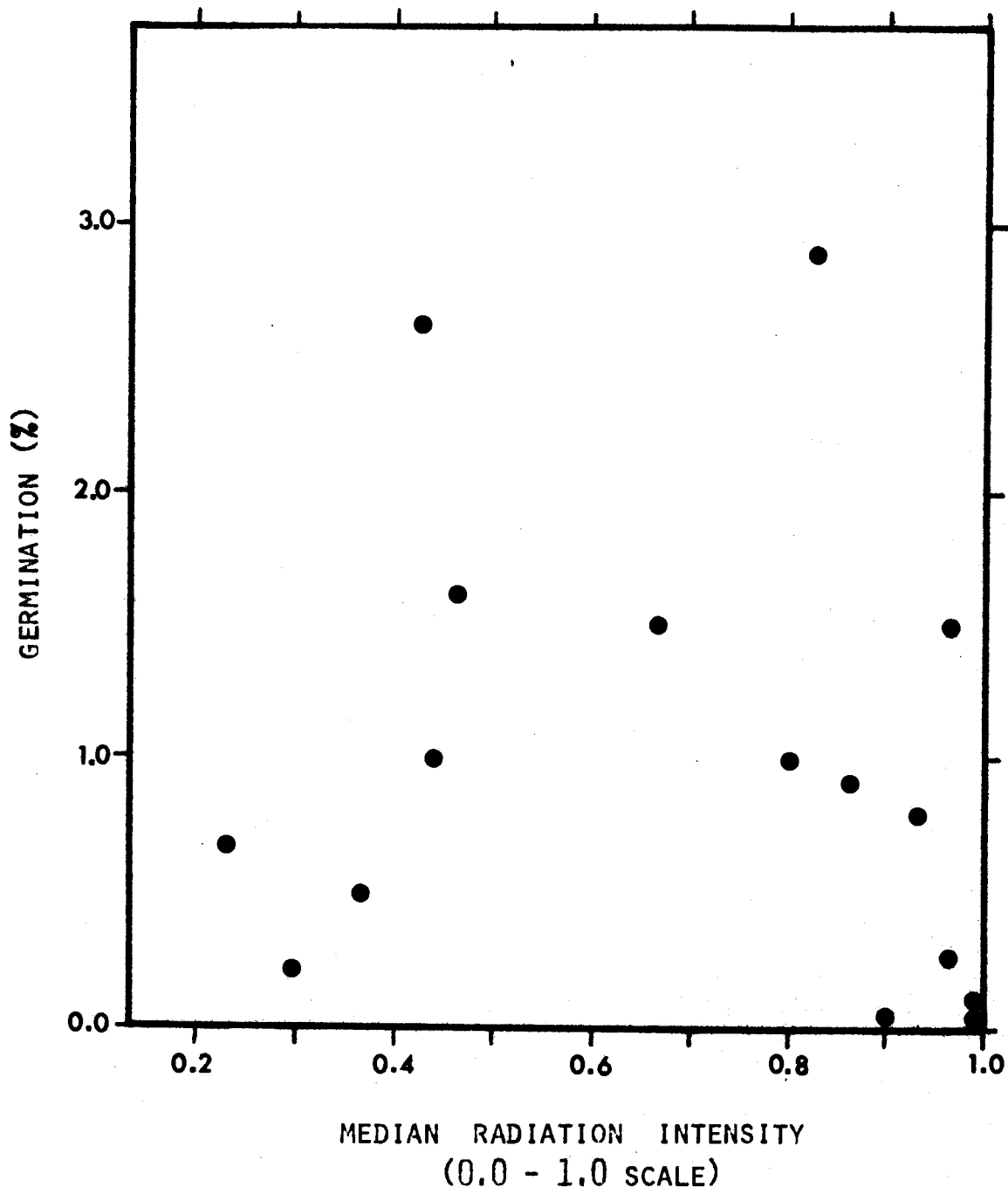


FIG. 5.14: PERCENTAGE GERMINATION OF *P. CARIBAEA* SEEDS IN THE TRNCHED AND CONTROL PLOTS AS A FUNCTION OF THE MEDIAN RADIATION-INTENSITY IN THE SAMPLE STANDS. GERMINATION DATA ARE DERIVED FROM THE FIRST CENSUS OF THE TREATMENT PLOTS 15 DAYS AFTER SOWING.

TABLE V.14: KOLMOGOROV-SMIRNOV TEST ON RADIATION LEVELS IN STANDS OF < 5 YEARS OF AGE COMPARED TO STANDS OF 5 - 15 YEARS OF AGE.

H₀: That radiation levels in stands of less than 5 years are not significantly greater than those in stands of 5 - 15 years (1-tailed test).

Cumulative Frequency Data

| Stand | Radiation - Intensity | | | | | | | | | | | |
|-----------------|-----------------------|-----|------|------|------|------|------|------|------|------|-----|-----|
| | Age | 0.0 | 0.1 | 0.2 | 0.3 | 0.4 | 0.5 | 0.6 | 0.7 | 0.8 | 0.9 | 1.0 |
| < 5 yrs. | | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 5 | 8 | 50 | |
| 5-15 yrs. | | 0 | 1 | 7 | 12 | 20 | 25 | 29 | 32 | 48 | 125 | |
| Sn1(x) - Sn2(x) | | 0 | .008 | .056 | .076 | .140 | .180 | .162 | .156 | .224 | 0 | |

$$D = \max [Sn1(x) - Sn2(x)] = 0.224$$

$$\chi^2 = 4 \cdot D^2 \cdot ((n1)(n2)/(n1 + n2))$$

$$= 4 \cdot (0.224)^2 \cdot (35.740)$$

$$= 7.17$$

$$df = 2$$

Since $\chi^2_{0.05[2]} = 5.99$, the D value is significant, and the null hypothesis (H₀) is rejected.

of pine stands to germinate in these stands may be primarily due to low moisture-availability caused by high radiation intensities.

5.342: Litter depth and seed germination

It was suggested in the introductory statement to this section that there is a complex interaction between the depth of litter in a stand and moisture availability to the seed. It was further hypothesised that pine seedlings would only become established in a favourable "window" of litter depths, being excluded from the tails of the distribution by moisture stress.

Pearson (1923) encountered this phenomenon in his work on the regeneration of *P. ponderosa* stands in the southwestern U.S.A. He noted the beneficial effects of a light litter cover on surface soil moisture and seedling establishment:

"Where the surface mat becomes thick it interferes with germination and induces shallow root development. Where it is not over one-half inch thick, however, it is a distinct aid to germination, especially on soils which have a tendency to dry out quickly at the surface....."

Pearson, *ibid.*, p.98.

If Pearson's conclusions hold true for *P. caribaea* then we should expect that seedlings would in general be restricted to only a short segment of the continuum of litter depths, failing to germinate at both 'tails' of the distribution because of the perching effect of thick litter mats and the low moisture

availability in areas with very thin litter mats.

In order to test this hypothesis, and delimit the range of such a "window", the litter depth measurements taken at random in the sample stands (Section 4.33), were compared to the litter depths at the base of extant first-year seedlings in a 100 sq. m. subplot in each stand. A Kolmogorov-Smirnov two-sample test on the cumulative frequency distributions of randomly-sampled and seedling-sampled litter depths (Tables V.15 and V.16), demonstrated that the seedlings are indeed restricted to a limited range of the litter depth continuum. In Table V.16 the number of points in the random litter-sample in each stand is equal to the number of seedlings sampled. In Table V.15 all the random litter-sample points (40 per stand) are employed. Table V.16 is formed from a random subset of the data used in Table V.15.

Seedlings are encountered less frequently than might be expected by chance in microsites where the litter mat is less than 0.5 cms. or more than 3.5 cms. in thickness. The favourable "window" would therefore appear to be the range between these two values in the stands sampled.

Microsites where litter is absent or very thin (< 0.5 cms. in depth), are usually associated with recent burns or areas where pine density is low. The lack of a litter layer and concomitant high intensity of solar radiation in these young

TABLE V.15: KOLMOGOROV-SMIRNOV TEST ON ASSOCIATION BETWEEN LITTER DEPTH AND SEEDLING ESTABLISHMENT - UNWEIGHTED DATA

H₀: That there is no difference in seedling establishment with changing litter depth (2-tailed test).

Cumulative Frequency Data

| Sample Type | Litter Depth (to nearest 0.5 cms.) | | | | | | | | | | | |
|-----------------|------------------------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| | 0.0 | 1.0 | 2.0 | 3.0 | 4.0 | 5.0 | | | | | | |
| Random* | 20 | 116 | 185 | 260 | 348 | 394 | 439 | 479 | 513 | 527 | 541 | 600 |
| Seedling | 2 | 21 | 32 | 50 | 66 | 77 | 86 | 89 | 89 | 89 | 90 | 90 |
| Sn1(x) - Sn2(x) | .01 | .04 | .05 | .12 | .15 | .20 | .22 | .19 | .13 | .11 | .10 | .00 |

* This random sample consists of all litter-depth measurements in all sample stands (cf. Table V.16)

$$D = \max [Sn1(x) - Sn2(x)] = 0.223$$

$$\chi^2 = 4 \cdot D^2 \cdot ((n1)(n2)/(n1 + n2))$$

$$= 4 \cdot (0.223)^2 \cdot (78.261)$$

$$= 15.567$$

$$df = 2$$

Since $\chi^2_{0.001(2)} = 13.82$, the D value is significant, and the null hypothesis (H₀) is rejected.

TABLE V.16: KOLMOGOROV-SMIRNOV TEST ON ASSOCIATION BETWEEN LITTER DEPTH AND SEEDLING ESTABLISHMENT - WEIGHTED DATA

Ho: That there is no difference in seedling establishment with changing litter depth (2-tailed test).

Cumulative Frequency Data

| Sample | Litter Depth (to nearest 0.5 cms.) | | | | | | | | | | | |
|-------------------------|------------------------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| Type | 0.0 | 1.0 | 2.0 | 3.0 | 4.0 | 5.0 | | | | | | |
| Random* | 4 | 8 | 15 | 28 | 48 | 54 | 64 | 70 | 74 | 76 | 77 | 90 |
| Seedling | 2 | 21 | 32 | 50 | 66 | 77 | 86 | 89 | 89 | 89 | 90 | 90 |
| $S_{n1}(x) - S_{n2}(x)$ | .02 | .14 | .19 | .24 | .20 | .26 | .24 | .21 | .17 | .14 | .14 | .00 |

* This is a subset of the data employed in Table V.16. The subset is a random sample of litter-depth measurements, selected so that the number of random observations in each stand is equal to the number of seedling observations.

$$D = \max [S_{n1}(x) - S_{n2}(x)] = 0.256$$

$$\chi^2 = 4 \cdot D^2 \cdot ((n1)(n2)/(n1 + n2))$$

$$= 4 \cdot (0.256)^2 \cdot (45.0)$$

$$= 9.21$$

$$df = 2$$

Since $\chi^2_{0.01[2]} = 9.21$, the D value is significant, and the null hypothesis (Ho) is rejected.

stands results in rapid dessication of the soil surface after a rainstorm. As the pine canopy closes and the litter layer increases in depth, the severe moisture conditions of these mineral soil seedbeds become ameliorated.

Nerpin, Pakshina and Bondarenko (1969) show that a 1 cm mulch layer can decrease evaporation by a factor of two and a 2 cm layer by a factor of three. Bond and Willis (1969) demonstrate that the evaporation rate is negatively correlated with the amount of plant residue remaining on the soil surface to act as a mulch. If their results are applied directly to pine litter residues then 450 g /sq. m. (~1 cm. thick) should lead to a 50% reduction in evaporation over the ten day pre-germination period and 670 g /sq. m. (~1.5 cm.) to a 65% reduction over the same period.

The hypothesis that moisture-stress is high in areas of thin litter was further tested by examining the numbers of seedlings that germinated in the control plots in open stands (> 80 % full radiation), as a function of mean litter thickness. A Mann-Whitney U-test (Table V.17), demonstrated that seedling emergence in the controls was significantly lower in those plots with mean litter depths of 0.6 cms. or less. The failure of pine regeneration in the youngest stands can therefore be construed as due to the interaction of high radiation-levels and thin litter layers.

TABLE V.17: MANN-WHITNEY U-TEST ON THE AMOUNT OF GERMINATION IN OPEN STANDS AS A FUNCTION OF LITTER DEPTH.

H₀: That there is no significant difference in seedling establishment in open (> 80% full radiation) stands where the litter depth is < 1 cm., compared to open stands where the litter depth is > 1 cm.

Control Plot Data

| Stand # | Litter Depth | # Seedlings | Rank | Stand # | Litter Depth | # Seedlings | Rank |
|-----------------|--------------|-------------|------|----------------|--------------|-------------|------|
| 1 | 1.65 | 1 | 5 | 4 | 0.53 | 0 | 2.5 |
| 3 | 1.15 | 5 | 6 | 16 | 0.19 | 0 | 2.5 |
| 8 | 1.19 | 16 | 8 | 17 | 0.55 | 0 | 2.5 |
| 9 | 1.76 | 0 | 2.5 | | | | |
| 14 | 1.56 | 10 | 7 | | | | |
| Rank sum = 28.5 | | | | Rank sum = 7.5 | | | |

$$U' = (3)(5) + (3)(3+1/2) - 7.5 = 13.5$$

$$U = (3)(5) - 13.5 = 1.5$$

$$p(U) = 0.05$$

Since $U_{0.05} = 1.5$, the difference in seedling establishment rates is significant, and the null hypothesis (H₀) is rejected.

The co-occurrence of these conditions, exacerbated by the effects of rain-splash on the mineral soil, combine to produce a rapidly desiccated, crusted soil surface which inhibits germination and mechanically impedes the extension of the radicles of those seeds that do germinate. Billings (1938), reported that the build-up of a litter layer with time in stands of P. echinata was the major cause of reduced pine germination in older stands. Litter mats > 2.5 cms (1.25 ins) in thickness were impenetrable to the light pine seeds of shortleaf pine, which were in consequence unable to obtain sufficient moisture for germination. It is postulated that the same phenomenon reduces the germination success of P. caribaea in older stands, but that the upper limit of litter thickness for seedling establishment is 3.5 cms. in this case. The difference in litter thresholds for the two species is probably a response to the differential penetrability of the seeds of the two species, as the seeds of P. caribaea from the study area are twice as heavy as those of P. echinata (Lamb, 1973; Fowells, 1965).

Two experiments were undertaken to determine whether perching of pine seeds on thick litter mats results in lowered seedling establishment. One experiment was undertaken in the field, the other in the laboratory.

A series of small quadrats were established in a fenced, open area 8 kms. north of Augustine (Fig. 4.5). Pine litter was spread to various depths (0 - 5 cms. range), over these

quadrats, which were then enclosed by chicken-wire to exclude predators. Seeds of P. caribaea were sown at a density of 200 seeds/sq. m. over the experimental treatments but none of the seeds germinated. The quadrats were re-established the following year and the sowing density was doubled, but again there was a total germination failure.

The reason for this failure is obscure, but may well be due to the presence of a surface soil crust in this open area. Surface crusts result from the mechanical action of raindrops which tend to produce a patina of fine grained-material on the surface of sandy or clayey soils. Such surface crusts dry out very rapidly after rain and also are a mechanical impediment to radicle extension in newly - germinated seedlings. Even when covered with litter, as in some of the treatment plots, it is doubtful whether these surfaces were sufficiently modified to offer a suitable seedbed for germination.

To insure against further failure an experiment was established in the laboratory. The experiment was set up in the incubators described in the earlier section on shading, with a 12-hour photoperiod, 20 - 30 ° C thermoperiod, and a light intensity of 2000 ft.-c. Plastic pots of 57 sq. cm. surface area and 7 cm. depth were filled with bulked sterilised soil samples from Mountain Pine Ridge. Air-dried pine needles were chopped into 4 - 5 cm. lengths and pressed firmly onto the soil surface. Litter weights equivalent to 0, 100, 500, 1000 and 1500

gms/sq. m. were spread across the surface of the soil to model field conditions. These litter weights represent approximate litter depths of 0, 0.2, 1.25, 2.5 and 3.75 cms. respectively. The pots were freely watered for a week and the evaporation rates in the incubators were determined daily using a Piche evaporimeter. Moisture loss during this period averaged 0.387 ± 0.053 ml/ sq. cm./day. The pots were planted with 10 seeds of P. caribaea, and one set of 4 replicates watered at a rate equivalent to the rate of moisture loss from the evaporimeter and another set of 4 replicates watered at half this amount. The course of germination was monitored for a 40 day period.

As can be seen from Fig. 5.15, the total number of seeds germinating decreases rapidly with increased litter weight under both moisture regimes, and the relationship between the two variables can be represented as a power function.

This relationship is analogous to that described by Billings (1938), indicating the depressant effect of thick pine litter on pine germination. The data previously presented on the relationship between seedling establishment and litter thickness in the sample stands (Tables V.15,16), show a great discrepancy with these results, as maximum establishment has earlier been stated to occur in the mid-range of litter depths. The reason for this divergence in results is almost certainly due to the great differences in substrate dessication between laboratory and field seedbeds in sites with thin litter.

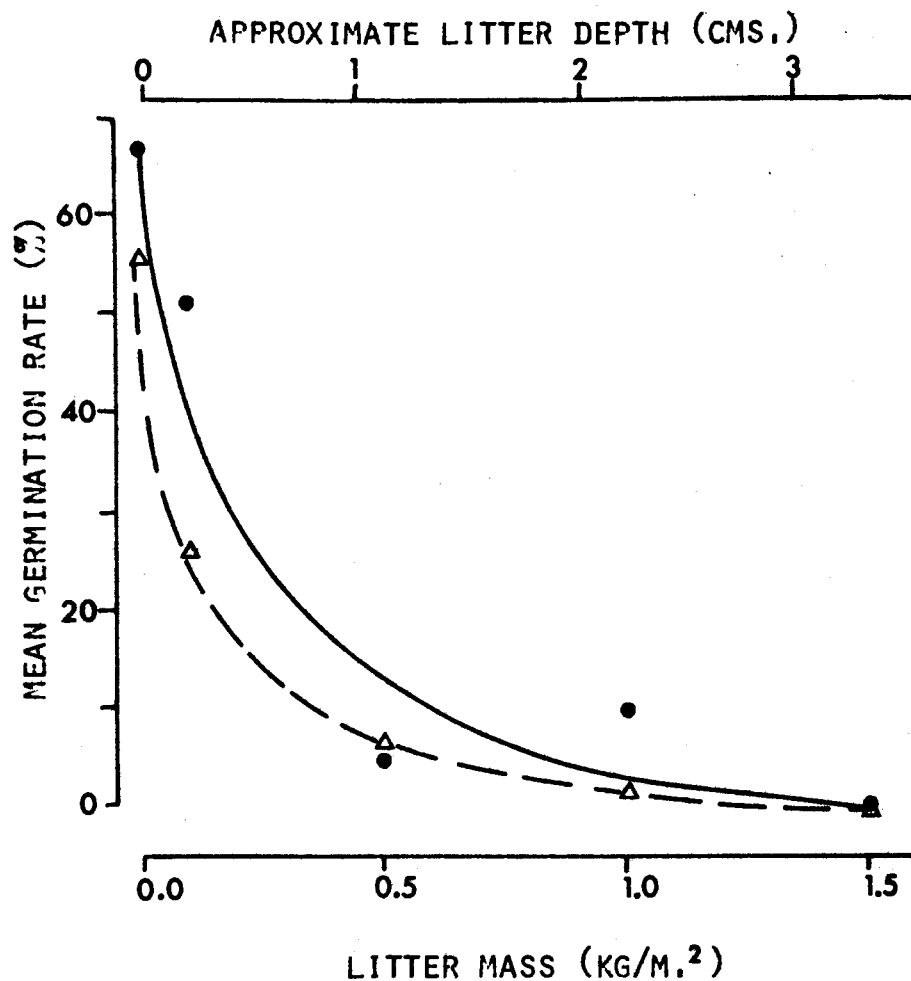


FIG. 5.15: PERCENTAGE GERMINATION OF SEEDS OF P. CARIBAEA AS A FUNCTION OF THE MASS OF THE LITTER SUBSTRATE. THE (●) POINTS REPRESENT POTS THAT WERE WATERED AT A RATE EQUAL TO THE EVAPORATION RATE FROM A PICHE EVAPORIMETER. THE OTHER (Δ) TREATMENT WAS WATERED AT 50% OF THIS RATE.

5.343: The herbaceous layer and seed germination

The grass and herb stratum may be analogous to the litter layer in its effects on pine germination. It is postulated that a light herbaceous biomass depresses germination success through exposure of the soil surface to high radiation-levels, whereas heavy herbaceous growth represents a variant on the perching phenomenon described in the previous section, that is, the light pine seeds are unable to penetrate the thick clumps of bunchgrasses. However, it should be noted that the biomass of the herbaceous layer is inversely related to litter mass. Thus, it is the perching effect of grasses that should be operative in the youngest stands, and not in the oldest stands as is the case with the litter layer.

A further series of experimental plots were established in the sample stands to examine the relationship between germination rates and grass biomass. Two 0.25 sq. m. quadrats were clipped in each sample stand and all grasses and herbs removed. These plots were sown at the same density and on the same day as the control plots, and the course of seedling establishment and survival was followed for the succeeding year.

In the clipped plots the overall maximum germination rates were the same as in the control and trenched plots (0.88 %), but seedling emergence was delayed, and maximum rates were reached some 2 - 3 months after the control treatments peaked (Fig.

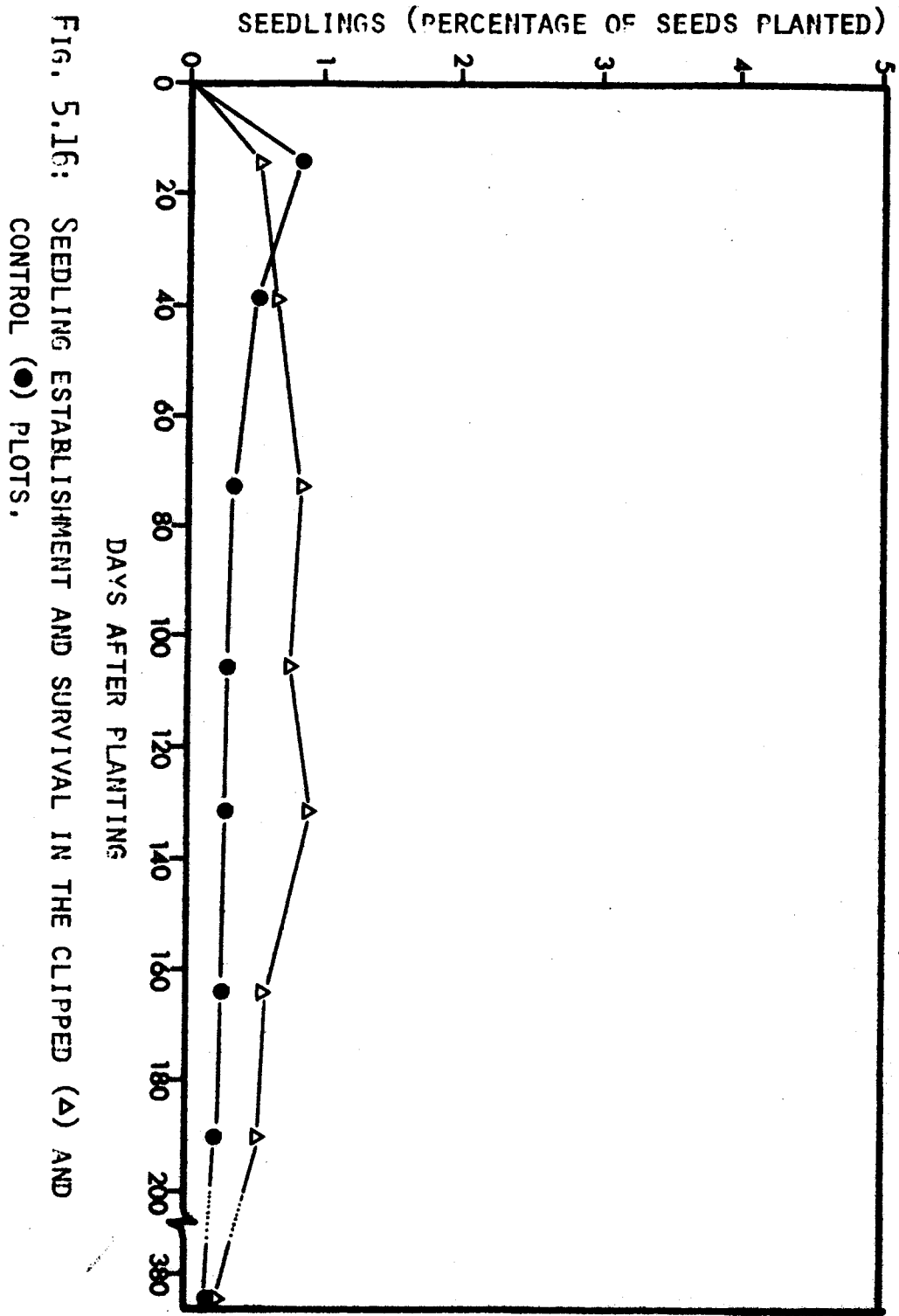


FIG. 5.16: SEEDLING ESTABLISHMENT AND SURVIVAL IN THE CLIPPED (△) AND CONTROL (●) PLOTS.

5.16). The reason for this delay in germination is presumably the decrease in surface soil moisture prompted by the removal of the grass cover.

A G-test of association (Table V.18), demonstrated that initial seedling establishment on the control plots does fluctuate with changing herbaceous biomass, with seedling emergence being most prolific at intermediate levels (0.2 - 0.4 kg./sq.m.).

The germination failure of pine seeds in very young stands can therefore be ascribed to seed-dessication due to high radiation intensities, thin litter layers and the lack of a herbaceous stratum in these recently burnt, open areas. It was postulated in Section 5.34 that the primary control on seedling survival in the first year was also moisture stress, resulting again from high radiation-levels, thin litter mats, competition for moisture with other plants, or combinations of these variables. Because of the very low initial establishment of seedlings in open stands with thin litter layers and high radiation-levels, no test can be made on the effects of these variables on seedling survival. However, the effects of inter-plant competition can be assessed.

5.344: Seedling survival and root competition

Much of the classic literature in forest ecology attempts to discriminate between the roles of shading and moisture levels as

TABLE V. 18: G-TEST OF ASSOCIATION BETWEEN GRASS BIOMASS AND STAND AGE

H₀: That there is no difference in seedling establishment rates with changing grass biomass (2-tailed test).

Treatments (a=2)
Categories (b=3)

| Grass Biomass (kg/m.) | Control Plots (day 15) | Clipped Plots (day 132) | Row Sum | Control/ Total |
|------------------------|------------------------|-------------------------|---------|----------------|
| 0.20 | 68 | 17 | 85 | 0.80 |
| 0.2 - 0.4 | 95 | 3 | 98 | 0.97 |
| 0.40 | 77 | 10 | 87 | 0.88 |
| Column Sum | 240 | 30 | 270 | |

(See Table V.5 for G-test methodology)

$$\begin{aligned}
 G &= 2 [1128.504 - 1215.486 - 1417.389 + 1511.574] \\
 &= 2 [7.203] \\
 &= 14.406
 \end{aligned}$$

$$df = (a-1)(b-1) = 2$$

Since $\chi^2_{0.01}[2] = 10.597$, the G value is significant, and the null hypothesis (H₀) is rejected.

controls on the dynamics of forest stands. A comprehensive review of this literature is found in Kozlowski (1949). Nineteenth century workers (e.g. Heyer, 1852) emphasised the importance of shading as a limiting factor in the regeneration of pioneer successional species like pines. However in the first three decades of this century a number of researchers (Fricke, 1904; Cieslar, 1909; Fabricius, 1927 and Craib, 1929) analysed the role of soil moisture as a control on the regeneration of early successional tree species, and concluded that competition for moisture in forest stands was often a more important regulatory mechanism than shading. The technique on which this conclusion was based was that of trenched quadrats, in which experimental plots on the forest floor were surrounded by a trench in which all superficial root systems were severed. This effectively eliminated root competition, and soil moisture availability in the plots increased (Craib, op. cit.), ensuring more rapid growth and greater survival of tree seedlings located there.

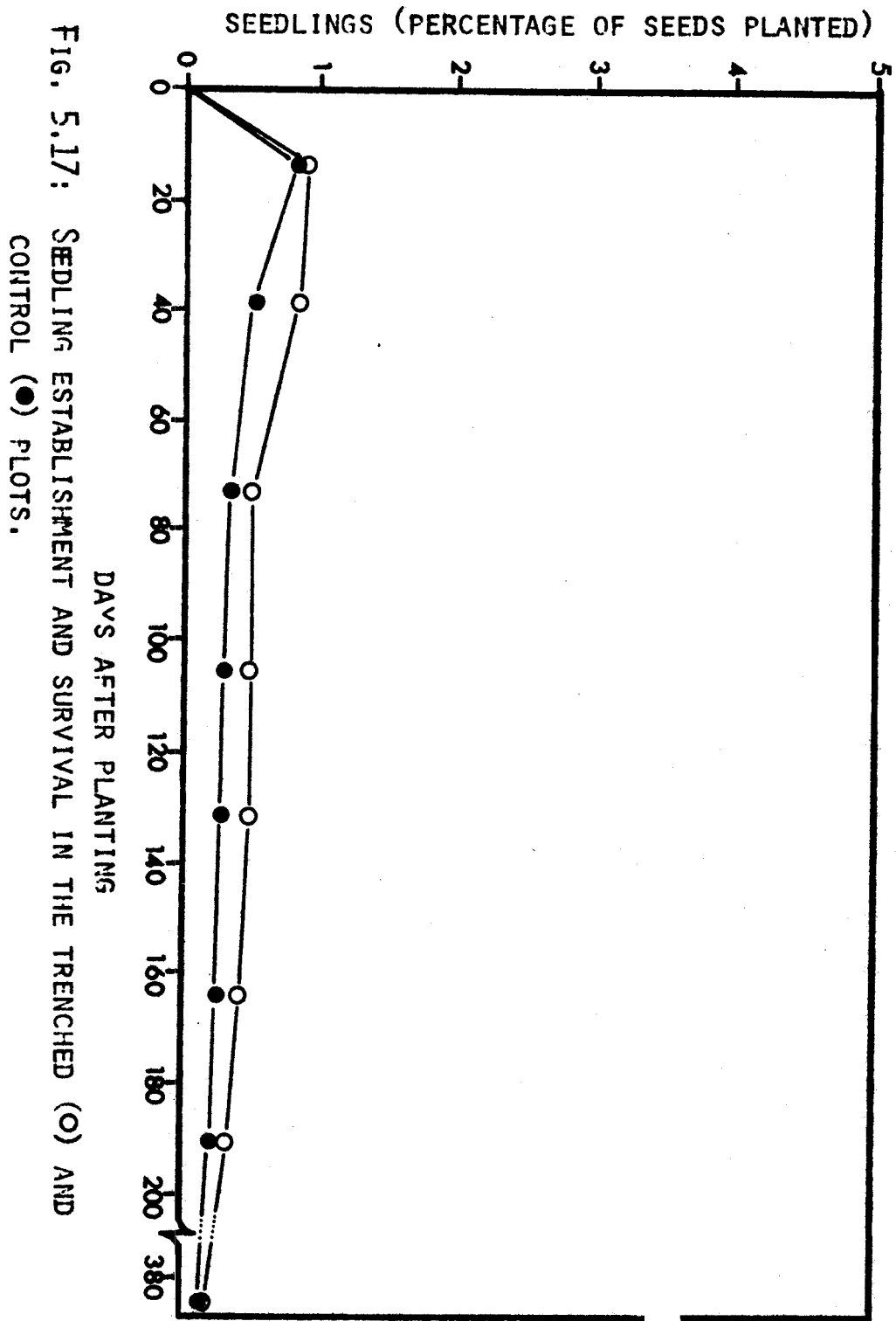
Pearson (1930), working with trenched and control plots in stands of Pinus ponderosa, demonstrated that the relative importance of these two factors varied according to the local climate and tree spacing. Korstian and Coile (1938) used the same technique in forest stands of the Piedmont of the U.S.A. and noted the stimulatory effect of trenching on the seedling populations. They concluded that the factor responsible for

inhibiting seedling regeneration was therefore competition for soil moisture with established trees.

A more comprehensive experiment by Shirley (1945) on the controls of reproduction of Pinus resinosa, P. strobus, P. banksiana and Picea glauca concluded that either shade or moisture may regulate the population dynamics of the young conifers, depending on stand composition. Nevertheless, Shirley considered that in general seedling survival was more dependent on light intensity than root competition.

To test the hypothesis that root competition for moisture with neighbouring trees produces high seedling mortality in the oldest stand age-category, trenches were dug around two 1 sq. m. quadrats in each sample stand to a depth of 15 cms. to sever surficial roots of pine and hardwoods. These quadrats were sown at the same density and on the same day as the control plots.

Initial rates of germination in the trenched and control plots were almost identical. Fifteen days after sowing 0.90 % of the seeds planted in the trenched plots had germinated compared to 0.89 % of the seeds in the control. Six months after sowing the number of seedlings remaining in the trenched plots was significantly greater than the numbers of seedlings in the control but in subsequent months this difference gradually declined. At the final count on day 388 there was no significant difference between the two treatments (Fig. 5.17). It may be



possible that this lack of statistical significance is caused by the inclusion of plots with only low competitive stress, thereby masking the more substantial competitive effects to be found in older stands. Table V.19 presents the results of a division of the sample stands into three groups based on their total tree basal area. It is apparent that there is no difference in the seedling survivorship rates between trenched plots and controls in the older sites where competition should be greatest, for in both treatments seedling populations are virtually eliminated.

Consequently we can conclude that competition for soil moisture with established trees, either pines or hardwoods, does not play a causative role in the inability of seedlings to establish in these older stands.

Competition for moisture and nutrients can also exist between seedlings and the plants of the herbaceous layer. If competition with the herbaceous layer is severe, then the overall mortality of seedlings in the clipped plots should be less than the mortality rate in the control plots. The reverse however is true. Seedling mortality rates in the clipped plots (Fig. 5.16), were slightly higher than those in the control plots, indicating that competition for moisture with the herbaceous layer does not lower seedling survivorship.

TABLE V.19: SURVIVORSHIP OF FIRST-YEAR SEEDLINGS OF *P. CARIBAEA* IN TRENCHED AND UNTRENCHED PLOTS AS A FUNCTION OF STAND BASAL-AREA.

| Basal-Area Sum | Trench | Cntrl. | Trench | Cntrl. | Trench | Cntrl. |
|------------------------|--------|--------|---------|--------|---------|--------|
| <0.5 <5.4 | 10.4 | 10.6 | 5.9 | 3.6 | 4.0 | 3.2 |
| 0.5- 5.4- 0.99 10.8 | 17.5 | 6.0 | 0.5 | 1.0 | 0.0 | 1.0 |
| >1.0 >10.8 | 7.5 | 8.6 | 0.0 | 0.60 | 0.0 | 0.5 |
| sq.m. sq.ft. | Day 15 | | Day 192 | | Day 388 | |

5.345: Seedling survival and thick litter layers

Pearson (1923), contends that survivorship of seedlings of P. ponderosa declined with increasing litter thickness as a result of root inhibition. Bilan (1960), reported the same phenomenon in seedling populations of P. taeda grown in thick litter, and shading of the soil surface also arrests root development according to Kozlowski (1949). The continued growth of roots and shoots of pine seedlings depends also upon the infection of their roots by ectomycorrhizae, and the consequent increase in nutrient supply to the higher plant. In normal circumstances (e.g. in nurseries), infection by mycobionts occurs 3 - 6 weeks after germination (Zak, 1964).

Mycorrhizal fungi may themselves be inhibited by certain environmental factors, and consequently the seedlings in these environments are less vigorous (due to decreased uptake of nutrients, particularly phosphorus), and more prone to disease (Sasek, 1967). The conditions that inhibit mycorrhizae are the same as those that favour pathogenic fungi - low light intensities (Hacskaylo and Snow, 1959; Wilde, 1968) and thick litter layers (Bilan, 1960). It is proposed therefore that this combination of circumstances of thick litter layers, shaded and moist surface soils, inhibits formation of mycorrhizae on the roots of pine seedlings in older stands. In consequence the seedlings become less vigorous and more vulnerable to disease, and the mortality rate may therefore be much greater in these

older stands.

Whatever the operative mechanism, the data from the control plots do demonstrate a strong positive correlation (Table V.20), between litter depth and seedling mortality. In addition, the litter depth is significantly greater (Table V.21), in stands older than 15 years, than in intermediate-aged stands. It is proposed therefore that the massive decline in seedling populations in these older stands is primarily a response to decreased root growth mediated by thick litter layers, and exacerbated by low light intensities and a possible failure of the pine-fungus symbiosis.

5.4: SUMMARY OF CONCLUSIONS

We have seen that the overall small size of the seedling population in *P. caribaea* stands is primarily a result of severe seed-predation. Although the relationship between seed density and seed-harvesting rate has not been investigated, it is likely that the seed population is reduced by some 60 % during the pre-germination period. Seed-predation during the main period of germination (10 - 40 days after dispersal) may account for almost all the remaining seeds. In consequence, the mean maximum germination in the control plots was only 0.89 % of the seed population.

TABLE V.20: SPEARMAN'S RANK CORRELATION BETWEEN MEAN LITTER DEPTH AND MORTALITY OF FIRST-YEAR SEEDLINGS.

H₀: That there is no positive association between mean litter depth and seedling mortality.

| Stand # | Litter Depth (cms.) | Rank | Mort. (%) | Rank | di | di ² |
|---------|---------------------|------|-----------|------|---------------------|-----------------|
| 1 | 1.65 | 5 | 81 | 2.5 | 2.5 | 6.25 |
| 2 | 3.92 | 12 | 100 | 12 | 0 | 0 |
| 3 | 1.15 | 2 | 95 | 6 | 4 | 16 |
| 4 | 0.53 | 1 | 85 | 4 | 3 | 9 |
| 5 | 4.06 | 13 | 97 | 9 | 5 | 25 |
| 6 | 2.39 | 7 | 86 | 5 | 2 | 4 |
| 7 | 3.19 | 9 | 100 | 12 | 3 | 9 |
| 8 | 1.19 | 3 | 15 | 1 | 2 | 4 |
| 10 | 3.66 | 11 | 87 | 6.5 | 4.5 | 20.25 |
| 12 | 2.36 | 6 | 98 | 10 | 3 | 9 |
| 13 | 3.65 | 10 | 87 | 6.5 | 3.5 | 12.25 |
| 14 | 1.56 | 4 | 81 | 2.5 | 1.5 | 2.25 |
| 15 | 2.49 | 8 | 100 | 12 | 4 | 16 |
| | | | | | $\sum di^2 = 144.0$ | |

$$rs = 1 - \frac{6 \sum_{i=1}^N di^2}{N^3 - N} = + 0.605$$

$$t = rs \sqrt{\frac{N - 2}{1 - rs}} = 2.44$$

$$df = N - 2 = 11$$

Since $t_{0.01} = 2.201$, the rs value is significant in a one-tailed test, and seedling mortality is positively correlated with increasing litter depth.

TABLE V.21: MANN-WHITNEY U - TEST ON MEAN LITTER DEPTH
IN STANDS BETWEEN 5 - 15 YEARS AND STANDS
OLDER THAN 15 YEARS.

H₀: That the mean litter depths in older stands are not significantly greater than mean litter depths in stands of intermediate age (1 - tailed test)

| STAND | | AGE | |
|--------------|------|--------------|-------|
| 5 - 15 Yrs. | | > 15 Yrs. | |
| Litter Depth | Rank | Litter Depth | Rank |
| 0.53 | 1 | 1.65 | 4.5 |
| 1.15 | 2 | 2.36 | 7 |
| 1.19 | 3 | 2.39 | 8 |
| 1.65 | 4.5 | 2.49 | 9 |
| 1.76 | 6 | 3.19 | 10 |
| | | 3.65 | 11 |
| | | 3.66 | 12 |
| | | 3.92 | 13 |
| | | 3.93 | 14 |
| | | 4.06 | 15 |
| CMS. | 16.5 | CMS. | 103.5 |

$$U' = (5)(10) + \frac{5(5+1)}{2} - 16.5$$

$$= 48.5$$

$$U = (5)(10) - 48.5 = 1.5$$

$$p(U) < 0.001$$

Since $U_{0.05} \leq 11$ for a one-tailed test, the difference in mean litter depths is significant, and H₀ is rejected.

Although predation of seed populations is intense, it is apparently uniform in stands of varying age, and cannot explain the observed differentials in seedling establishment with stand age. These differentials consisted of a massive failure of seeds to germinate in very young stands (< 5 years), and very heavy mortality of seedlings in stands > 15 years of age. Germination and survivorship were both maximised in stands of intermediate age (5 - 15 years). Statistical analysis of stand data demonstrate that light intensity does not become limiting for seedling establishment in the stands sampled, and that neither competition for soil resources with neighbouring trees, nor inter- or intra-specific allelopathy had any significant effect on seedling recruitment.

However, seedlings were restricted almost entirely to microsites where the litter was between 0.5 and 3.5 cms. in thickness. A litter depth of 0.5 cms. may be attained 1 - 2 years after a fire in dense pine stands, but may only be reached after a decade in very open areas. Litter layers less than the lower threshold are associated with significantly higher radiation-intensities, and the interaction of these two variables promotes dessication and crusting of the soil surface which in turn inhibit germination and impede seedling emergence. Litter thicknesses between 0.5 and 3.5 cms. act as a mulch to conserve surface soil moisture and promote seed germination. This accounts for the highest seedling germination rates in stands

between 5 and 15 years of age. Above the 3.5 cms. threshold (attained in all but the most open stands 20 - 25 years after disturbance), the litter layer forms a barrier to seed penetration. Seeds which are washed down through the litter may germinate, but have reduced survivorship due to shallow root development, which is a result of lowered light intensity and the thickness of the litter mat. These environmental conditions may inhibit infection of the young pine roots by ectomycorrhizae and seedlings become less vigorous and less resistant to parasites and disease. In addition, predation of seedlings by phytophagous insects exacerbates the severe mortality rates in stands over 15 years of age.

Consequently, the population dynamics of P. caribaea seedlings appear to be subject to two major controls: (1) severe overall decimation by post-dispersal predators, and (2) differential success of those surviving this predation as a consequence of changing seedbed conditions (primarily a response to litter depth) as stands age.

CHAPTER SIX: CONSTRUCTING THE SIMULATION MODEL.

6.1: INTRODUCTION

The previous chapter has dealt in some detail with the dynamics of seedling populations of Pinus caribaea, and the environmental controls on seedling dynamics. Because of the longevity of mature trees, it is exceedingly difficult to examine stand dynamics through field observation and experimentation. In consequence a simulation model is employed to analyse the changes in mature tree populations.

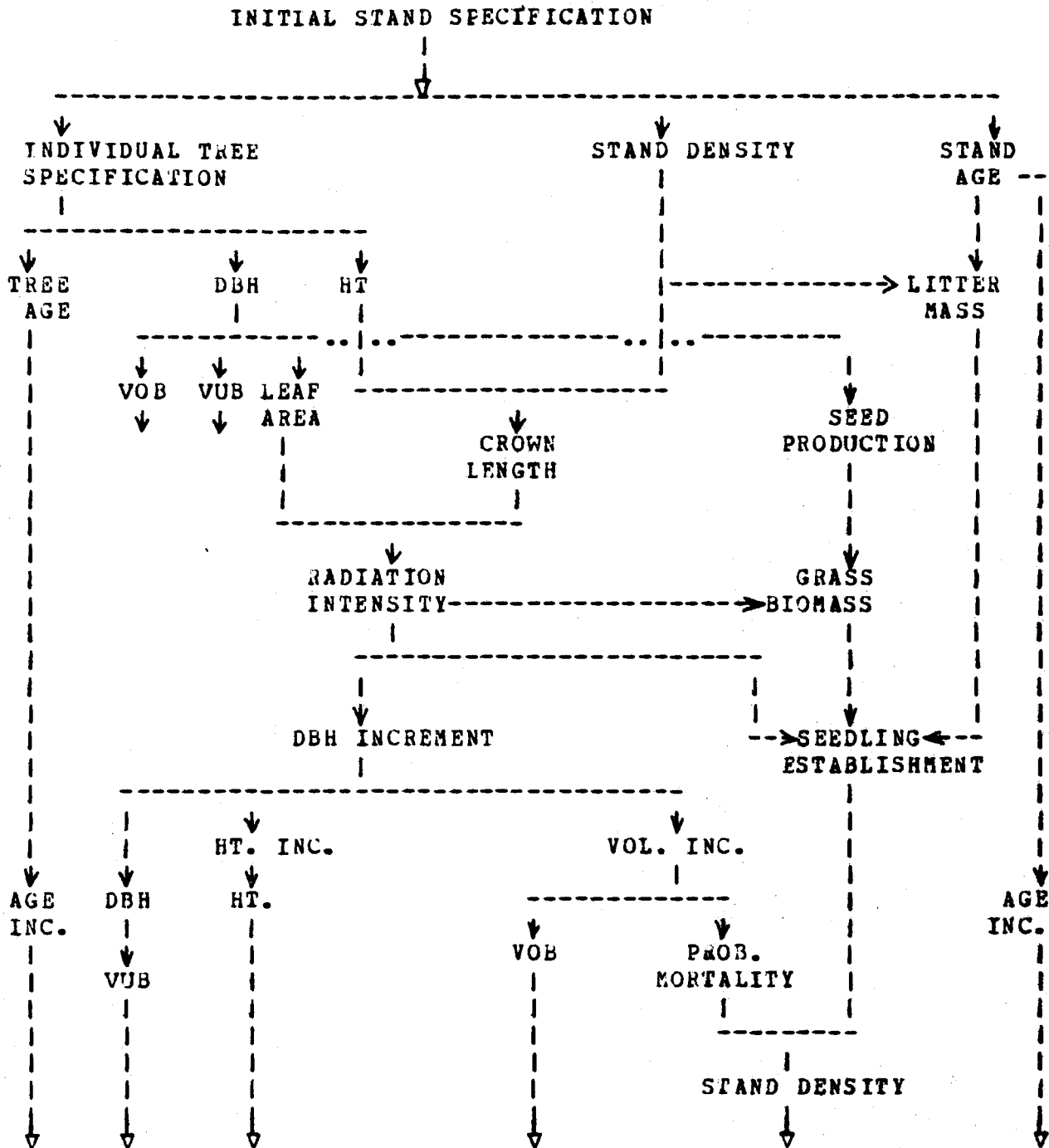
The model outlined here only considers intra-specific interactions in the development of stands of P. caribaea. This can be justified on the grounds that the hardwood species associated with Caribbean pine form a very small proportion of the total biomass of the sample stands, and therefore their influence on stand development can be considered to be slight. This assumption was confirmed by Kellman (1976, p. 14), who states: "Neither broad-leaved tree abundance, (nor) shrub abundance appear to have any significant effect on pine growth".

Data on the growth, yield and mortality of P. caribaea in Mountain Pine Ridge are limited. Increment plots and thinning plots were established by Lamb and Wolffsohn in the late 1950's but all the records from these were lost in Hurricane Hattie in

1961, when the entire research laboratory was destroyed. The only data available come from a single plantation set up close to of Augustine in 1959 which has been censused irregularly since then, and from a further series of increment plots which were laid out in 1967, censused yearly.

In order to model the growth and yield of stands by the individual tree method, the important characteristics of each tree in the stand must be accurately specified, and incremented on an annual basis. There is general agreement as to what constitute the important variables to be examined in a stand: height, dbh, stem volume, crown size for each tree, and mortality, fecundity, density and spatial distribution of trees for the stand as a whole.

In PINUS, the model to be developed here, each of the above components with the exception of tree location is specified and incremented in the sequence outlined in Fig. 6.1. The locational variable is necessary in those simulators which estimate the competitive status of an individual tree based on the density and size of its immediate neighbours. A more general method of calculating inter-tree competition is employed in PINUS, for which the spatial distribution of individual trees is not a prerequisite. The rationale of this alternative approach is discussed in detail in section 6.4 of this chapter. PINUS generates and grows a stand and performs an annual update by calling six workhorse subroutines:



 * FIG. 6.1: LOGICAL STRUCTURE OF THE PINUS MODEL *

Subroutine BIRTH - inputs new seedlings into the stand.

Subroutine LEAF - calculates crown characteristics for each tree in the stand and for the stand as a whole.

Subroutine GROW - grows each tree in the stand.

Subroutine MORT - allocates mortality between trees.

Subroutine THIN - provides flexible thinning and logging schedules.

Subroutine LIST - accounting procedure to keep track of trees culled by MORT or THIN.

In addition, there are two subroutines (RANDU and GAUSS) which generate uniform and normally distributed pseudo-random numbers respectively. The main program requires as input five items of data:

- a) Number, diameter and age of initial tree population. These may be seedlings in a plantation, trees in an uneven-aged stand, or seedtrees left after tree-harvesting.
- b) Age of the plot in years. Usually set to zero.
- c) Thinning schedule. Intensity and frequency options.
- d) Time span for simulation in years; and time period between printouts.
- e) An initial random-number for RANDU and GAUSS.

PINUS then proceeds to update the changes in population structure and individual tree growth annually, until a maximum age of 50 years is reached. This limited time span was chosen because only a very small number of trees in the study area were

over 35-40 years of age, due to the combined effects of logging and wildfires, and validation of the model output for older stands was therefore impossible.

The successful implementation of PINUS required the development and validation of four procedures, which are described in detail in the rest of the chapter:

- 1) Development of a procedure to model pine seedling establishment over time.
- 2) Development of a procedure to model the morphology and growth of each tree based on its competitive status.
- 3) Development of a procedure to allocate individual-tree mortality as a function of its competitive status.
- 4) Development of a procedure to implement flexible logging and thinning schedules.

The functional relationships used to model these parameters were not always the most biologically meaningful relationships. In a few cases intermediate or surrogate variables were employed in place of "proven" functional variables in order to facilitate mathematical computation.

6.2: SEEDLING ESTABLISHMENT

The input of new seedlings to the stand is handled by subroutine BIRTH. BIRTH requires data on the following variables:

- a) Seed production as a function of tree size

- b) Total seed production in the stand
- c) Potential germination of dispersed seeds

The field data on cone and seed yields per tree in 1973 (Fig. 5.2), are employed to generate seed production for each tree in the BIRTH subroutine (= FECU vector). The main program first calls subroutine STAGES which groups the trees on the plot into 13 size classes (vector STRUC), and then BIRTH obtains the total seed-production (SEEDP) from:

$$SEEDP = \sum_{i=1}^{13} (FECU_i \cdot STRUC_i)$$

As we have seen in Chapter Five the environmental controls on germination are very intricate. Although radiation intensity per se does not control seedling establishment, interactions between radiation intensity and substrate jointly determine local soil moisture availability. This in turn regulates seed germination and survivorship. Ideally we should like to calculate soil moisture directly from physical principles in the manner of Janssen (1974), but this would involve a considerable, probably unwarranted, increase in the computational complexity of the model. Not only that, but field data to validate the necessary equations are not available for the study area.

Consequently the variables of radiation intensity, litter weight and grass biomass are used as surrogates for moisture availability in this section. The relationship between these variables and germination was discussed in Chapter Five. The

relationship between median radiation-intensity and initial seedling-establishment can be approximated by a third-degree polynomial (Fig. 6.2) of the form:

$$Y = 5.36 - 23.34(\text{SLITE}) + 209.8(\text{SLITE})^2 - 192.06(\text{SLITE})^3 \quad (1)$$

where SLITE is the median radiation-level on the forest floor. Although the analysis of variance for this regression equation indicates that the overall regression is not significant ($F = 1.04$; $df(n1) = 3$, $df(n2) = 13$) at an $\alpha = 5\%$ level, the regression does account for 20 % of the total variance in the germination data, and will be retained as a basis for the next step.

The residuals from this regression equation can be decomposed into the effects of a number of factors; local variations in radiation intensity, the variable thickness of the litter substrate, variations in grass growth, measurement errors, and so on. Field data on two of these variables exist, namely, litter and grass mass on the forest floor.

The mass of litter at a site can be calculated as a function of the total basal area (BASUM), the stand age (MAYR), and the number of dominant trees on the plot (DOMT = trees >400 sq. cm. basal area) A multiple regression analysis of the field data (Table VI.1; Fig. 6.3) produces the following equation:

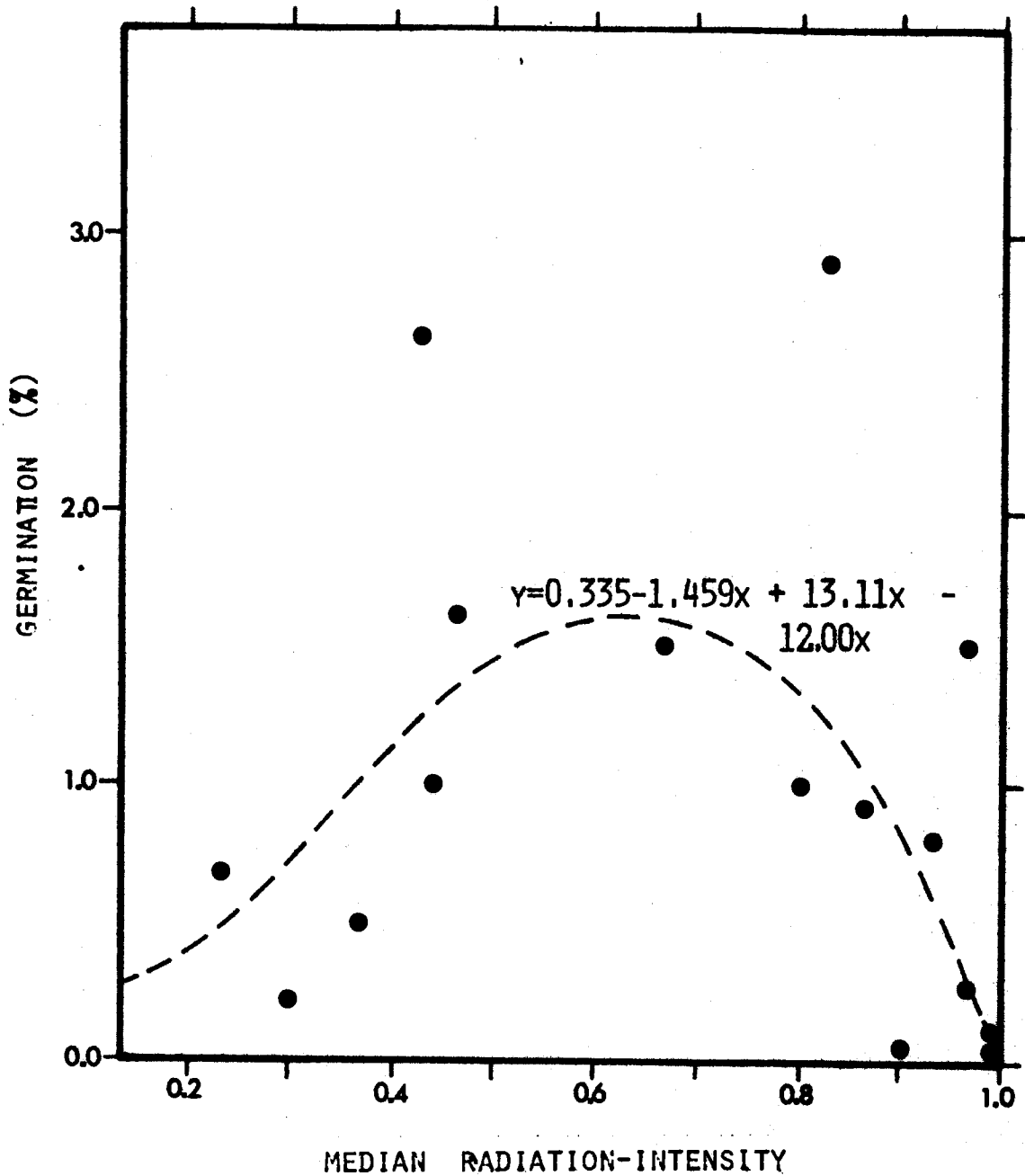


FIG. 6.2: THIRD-DEGREE TREND BETWEEN PERCENTAGE GERMINATION IN THE TRENCHED AND CONTROL PLOTS AND MEDIAN RADIATION INTENSITY IN EACH SAMPLE STAND.

TABLE VI.1: MULTIPLE REGRESSION ANALYSIS OF THE EFFECTS OF PINE BASAL AREA, STAND AGE AND DENSITY OF DOMINANT TREES ON LITTER WEIGHT.

Multiple Correlation

| <u>Variables</u> | <u>Multiple r</u> | <u>% explanation</u> |
|------------------|-------------------|----------------------|
| Pine Basal Area | 0.615 | 37.77 |
| Stand Age | 0.748 | 18.23 |
| Dominants | 0.804 | 8.63 |

Regression Coefficients

| <u>Variables</u> | <u>Coefficient</u> | <u>Beta Coefficient</u> |
|------------------|--------------------|-------------------------|
| Constant | 16.8200 | |
| Pine Basal Area | 0.0134 | 0.4163 |
| Stand Age | 2.5191 | 0.1847 |
| Dominants | 6.5150 | 0.3776 |

Partial Correlation

| <u>Variables</u> | <u>Partial Corr. Coeff.</u> | <u>Prob. Level</u> |
|------------------|-----------------------------|--------------------|
| Pine Basal Area | 0.4886 | 0.04 |
| Stand Age | 0.0283 | 0.32 |
| Dominants | 0.4342 | 0.11 |

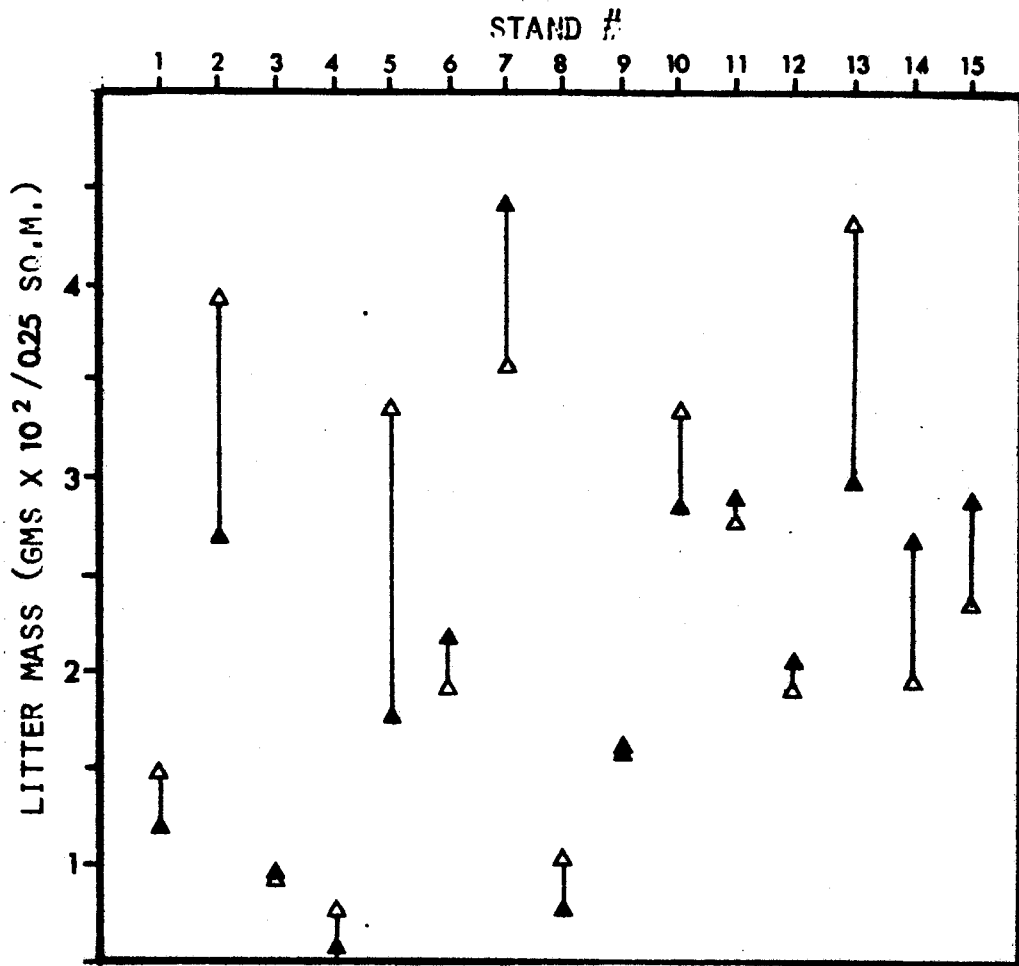


FIG. 6.3: PREDICTED (▲) AND OBSERVED (△) LITTER WEIGHTS IN THE SAMPLE STANDS.

$$ALITT = 16.82 + 0.01337(BASUM) + 2.5191(MAYR) + 6.515(DOMT)$$

The mean grass biomass at a site is correlated with the median radiation intensity ($r = 0.550$; $df = 14$), and can be estimated (Fig. 6.4) by the linear regression equation:

$$GRASS = 30.47 + 91.00 (SLITE)$$

When taken singly both litter and grass weight proved to be poor predictors of the direction and magnitude of the residuals from equation [1]. In consequence these two variables were combined, and their product proves to be of predictive value (Fig. 6.5). At low combined grass and litter weights pine germination is inhibited, presumably due to desiccation of the soil surface. High values of the litter-grass index are also associated with depressed germination rates, probably due to the thick litter barrier, associated with heavy grass cover. All the positive residuals are found associated with intermediate values of the grass-litter index.

The predictive function fitted to this data is discontinuous, and is of the form:

$$y = a \cdot GRLT \cdot e^{-GRLT \cdot s}$$

where the y values are the residuals, and the $GRLT$ values represent the grass-litter index. The values of the coefficients in the equation are:

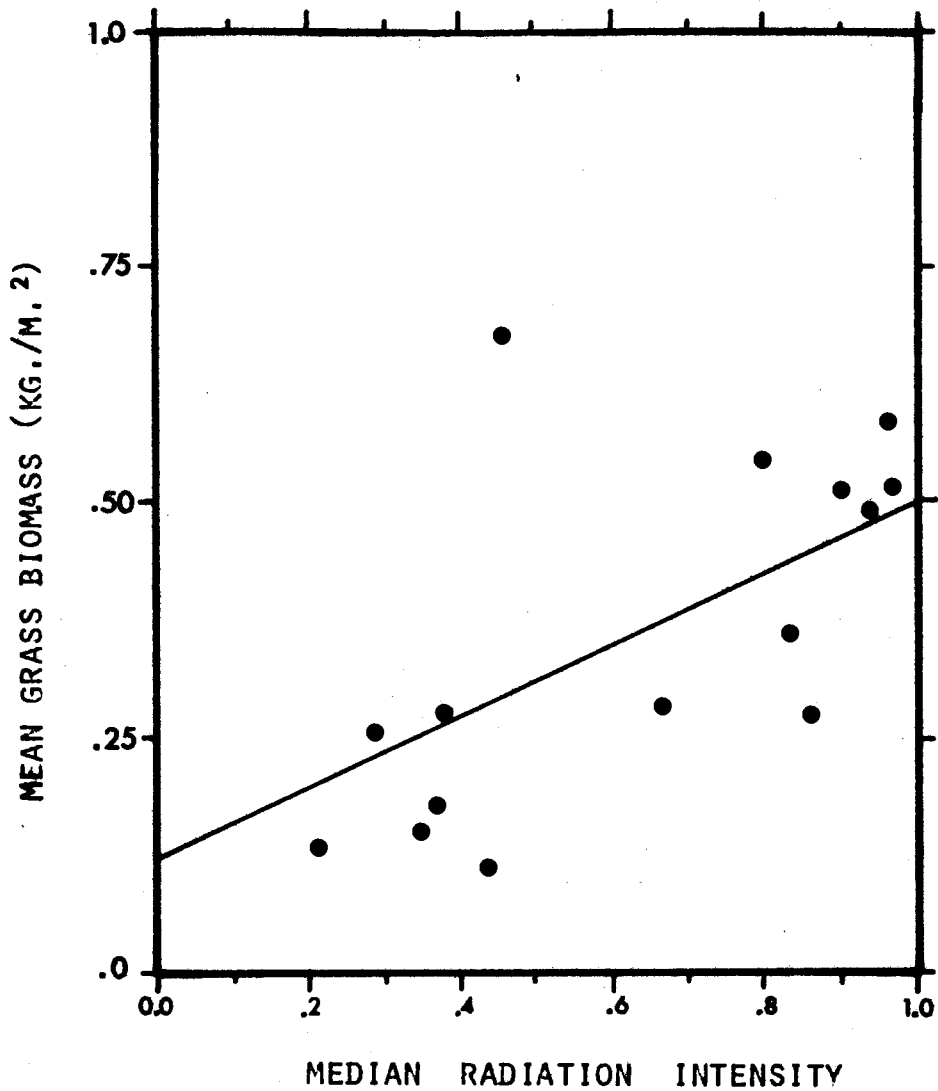


FIG. 6.4: MEAN GRASS BIOMASS IN THE SAMPLE STANDS EXPRESSED AS A FUNCTION OF THE MEDIAN RADIATION INTENSITY IN THAT STAND.

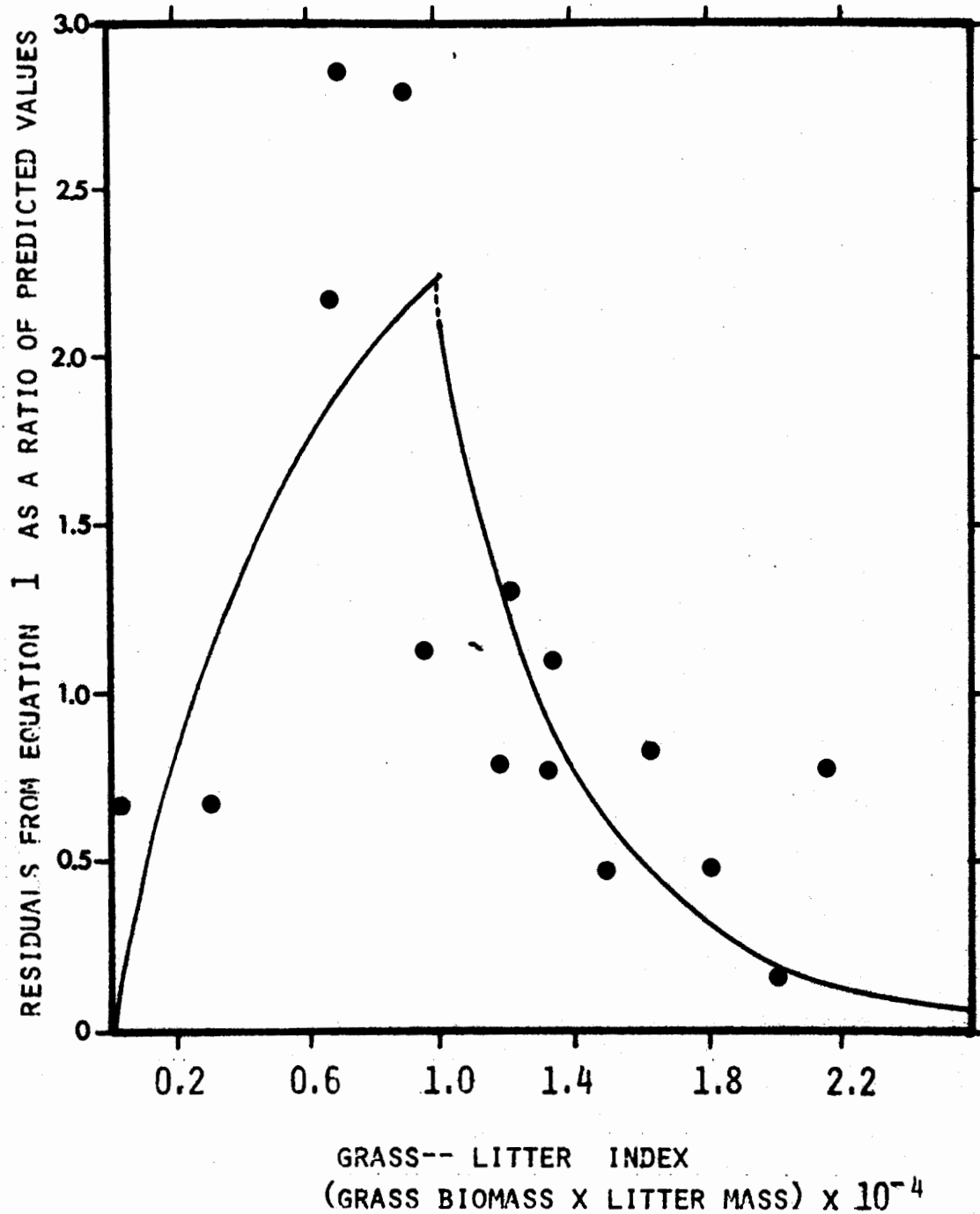


FIG. 6.5: RESIDUALS FROM THE THIRD-DEGREE POLYNOMIAL REGRESSION BETWEEN GERMINATION RATE AND MEDIAN RADIATION-INTENSITY EXPRESSED AS A FUNCTION OF THE GRASS-LITTER INDEX.

GRLT < 1.0: s = 0.8; a = 5.0.

GRLT > 1.0: s = 3.2; a = 50.0.

This function explains some 78 % of the residual variance and therefore SLITE and GRLT account for 82 % of the total variance in the germination data.

These combined equations are used to calculate the input of seedlings to PINUS. Because of the large amount of computer memory required to keep track of these young seedlings, the BIRTH subroutine also calculates first-year mortality and culls the number of seedlings accordingly. This is accomplished by an algorithm which expresses first-year mortality as a function of stand basal area (BASUM). Although the survivorship of first-year seedlings has been shown (Section 5.345) to be inversely correlated with litter depth, the relationship between survivorship and total stem basal-area (which is highly correlated with litter depth), is more mathematically tractable, and is substituted for litter depth in this section. The number of germinated seedlings (BORN) is derived by a logistic equation expressing the probability of surviving in each year (Fig. 6.6) according to this equation:

$$\text{BORN} = \text{BORN. 100} - \frac{95.0}{1 + e^{4.8+0.00076(\text{BASUM})}}$$

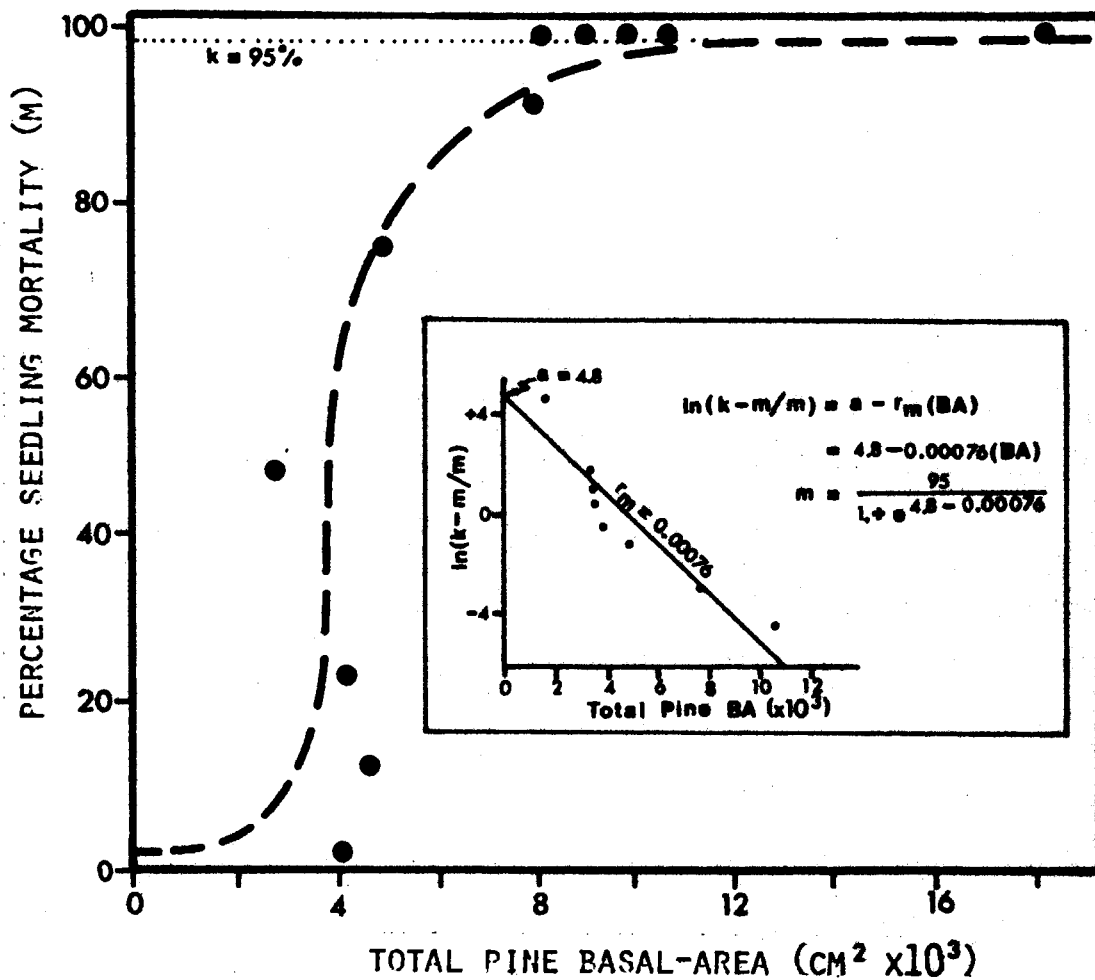


FIG. 6.6: MORTALITY OF SEEDLINGS OF P. CARIBAEA IN THEIR FIRST YEAR OF EXISTENCE AS A FUNCTION OF THE TOAL PINE BASAL-AREA IN THE STAND. INSERT SHOWS METHOD OF CALCULATING THE LOGISTIC EQUATION.

6.3: TREE MORPHOLOGY

The variability of tree dbh and height distributions in stands has been the subject of a number of studies (Meyer, 1930; Nelson, 1964; Bonnor, 1967). Attempts to model dbh distributions for instance have employed the geometric series (de Liocourt, 1898), the normal distribution (Lee, 1967), the gamma (Nelson, 1964, Hatch, 1971), the beta (Clutter and Bennett, 1965) or Charlier's distribution (Meyer, 1930). These approaches have been necessitated by the fact that all the above models omit the seedling stage, and therefore some means of generating an instantaneous stand is necessary. In models which incorporate seedling dynamics, no such artificial techniques are needed. In PINUS, as each stem attains breast height it is assigned a dbh of 2 cm. and the stochastic nature of seedling growth produces variable dbh distributions. The height of each seedling is assigned on the basis of its age-class, and is generated by the subroutine GAUSS, which calculates normally distributed random numbers based on the mean and standard deviations of the seedling height - age structure relations plotted in Fig. 5.3.

Height characteristics are generated by procedures outlined in the section on growth components. Tree volume (in cu.m.) is specified both as over-bark volume (VOB) and under-bark volume (VUB). These are two of the principal output variables in the model and are used to estimate stand yields.

$$VOB = 0.0001(BA:H.FF)$$

$$VUB = 0.00001198.DBH^{3.028}$$

where BA is the basal area of the tree and H is the height. The form-factor (FF) of 0.40 is the mean value found from increment plots in Mountain Pine Ridge. The equation for VUB is taken from Johnson and Chaffey (1973) for *P. caribaea* in Mountain Pine Ridge.

6.4: COMPETITION AND TREE GROWTH

The growth rate of a tree is a function not only of its genetic preadaptations to the environment, but also of the degree of competition it receives for radiant-energy, moisture and nutrients from neighbouring trees. For most pine species (see: Stiel, 1970) competition for radiant-energy appears to be the most limiting of the three. Several authors have proposed measures for quantifying competitive stress in forest stands. The area occupied by branches and roots varies with the size of the tree and can be considered the tree's "influence zone" (Zinke, 1962; Opie, 1968). The degree of invasion of the influence zone of one tree by those of its neighbours can then be utilised as an index of competition. Several such indices have been proposed (Lin, 1969; Newham, 1964; 1966; Mitchell, 1969; Bella, 1971; Lee, 1970; Keister, 1971; 1972; Hatch, 1971; Arney, 1971; 1973; 1974). All these measures require data on tree location so that the degree of overlap can be computed.

Where the locational variable is not taken into account, as in this simulator, some other criterion of the degree of competition is required. Botkin, Janak and Wallis (1970, 1972) propose that in small research plots, the radiation-intensity at the top of an individual crown at depth d in the canopy, can serve as such a measure. Their procedure entails the calculation of the total leaf-area of all other trees on the plot to express the degree of mutual shading of neighbouring trees. This can then be used as a surrogate for the more traditional competition index. Annual growth increments are then calculated directly based on the degree of shading. To utilise this technique data are required on the relationships between canopy structure, the radiation-intensity at the top of the canopy, and stem growth rate

6.41: Leaf Area, Foliage Distribution, and Radiation Intensity

There are several successive growth flushes each year in the pine stands of the research area, and each one is represented by repeated formation and release of terminal buds. Repeated elongation of the shoot apices produces a branching system which consists of an unneedled branch, about 50 - 100 cms. in length, from which the needles have aborted; followed by a thinly-needled portion, representing the oldest part of the current flush. This grades into a shoot on which the needles are much denser, culminating in a terminal bud surrounded by expanding

leaf primordia. Lateral shoots off the main branches possess the same sequence of features on a smaller scale.

Each growth flush is therefore represented by a distinct 'clump' of needle fascicles, separated from other such 'clumps' by unneedled or sparsely-needled branches. The size of these needle clumps varies somewhat with shoot vigour, decreasing in size with increasing shade towards the base and to the interior of the crown, but each needle clump forms a unit from which the total needle area and foliage profile of a pine crown can be computed.

In order to describe the relationship between leaf area, crown depth and foliage distribution in Pinus caribaea the following technique was employed. A sample of eight open-grown trees in the 15-20 year age-class was climbed and the number of needle clumps in 1-metre vertical intervals was estimated by measuring the height of the junction of the trunk with every branch, and counting the number of clumps on each branch. This method underestimates the amount of foliage at the top of each crown because of the negative geotropic response of pine branches particularly in the top 20% of the crown (Fig. 6.7), but these inaccuracies will be ignored in this discussion.

Two "average" branches were selected from the mid-portion of each crown, and were removed to determine the photosynthetic area of each needle clump. The length and width of each needle was



FIG. 6.7: AN OPEN-GROWN INDIVIDUAL OF PINUS
CARIBAEA, ILLUSTRATING THE DISTRIBUTION
OF NEEDLE "CLUMPS" AND THE FOLIAGE
PROFILE. (PHOTO BY LAMB, 1973.)

recorded, and the photosynthetic area of a single needle was estimated as simply $2(L \cdot W)$, where L and W are the needle length and width respectively. Each clump (Table VI.2) contained 100 - 300 needle fascicles (300 - 900 needles) representing 0.25 sq. m. photosynthetic area per clump, with both sides of the needles being measured.

The vertical distribution of needle area can be calculated using this data base (Fig. 6.8) and it can be seen that there is considerable variation in the canopy morphology between the sampled trees. The subject of foliage distribution and canopy geometry is discussed by Horn (1972), who contends that the optimum profile for early successional tree species, including pines, is an evenly-distributed array of foliage clusters throughout the depth of the canopy (= multi-layer strategy). Actual foliage distributions in pine canopies are described by Storey, Fons and Sauer (1955), Stiel (1962), Kinerson and Fritschen (1971), and Kinerson, Higginbotham and Chapman (1974). Their results indicate that foliage distributions may be approximated by a normal distribution, but Hall (1965) presents evidence which indicates that in older pine canopies this simple relationship breaks down, and there is considerable variation in the foliage profile of mature dominants.

Of the eight trees sampled, three (#3, 5 and 8) exhibit normal leaf-area distributions with canopy height, two, (1, 6) are log-normal, and the others are approximately uniform or

TABLE VI.2: MORPHOLOGY OF NEEDLE CLUMPS OF *P. CARIBAEA*.

| Length of Unneeded Branch (cm.) | Length of "Clump" (cm.) | # of Fascicles | Needle Density (needles/cm.) | Needle Area § (sq. m./"clump") |
|---------------------------------|-------------------------|----------------|------------------------------|--------------------------------|
| 96.5 | 15.2 | 198 | 39.1 | 0.25 |
| 79.0 | 26.0 | 210 | 24.2 | 0.27 |
| 53.0 | 32.0 | 268 | 25.1 | 0.34 |
| 18.5 | 10.0 | 90 | 27.0 | 0.16 |
| 25.0 | 16.0 | 146 | 27.4 | 0.26 |
| 62.0 | 8.0 | 84 | 31.5 | 0.15 |
| 31.0 | 10.2 | 188 | 27.6 | 0.33 |
| 25.0 | 13.0 | 132 | 30.5 | 0.23 |
| 19.0 | 33.0 | 250 | 22.7 | 0.45 |
| 42.0 | 26.5 | 233 | 26.4 | 0.30 |
| 53.0 | 18.0 | 170 | 28.3 | 0.22 |
| 67.0 | 28.0 | 274 | 29.4 | 0.35 |
| 29.5 | 15.5 | 135 | 26.2 | 0.17 |
| 17.0 | 11.0 | 137 | 37.4 | 0.17 |
| 48.0 | 29.5 | 237 | 24.1 | 0.30 |
| 51.0 | 31.0 | 317 | 30.5 | 0.40 |
| \bar{x} 41.6 | 20.2 | 192 | 28.6 | 0.25 |

§

Mean Surface Area of an Individual Needle = 4.22 sq. cm.
(n = 100 needles)

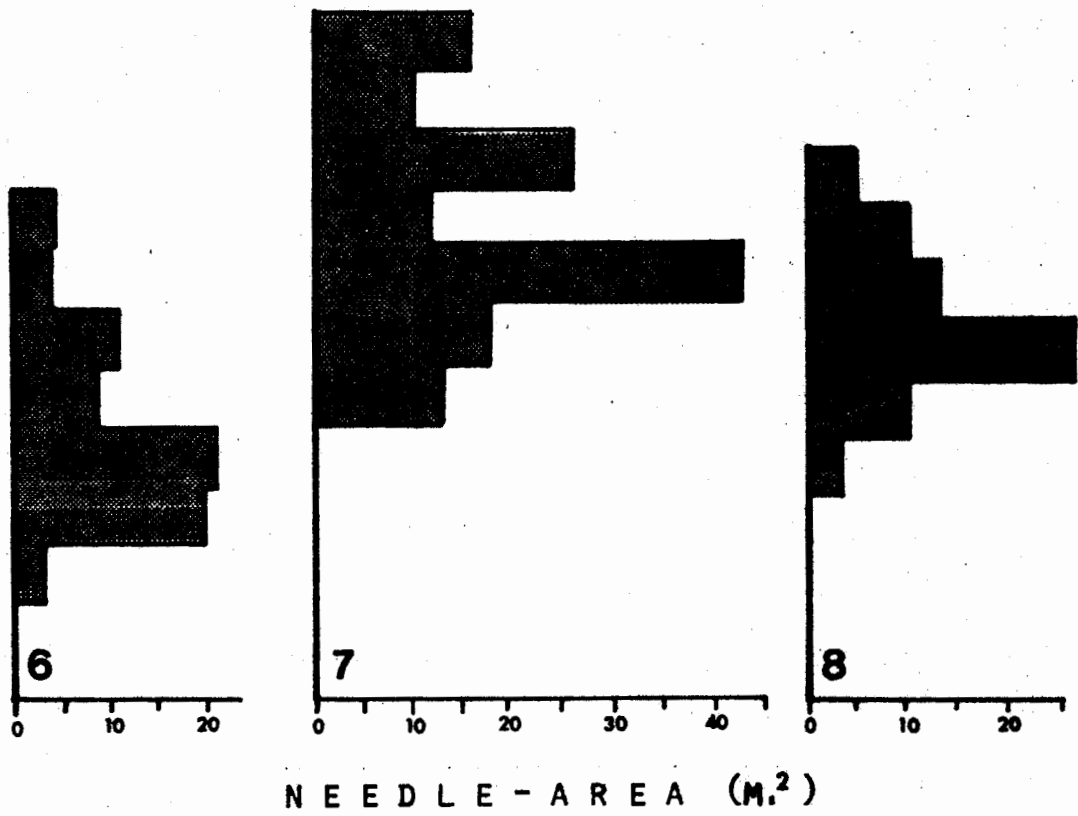
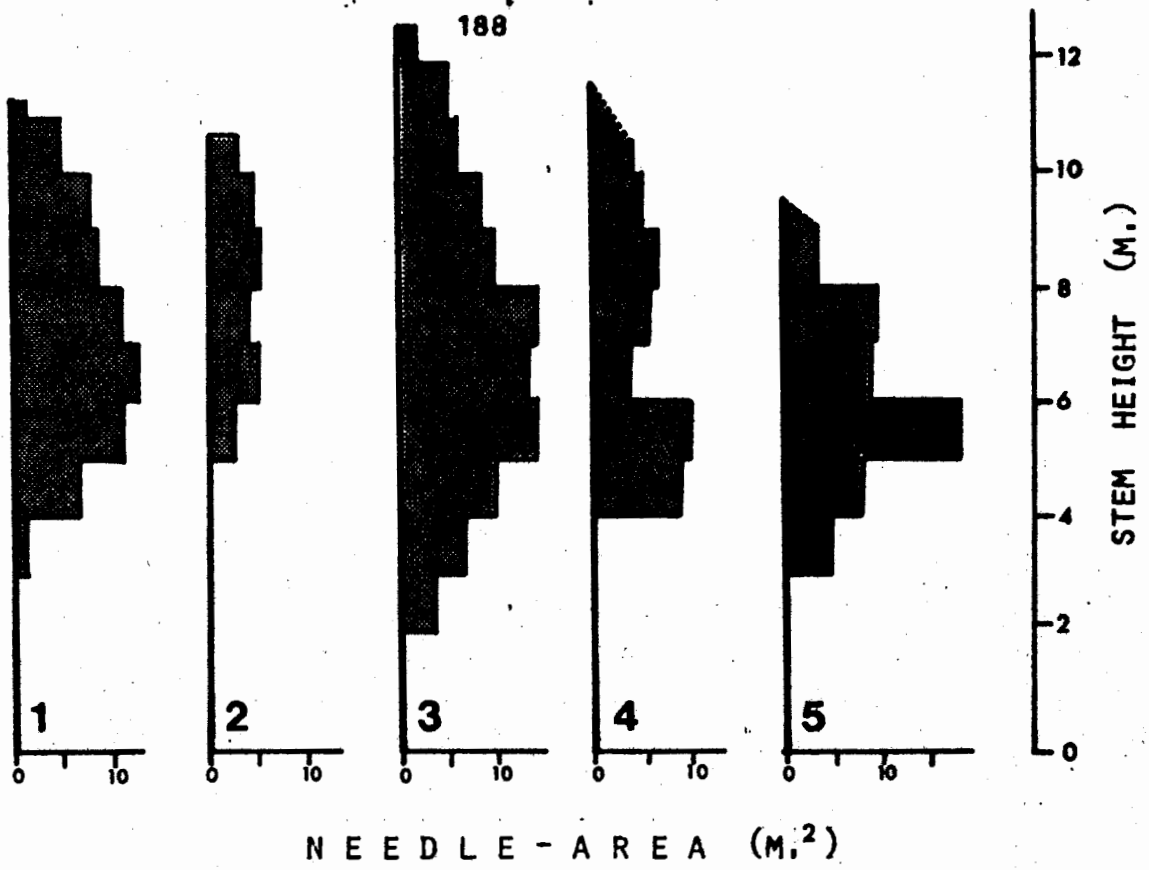


FIG. 6.8: NEEDLE-DISTRIBUTION PROFILES OF *P. CARIBAEA* TREES IN MOUNTAIN PINE RIDGE, BELIZE.

multimodal. These individual foliage profiles were averaged to form a composite profile. In Fig. 6.9a the composite profile represents the mean for all trees at all heights, whereas in Fig. 6.9b the profile is the mean for each one-third of the crown. Depending on the method used, either a log-normal profile (Fig. 6.9a), or an approximately uniform distribution (Fig. 6.9b), can be produced. Because of the ambiguous nature of these results, it was decided to proceed with the simplest distribution, the uniform (Fig. 6.9b), as a model for needle distribution in the canopy, as this entails fewer assumptions about the exact form of the distribution than with the alternative normal or log-normal distributions. The crown of P. caribaea is therefore represented by a cylinder with uniform foliage-distribution throughout its length.

There is a complex feedback mechanism linking needle area, productivity, tree size and radiation interception by the canopy. As early as 1864 Pressler proposed growth laws for forest trees, each of which stressed the controlling influence of crown-size on stem growth and morphology. Several authors have noted that this relationship can be investigated by regression analysis of stem morphology against foliage amount. Loomis, Phares and Crosby (1966) note that the slope of such a regression equation does not change with increasing stand density in plantations of P. echinata, so stand variables were omitted from the following analysis. Data on three morphological variables (Tree height,

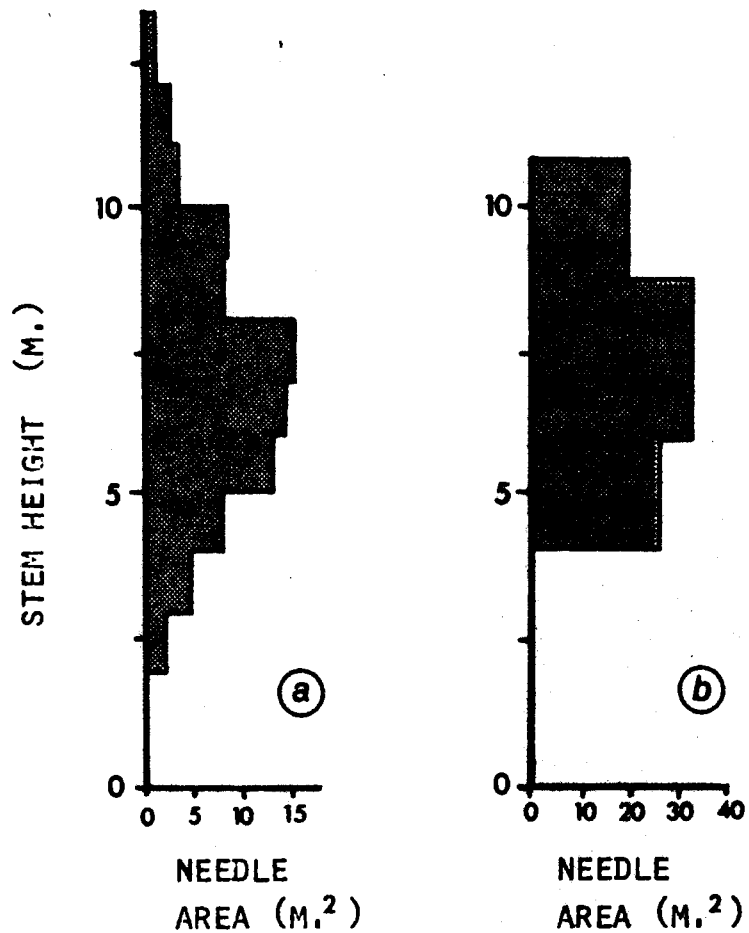


FIG. 6.9: MEAN NEEDLE-DISTRIBUTION PROFILES FOR THE SAMPLE OF *P. CARIBAEA* TREES PLOTTED IN FIG. 6.8.

IN (A) THE PROFILE IS FORMED BY CALCULATING THE MEAN FOR ALL TREES AT ALL STEM HEIGHTS.

IN (B) THE PROFILE REPRESENTS THE MEAN VALUE FOR EACH ONE-THIRD OF THE PROFILE OF EACH INDIVIDUAL TREE.

Basal area and Crown length) and the total needle area were recorded for a sample of 38 trees in stands of varying density in order to analyse their relationship. Linear regression analysis of the raw data indicated that all three morphological variables were highly correlated ($P=99\%$) with needle area, but that Basal area had the greatest predictive value (Fig. 6.10). The linearity of the relationship between the two variables is questionable however, and log-log transformation of the field data yields an r value of 0.88, compared to 0.82 for the linear model. This transformation produces an equation of the form:

$$ELA = 0.10.BA^{1.0} \quad [2]$$

where ELA is the estimated needle area for each tree. The predicted values of this equation are compared with those of Kinerson, Higgingbotham and Chapman (op.cit.) for *P. taeda* in Fig. 6.11. It can be seen that there is a fairly close correspondence between the two over the range of common values.

The subject of the relationship between foliage distribution, canopy depth, leaf area and radiation intensity has been treated in a number of theoretical papers (see for example: Monsi and Saeki, 1953; Kasanga and Monsi, 1954; Saeki, 1960; Donald, 1961; Verhagen, Wilson and Britten, 1963; Loomis, Williams and Duncan, 1967; Monsi, 1968; Monsi, Uchijima and Oikawa, 1973). These workers describe the interception of solar radiation by the plant canopy as conforming to a negative exponential relationship, generally expressed as Beer's Law:

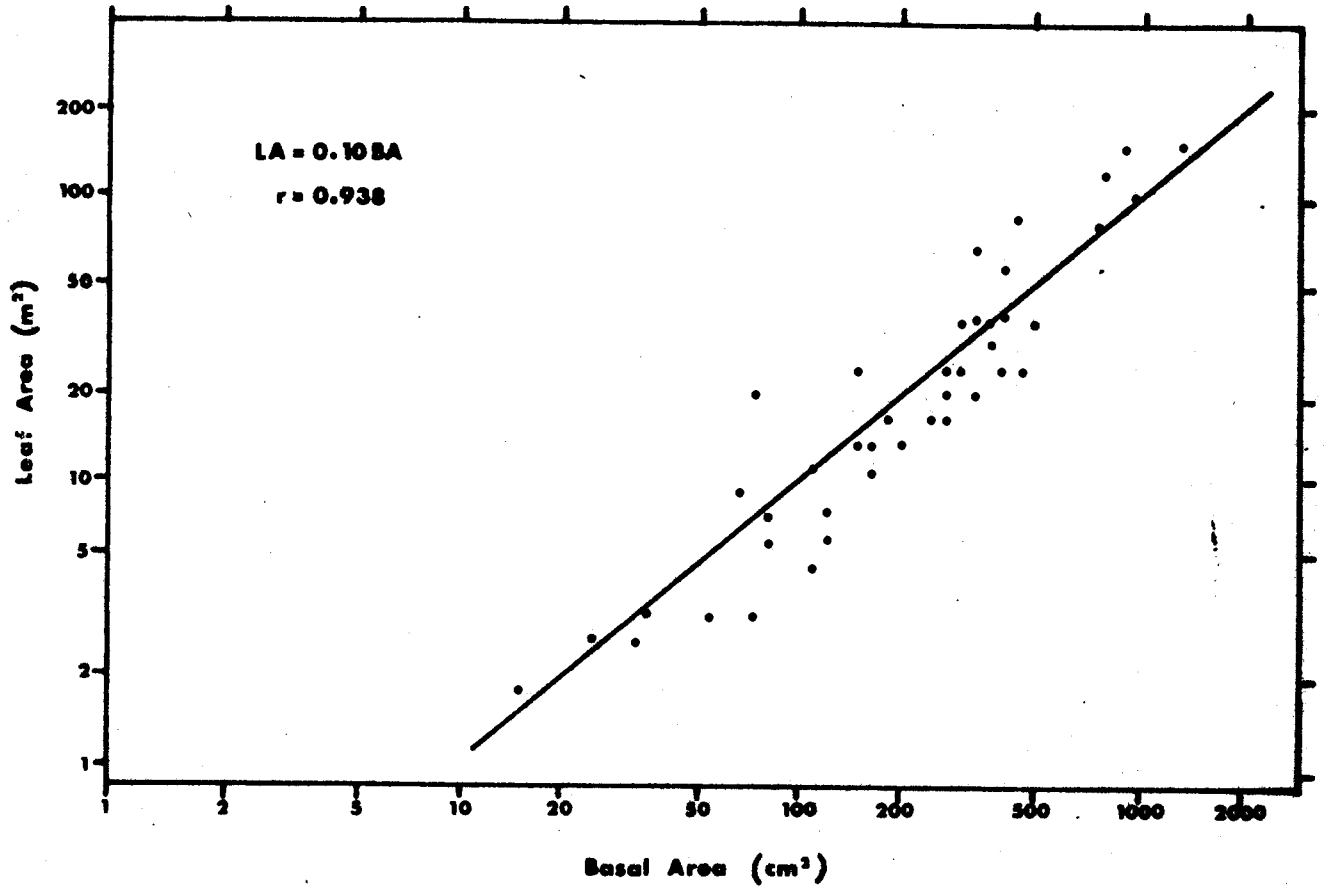


FIG. 6.10; NEEDLE-AREA AS A FUNCTION OF STEM BASAL-AREA FOR INDIVIDUALS OF *P. CARIBAEA*.

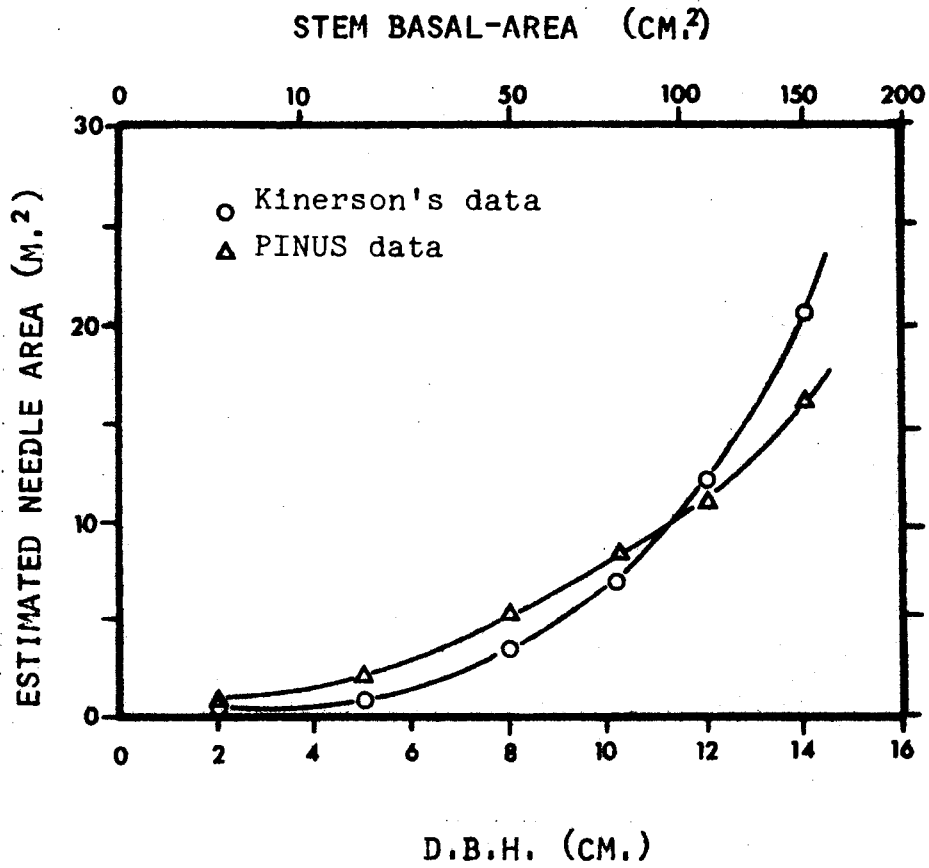


FIG. 6.11: NEEDLE-AREA ESTIMATES USED IN THE PINUS MODEL AND IN KINERSON ET ALIA (1974).

$$I_d = I_0 \cdot e^{-k \cdot L} \quad [3]$$

where: I_d = radiation intensity at depth d in the canopy

I_0 = radiation intensity at the top of the canopy

k = extinction coefficient

L = leaf area index (=leaf area per unit ground area)

For single plants this relationship holds true only if the leaves are arranged randomly in the horizontal plane, which is patently not the case for most species. Alternative radiation penetration models which incorporate information on phyllotaxy and leaf inclination angles have been developed, notably by Saeki, Iwaka and Monsi (1965) Nichiporovich (1963) and Monsi, Uchijima and Oikawa (op.cit.), but the advantage of increased resolution of these models is offset by such greater data-gathering effort in the field. The regular spacing of crop plants, and their fairly simple foliage architecture make this increase in data collection viable in agronomic research, but in silvicultural applications the environmental patchiness that is a feature of forest stands before the canopy has closed produces a very complex and variable woodland radiation environment, and, as far as is known, no attempt has yet been made to apply non-random foliage distribution models to tree canopies. Consequently in the present study Beer's law will be retained as a working model of canopy illumination.

The only modification that is made is that the subroutine GROW does not calculate the total leaf-area of the canopy but instead sums the needle areas of all partial or complete crowns above depth d to compute the radiation intensity on that plane (Fig. 6.12). Radiation-intensity in the model is expressed on a dimensionless scale from 1.0 (full sun) to 0.0 (full shade).

The magnitude of the extinction coefficient k in equation [3] can be calculated from field data on the radiant-energy reaching the forest floor at solar noon presented in Chapter Four. Although these data were collected at forest floor level, it is presumed that a constant relationship exists between total leaf area and the degree of shading at all levels in the canopy. Computing the total needle-areas on each plot using equation [2] and plotting these against recorded median-radiation data transformed to a 0.0 - 1.0 scale (Fig. 6.13) yields the following relationship:

$$AL = I_d = I_o \cdot e^{-0.00058 \cdot SLA} \quad [4]$$

where SLA is the summed needle area of all higher canopies. This is equivalent to a radiation extinction coefficient of 0.23, which is close to values quoted by Satoo (1967) for stands of *P. densiflora* in Japan.

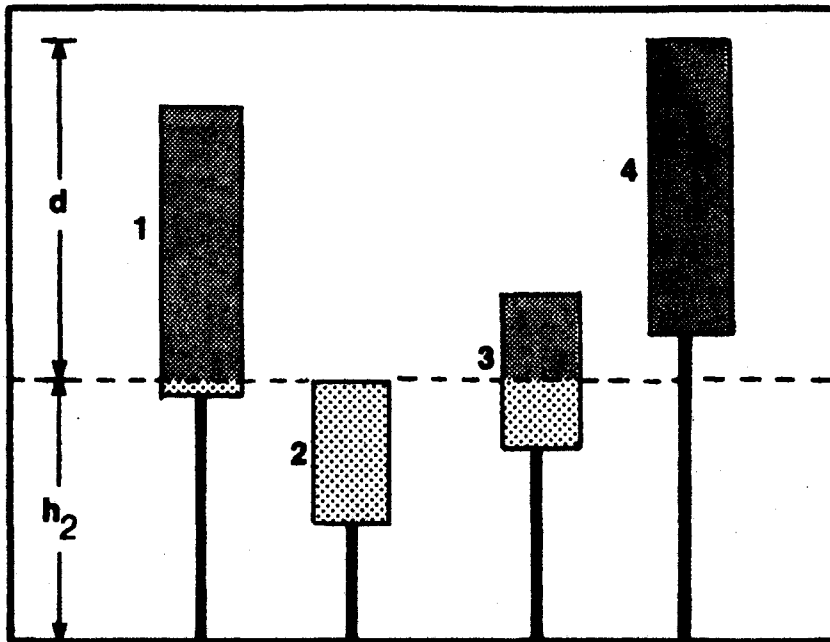


FIG. 6.12: METHOD OF CALCULATING RADIATION-INTENSITIES IN THE TREE CANOPY ADOPTED IN THE PINUS MODEL. FOR EXAMPLE, THE RADIATION INTENSITY AT DEPTH d IN THE CANOPY (AT THE TOP OF TREE #2), IS CALCULATED BY SUMMING THE LEAF-AREAS OF ALL ENTIRE OR PARTIAL CANOPIES ABOVE THE HEIGHT OF THIS INDIVIDUAL (h_2).

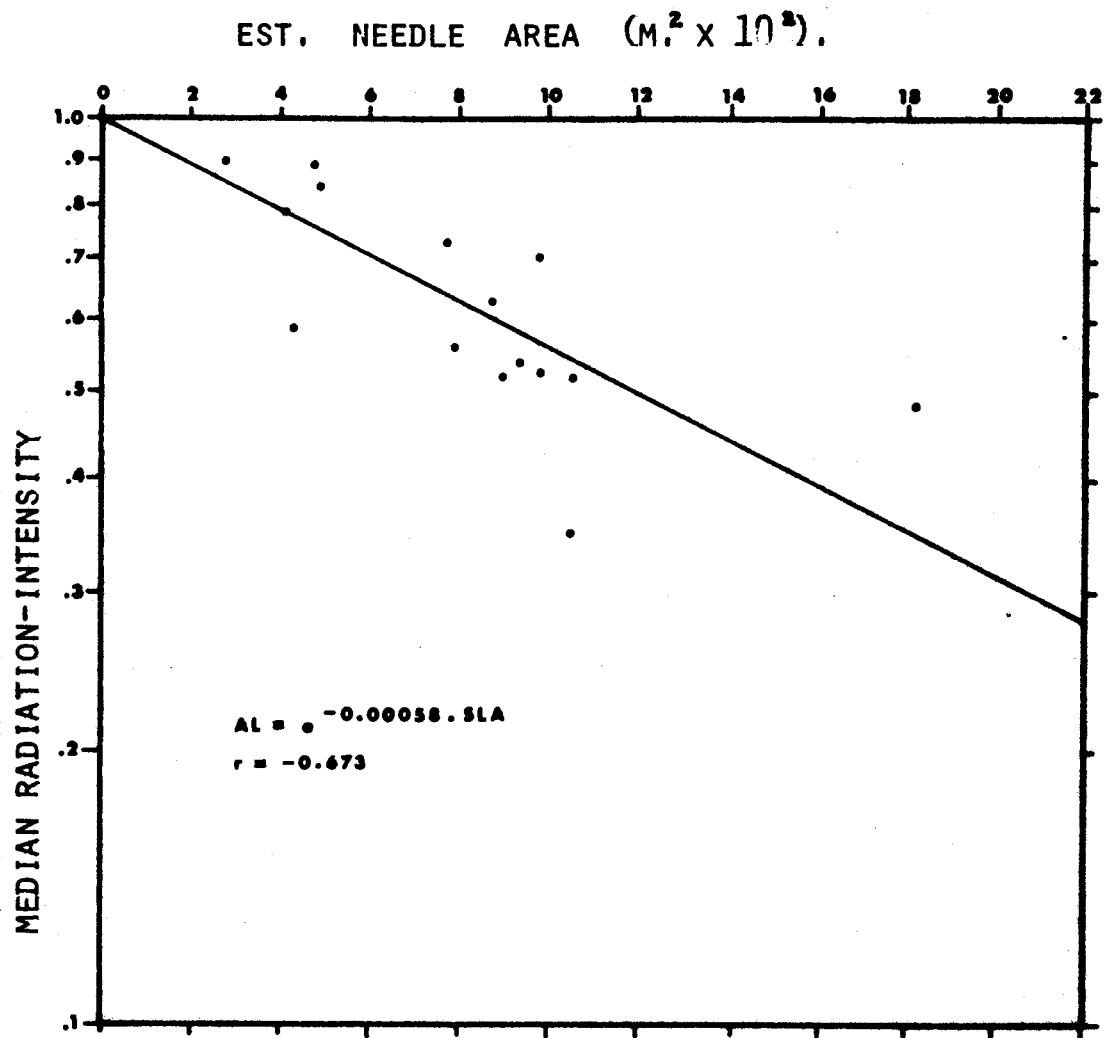


FIG. 6.13: MEDIAN RADIATION-INTENSITY AS A FUNCTION OF THE TOTAL NEEDLE AREA IN A STAND.

6.42: Crown Length

In order to employ equation [4] to calculate the degree of mutual shading in the stand, the canopy depth of individual trees must be known. The length of the crown is influenced both by tree size and the degree of canopy closure. Ware and Stahelin (1948) show that the mean crown-length ratio (C.L.R. = crown length as a proportion of total tree height) in 14 year-old plantations of various southern pine species is strongly correlated with stand density. To check these interrelationships the crown-lengths of all the trees (n= 1007) on 18 0.04 ha. (0.1 acre) quadrats were measured in the Granite Basin Area. The base of the crown was taken as the height of the lowest live branch in each case. Plotting of the C.L.R. of individual trees against tree height in two plantation stands (Fig. 6.14) gives some indication of the variability of these data. It is apparent that the morphology of the stem is of little predictive value in determining the C.L.R. of the individual. Consequently an attempt was made to predict mean C.L.R.'s per stand using two stand variables (density and age of dominants), and then apply these mean values to individual trees. A multiple linear regression analysis (Table VI.4) of the stand data indicated that only one regression coefficient was significant ($t = 1.75$; $p = 95\%$) and so we can conclude that the mean C.L.R. of a stand may be predicted from the relation

$$\text{C.L.R.} = 0.0672 - 0.002.D \quad (r^2 = 0.619)$$

STEM HEIGHT (M.)

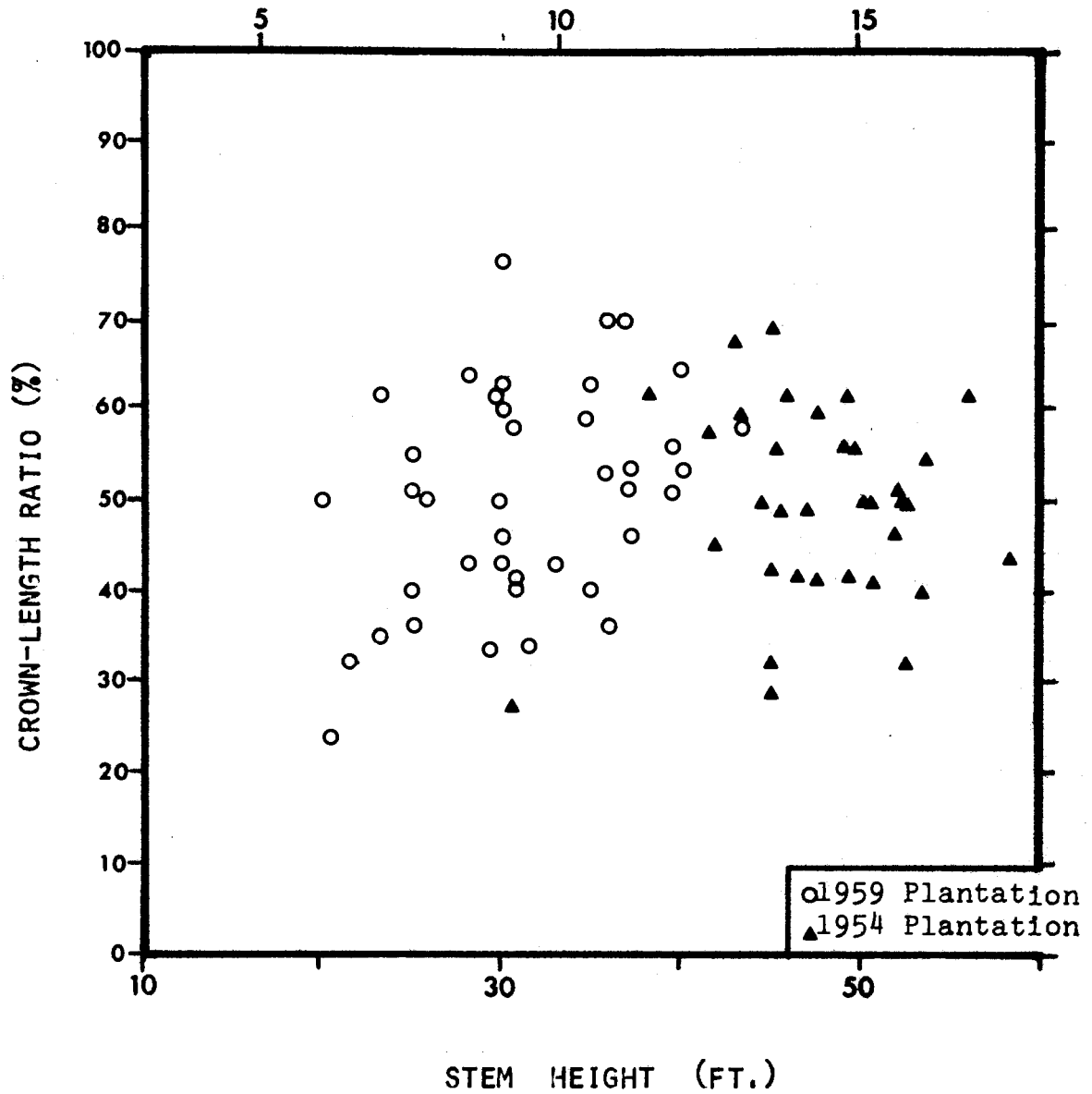


FIG. 6.14: THE CROWN-LENGTH RATIO OF INDIVIDUAL TREES OF P. CARIBAEA EXPRESSED AS A FUNCTION OF STEM HEIGHT

TABLE VI.3: ANALYSIS OF THE EFFECTS OF STAND AGE AND DENSITY ON THE MEAN CROWN LENGTH RATION IN A STAND.

Multiple Correlation

| <u>Variables</u> | <u>Multiple r</u> | <u>% explanation</u> |
|------------------|-------------------|----------------------|
| Stand Density | - 0.787 | 61.94 |
| Stand Age | - 0.803 | 2.54 |

Regression Coefficients

| <u>Variables</u> | <u>Coefficient</u> | <u>Beta Coefficient</u> |
|------------------|--------------------|-------------------------|
| Constant | 0.672 | |
| Stand Density | - 0.002 | - 0.850 |
| Stand Age | - 0.0014 | - 0.123 |

Partial Correlation

| <u>Variables</u> | <u>Partial Corr. Coeff.</u> | <u>R² - Delete</u> |
|------------------|-----------------------------|-------------------------------|
| Stand Density | - 0.787 | 0.065 |
| Stand Age | - 0.182 | 0.632 |

where D is the stem density / quadrat. Plotting of these results alongside those of Ware and Stahelin (op. cit.; Fig. 6.15) indicates a close correspondence in the response of the three tree species to canopy closure.

6.43: Growth Components

The growth rate equations presented here are taken directly from the JABOWA stand simulator of Botkin, Janak and Wallis (1970, 1972).

"The model consists of a basic growth rate equation ... that may be taken to represent the rate of growth of a tree with optimum site quality and no competition from other trees. For each plot-year this growth rate is decreased by factors taking into account shading and shade-tolerance, soil quality, and average climate as measured by the number of growing degree-days".

Botkin, Janak and Wallis, 1972: p. 853.

As the study area is only 600 sq. km. in areal extent and restricted to one lithological unit, the climatic and edaphic variables are omitted from this model, and shading alone is retained. The PINUS equation for a tree growing under optimum conditions becomes:

$$(D^2H) = R \cdot ELA \cdot \left(1 - \frac{D \cdot H}{D_{\max} \cdot H_{\max}}\right) \quad [5]$$

in which D is tree dbh, H is its height, with DMAX and HMAX being maximum values of these quantities. ELA is the estimated leaf area, and R is a constant. For P. caribaea the maximum

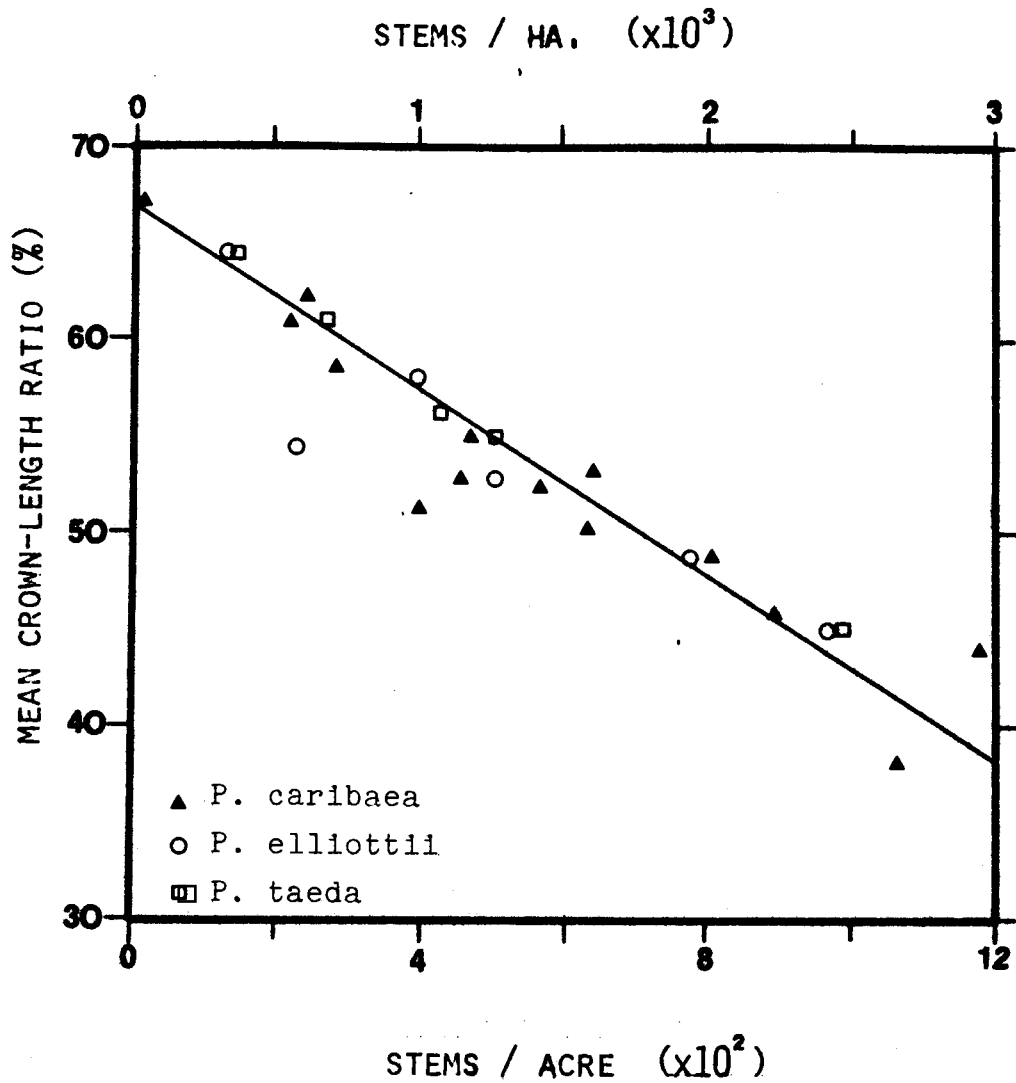


FIG. 6.15: THE MEAN CROWN-LENGTH RATIO IN A STAND EXPRESSED AS A FUNCTION OF STAND DENSITY.

values of these size variables in the study area are:

$$D_{MAX} = 50 \text{ cms.}, H_{MAX} = 3300 \text{ cms.}$$

The model assumes that the annual growth increment of a tree is proportional to the radiation it receives, derated by a factor $(1 - DH/D_{MAX} \cdot H_{MAX})$ which represents the respiratory activity of the tree over the same period. In other words it is assumed that there is a linear increase in maintenance metabolic activity with increasing tree size ($D^2 H$), and consequently growth becomes asymptotic to D_{MAX} , H_{MAX} as $t \rightarrow \infty$.

The height of a tree (in cm.) with dbh D (in cm.) is given by the polynomial:

$$H = 137.0 + b_2 D - b_3 D^2$$

derived from Ker and Smith (1955). The constants b_2 and b_3 are calculated by:

$$b_2 = 2(H_{max} - 137)/D_{max}$$

$$b_3 = (H_{max} - 137)/D_{max}^2$$

so that when $D=D_{MAX}$, $H=H_{MAX}$ and $dH/dD = 0$. Equation [5] can be rewritten in the form:

$$DEST = G \cdot D \cdot \frac{(1 - D \cdot H / D_{max} \cdot H_{max})}{(274 + 3b_2 D - 4b_3 D^2)} \quad [6]$$

where $DEST$ is the annual dbh increment. The constant G in this equation sets the initial growth rate of young pines, and is chosen so that the ratio of $D/D_{MAX} = 2/3$ for a tree of half the maximum age (Botkin, Janak and Wallis, op. cit.). The maximum

age of P. caribaea is unknown, but is taken as 100 years, as the oldest tree cored in Mountain Pine Ridge gave an estimated age of 85 years. Although site conditions are initially assumed to be constant, variations in site quality can be incorporated into PINUS by altering the value of G, such that:

$$G = 13 (SI)$$

where the site index (SI) is the mean height of the dominants at 25 years (in meters).

Equation [6] models the optimum growth rate for a tree growing in the absence of competition. In sub-optimal conditions this growth-rate is derated by the function $r(AL)$ which relates growth rate to the effects of radiation competition in the canopy.

No data are available in the research literature on the photosynthetic rate of P. caribaea at various radiation intensities, but it is unlikely to be significantly different from that of other pines (see: Logan, 1966; and Fig. 6.16). Utilising these data the photosynthetic rate of P. caribaea can be expressed as:

$$r(AL) = 2.24(1 - e^{-1.136(AL - 0.08)})$$

where AL is the available radiation calculated by equation [4]. The growth rate of each tree is therefore determined by the radiation intensity at the top of the crown (Fig. 6.12). In

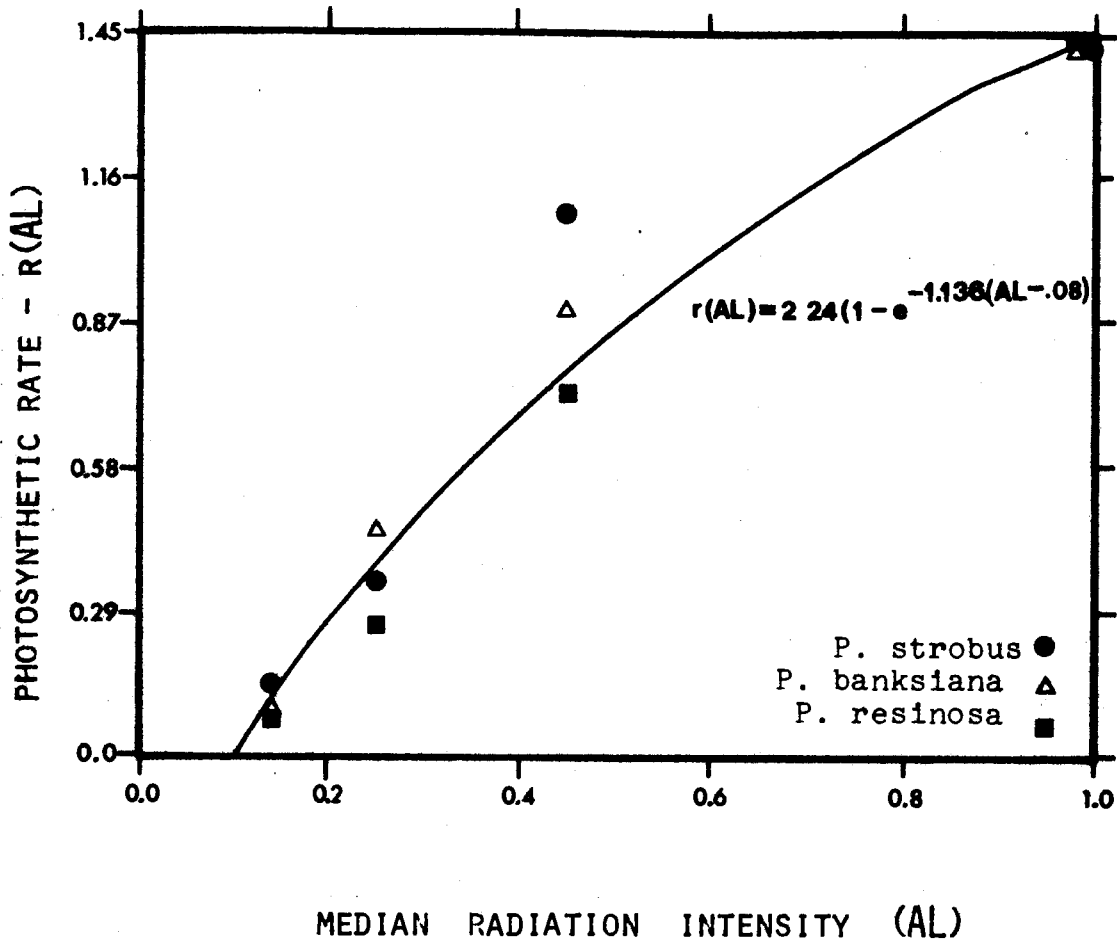


FIG. 6.16: PHOTOSYNTHETIC RATE EXPRESSED AS A FUNCTION OF MEDIAN RADIATION INTENSITY (AL) FOR THREE SPECIES OF PINES (DATA SOURCE: LOGAN, 196).

reality however, genotypic and phenotypic factors also play a role in determining tree growth rate. These can range from variables such as the location of the tree relative to its neighbours, which affects radial growth of the crown and moisture and nutrient competition, to relatively minor variables such as the susceptibility of the tree to folivore attack. These other factors are lumped together by PINUS in an algorithm which calculates the diameter growth of the tree, in a stochastic fashion.

Analysis of the annual growth data from a single increment plot (A21) in the study area over a seven-year period demonstrate that there is considerable variation in annual growth by individual trees, possibly as a response to variable moisture levels. These annual growth values can be approximated by a log-normal distribution, in which the standard deviation of the data values can be estimated by the relation $S.D = 0.2 (DEST)$ where DEST is the mean annual increment in diameter calculated by equation [6]. The GROW subroutine models annual growth variations by generating a normally-distributed pseudo-random number with mean DEST and standard deviation DSTD by a call to subroutine GAUSS. Annual height increments are calculated from the regression:

$$HEST = 0.60.DINC^{0.60}$$

where DINC is the stochastic dbh increment returned by GAUSS. This regression is based on an analysis of the diameter -

height increment relations of a random sample of 100 trees from the increment plots in Mountain Pine Ridge.

6.5: MORTALITY

Although data on seedling mortality rates are available for a few species, (Hett and Loucks 1968; Campbell and Mann, 1973) there is very little information on the mortality rates of mature trees. Most information of this sort is contained in reports on the yield and survival of a few commercial species in plantations (eg. Bennett, 1956, 1963; Ware and Stahelin, 1948; Enghardt and Mann, 1972). Because of constraints such as the regularity of spacing and frequent cleaning and thinning of these stands their application to natural stands may be questionable.

Survivorship data for P. caribaea in Mountain Pine Ridge are equally sparse. None of the trees included in the increment plots laid out in 1967 have as yet died, and these data serve only to indicate the low degree of competition and high survivorship rates of trees between 15-30 years old in this environment. The 1959 planting of P. caribaea was divided into two plots, and each was planted with 3 month old seedlings with a 8 x 8 ft (2.4 x 2.4 m) spacing. Over the first four years seedling mortality averaged 6.5% p.a. (Fig. 6.17), but in the ensuing decade this was sharply reduced to 0.4 % mortality per year.

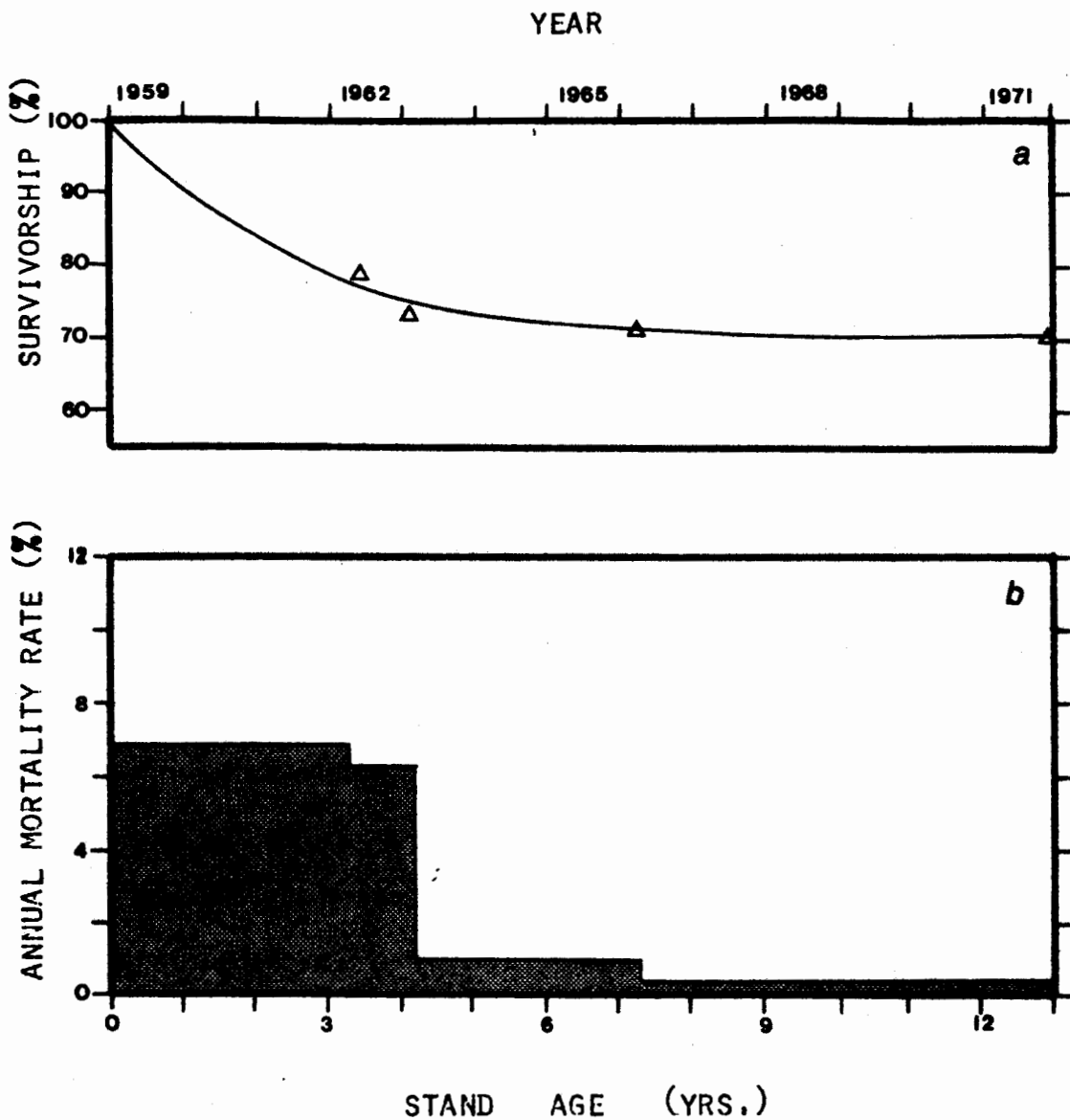


FIG. 6.17: PERCENTAGE SURVIVORSHIP AND ANNUAL MORTALITY RATES IN A PLANTATION OF PINUS CARIBAEA, ESTABLISHED IN 1959, MOUNTAIN PINE RIDGE, BELIZE.

It is necessary in an individual tree model to simulate mortality not only in terms of annual rates in the stand, but also in terms of assigning individual trees to be killed. Trees can die from processes that may be entirely random such as lightning, fire, windthrow; semi-random, such as infection by pathogens, or from non-random processes such as suppression. The first group of processes can be easily simulated if the probabilities of occurrence of these events are known. Mortality from competitive stress presents a more difficult problem however.

The progressive decrease in crown size in relation to the stem volume of an aging or suppressed tree results in a decrease in the ratio of photosynthetic output to respiratory consumption (Kozlowski, 1971). Translocation of water and essential compounds becomes increasingly difficult and enzymatic and hormonal activity decline.

The probability of mortality can thus be assessed on the basis of the competitive status of the individual tree. Most authors have adopted fairly arbitrary decision rules at this point. For instance, Newnham (1964) assumed that a tree died when its growth rate over a five-year period fell below a threshold value. Lin (1969), working with a stand simulator for Tsuga heterophylla in Oregon, used certain competition criteria to define suppression, and any tree remaining suppressed over a six year period was considered dead.

Keister (1972) employed two variables as predictors of mortality: his competition index (I) (Keister, 1971) and the average competition (R) of neighbouring trees (n) such that $R=I/n$. Field tests of the method indicated that trees with R values $> .5$ had a high risk of mortality ($p= 0.61$ over 5 years) compared with trees with lower R values ($p = .08$ over the same period).

The assumption made in PINUS is that the annual volume increment of a tree relative to the maximum volume-increment of trees in its age-class is a direct measure of the degree of competition the tree is suffering. Dr. Keister kindly made his field data on the causes and amount of mortality in P. elliotii and P. taeda plantations in Louisiana available to me in order to test this assumption. This somewhat desperate expedient was necessitated by the complete absence of such data for P. caribaea in Belize.

The similarity of ecological response to competition and canopy closure of the three species is evidenced by Fig. 6.15, and it is presumed that this similarity extends to mortality induced by competitive stress. The available evidence indicates that mortality rates in plantations of the three species are similar over common stocking levels (Fig. 6.18).

The Louisiana data are based on eight pine plantations (mainly of P. elliotii), ranging in age at initial measurement from 9 - 16 years. In the first four years of data collection

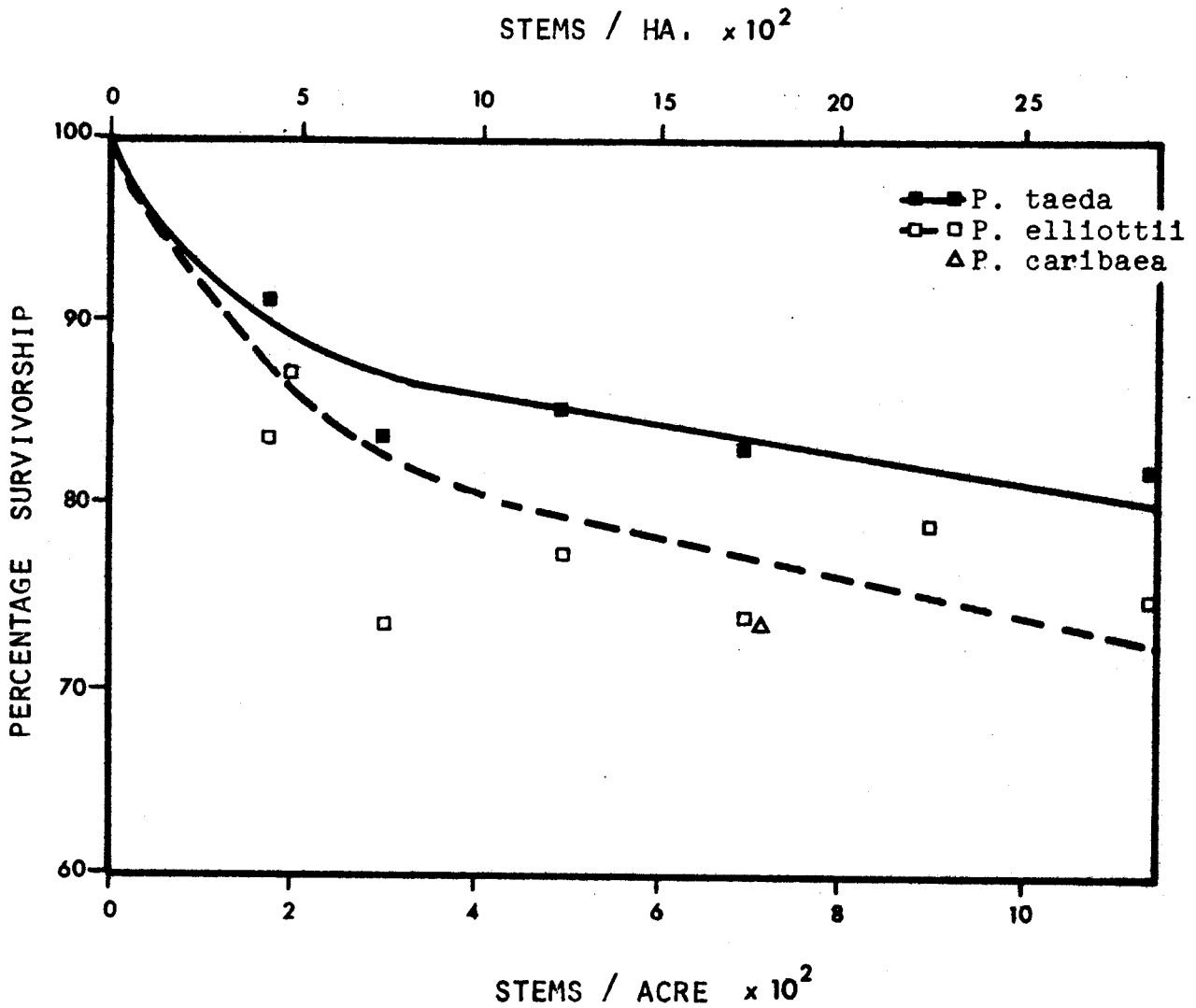


FIG. 6.18: PERCENTAGE SURVIVORSHIP OVER THE INITIAL 15 - YEAR PERIOD AS A FUNCTION OF INITIAL STAND DENSITY IN PLANTATIONS OF PINUS TAEDA, P. ELLIOTTII, AND P. CARIBAEA

201 of the initial population of 2485 trees died, of which 13 (= 0.1 % p.a. mortality) died from windthrow, fire and lightning. The other 188 apparently died from suppression; most of these were small, averaging 2.4 " (6 cms.) less than the plot mean in dbh, indicating a suppression-mortality rate of 1.9 % p.a. overall. Lee (1970), reported similar results for young stands of P. contorta. His data show that trees dying from competition were on average 2" (5 cms.) smaller in dbh than the stand mean.

When the mortality rates of trees in successive volume-increment classes are computed (Table VI.4), it can be seen that mean annual volume-increment does correlate closely with declining mortality rates (Fig. 6.19; $r = -.954$). Assuming this relationship holds true for P. caribaea, we can therefore establish the probability of mortality of an individual tree as:

$$P_{\text{mort}} = 0.04467(e^{-0.004(\text{vinc}/\text{vcoef})})$$

where VINC is the calculated overbark increment in volume (in cm.) and VCOEF is a proportionality coefficient; the ratio between mean volume increments in successive age-classes relative to the mean age-class (10-15 years) in Keister's data. The ratio indicates that mortality is not dependent upon absolute increment, but is proportional to the potential increment in each age-class. The values of the VCOEF index are computed by comparing the volume-increment /stem-volume ratio for fully-stocked stands of various ages with this same ratio for stands

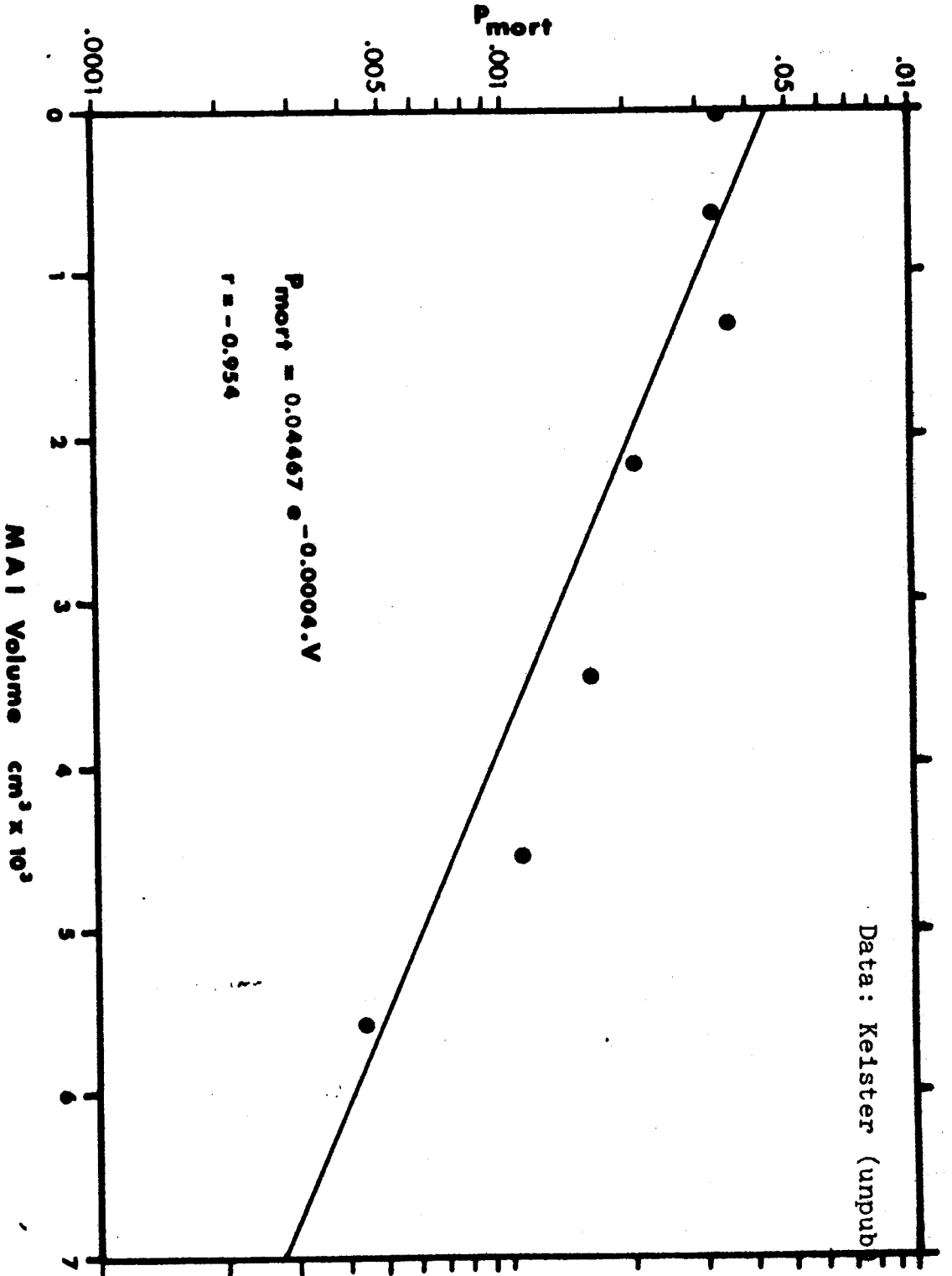


FIG. 6.19: PROBABILITY OF MORTALITY AS A FUNCTION OF ANNUAL VOLUME-INCREMENT IN PLANTATION-GROWN P. ELLIOTTII AND P. TAEDA.

TABLE VI.4: COMPETITION-RELATED MORTALITY AS A FUNCTION
OF CURRENT VOLUME-INCREMENT IN PLANTATIONS OF
PINUS TAEDA AND P. ELLIOTTII FROM LOUISIANA.

| Mean Volume Increment (cu. cm.) | # Alive | # Dying | Probability of Mortality (%) |
|---------------------------------------|------------|------------|--------------------------------------|
| 0 | 2639 | 91 | 3.45 |
| 622 | 119 | 4 | 3.36 |
| 1300 | 110 | 4 | 3.64 |
| 2180 | 145 | 3 | 2.07 |
| 3460 | 241 | 4 | 1.66 |
| 4530 | 186 | 2 | 1.07 |
| 5600 | 228 | 1 | 0.44 |
| 6700 | 217 | 0 | - |
| 7800 | 172 | 0 | - |
| 8900 | 144 | 0 | - |
| 10000 | 201 | 0 | - |

in the 10-15 year age-class (Table VI.5). The data are taken from yield tables for *P. taeda* prepared by Wahlenberg (1960).

The MORT subroutine calculates PMORT for each tree in the stand and then summons the subroutine RANDU to generate a uniform random number between 0 and 1. If the calculated value of PMORT is greater than the random number then the tree is killed. For example, a 10-15 year-old tree making no growth in any one year has a probability of mortality of 0.0446 in that year. If a random number smaller than this value is generated, the individual would be recorded as having died.

Juvenile mortality cannot be estimated by this technique as volume increment is not calculated. Therefore mortality at this stage is programmed as a function of the height of the seedling and the amount of radiation it receives at the top of the crown (Fig. 6.20). This approach is consistent with that adopted for mature individuals, as the annual volume increment is directly dependent on the available radiation received by the tree. It can also be justified on theoretical grounds. Pine seedlings with primary needles, alone or mixed with secondary needles, attain maximum photosynthesis at ~2500 ft-c (Kozlowski, 1972). This is because the photosynthetic apparatus of individual needles saturates out at this radiation intensity, and the lack of mutual shading of needles in very young seedlings, (< 1 year) means that the whole seedling saturates at ~ 2500 ft-c. As the seedling ages secondary needles grow and clusters of needles

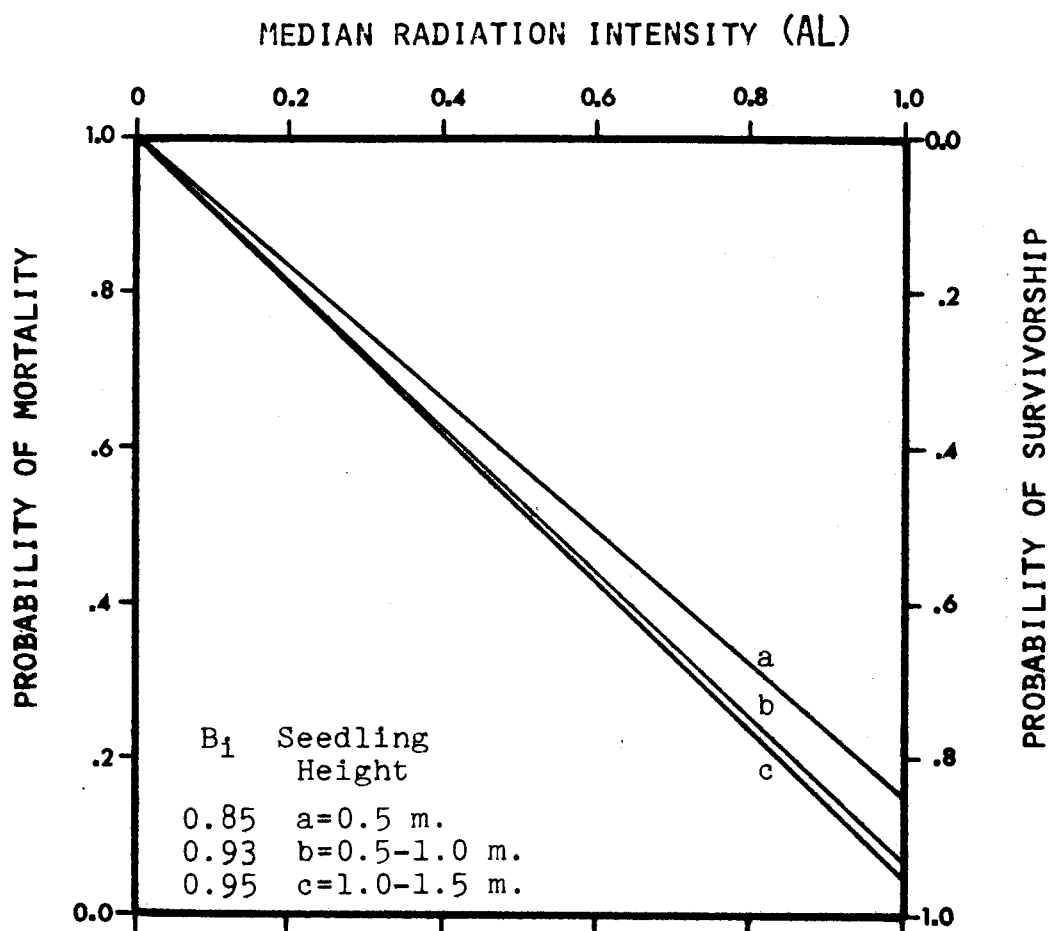


FIG. 6.19: PROBABILITY OF SEEDLING MORTALITY AS A FUNCTION OF MEDIAN RADIATION INTENSITY. THE INTERCEPTS (B_i VALUES), ARE DERIVED FROM AN ANALYSIS OF MORTALITY IN THE 1959 PLANTATION OF PINUS CARIBAEA (SEE FIG. 6.16).

develop. In this situation self-shading of needles occurs, and the apparent photosynthesis of young seedlings over 1 year-old declines with lower radiation intensities, and photosynthesis becomes almost a linear function of radiation intensity over the 1,000 - 10,000 ft-c. range as the seedling ages (Bormann, 1956).

PINUS assumes that survivorship also declines linearly with ambient radiation intensity (Fig. 6.20). Mortality of seedlings can therefore be modelled as:

$$P_{\text{mort}} = B_1 \cdot AL$$

where the B_i are constants for various seedling height classes estimated from the available plantation data. The procedure used to kill seedlings is the same from this point on as that for killing mature trees.

Finally MORT summons an accounting subroutine LIST which keeps track of the number of trees dying, their individual characteristics, then condenses the live-tree array by removing all dead trees. On return, MORT calculates summary statistics for the mortality in each year, and accumulates these values.

Output from the model consists of a list of the values of environmental variables (litter and grass weight); birth data (seed production, germination rate); and the characteristics of each tree in the stand (height, dbh, basal area, volume over-bark, current volume increment, crown length, leaf area,

TABLE VI.5: VALUES OF THE VCOEF COEFFICIENT FOR TREES OF VARIOUS AGES.

VCOEF is calculated as the ratio of annual volume growth to current tree volume. The data are derived from a yield table for fully-stocked stands of Pinus taeda in the U.S.A.

$$\text{VCOEF Index} = \frac{(\text{Growth/volume in 15-yr. age-class})}{(\text{Growth/volume in other age-classes})}$$

Data Source: Wahlenberg (1960)

| Tree Age | Mean Tree Volume | Ann. Vol. Increment | Growth/Volume | VCOEF Index |
|----------|------------------|---------------------|---------------|-------------|
| 15 | 4.48 | 0.725 | 0.1618 | 1.0 |
| 20 | 9.77 | 0.688 | 0.0704 | 2.3 |
| 25 | 15.40 | 0.645 | 0.0419 | 3.9 |
| 30 | 22.63 | 0.601 | 0.0266 | 6.1 |
| 35 | 28.83 | 0.543 | 0.0188 | 8.6 |
| 40 | 34.24 | 0.484 | 0.0141 | 11.4 |
| 45 | 38.52 | 0.423 | 0.0110 | 14.7 |
| 50 | 43.61 | 0.342 | 0.0078 | 20.6 |
| | cu.ft. | cu.ft. | | |

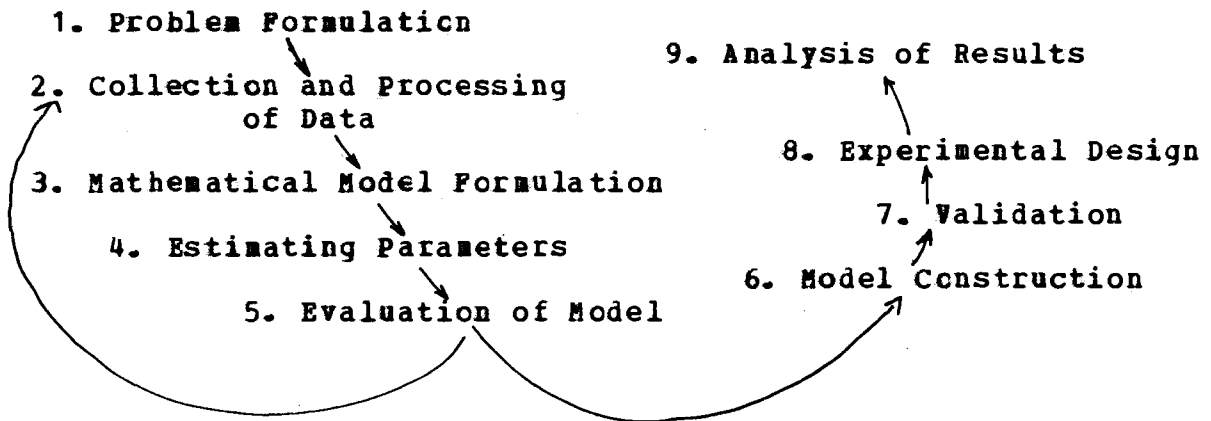
radiation level at top of the tree, and stem age). In addition, summary statistics on mortality rates, mean tree height and dbh, total leaf area, stand basal area, and total underbark volume are also printed. The program has an optional plotting routine (call to MPLOTS) which produces graphs on a Calcomp plotter. The graphs consist of the values of most of the variables listed above, plotted as a function of stand age.

CHAPTER SEVEN: VERIFICATION OF THE SIMULATION MODEL

7.1: THEORY OF MODEL VERIFICATION

Naylor et alia (1966), in an article on the theoretical aspects of simulation in business management, outline a nine-stage procedure for the construction of a simulation model.

This procedure involves:



The sequential process above is similar to an earlier "model of a model" produced by Forrester (1960). Both designs stress the importance of the model verification and validation stage, and the cyclical nature of the modelling process. Recycling takes place at a preliminary stage (5), when lacunae in model linkages or inappropriate parameters are evident. Often detection of model failure at this stage is based solely on the intuition of the modeller. A further series of model-performance tests should be made (stage 7) before extensive experimentation begins.

In many of the modelling efforts in the natural sciences, including ecology, the process of construction of a simulation model is often limited to a single pass through the nine stages, with scant attention being paid to model validation. Kenneth Watt, in a critique of the state-of-the-art in biome modelling, notes:

"The vast majority of the models put into the literature,... either do not describe the phenomena they purport to describe, or contain internal mathematical difficulties.."

1975; p. 143.

Confidence in a model's output should therefore vary directly with the amount of testing to which it has been subjected. The type of tests vary between different classes of models. Theoretical, or strategic models, can be regarded as extensions of scientific theories in general, and can be corroborated by failure to disprove the hypotheses generated by the model (Popper, 1959; Platt, 1964). A single instance of disagreement between model predictions and reality therefore refutes the model (Caswell, 1976).

Predictive models cannot be verified in the same manner. The performance of the model (its predicted results), are judged against empirical data, and the model is either accepted or rejected. The probability of rejection increases as the test becomes more powerful; failure becomes inevitable after a certain point, as no simulation model is an exact replica of observed

reality. Model rejection can be ascribed to several causes.

Wright lists the most common as:

- "(1) Incomplete scope: missing components.
- (2) Incorrect or over-simplified functional forms.....
- (3) Misestimation of parameters....
- (4) Uncertain initial conditions.
- (5) Stochastic variation of exogeneous inputs...
- (6) Noise and misspecification in the measurement process."

1972; p. 1287.

7.2: TECHNIQUES OF MODEL VALIDATION

The stage of model validation in Naylor's (op. cit.) model can be further subdivided. Naylor and Finger (1967) propose a three-stage sequence for validation of components of the model:

- 1: Construct a set of hypotheses for the process using all available knowledge. Hence models incorporating such knowledge should exhibit a priori confidence.
- 2: Verify assumptions by empirical testing.
- 3: Test model's ability to predict behaviour of the real system.

Stages two and three comprise the initial evaluation procedure and confirm that the coefficients, functions or sub-models produce acceptable results. Once these sub-models are linked together however there is no guarantee that the whole-model output will mimic the dynamics of the real-world

system. The modeller must test whether the observed and predicted systems are samples from the same stochastic process. Five techniques are commonly used to achieve this end: namely, graphical methods, sensitivity analyses, "Turing" tests, goodness-of-fit tests, and field tests.

Most ecological modellers have restricted themselves to the first technique. The model is judged to be acceptable if the time paths of the plotted variables of interest exhibit similar oscillations or time-delay responses. Sensitivity analysis of model behaviour is based on the assignation of modified values to the model parameters, for example, by changing the magnitude of a parameter by $\pm 10\%$. This kind of analysis focusses attention on system attributes which are highly sensitive to small changes in magnitude, and which hence must be modelled with considerable accuracy. A refinement of this technique was proposed by Tomovic (1963), and involves the calculation of 'sensitivity coefficients', which are solved simultaneously during model execution.

Wright (op. cit.), notes that a real test of the acceptability of a model is whether it gains the confidence of the academic audience (or funding group) for whom it was intended, and this can be regarded as a variant on Turing's "model output fools experts" test. Turing (1950), suggested that a measure of the I.Q. of an artificial intelligence could be obtained by testing whether experts could discriminate between it

and a human intelligence. The equivalent test in ecology would be whether ecologists or foresters could differentiate between model output and observed data.

Goodness-of-fit tests measure the statistical coincidence of model predictions against empirical data. These usually consist of tests of analysis of variance, chi-squared tests, t-tests, and correlation-regression analysis. Field tests usually involve the manipulation of real world systems to attempt to verify the predictions of the model.

7.3: VERIFICATION OF PINUS

PINUS can be verified by goodness-of-fit tests of its growth, yield and mortality predictions against real stands in Mountain Pine Ridge. The only suitable empirical data source is from the increment plots established in 1967. Each one of these covers 0.1 acres (400 sq. m.), the same size as the plots in the sample stands. Increment plots located in the hilly areas to the south and east of the Granite Basin were considered unsuitable for verification purposes, and these were discarded. Eight plots in the Granite Basin were finally utilised for the verification procedure. As these plots represent only a very limited range of forest conditions, they severely restrict the usefulness of the model verification procedure. However, for the sake of completeness, verification tests are undertaken. PINUS can be tested by assessing whether:

- a) the mean predicted stand growth rates are significantly different from growth in the increment plots.

- b) the mean predicted growth rates of individual trees are significantly different from growth of trees in the increment plots.
- c) the mortality in the simulated stands is not significantly different from that taking place in the increment plots.

The input for each verification run consisted of the stand data from the original census in 1967. PINUS then updated the growth of each tree in each of the eight sample stands on an annual basis over a six-year period. This procedure was repeated for a total of ten runs per increment plot, in order to obtain a probability distribution for each variable of interest. The real growth, yield and mortality values for 1973 were then compared with the simulated values.

7.31: Growth predictions

The mean simulated dbh increments for each tree in the sample runs are given in Table VII.1. These values were tested against actual increments using a t-test (Table VII.2). In only one case is there any difference between observed and simulated dbh increment. The distribution of dbh increments in the observed and simulated stands may be tested using a Kolmogorov-Smirnov two-sample test. For the purposes of this test only the first simulation run in each series was compared to the observed values. PINUS performed acceptably in all of the eight sampled stands (Fig. 7.1); in none of the cases was the predicted distribution significantly different from the observed.

TABLE VII.1: MEAN INCREMENTS OF HEIGHT, DGM, TOTAL STEW BASAL-AREA AND SURVIVORSHIP IN THE INCREMENT PLLOTS AND THEIR SIMULATED EQUIVALENTS.

| INCREMENT | VARI | RUN # | | | | | | | | | | FINAL | VALUES | INITIAL | | |
|-----------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|--------|---------|-------|-------|
| PLCT # | ABLES | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 5 | 1 | 1 | 1 | 1 | |
| A27 | HT | 21.2 | 21.3 | 21.3 | 21.2 | 21.3 | 21.3 | 21.3 | 21.3 | 21.3 | 21.3 | 21.3 | 21.3 | 21.3 | 21.3 | 21.3 |
| | DGM | 31.1 | 31.4 | 30.5 | 30.4 | 30.7 | 30.6 | 30.6 | 30.6 | 30.6 | 30.6 | 30.6 | 30.6 | 30.6 | 30.6 | 30.6 |
| | SA | 11613 | 11795 | 11850 | 11871 | 12024 | 11544 | 11977 | 11623 | 11974 | 11967 | 11876 | 11876 | 11876 | 11876 | 11876 |
| A29 | SUBV. | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 |
| | HT | 15.3 | 15.3 | 15.3 | 15.3 | 15.7 | 15.5 | 15.5 | 15.5 | 15.5 | 15.5 | 15.5 | 15.5 | 15.5 | 15.5 | 15.5 |
| | DGM | 20.5 | 20.6 | 20.5 | 20.5 | 20.7 | 20.8 | 20.9 | 20.7 | 20.7 | 20.5 | 20.5 | 20.5 | 20.5 | 20.5 | 20.5 |
| A34 | SA | 8340 | 8374 | 8172 | 8098 | 7931 | 8328 | 8187 | 8045 | 8046 | 8046 | 8046 | 8046 | 8046 | 8046 | 8046 |
| | SUBV. | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 |
| | HT | 14.0 | 14.0 | 13.9 | 13.9 | 13.9 | 13.5 | 14.0 | 14.1 | 13.8 | 14.0 | 14.0 | 14.0 | 14.0 | 14.0 | 14.0 |
| A35 | DGM | 16.7 | 16.7 | 16.6 | 16.7 | 16.2 | 16.8 | 16.5 | 16.6 | 16.6 | 16.6 | 16.6 | 16.6 | 16.6 | 16.6 | 16.6 |
| | SA | 8021 | 8257 | 8137 | 8041 | 8275 | 8167 | 8317 | 800 | 8365 | 8365 | 8365 | 8365 | 8365 | 8365 | |
| | SUBV. | 94.6 | 97.3 | 97.3 | 92.6 | 100 | 94.6 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 |
| A25 | HT | 14.5 | 14.8 | 14.5 | 14.9 | 14.5 | 14.9 | 14.8 | 14.9 | 14.9 | 14.9 | 14.9 | 14.9 | 14.9 | 14.9 | 14.9 |
| | DGM | 20.9 | 20.8 | 21.3 | 21.3 | 21.3 | 21.2 | 21.2 | 21.2 | 21.2 | 21.2 | 21.2 | 21.2 | 21.2 | 21.2 | 21.2 |
| | SA | 6348 | 6263 | 5531 | 6325 | 6266 | 6376 | 6235 | 6311 | 6261 | 6306 | 6306 | 6306 | 6306 | 6306 | 6306 |
| A24 | SUBV. | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 |
| | HT | 23.8 | 23.4 | 23.5 | 23.5 | 23.4 | 23.7 | 23.5 | 23.4 | 23.7 | 23.4 | 23.7 | 23.4 | 23.7 | 23.4 | 23.7 |
| | DGM | 31.0 | 30.2 | 31.8 | 31.8 | 30.3 | 30.4 | 30.1 | 30.2 | 30.6 | 30.5 | 30.5 | 30.5 | 30.5 | 30.5 | 30.5 |
| A22 | SA | 6925 | 6555 | 6422 | 6616 | 6667 | 6587 | 6587 | 6580 | 6580 | 6580 | 6580 | 6580 | 6580 | 6580 | 6580 |
| | SUBV. | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 |
| | HT | 14.3 | 14.3 | 14.3 | 14.4 | 14.2 | 14.3 | 14.4 | 14.1 | 14.4 | 14.4 | 14.4 | 14.4 | 14.4 | 14.4 | 14.4 |
| A23 | DGM | 19.4 | 18.2 | 16.6 | 18.8 | 18.3 | 18.2 | 18.6 | 18.3 | 18.6 | 18.3 | 18.3 | 18.3 | 18.3 | 18.3 | 18.3 |
| | SA | 9833 | 9668 | 10115 | 9960 | 9504 | 9723 | 9723 | 9769 | 10004 | 9722 | 9792 | 9792 | 9792 | 9792 | |
| | SUBV. | 100 | 100 | 100 | 97.1 | 97.1 | 94.3 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 |
| A22 | HT | 15.1 | 15.4 | 15.1 | 15.1 | 15.1 | 15.2 | 15.3 | 15.3 | 15.3 | 15.3 | 15.3 | 15.3 | 15.3 | 15.3 | 15.3 |
| | DGM | 17.8 | 17.8 | 17.3 | 17.8 | 17.5 | 17.8 | 17.8 | 17.8 | 17.8 | 17.8 | 17.8 | 17.8 | 17.8 | 17.8 | 17.8 |
| | SA | 1008 | 1046 | 1003 | 10237 | 1227 | 1008 | 1008 | 1008 | 1008 | 1008 | 1008 | 1008 | 1008 | 1008 | 1008 |
| A22 | SUBV. | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 |
| | HT | 15.1 | 15.4 | 15.1 | 15.1 | 15.1 | 15.2 | 15.3 | 15.3 | 15.3 | 15.3 | 15.3 | 15.3 | 15.3 | 15.3 | 15.3 |
| | DGM | 17.8 | 17.8 | 17.3 | 17.8 | 17.5 | 17.8 | 17.8 | 17.8 | 17.8 | 17.8 | 17.8 | 17.8 | 17.8 | 17.8 | 17.8 |
| A22 | SA | 1008 | 1046 | 1003 | 10237 | 1227 | 1008 | 1008 | 1008 | 1008 | 1008 | 1008 | 1008 | 1008 | 1008 | 1008 |
| | SUBV. | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 |

N.B. THE FINAL SIMULATED VALUES ARE THE MEANS OF THE 10 SIMULATION RUNS.

TABLE VII.2: "t"- TEST ON MEAN DBH GROWTH OF TREES IN
THE INCREMENT PLOTS AND THE SIMULATED STANDS.

Ho: That there is no significant difference in dbh
increment between real stands and their simulated
equivalents.

| Stand | Actual dbh growth | Simulated growth | Mean Absolute Deviation | t value | P |
|-------|----------------------|---------------------|----------------------------|------------|-------|
| A35 | 2.34 | 2.47 | 0.13 | 0.56 | N.S. |
| A24 | 3.60 | 3.56 | 0.04 | 0.12 | N.S. |
| A22 | 3.19 | 3.39 | 0.20 | 1.10 | N.S. |
| A25 | 3.61 | 3.73 | 0.12 | 0.49 | N.S. |
| A29 | 2.84 | 3.27 | 0.43 | 1.85 | N.S. |
| A27 | 3.51 | 3.46 | 0.04 | 0.12 | N.S. |
| A34 | 2.50 | 2.93 | 0.43 | 2.67 | 0.05* |
| A20 | 4.09 | 3.69 | 0.35 | 1.68 | N.S. |

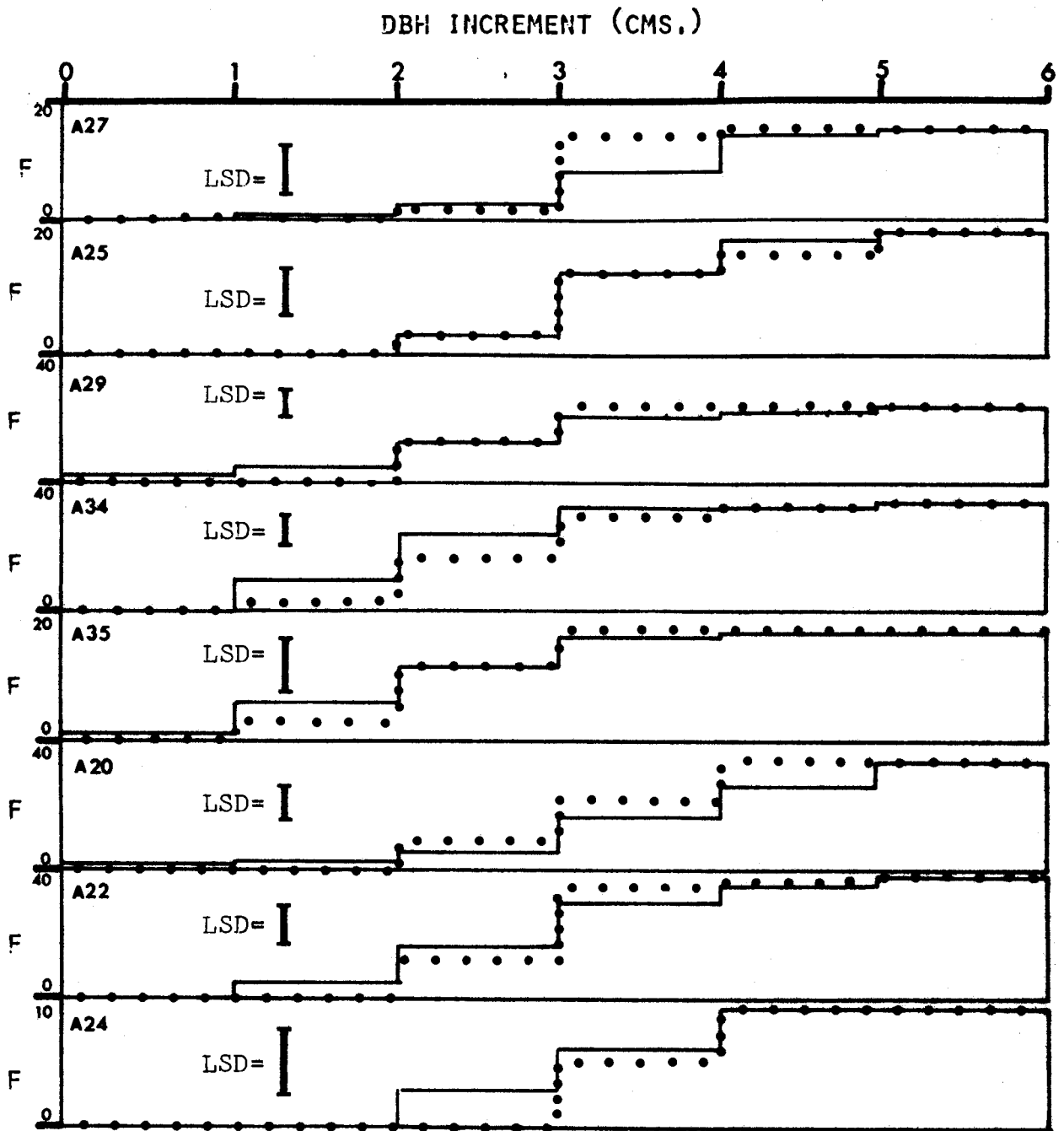


FIG. 7.1: CUMULATIVE FREQUENCY-DISTRIBUTIONS OF DBH INCREMENTS IN THE REAL (—) AND SIMULATED (••) STANDS. THE LEAST SIGNIFICANT DIFFERENCE (LSD) BY THE KOLMOGOROV-SMIRNOV TWO-SAMPLE TEST IS INCLUDED FOR COMPARISON ON EACH PLOT. THE LSD IS GRAPHED FOR A $p=10\%$ LEVEL.

TABLE VII.3: MEAN DBH INCREMENTS IN REAL AND SIMULATED STANDS.

Ho: That there is no significant difference between DBH increments in the real and simulated stands.

| Site # | Site Index (m. @ 25 yrs.) | Initial DBH (cms) | Real Growth | Simulated Growth | Deviation (R - S) |
|--------|------------------------------|-------------------|-------------|------------------|----------------------|
| A27 | 21 | 26.52 | 3.51 | 3.46 | +0.04 |
| A29 | 13 | 17.40 | 2.84 | 3.27 | -0.43 |
| A34 | 15 | 13.40 | 2.50 | 2.94 | -0.44 |
| A35 | 12 | 18.40 | 2.34 | 2.47 | -0.13 |
| A25 | 24 | 27.25 | 3.61 | 3.73 | -0.12 |
| A24 | 23 | 26.77 | 3.60 | 3.56 | +0.04 |
| A20 | 20 | 14.79 | 4.09 | 3.69 | +0.40 |
| A22 | 18 | 13.90 | 3.19 | 3.39 | -0.20 |

$$\bar{x} = 3.21 \quad \bar{y} = 3.31$$

$$s_x = 0.787 \quad s_y = 0.182$$

$$(\bar{x} - \bar{y}) = 0.10$$

$$"t" = 0.41 \quad (N.S.)$$

TABLE VII.4: MEAN HEIGHT INCREMENTS IN REAL AND SIMULATED STANDS.

H₀: That there is no significant difference between height increments in the real and simulated stands.

| Site # | Site Index (m. @ 25 yrs.) | Initial Ht. (m) | Real Growth | Simulated Growth | Deviation (R - S) |
|--------|------------------------------|--------------------|----------------|---------------------|----------------------|
| A27 | 21 | 17.93 | 3.46 | 3.38 | +0.08 |
| A29 | 18 | 12.20 | 2.64 | 3.21 | -0.57 |
| A34 | 15 | 10.67 | 3.04 | 3.29 | -0.25 |
| A35 | 12 | 11.83 | 2.34 | 3.06 | -0.72 |
| A25 | 24 | 21.77 | 3.55 | 3.73 | -0.18 |
| A24 | 23 | 20.17 | 2.54 | 3.37 | -0.83 |
| A20 | 20 | 10.86 | 5.00 | 3.44 | +1.56 |
| A22 | 18 | 11.95 | 3.38 | 3.27 | +0.11 |

$$\bar{x} = 3.24 \quad \bar{y} = 3.34$$

$$s_x = 0.787 \quad s_y = 0.182$$

$$(\bar{x} - \bar{y}) = 0.10$$

$$"t" = 0.3276 \quad (\text{N.S.})$$

TABLE VII.5: BINOMIAL TEST ON THE DIFFERENCE BETWEEN MORTALITY IN THE INCREMENT PLOTS AND THAT IN THE SIMULATED STANDS.

H₀: That the mortality rates predicted by PINUS are not significantly greater than the mortality rates in real stands (1-tailed test).

| | Sample Size (N) | # Dead (A) | % Mortality (p) |
|------------|-----------------|------------|-----------------|
| Real | 197 | 0 | 0.0 |
| Simulated' | 1970 | 22 | 1.117 |

$$\text{Pooled } p = (A+A')/(N+N') = 22/2167 = 1.015$$

$$\text{Pooled } s^2 = 1.015(98.985) = 100.492$$

$$sp^2 = 100.492/197 = 0.510$$

$$sp'^2 = 100.492/1970 = 0.051$$

$$sd^2 = 0.510 + 0.051 = 0.561$$

$$sd = 0.749$$

$$x^* = (p-p')/sd = -1.117/0.749 = -1.49$$

Since $x^*_{0.05} = -1.64$ in a one-tailed test, the differences are not significant and the null hypothesis (H₀) is accepted.

The results of these tests confirm that PINUS models stand growth reasonably well, but there are considerable deviations from observed dbh increments on an individual tree basis. PINUS computes dbh increments for each tree based on the available light at the top of the crown of that tree, and assumes a uniform distribution of foliage in the crowns of individuals, and a uniform spacing of trees in the stand. Discrepancies between predicted and observed values are undoubtedly due to these two assumptions being violated in the increment plots.

On an overall basis PINUS calculates growth rates to within 10 % of their real values in the plots sampled (Tables VII.3 and VII.4), and is therefore judged an acceptable model of stand growth.

7.32: Mortality Predictions

None of the 197 trees in the increment plots died over the six-year census period for which the simulation was performed. In the simulation runs the following results were obtained:

| | REAL : | SIMULATION RUNS | | | | | | | | | |
|---|--------|-----------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| | : | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| I | 197 | 197 | 197 | 197 | 197 | 197 | 197 | 197 | 197 | 197 | 197 |
| F | 197 | 195 | 195 | 196 | 195 | 195 | 193 | 195 | 197 | 195 | 192 |

where I is the initial number of stems, and F is the final quantity. The simulation runs indicate that the death of 2.2 stems can be expected on average, with zero mortality occurring

some 10 % of the time. Using a Poisson distribution to calculate the 95 % confidence interval about a count of 0 (the observed mortality), we obtain values of 0.0 - 3.6. In other words a predicted mortality of < 3.6 stems is not significantly different from zero (Fisher and Yates, 1963; Biometric tables, p.65). The simulation runs produce results within the appropriate confidence interval 80 % of the time.

The difference between observed and simulated mortality can be also tested using the binomial distribution (Table VII.5). Since the calculated value of x^* falls short of the tabulated 1.64 at $P=0.05$ in a one-tail test, we can conclude that the model mimics the mortality in real world situations reasonably well.

Although the verification tests are not very rigorous, and the model has only been tested over the short term, it can be concluded that PINUS is a reasonable analogue of the stand behaviour of *P. caribaea*. It will therefore be employed to test the effects of various forest management strategies on stand structure and timber yields.

CHAPTER EIGHT: RESULTS OF THE SIMULATION RUNS

8.1: APPLICATION OF PINUS TO FOREST MANAGEMENT PROBLEMS

The primary goals of forest management in Mountain Pine Ridge, as in the other Central American pinelands, have been the conservation of the pine resource and the stimulation of pine regeneration through fire control and protection of stands from over-cutting. Most forest management to date has concentrated on fire-suppression. In order to implement the second objective data are expressly required on the cutting/regeneration system to be employed in P. caribaea stands, the length of the rotation, and the response of stands to various levels of thinning intensity and frequency.

Caribbean pine can be managed in either all-aged or even-aged stands. Under the former, the intermediate shade-tolerance of the species allows a group-selection system to be applied, with regenerating pine restricted to small gaps in the canopy. This method has two drawbacks. Competition of regeneration with the unharvested mature pine may induce suppression, and the system is not feasible in areas where low-cost management should be practiced. Even-aged management is preferable as the trees can be harvested in one operation, prescribed burning of even-aged stands for fire-hazard reduction and range management results in less damage to young pine, and competition between mature trees and regeneration is reduced.

Several alternative silvicultural systems may be employed to obtain regeneration under even-aged management. Clearcutting the entire stand and then planting seedlings or seeding onto prepared (burned, disked, etc.) seedbeds is widespread in areas of intensive tree cultivation where heavy equipment is used in the logging operation. In areas of extensive low-cost management such as Mountain Pine Ridge vigorous and expensive site preparations are not feasible and natural regeneration of stands is mandatory. The recommended methods for supplying a seed source under low-cost management have been: to either leave scattered or clumped trees to act as seed-bearers (35 trees/ha. [14/ac.] generally being considered the economic limit); or to apply the shelterwood system, where 60-100 trees/ha. (25-40/ac.) may be retained in strips at right angles to the principal wind-direction. In Mountain Pine Ridge, Wolffsohn (1956), envisaged that the pine stands would be managed according to the seed-tree system, and PINUS was therefore employed to predict the response of stands of P. caribaea to this form of management.

8.2: MANAGEMENT BY THE SEED-TREE SYSTEM.

Several logical problems are encountered in adapting PINUS to model a seed-tree regeneration system. The first of these is that seed-dispersal from the remnant seed-bearers is presumably patchy in nature, dependent upon interactions between wind-speed, direction, and local topography. No data are available on seed dissemination distances for P. caribaea, but most pine species

attain mean dispersal distances of 100 metres (Baker, 1934), apparently due to the similarity of seed-weight/surface-area ratios between species (Gemmer, 1940; quoted in Wahlenberg, 1960). This complex of factors will in most cases give rise to a seed-shadow which covers a fairly narrow angle downwind of each seed-tree, with the density of seeds a function of distance from the parent tree. The inherent difficulty of producing a realistic model of this highly variable phenomenon led to the simplifying assumption that seed distribution in a stand should be treated as uniform.

Regeneration of a stand from seed-bearers depends not only upon their spacing, but also on the amount of seed produced by the remnant trees. The post-harvest release of seed-bearing trees from competition results in increased seed-yields, in some cases by as much as 500 % (Fowells, 1965). Although no data are available on the extent of this release in P. caribaea, it is clear that reduced competition induces an increase in the cone yield of dominant and co-dominant trees (Fig. 8.1) in sampled stands. PINUS however assumes that the seed production of trees of a particular basal area remains constant after harvesting. Thus it is more realistic to analyze the dynamics of the stand as a response to a specific seed-input to the system, rather than a response to a number of seed-trees per unit area. Thus, to simulate the regenerative response of a stand to a seed-rain produced by n trees/ha., it is assumed that a single seed-tree is

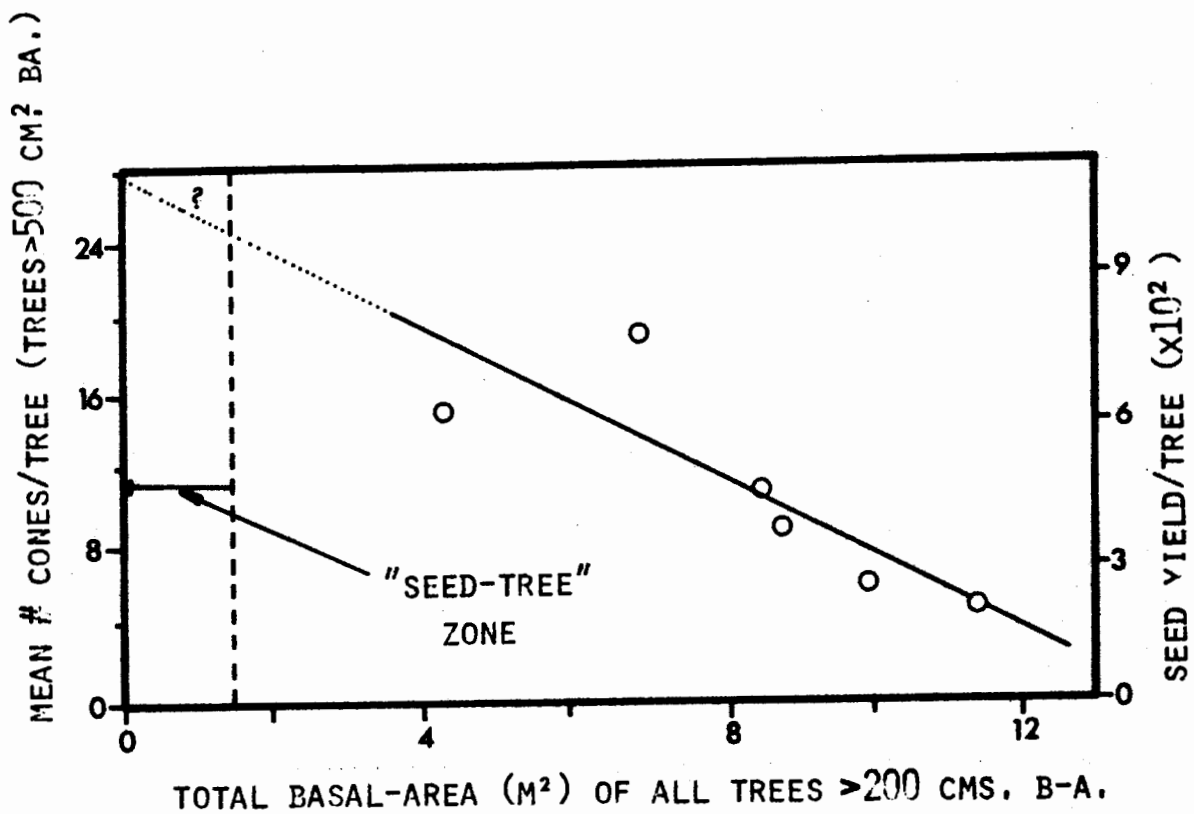


FIG. 8.1: SEED-YIELD PER TREE AS A FUNCTION OF THE DEGREE OF COMPETITION IN A STAND. THE "SEED-TREE" ZONE REPRESENTS THE RANGE OF TOTAL STEM BASAL-AREA TO BE EXPECTED IN A STAND AFTER HARVESTING UNDER A SEED-TREE REGENERATION SYSTEM.

located in the simulated 0.04 ha. (0.1 acre) plot, but that seedfall on this plot is equal to $0.04 \cdot \sum_{i=1}^m Sp_i$, where Sp_i is the total seed-production of the i th tree.

A further problem concerns the annual variability of seed-crops. Anecdotal information on cone-yields, based on the amount of seed collected commercially, indicates that *P. caribaea* is a more constant seed-bearer than most of its temperate congeners, and PINUS therefore assumes constant rates of seed-production by the unharvested trees. Within these constraints we can examine the response of stands to variable seed input.

The initial stand in each simulation run was comprised of trees bearing 1000 seeds each (> 800 cms. BA or 25 cms. {10"} DBH), equivalent to a mean annual-crop of 25 cones/tree. The experimental design consisted of testing five levels of initial seed-input. The seed inputs and their corresponding seed-tree requirements are listed in Table VIII.1.

The model was run for a simulated time-period of 50 years at least ten times for each experimental treatment. At some point in the 50-year period environmental conditions would preclude further pine seedling establishment. Runs in which seedtrees died before this regeneration phase was completed were discarded. These latter runs would have introduced a great deal of heterogeneity into the system, and their inclusion would have

TABLE VIII.1: INITIAL SEED-INPUTS IN PINUS SEED-TREE RUNS.

| Seed Input | | Estimated Number of Seed-Trees | |
|------------|-------|--------------------------------|---------|
| /ha. | (ac.) | Minimum | Maximum |
| 10 | (4) | 4 (2) | 10 (4) |
| 20 | (8) | 10 (4) | 20 (8) |
| 30 | (12) | 15 (6) | 30 (12) |
| 40 | (16) | 20 (8) | 40 (16) |
| 50 | (20) | 25 (10) | 50 (20) |

The estimated density of seed-trees corresponding to each level of seed-input is based upon an assumed seed-production of 1000 seeds/tree/annum.

necessitated a considerable increase in sample size (and computer execution time), and as they formed < 20 % of the run population they represent a fairly minor element in the behaviour of the system as a whole. The values reported below are therefore the means of the ten runs that were retained for each initial seed-input, and consequently represent the behaviour of fully-stocked stands derived from a given seedfall.

The simulation was performed for only a single site index. Site indices are calculated by measuring the height of stand dominants at either 25 or 50 years of age. No reliable data are available from the study area on the mean height of dominants or the range of expected values at either of these times, but it is unlikely that many stands have site indices much less than 15 m. (~50 ft.) at 25 years, and most stands probably fall in the 15 m. - 21 m. (~ 50 - 70 ft.) range. It was therefore decided to perform all simulations at a site index of 15 m., and so the yield data presented below probably represent a lower threshold for fully-stocked stands.

8.21: Results of the Seed-tree Runs

The use of the seed-tree system demands that the forester ensure adequate stocking and yields from the remnant trees, whilst maximising the wood production in the previous harvest. Analysis of the results of the seed-tree runs focusses on three variables: the stocking levels of natural regeneration; the

survivorship of recruited stems; and the yield of stands as a function of stand age and density.

8.211: Stand Dynamics: Regeneration

The graphs in Figs. 8.2 - 8.5 summarise the results of the simulation runs for the principal demographic variables in the stand. Figure 8.2 records the increases over time in annual seed production in the simulated plot for each of the initial seed-production levels. With an initial seed-input of 10,000 seeds/ha./yr., seed production by the regenerating stand attains some 29,000 seeds/ha./yr. at 50 years. At each of the higher seed-production levels a more rapid and earlier rise in seed-production occurs, so that an initial input of 50,000 seeds/ha./yr. gives rise to a stand capable of producing 168,000 seeds/ha./yr. at the end of the simulation. Most of this increase in seed-production takes place in the 30-50 year period, as the growing stand matures.

The number of seedlings produced per year from this seed population is plotted in Fig. 8.3. Annual seedling establishment can be characterised in all treatments as low during the first five-year period, attaining maximum levels during the next decade, and then falling off more or less rapidly in the period between 15 and 25 years. No seedlings become established in any treatments after the stand reaches 30 years of age. Despite these similarities, there are obvious differences

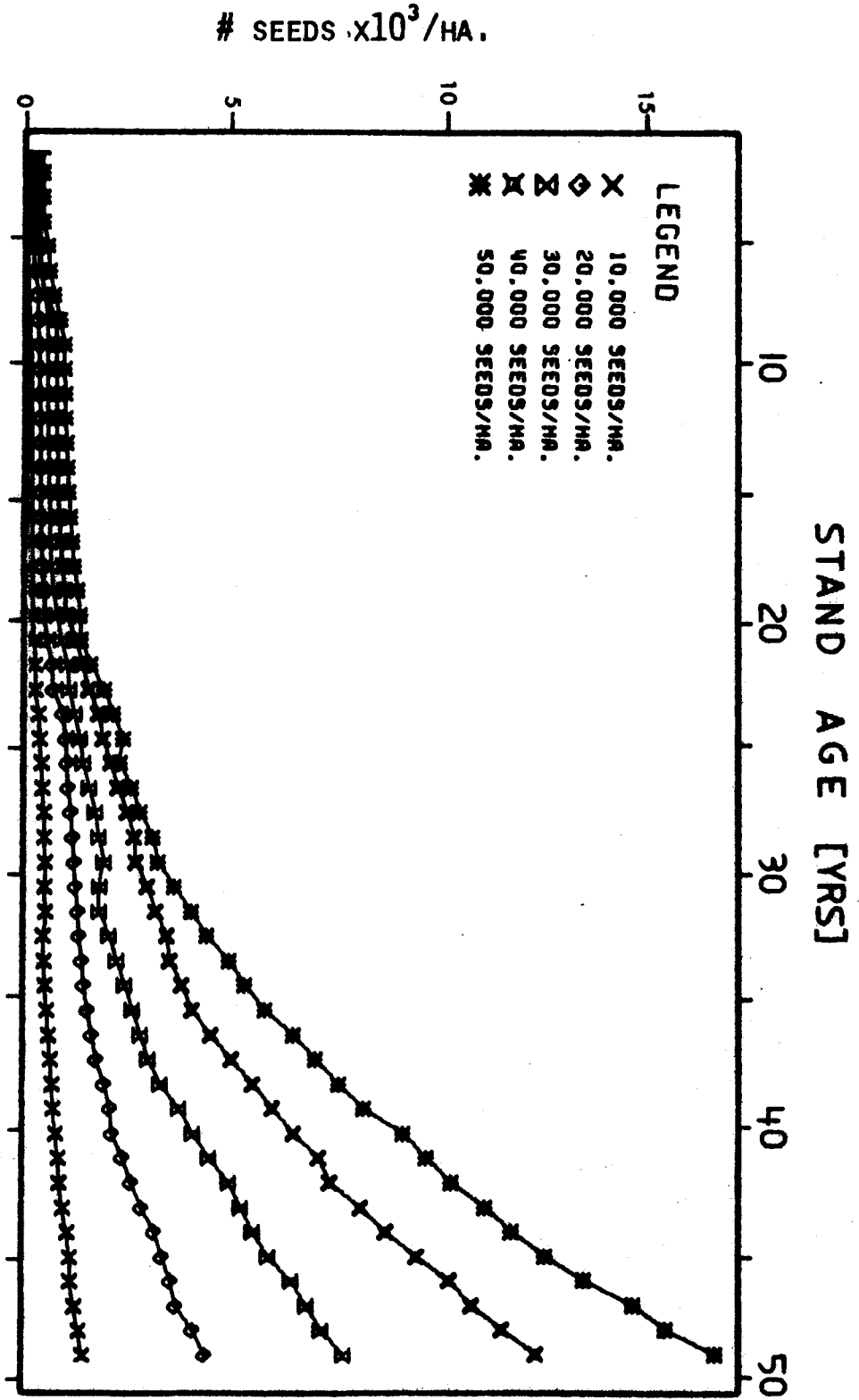


FIG. 8.2: SEED-PRODUCTION IN THE SIMULATED STANDS

ANNUAL SEEDLING RECRUITMENT /HA.

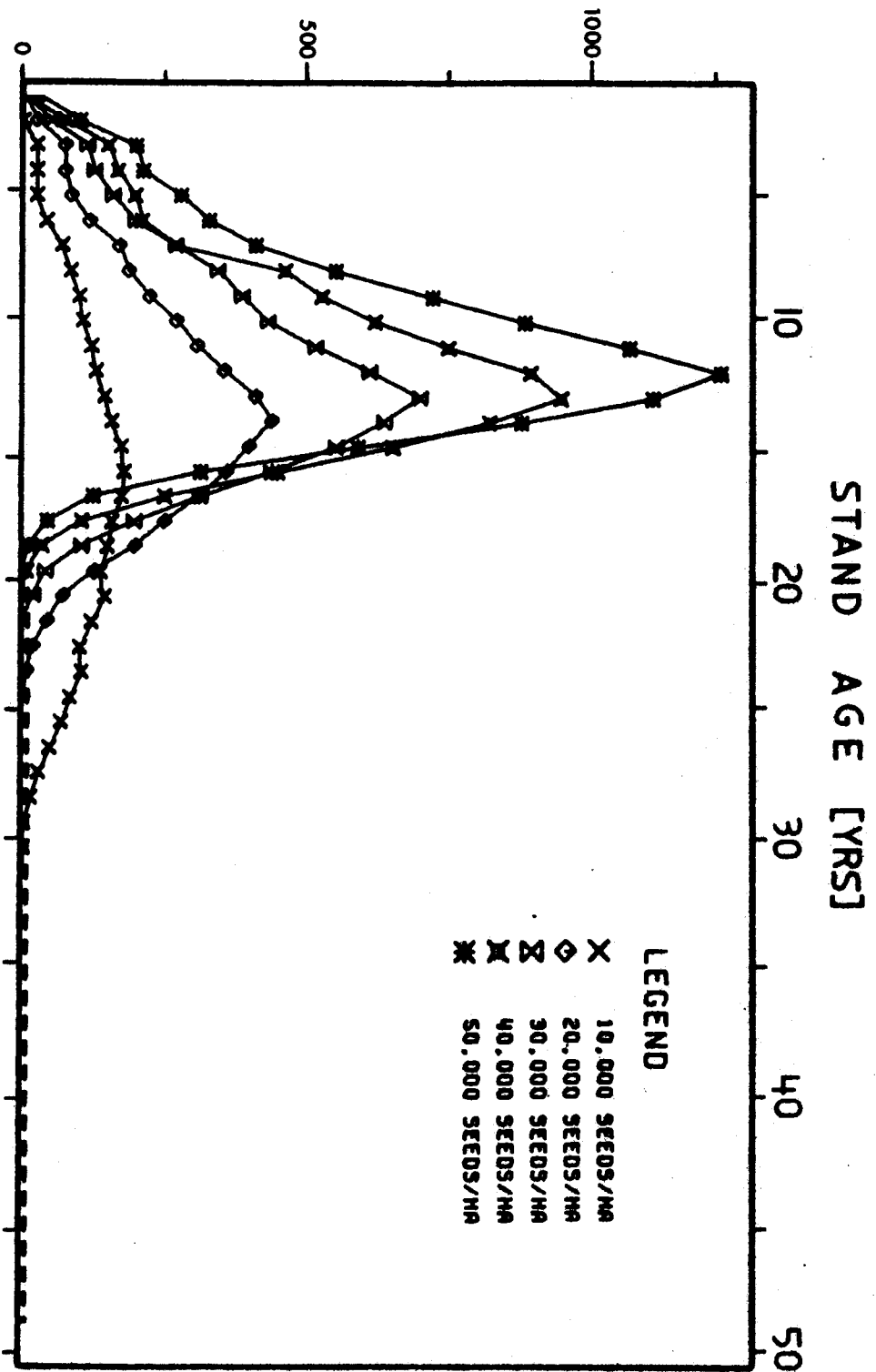


FIG. 8.3: ANNUAL SEEDLING RECRUITMENT IN THE SIMULATED STANDS

CUMULATIVE SEEDLING RECRUITMENT $\times 10^3/\text{HA.}$

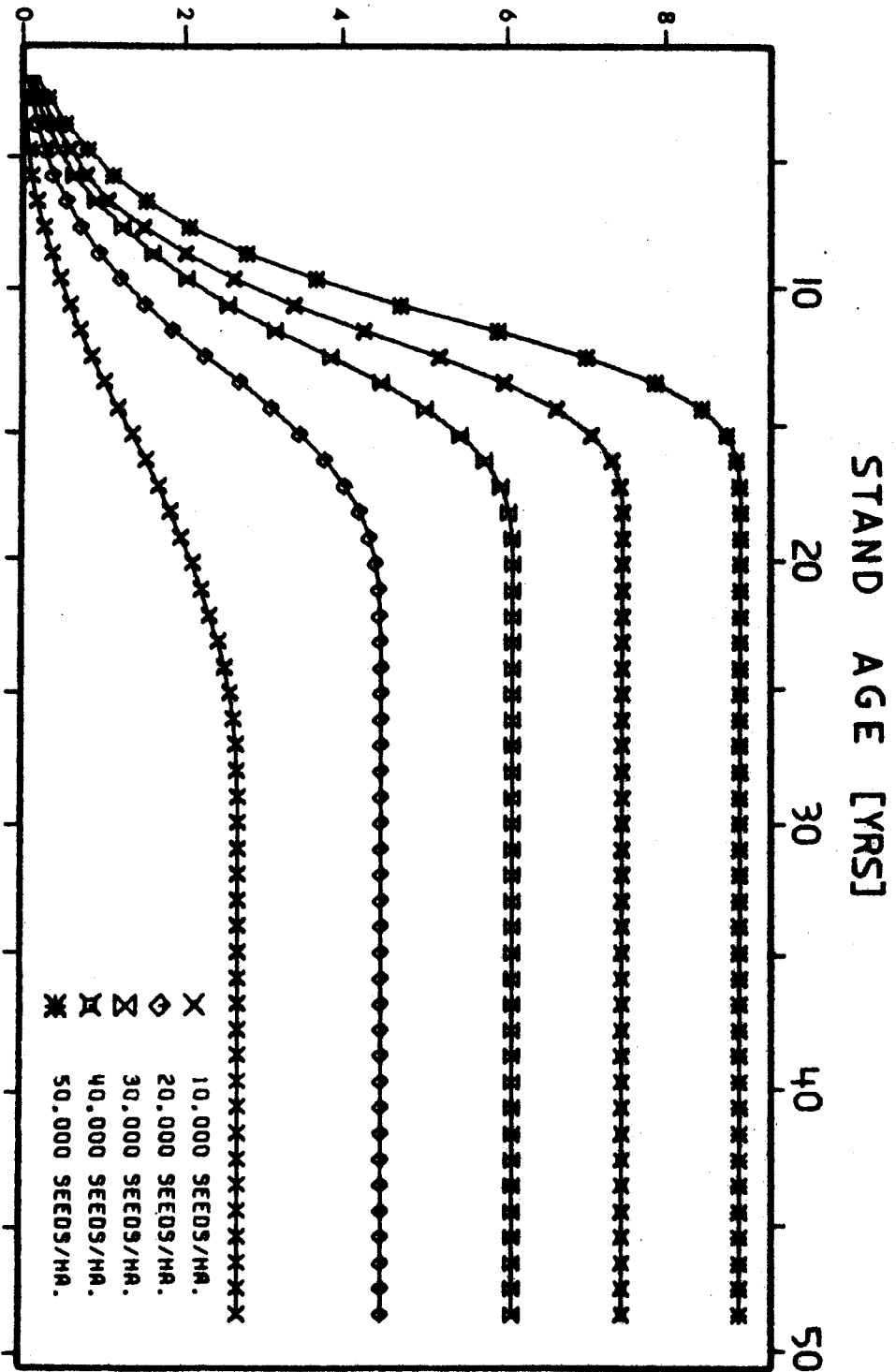


FIG. 8.4: CUMULATIVE SEEDLING RECRUITMENT IN THE SIMULATED STANDS.

PERCENTAGE GERMINATION

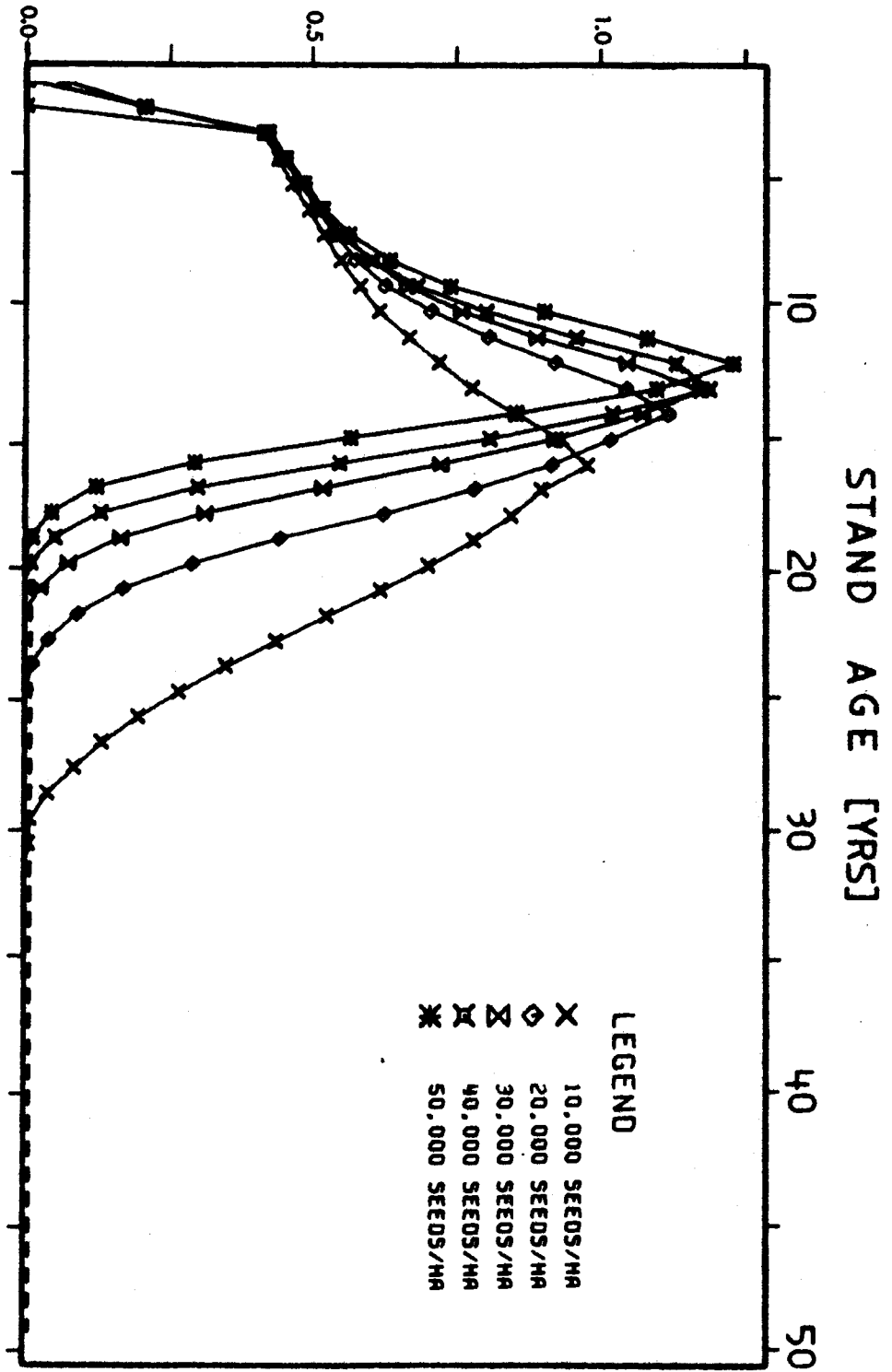


FIG. 8.5: PERCENTAGE GERMINATION-RATES IN THE SIMULATED STANDS.

between treatments in terms of the number of recruits that enter the seedling population during this favourable time-span. The higher the initial seed-input, the greater the total recruitment, the earlier high recruitment rate are attained and the more rapid the subsequent decline. Thus, with an initial seed input of 50,000 seeds/ha./yr. PINUS predicts that maximum seedling establishment takes place in year 12 (~ 1250 seedling/ha.yr.), and recruitment has dwindled to zero by year 20.

These data on seedling establishment are summarized in Fig. 8.4. The cumulative recruitment curves illustrate the rapid increase in seedling establishment and shortening span of the regeneration phase as the initial density of seed increases. The rate of seed input, rate of seedling establishment and growth of young pine all control the germinative success of seed in later years. There is little difference in the percentage germination rates between treatments (Fig. 8.5). Maximum germination rates vary between 1.00 - 1.25 % and are achieved in the 10-15 year period of stand development in all treatments. The total number of seedlings established is a linear function of initial seed input (Fig. 8.6a) over the domain of values tested. When the total number of recruits is graphed as a percentage of total seed input during the phase of seedling establishment, it is apparent that the efficiency of the system is constant at 0.5 - 0.6% germination over a wide range of values (750,000 - 1,600,000 seeds). Only at lower seed inputs (<700,000 seeds), does the

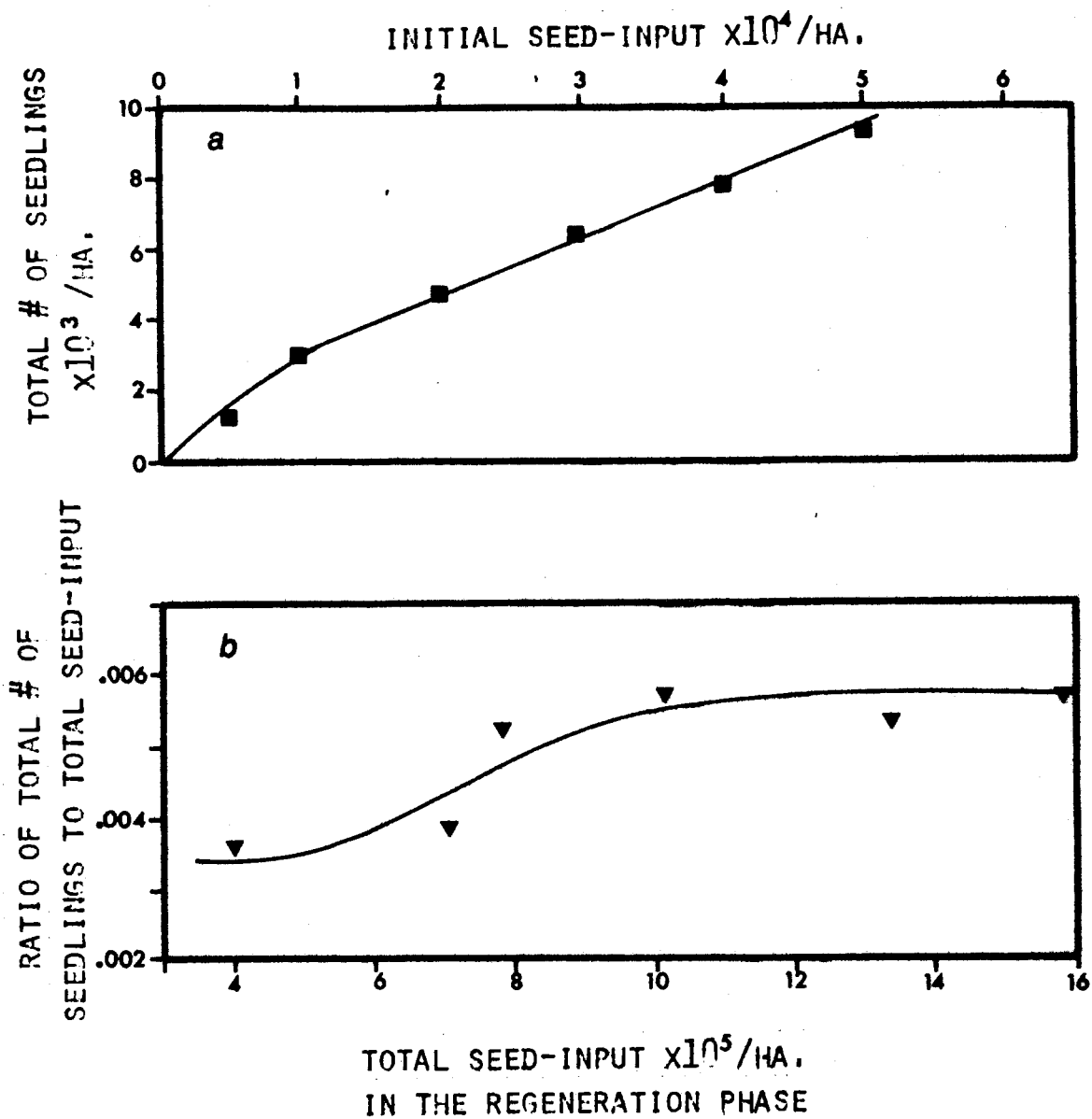


FIG. 8.6: SEEDLING RECRUITMENT AS A FUNCTION OF
 A) INITIAL LEVELS OF SEED-INPUT, AND
 B) TOTAL SEED-INPUT DURING THE PHASE IN
 WHICH THE STAND IS CAPABLE OF
 REGENERATION.

efficiency of the system decrease, falling to 0.36% germination at 400,000 seeds/ha. The demographic factors of primary importance to the forest manager are (a) the levels of stocking, expressed either as a percentage of plots containing seedlings, or as number of seedlings per unit area; and (b) the time delay between harvesting and attainment of adequate re-stocking.

Henry (1974), recognised five stocking levels as indicators of the relative success of Caribbean pine regeneration in the Bahamas (Table VIII.2). These levels were based on a survey of the % frequency of pine stems per unit area in sampled stands. The standard area adopted by Henry for this survey was 3m. x 3m. (9.8 x 9.8 ft.), which was considered by Luckhoff (1964), to produce optimal yields in South African plantations of *P. caribaea*. Thus, a "full" stocking would be one in which every 3 m. x 3 m. quadrat was occupied by one or more pine seedlings, equivalent to a stand density of at least 1100 seedlings/ha. (450/ac.). The first criterion of success for a seed-tree system must therefore be the attainment of Grade 1 or 2 stocking (>888 stems/ha) within a certain number of years after clear-cutting of the remainder of the stand.

The performance of each of the regeneration strategies is graphed in Figs. 8.7 and 8.8. An arbitrary (and lenient) criterion of regeneration success can be taken as the attainment of "adequate" stocking within 10 years. The lowest initial seed densities (<10,000 seeds/ha) can therefore be dismissed as a

TABLE VIII.2: STOCKING LEVELS FOR A 3 M. X 3 M. PLOT SIZE.

| Stocking Grade | % Stocked | Plants/ha. | Plants/acre |
|----------------|-----------|------------|-------------|
| 1) Full | 100 | > 1111 | > 449 |
| 2) Adequate | 80-95 | 888 - 1110 | 359 - 448 |
| 3) Moderate | 55-75 | 611 - 887 | 246 - 358 |
| 4) Poor | 30-50 | 333 - 610 | 135 - 245 |
| 5) Reseed | < 25 | < 332 | < 134 |

Source: Henry, 1974.

DENSITY OF STEMS $\times 10^3$ /HA.

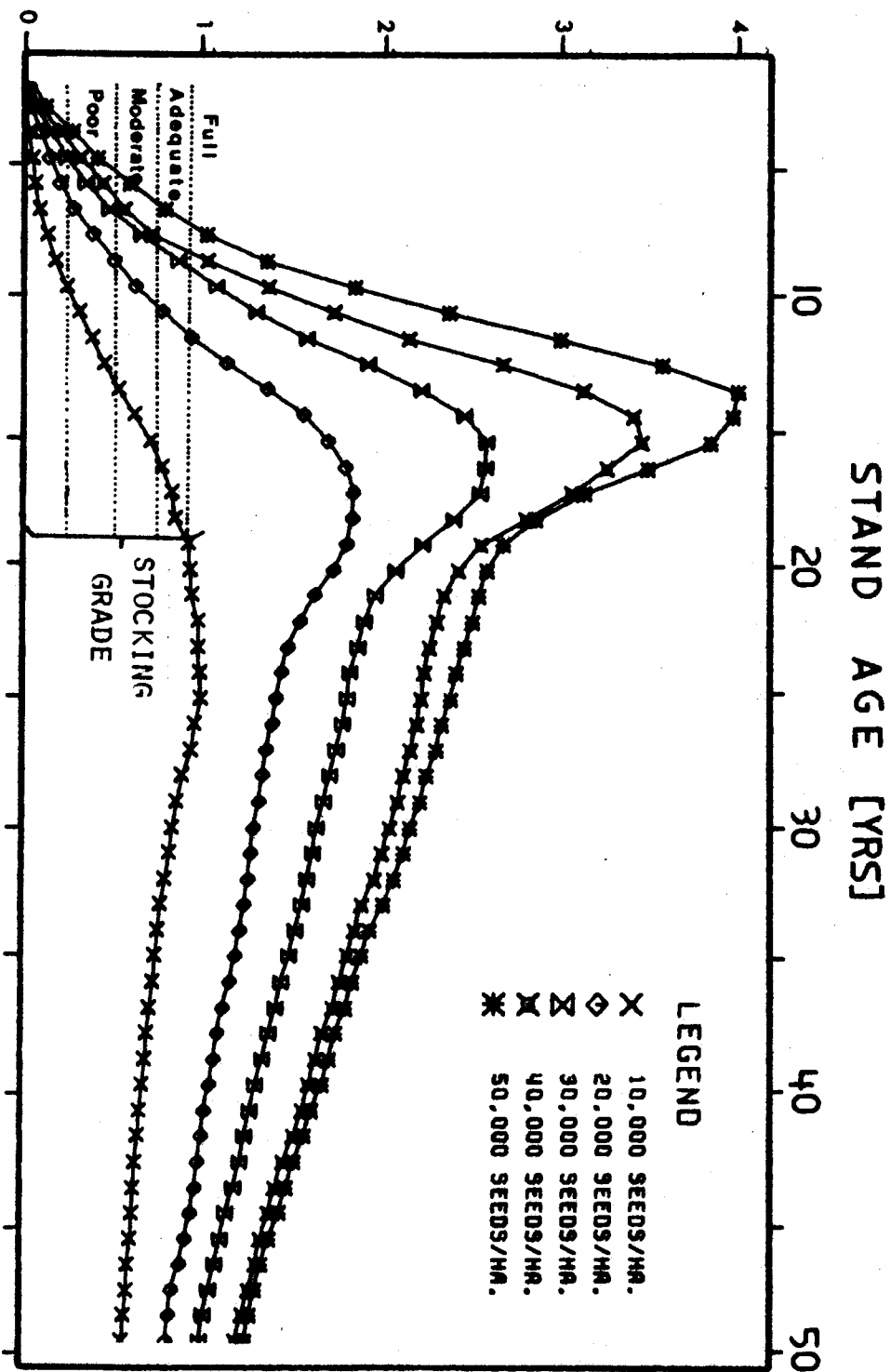


FIG. 8.7: SEEDLING STOCKING IN THE SIMULATED STANDS.

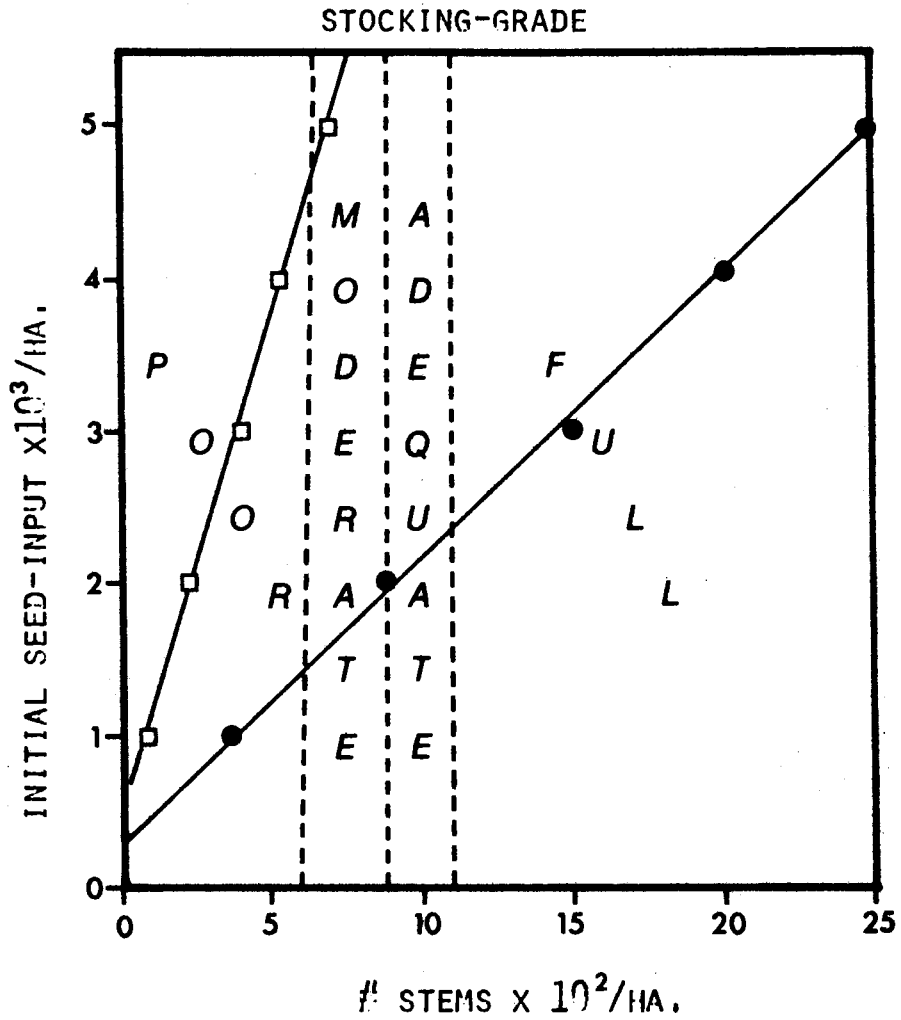


FIG. 8.8: PREDICTED STOCKING-GRADE AS A FUNCTION OF INITIAL SEED-INPUT, THE DATA POINTS REPRESENT THE STOCKING ATTAINED AFTER (□) FIVE AND TEN (●) YEARS.

regeneration strategy as "moderate" stocking is only achieved after an interval of 15 - 25 years. Only strategies supplying >20,000 seeds per ha. are acceptable, and this value must be regarded as a bare minimum. Referring back to Table VIII.1, it can be concluded that this minimum seed-input can be supplied by retaining 10 - 20 seed-trees/ha. (4 - 8/acre).

These data may be compared with the pine regeneration figures of Johnson and Chaffey (op. cit., Table 4, p.3) from Mountain Pine Ridge. Their inventory indicates that only 30% of the Granite Basin area can be considered to have attained Grade 3 (Moderate) status, the remainder of the project area being severely understocked as a result of past fires, over-cutting, and damage sustained as a result of Hurricane Hattie in 1961.

8.213: Stand Dynamics: Survivorship

The dynamics of pine populations can be studied most readily through an analysis of cohort survivorship. As an example, the survivorship of the seedlings establishing in the tenth year of stand development is graphed as a function of stand age in Fig. 8.9. The population is standardised to a cohort of 1000 individuals in each case. For each of the initial seed inputs the greatest seedling mortality occurs in the first decade of existence when some 40 - 60 % of the pine seedlings die. In the second decade death rates decline to 0 - 20 %, and then rise again to reach 5 - 30 % in the final ten years of the study. At

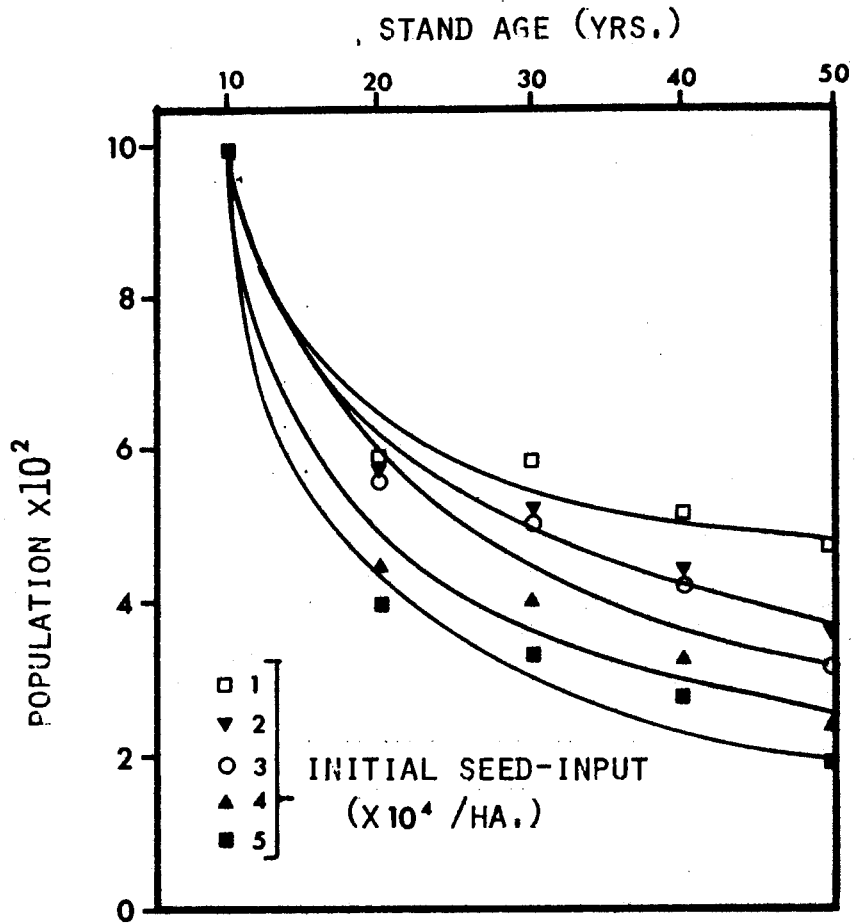


FIG. 8.9: SURVIVORSHIP OF THE COHORT OF P. CARIBAEA SEEDLINGS BORN IN THE TENTH YEAR OF THE STAND'S EXISTENCE AS A FUNCTION OF STAND AGE AND DENSITY. THE DATA ARE STANDARDISED TO A POPULATION COHORT OF 1000 INDIVIDUALS.

every stage of development mortality is density-dependent. In the stands with the smallest seed inputs PINUS predicts a survivorship of 43 % of all seedlings born in year 10 at the end of the simulation. In stands with an initial input of 20,000 seeds survivorship at the end of the run drops to 37 %, and then down to 30 %, 25 % and 20 % for inputs of 30,000, 40,000 and 50,000 seeds/ha. respectively.

8.214: Stand Dynamics: Yields

The pinelands of Mountain Pine Ridge are suitable only for the growing of saw-timber and for turpentine extraction. The domestic market is too small to support a local pulpwood industry, and the pinelands probably too restricted in size, and the pines too slow growing, to be exploited for export to the pulp mills of the U.S.A. Consequently, deciding upon the optimal rotation for saw-timber is of prime importance in Mountain Pine Ridge. Solving this problem depends on the acquisition of two items of information. Firstly, the relationship between wood production in the stand as a function of stand age must be known, and secondly, the costs and revenues associated with various rotation ages and harvesting methods must be taken into account. The second element is outside the domain of this thesis, but the first can be treated.

The age-dependent changes in the principal stem morphological variables predicted by PINUS are presented in Figs.

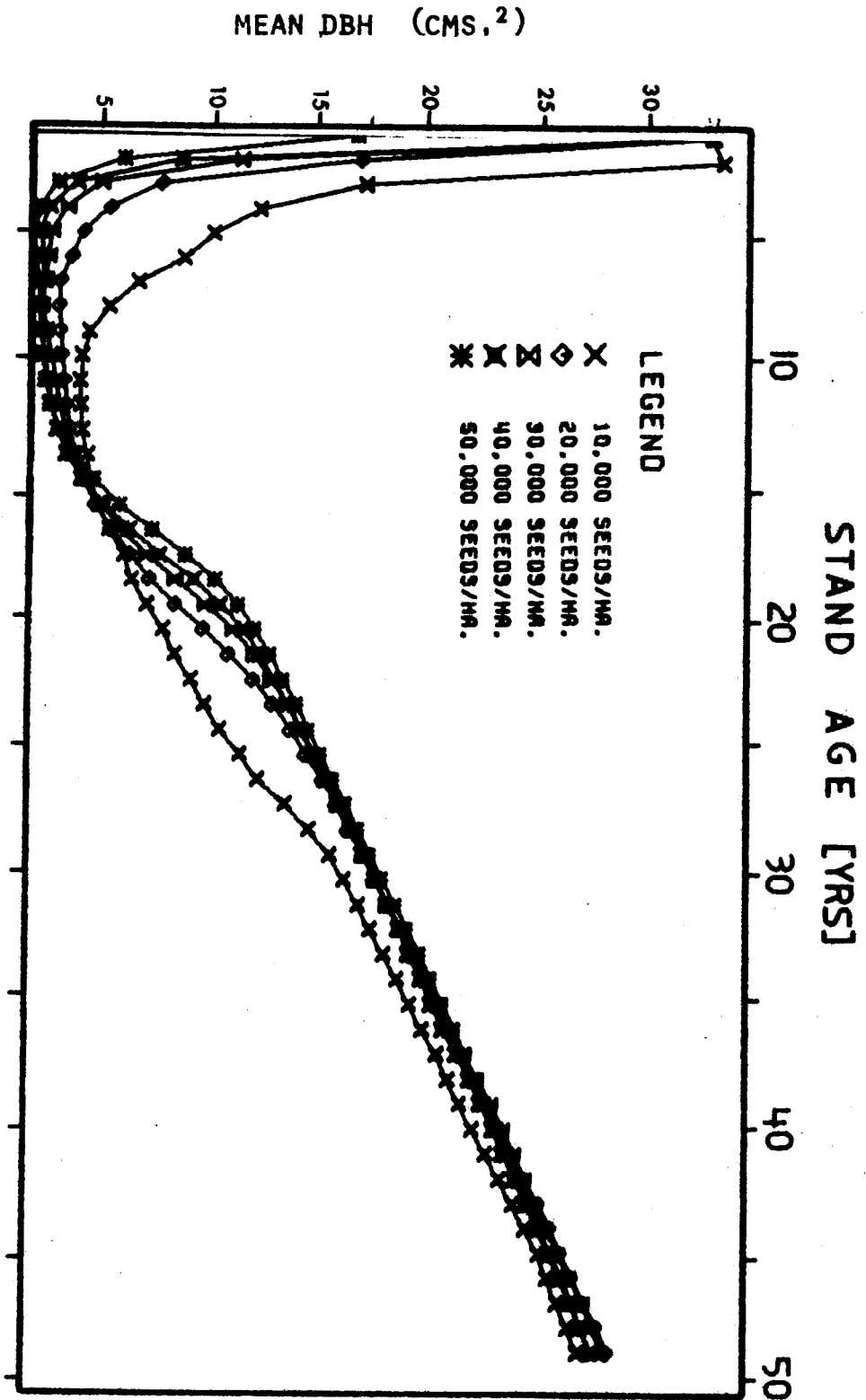


FIG. 8.10: MEAN DBH OF TREES IN THE SIMULATED STANDS.

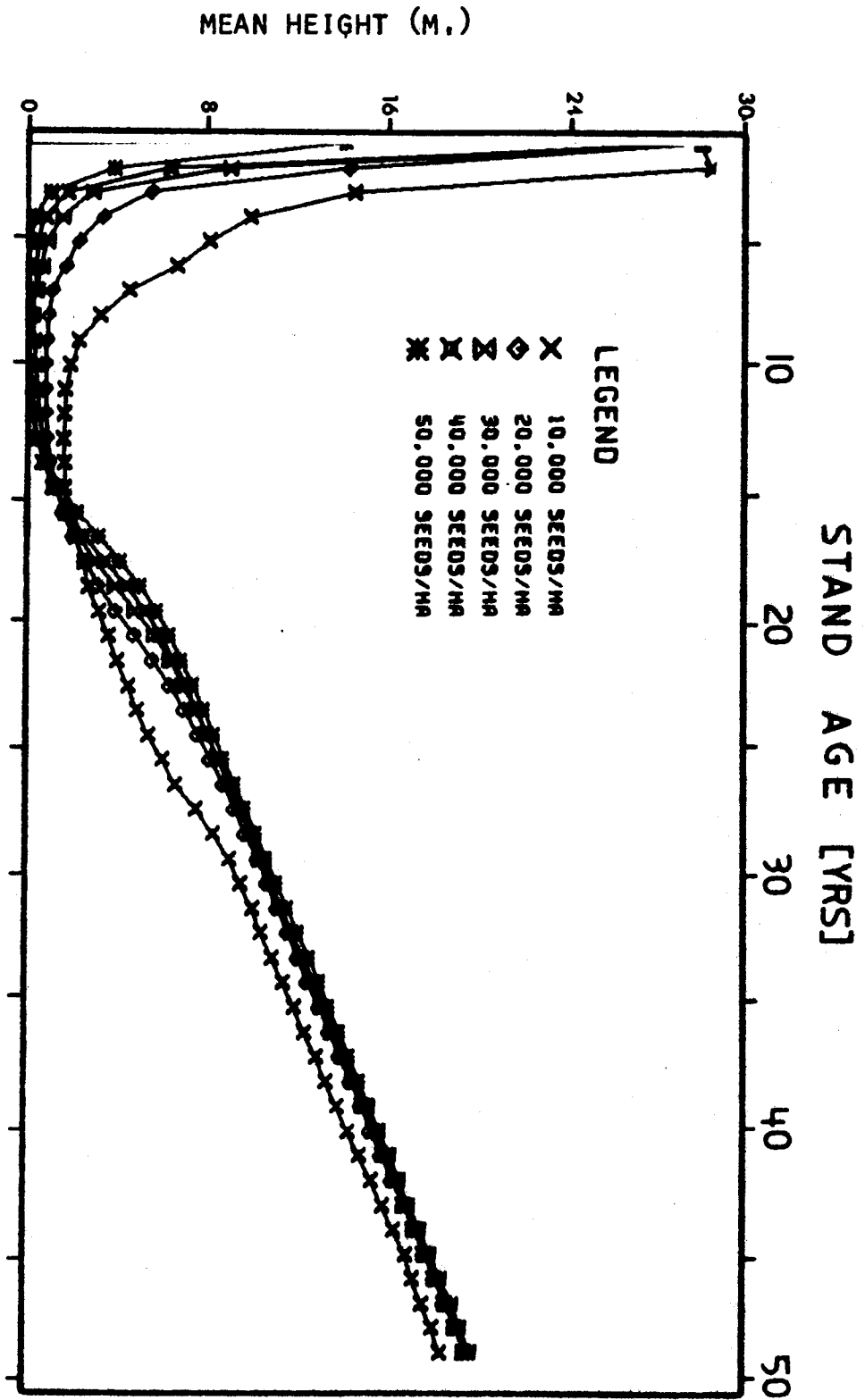


FIG. 8.11: MEAN HEIGHT OF TREES IN THE SIMULATED STANDS.

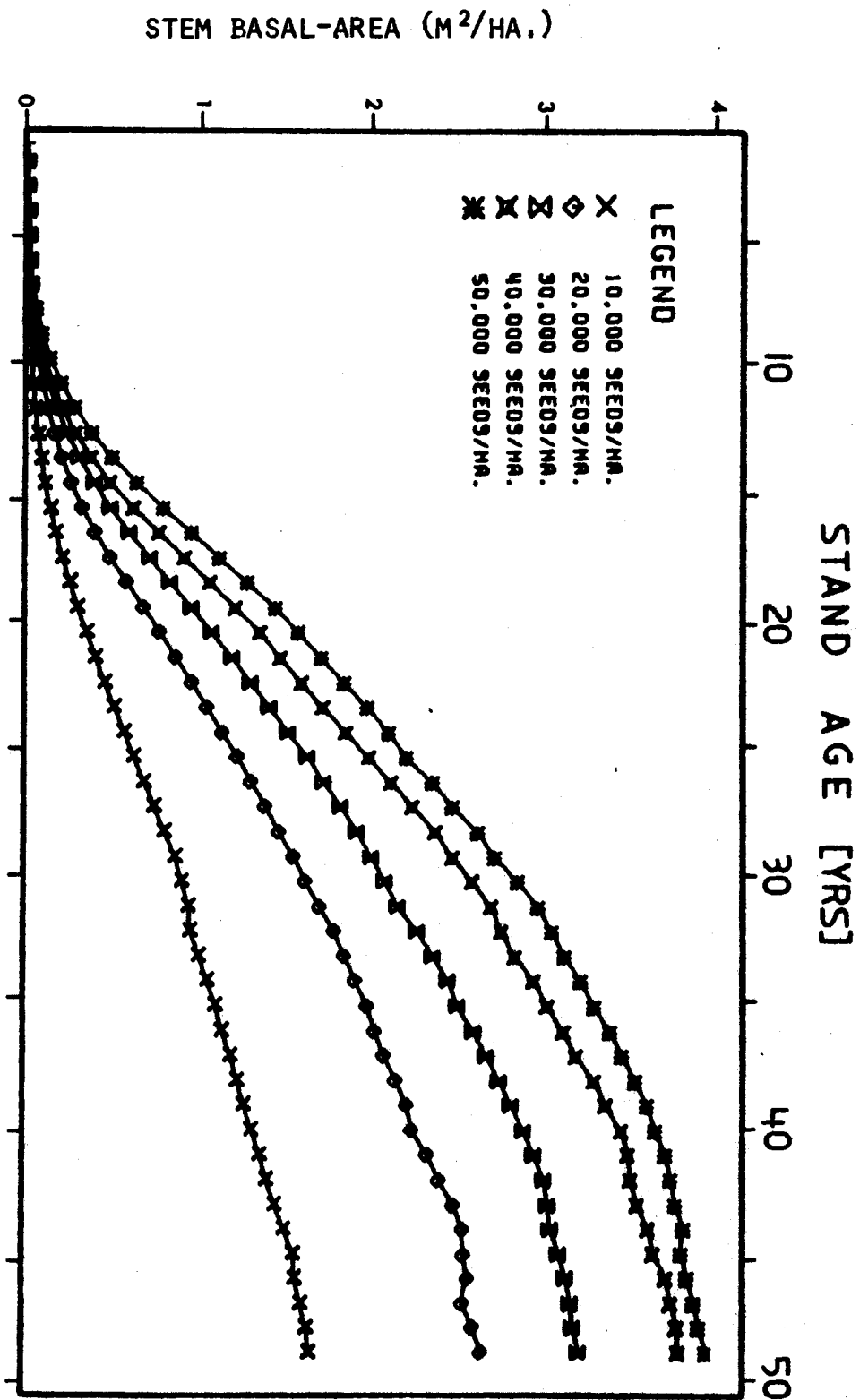


FIG. 8.12: TOTAL PINE BASAL-AREA IN THE SIMULATED STANDS

8.10 - 8.12. Although the stand dominants have completed 2/3 of their growth by the age of thirty years, mean height and D.B.H. characteristics for the stand have attained only 50% of their final (50 year) values at this time. At the end of the simulation run stand dominants have reached heights of 23 - 24 m. and basal area dimensions of 1000 - 1300 sq. cms.

The mean net volume yields of stands are graphed in Figs. 8.13 - 8.15 and summarized in Table VIII.3 and in Appendix G. In all these cases the stands are assumed to be unthinned. Net yields vary directly with the amount and rate of initial establishment of pine seedlings. In terms of volumetric yields, there is a rapid increase in all simulated treatments in the period from 20 - 50 years. PINUS predicts final yields of 300 - 800 cu. m./ha. overbark (4,310 - 11,436 cu. ft./ac) for the various simulated treatments. For the minimum acceptable initial seed input of 20,000 seeds/ha. an overbark yield of 520 ± 21 cu. m./ha. (7520 ± 370 cu. ft./ac) can be expected at 50 years. Underbark volumetric yields are some 37% below these overbark values (Fig. 8.14). Thus, for the 20,000 seeds/ha. initial input, a final (50 yr. old stand) yield of 330 ± 12 cu. m./ha. (4717 ± 170 cu. ft./ac) can be expected. The predicted board-foot yields are plotted in Fig. 8.15. Yields are computed only for trees attaining the minimal exploitable saw-timber diameter of 25 cms. (10 in.) at breast height. Trees of this size increase rapidly in number as stands attain 25 -30 years of age, which

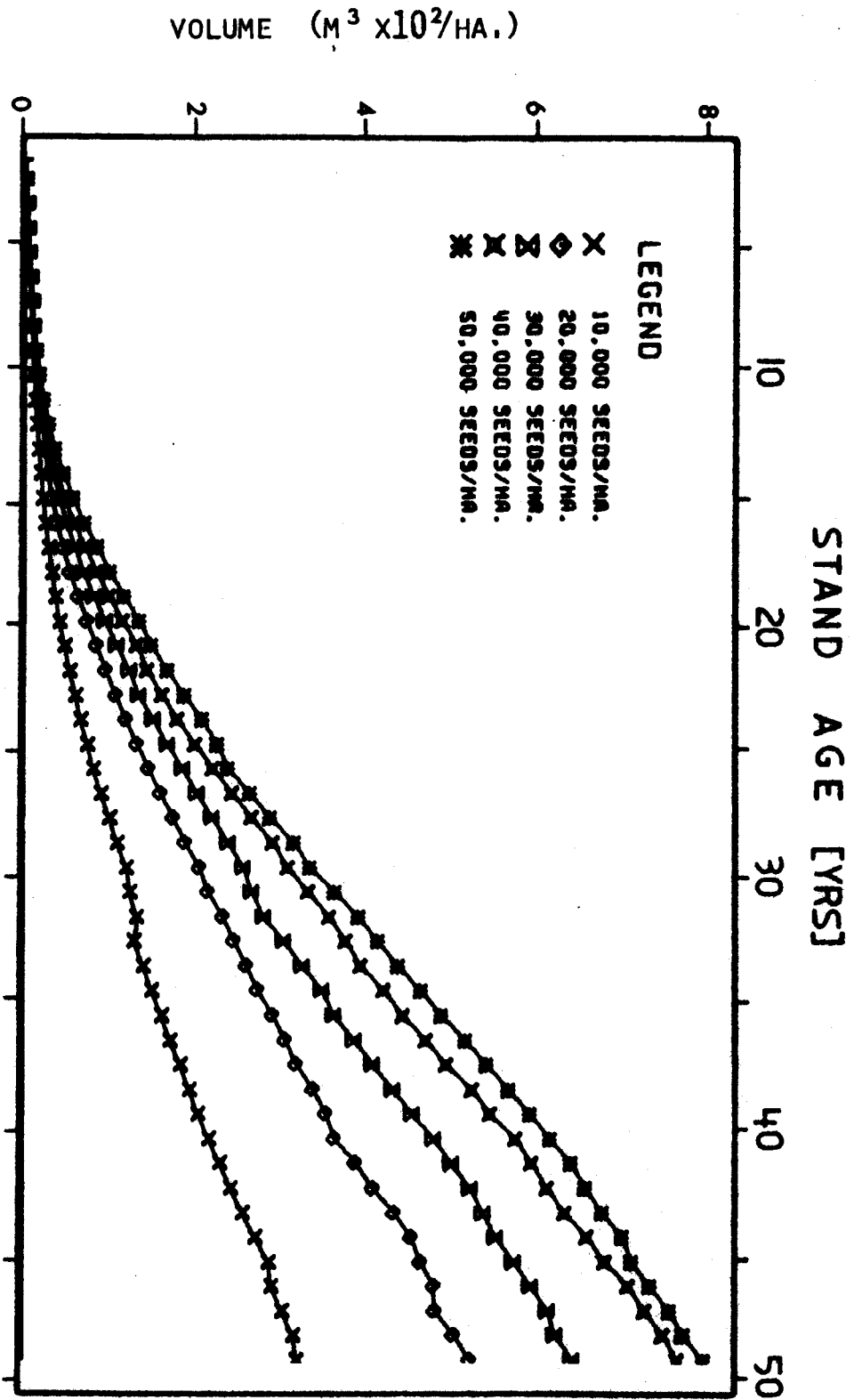


FIG. 8.13: TOTAL OVERPARK VOLUME IN THE SIMULATED STANDS

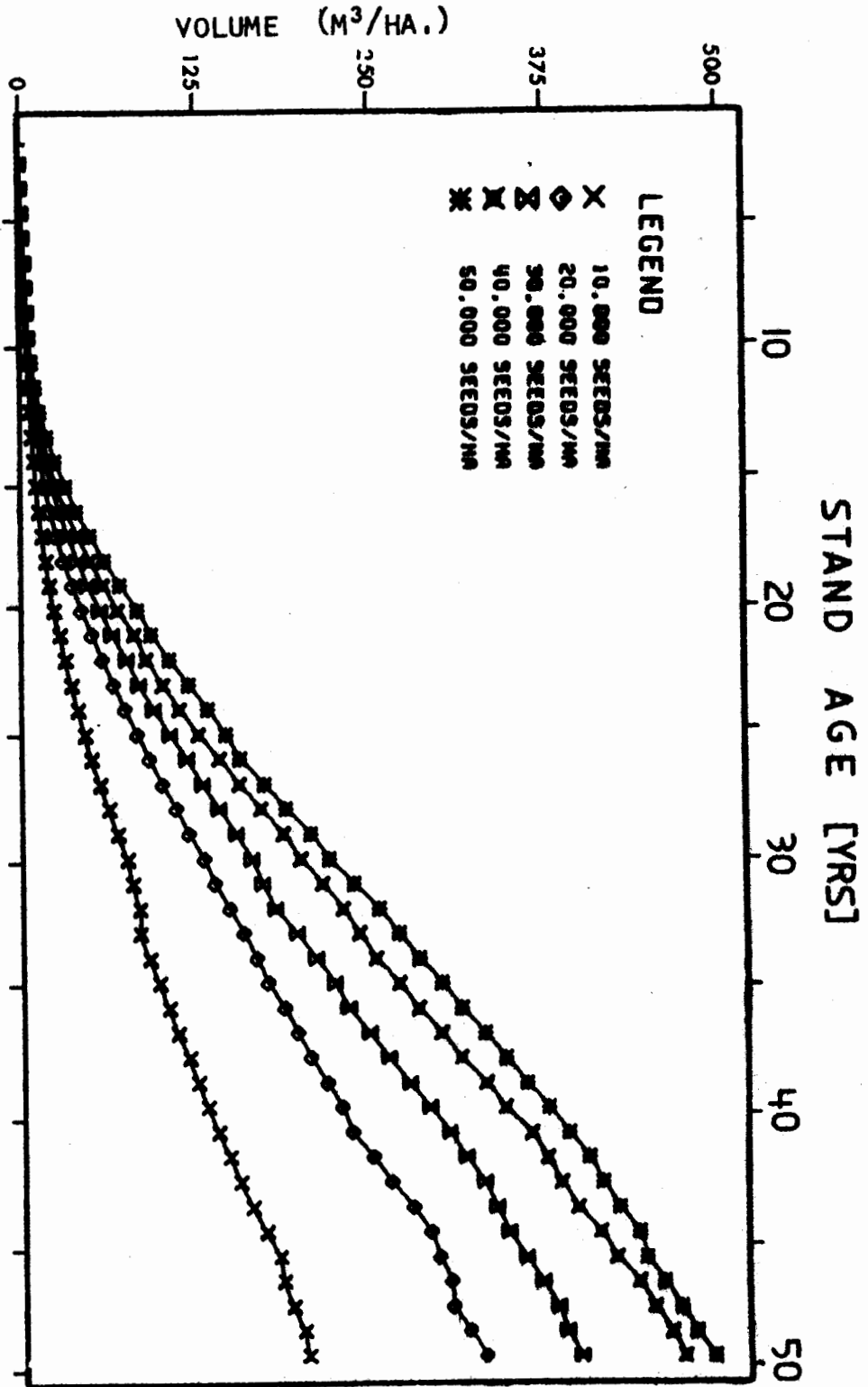


FIG. 8.14: TOTAL UNDERBARK VOLUME IN THE SIMULATED STANDS

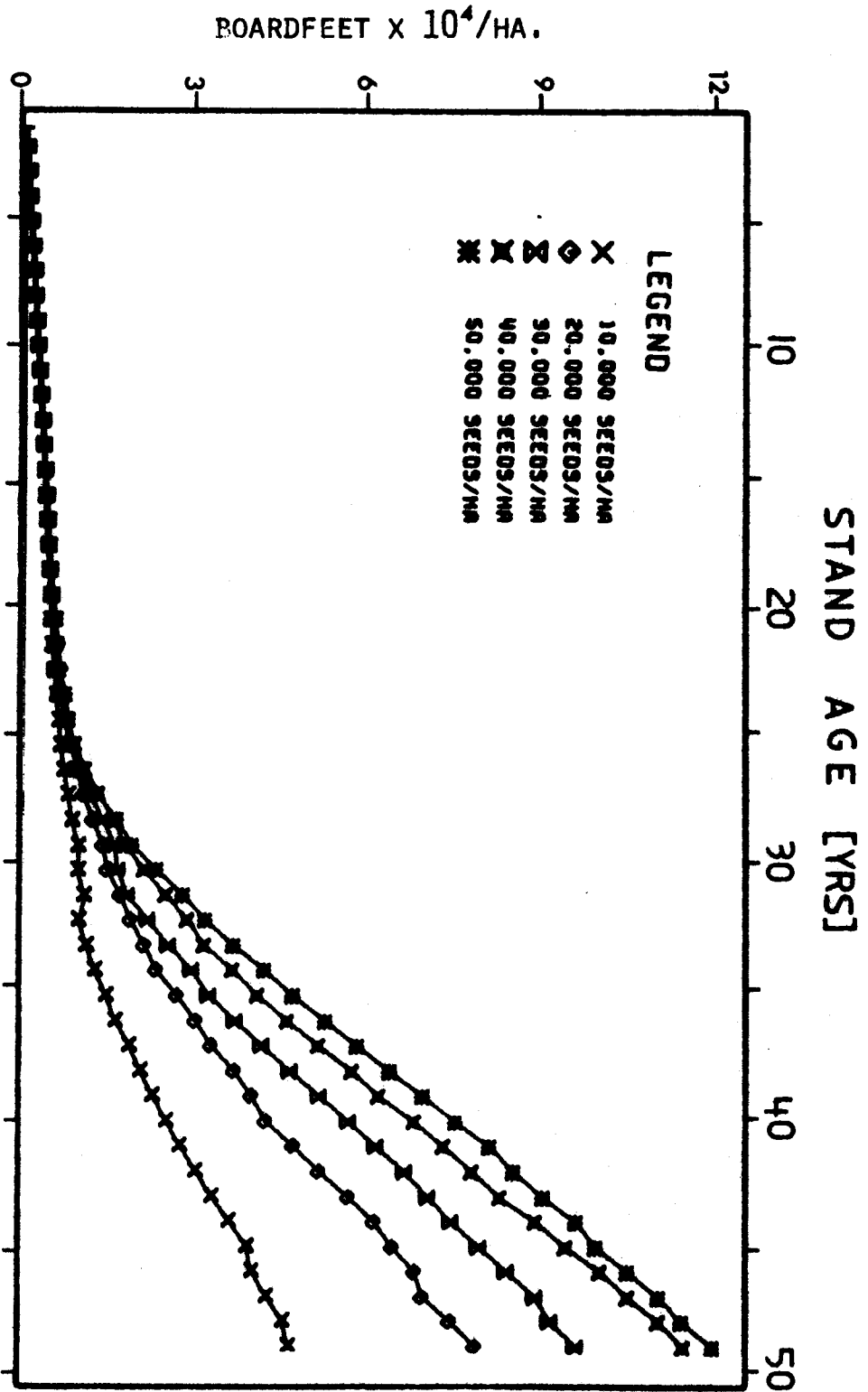


FIG. 8.15: TOTAL SAWTIMBER VOLUME IN THE SIMULATED STANDS.

TABLE VIII.3: PREDICTED YIELDS OF SIMULATED STANDS UNDER THE THE SEED-TREE MANAGEMENT SYSTEM.

| Seed Input | Yr. | Yield V.OB. | | Yield V.UB. | | Yield Bdft. | |
|---------------|-----|-------------|------|-------------|------|-------------|------|
| | | \bar{x} | s.e. | \bar{x} | s.e. | \bar{x} | s.e. |
| 10. | 20 | 64.5 | 1.3 | 34.8 | 0.8 | 7740 | 100 |
| | 30 | 138.6 | 3.0 | 83.5 | 2.1 | 12140 | 200 |
| | 40 | 219.4 | 10.2 | 137.6 | 5.7 | 232200 | 1520 |
| | 50 | 329.5 | 11.6 | 206.9 | 6.9 | 43640 | 1830 |
| 20. | 20 | 92.4 | 2.2 | 52.2 | 1.6 | 8030 | 100 |
| | 30 | 217.9 | 4.7 | 135.8 | 3.2 | 15530 | 430 |
| | 40 | 359.3 | 14.9 | 229.8 | 8.3 | 37680 | 2050 |
| | 50 | 520.4 | 20.7 | 329.6 | 12.0 | 70960 | 3030 |
| 30. | 20 | 112.2 | 2.7 | 64.5 | 1.8 | 7830 | 160 |
| | 30 | 267.1 | 8.5 | 168.2 | 4.9 | 17340 | 1280 |
| | 40 | 455.8 | 15.5 | 290.3 | 9.2 | 47860 | 2430 |
| | 50 | 632.8 | 10.4 | 395.3 | 6.2 | 85890 | 1550 |
| 40. | 20 | 132.2 | 2.6 | 77.3 | 1.5 | 8080 | 90 |
| | 30 | 317.3 | 9.2 | 202.3 | 5.4 | 18750 | 1280 |
| | 40 | 521.9 | 14.5 | 330.3 | 9.3 | 52750 | 1720 |
| | 50 | 750.2 | 20.6 | 466.2 | 13.9 | 101920 | 2750 |
| 50. | 20 | 151.5 | 3.2 | 90.9 | 2.2 | 8040 | 130 |
| | 30 | 341.9 | 10.5 | 222.4 | 5.6 | 19920 | 1590 |
| | 40 | 585.9 | 16.8 | 372.9 | 10.9 | 63180 | 2000 |
| | 50 | 779.4 | 38.0 | 487.1 | 23.1 | 106250 | 5400 |
| $\times 10^3$ | | cu.m./ha. | | cu.m./ha. | | /ha. | |

V.OB. = Volume Overbark
V.UB. = Volume Underbark
BDFT. = Boardfoot volume
 \bar{x} = mean
s.e. = standard error

accounts for the concomitant increase in saw-timber volume after this point in time. In the oldest stands the predicted yields are from 40,000 - 106,000 bd. ft./ha. (16,000 - 43,000 bd. ft./ac). A management strategy aimed at establishing full stocking by leaving a minimum of 20 seed-bearing trees/ha. (20,000 seeds/ha. input), can therefore expect yields of 71,000 3000 bdft./ha. at 50 years.

8.215: Stand Dynamics: Volume Increment and Rotation Age

The mean annual increment (M.A.I.) in volume for each of these three stand variables is graphed as a function of stand age in Figs. 8.16 - 8.18 and Table VIII.4. Maximum wood productivity in terms of volume overbark is attained in all stands during the final 5 year period of the simulation, when the curves of volume increment approach their asymptotes. The absolute values of M.A.I. volume are again density-dependent, with some tendency for stands with the densest initial conditions (>40,000 seeds/ha) to converge. In managing stands for pulpwood products the culmination of the m.a.i. volume (ob) curve indicates the period of maximum wood productivity in the stand, and hence the optimal length of the rotation. According to Davis (1954), the culmination of board-foot growth occurs some 10 - 15 years after maximum volume increment in southern pine stands. Assuming the same relationship holds true for P. caribaea, and Fig. 8.18 indicates that it well may, the optimal rotation length for saw-timber products in Mountain Pine Ridge should be

M²/HA.

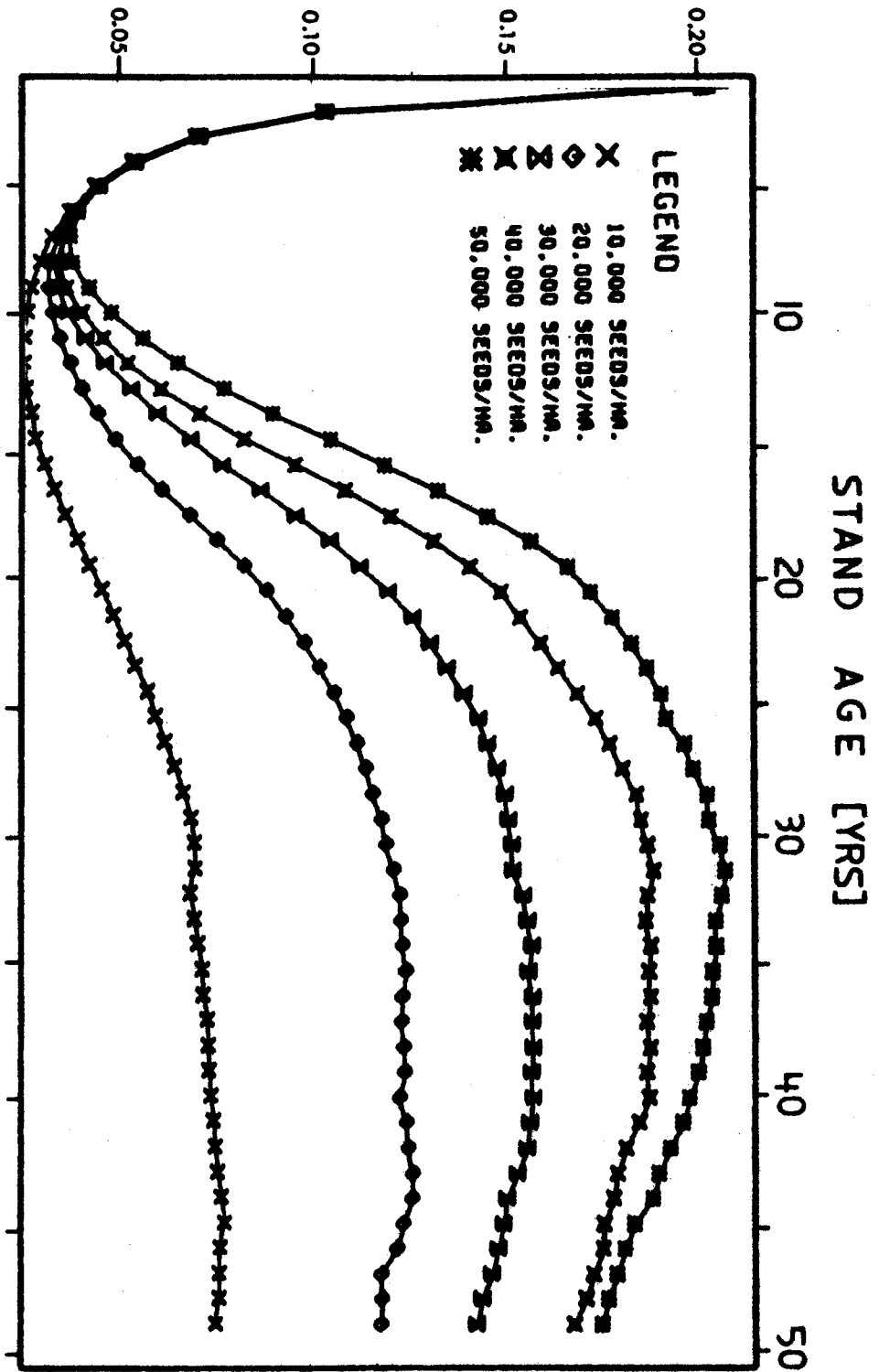


FIG. 8.16: MEAN ANNUAL INCREMENT IN STEM BASAL-AREA.

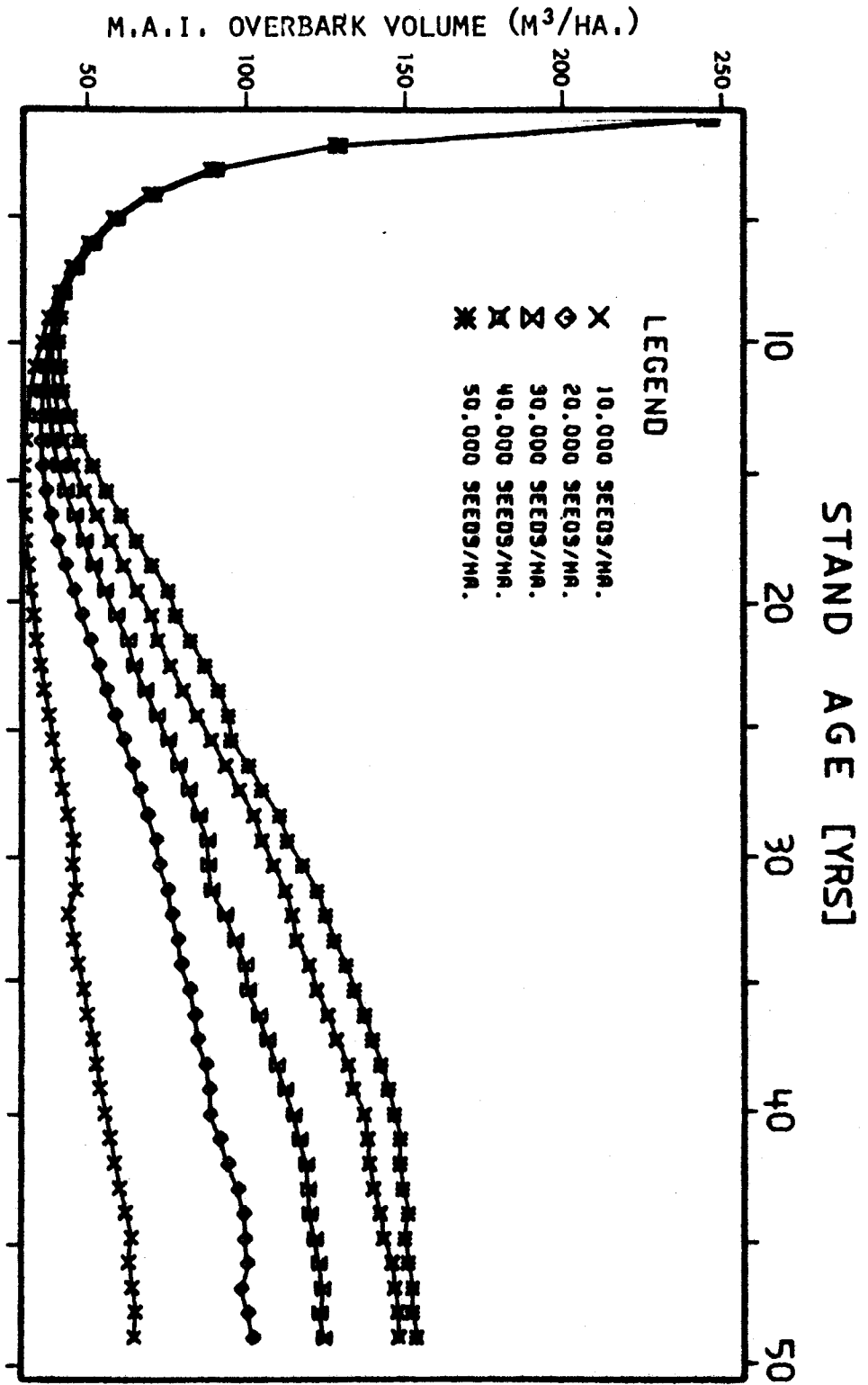


FIG. 8.17: MEAN ANNUAL INCREMENT IN TOTAL OVERBARK VOLUME

BOARDFEET $\times 10^2$ /HA.

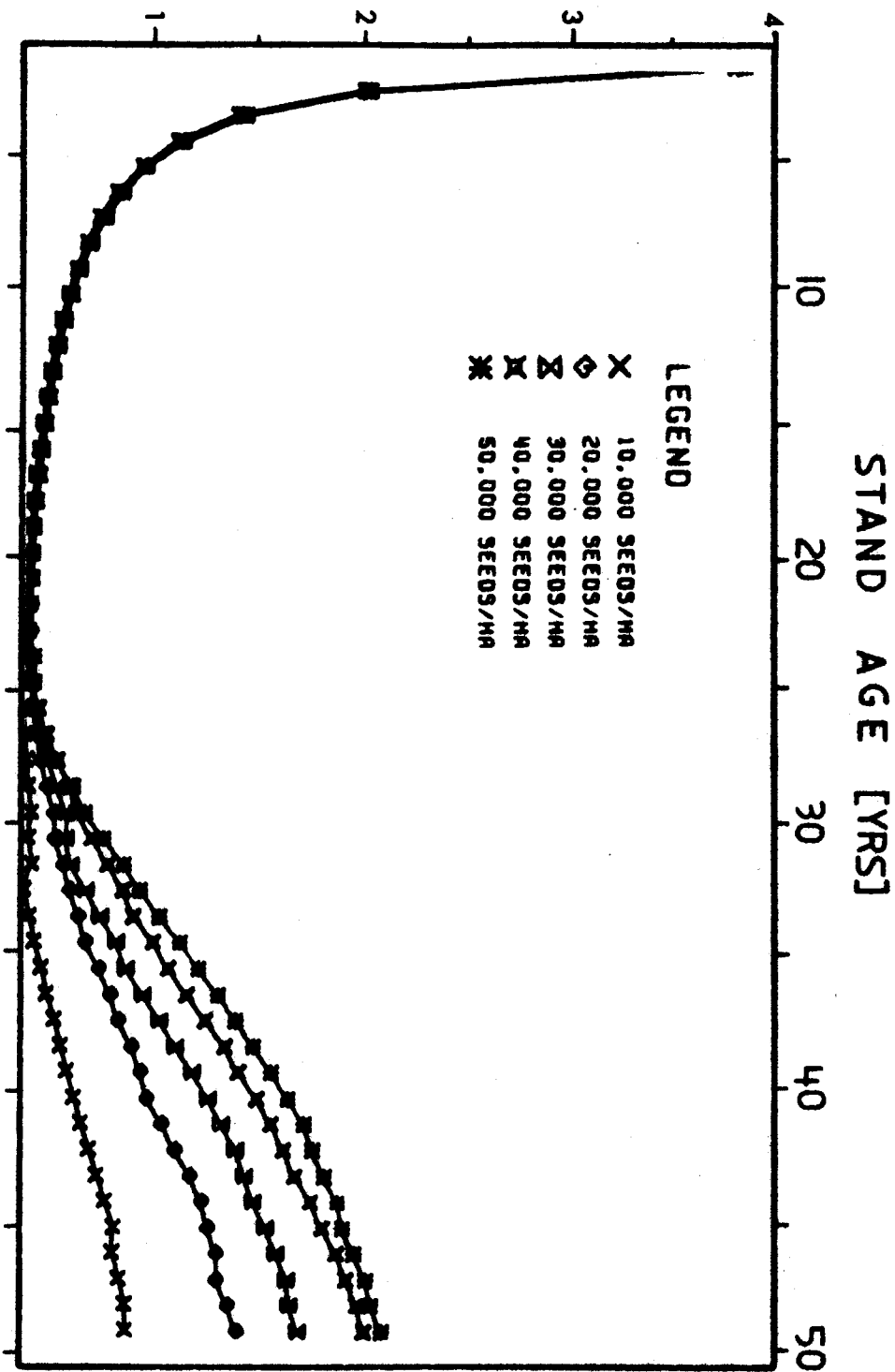


FIG. 8.18: MEAN ANNUAL INCREMENT IN TOTAL SAWTIMBER VOLUME.

TABLE VIII.4: MAXIMUM MEAN ANNUAL VOLUME INCREMENTS ("YIELD CLASSES") FOR THE SIMULATED STANDS

| Seed Input | Yield Class | | | Annual Thinning Rate | | |
|------------|----------------|------------------|--------|----------------------|------------------|--------|
| | m ³ | ft. ³ | hoppus | m ³ | ft. ³ | hoppus |
| 10,000 | 6.75 | 96.5 | 75.8 | 4.73 | 67.6 | 53.1 |
| 20,000 | 10.50 | 150.1 | 117.9 | 7.35 | 105.1 | 82.5 |
| 30,000 | 12.75 | 182.3 | 143.2 | 8.92 | 127.6 | 100.2 |
| 40,000 | 15.25 | 218.1 | 171.3 | 10.68 | 152.7 | 120.0 |
| 50,000 | 15.75 | 225.1 | 176.8 | 11.03 | 157.6 | 123.8 |
| /ha. | /ha. | /ac. | /ac. | /ha. | /ac. | /ac. |

1 hoppus foot = 1.2732 cu. ft.. This measure is the one commonly employed in British forest management, and is used to define Yield Classes by Bradley, Christie and Johnston (op. cit.).

at least 55 - 60 years. On the basis of his experience in the study area, Lamb (1973, p. 126), concluded that a 60-year rotation would be necessary for saw-timber production. Extrapolating the data in Fig. 8.18 into this time period indicates yields of between 60,000 - 135,000 bdft/ha. (25,000 - 55,000 bdft/ac) for the range of seed inputs tested.

Because of the constraints on the model imposed by the absence of such old stands in the study area, these results must be treated cautiously. However, it should be noted that a yield table for fully-stocked stands of loblolly pine in the southeastern U.S.A. (Wahlenberg, 1960, p. 502) lists a similar range of values at this age. Stands of P. taeda with similar site indices to those tested in the simulation (24 m. (80 ft.) at 50 years), are capable of producing 65,000 bdft/ha. at age 60. Board-foot yields in this yield table for loblolly pine are calculated for trees with a minimum D.B.H. of 32 cms. and not 25 cms., as in this study, and so the values are roughly comparable.

Thus, if a management plan to supply a seed input of 20,000 seeds/ha. is achieved, the forest manager can expect to harvest 100,000 bdft/ha. (40,000 bdft/ac) after 60 years in Mountain Pine Ridge, assuming that wildfires and/or hurricanes do not damage the growing crop.

The results of the simulation runs can also be placed in perspective by comparing their predictions with the status of the present crop of trees maturing in Mountain Pine Ridge. Johnson and Chaffey (op. cit.) present data on the standing volume of timber in the project area. Their data indicate that in their "pine forest" category the mean underbark stand volume is of the order of 20 - 30 cu. m. /ha. (280 - 430 cu. ft./ac). Most of these pine stands are approximately 20 years old, and because of wildfires and overcutting in the past, contain slightly less volume than the simulated stands derived from 10,000 seeds/ha. (Table VIII.3). The best of these areas can therefore be expected to produce some 200 cu. m./ha. (2850 cu. ft./ac) or 50,000 bdf./ha. (20,000 bdf./ac) at the end of a 60-year rotation.

8.3: STAND DYNAMICS AND THINNING TREATMENTS

The objective in thinning a forest stand is to "provide the greatest girth increment, consistent with maximum volume production" (Bradley, 1967). Thinning involves a reduction in the density of the stand, and therefore competitive stress, in order to stimulate growth and improve the quality of the remnant trees. Artificial thinning of forest stands generally proceeds according to empirically derived rules which often vary from species to species and from region to region. It has been found that such empirical rules are strikingly similar to the "3/2 power law" (White and Harper, 1969) which was initially derived

from natural, unthinned crop and forest stands (Yoda et al., 1963).

The latter authors examined the process of population reduction (self-thinning) in overcrowded pure populations of several herbs and trees, and found that the mean weight of plants surviving density-stress could be related to population size as $w = C.p$, where p is the number of survivors, and w is their corresponding mean weight. White and Harper demonstrated the application of this law to forest management by testing the fit of data derived from artificial thinning of stands of various forest species to the model. They state: "It is readily apparent that the thinning treatments...based upon an "arbitrary standard" to "maximize growth per tree and unit area" follows closely the empirical conclusion of the Japanese workers - "there is a maximum asymptotic density at each stage of growth and densities beyond this level cannot be realized, however high the initial density was, because of the regulation by self-thinning" (p. 480).

The degree of density stress and competition (and therefore the necessity of thinning) in the simulated stands can be evaluated using the "3/2 power law". The weight of a plant is proportional to its volume, and mean stem-volume/tree will be substituted for weight in this discussion. Plotting mean tree-volume against the stem-density of a stand at 1 year intervals from 15 years on in each of the simulated stands

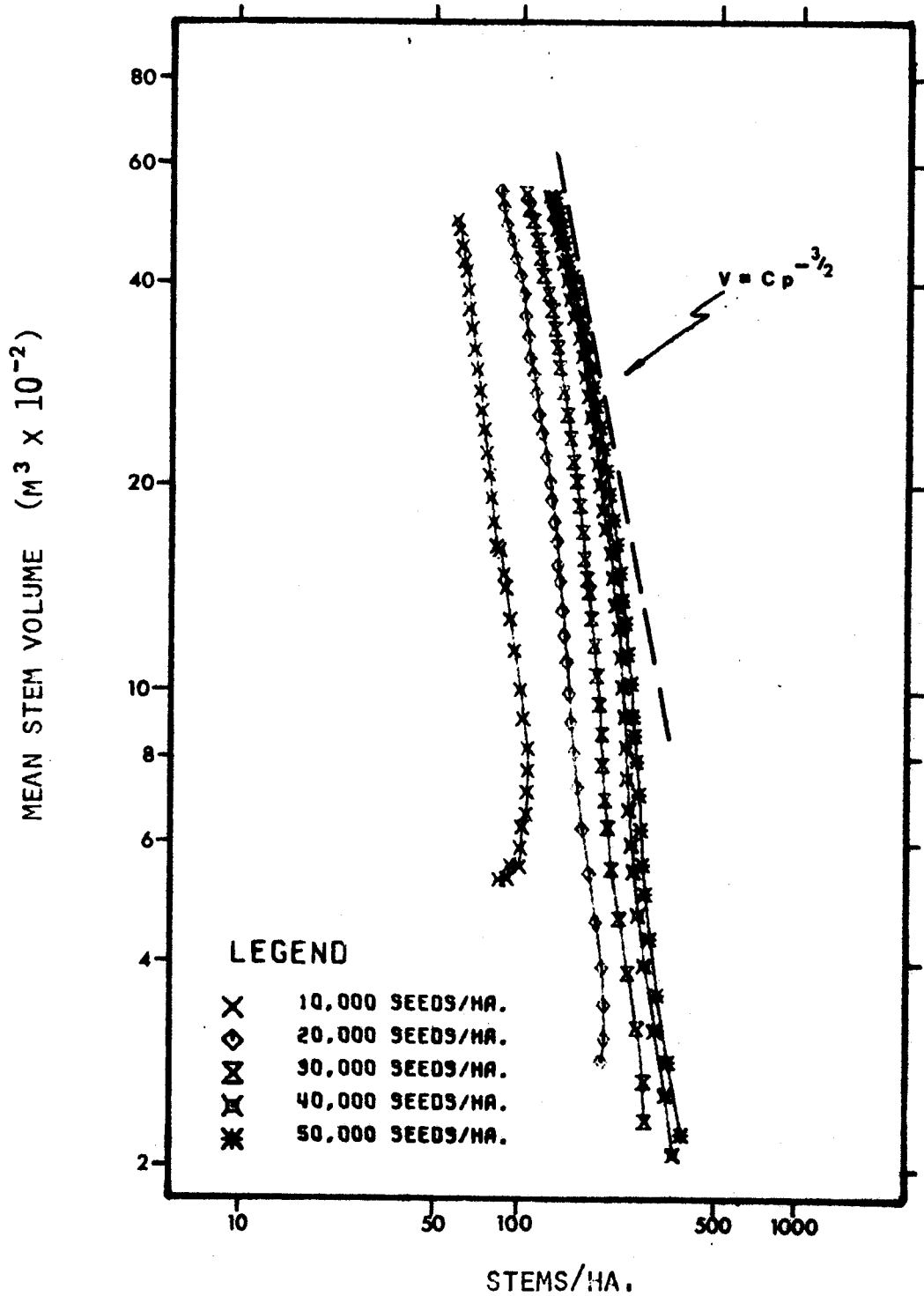


FIG. 8.10: TEST OF THE " $3/2$ POWER LAW" IN THE SIMULATED STANDS.

produces the series of graphs in Fig. 8.19. If self-thinning proceeds according to the "3/2 power law", the slope of each plot should be -1.5. A broken line with this gradient is included in Fig. 8.19 for comparison. It is clear that self-thinning in the youngest stands (15 - 35 years), in all treatments, proceeds along a much steeper gradient (c.4.7.) than the "3/2 power law" predicts. This is indicative of low density stress and competition in these stands. At ages of more than 35 years the slope of the volume - density regression line changes, and self-thinning proceeds at a gradient of 1.5 - 2.5. As might be expected, convergence to the -1.5 slope occurs most rapidly in the stands derived from the largest initial seed inputs, where density stress is greatest. In less dense stands (<20,000 seeds/ha. input), it is only in the final five-year period of the simulation that model and law converge. The close correspondence of the model to the law would indicate that the simulator mimics mortality and stand growth acceptably well.

We can conclude from these results that density stress and inter-tree competition are not severe in P. caribaea stands in Mountain Pine Ridge until the stand reaches 35 years of age. To allow the stand to progress to this point often reduces the productivity of the stand, and most foresters would contend that a stand should be artificially thinned at least a decade before severe self-thinning begins.

This conclusion may itself be tested against the more arbitrary thinning rules devised for forest stands. Two "rules" will be used as a test. The first of these is the "1.5D rule" in which the required spacing between neighbouring trees (in feet) is equal to the mean stem DBH (in inches) multiplied by 1.5. The metric equivalent of this rule is $0.21D'$ where D' is the stem DBH in cms. and spacing is calculated in meters. The second thinning method to be employed is the Yield Class system of Bradley, Christie and Johnston (1966)

As a preliminary step in using the 1.5D rule, the time-paths of mean DBH development in the three treatments to be tested (20,000, 30,000 and 50,000 seeds/ha) are plotted in Fig. 8.20. In the most densely-stocked stands (3,000 stems/ha. (1200 stems/ac)) thinning is required by the 1.5D rule when the stand is over 15 years of age. Minimal thinning-ages in less dense stands are 21 years (30,000 seeds input; 2500 stems/ha. (1000/ac)) at age 15, and 27 years (20,000 seeds/ha; 20 stems/ha. (800/ac) at age 15). The frequency of thinning after these dates is a subjective decision which must be based to some extent on the availability of local markets for thinned material.

A series of five replicate runs were made using PINUS to simulate the effects of thinning in each of the densest stands. Thinnings were made at years 18, 24 and 30 according to the 1.5D rule. The numbers of stems (S) required in each thinning was $S = 400/(D \cdot 0.21)$, equivalent to a total stem basal area per plot

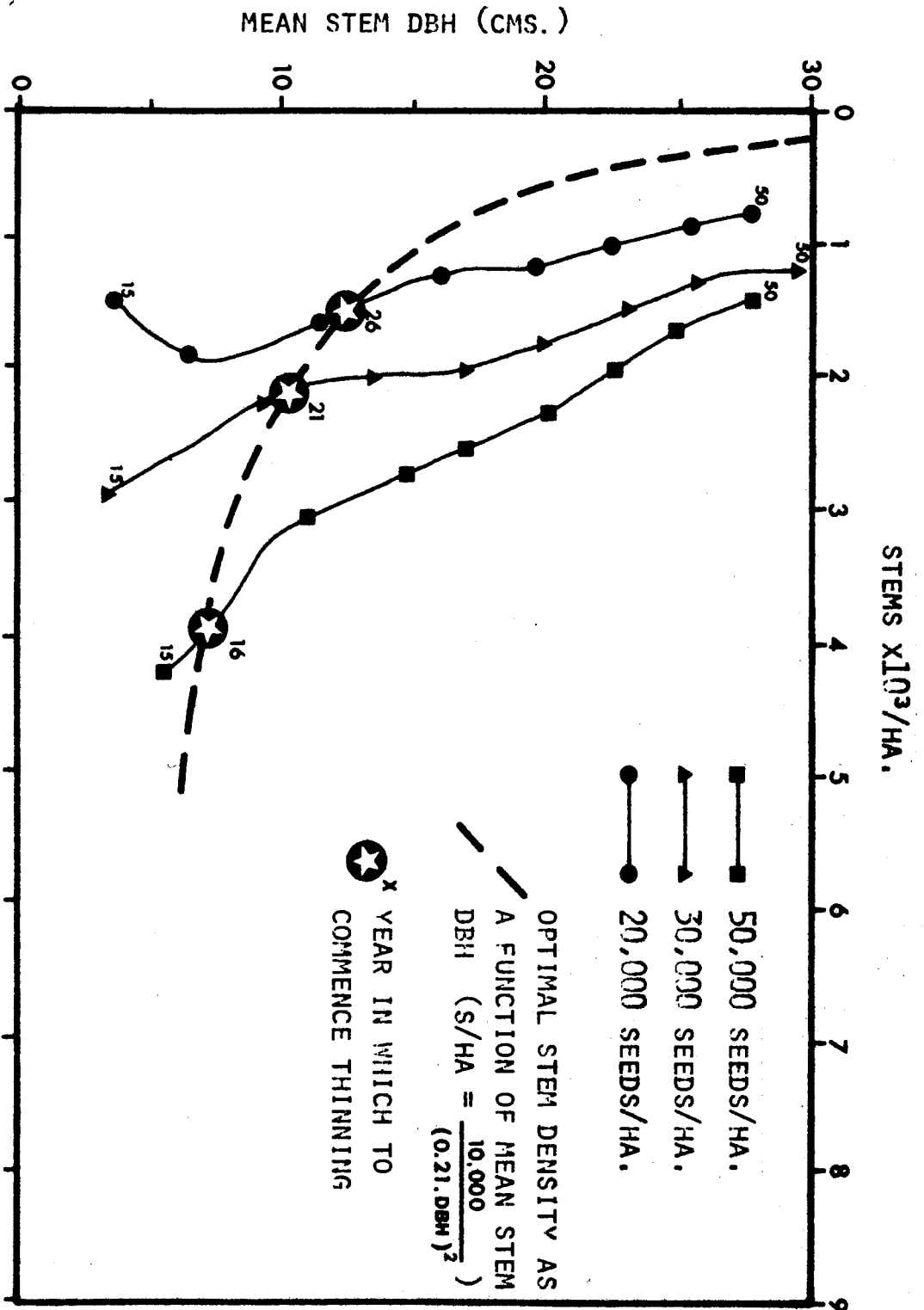


FIG. 8.20: OPTIMAL STEM DENSITY (1.5D RULE), AND TIME-PATHS OF MEAN DBH DEVELOPMENT (YEAR 15-50 AT 5 YEAR INTERVALS), OF SIMULATED STANDS AT THREE INITIAL SEED-INPUTS.

of S. (D/2) . To conduct the thinning trees of progressively greater basal area were removed (Subroutine SORT), until the total basal area of the plot was equivalent to this value, which is constant in all thinnings at 17.8 sq. m./ha. (77 sq. ft./ac). The mean results of the five runs are presented in Fig. 8.21 where stand yields in the thinned and unthinned modes are compared. Net volumetric yield in the unthinned stands is high, amounting to some 500 cu. m./ha. at 50 years. In contrast, the three thinnings retard volume yield, and net volume and volume of thinnings is only of the order of 40% of that in the unthinned mode. Using the international 1/4" rule to calculate board-foot yields, the thinned stands perform somewhat better. At 50 years of age the remnant stand is capable of producing net yields of 25,000 - 30,000 bdft./ha. (10 - 12,000 bdft./ac) compared to 80,00 - 95,000 bdft/ha. (32 - 40,000/ac) in the unthinned model. These yields, plus intermediate yields from thinnings, indicate that saw-timber yields in thinned stands may be only 50% of those in the unthinned stands.

The second thinning technique to be employed is one developed by the Forestry Commission in Britain, which is claimed to be suitable for all commercial species and site classes in that country. The system is based on the "yield class" of a stand, where "yield class" is defined as the maximum mean annual volume increment of the growing crop. Management of the stand consists primarily of removing on an annual basis a volume

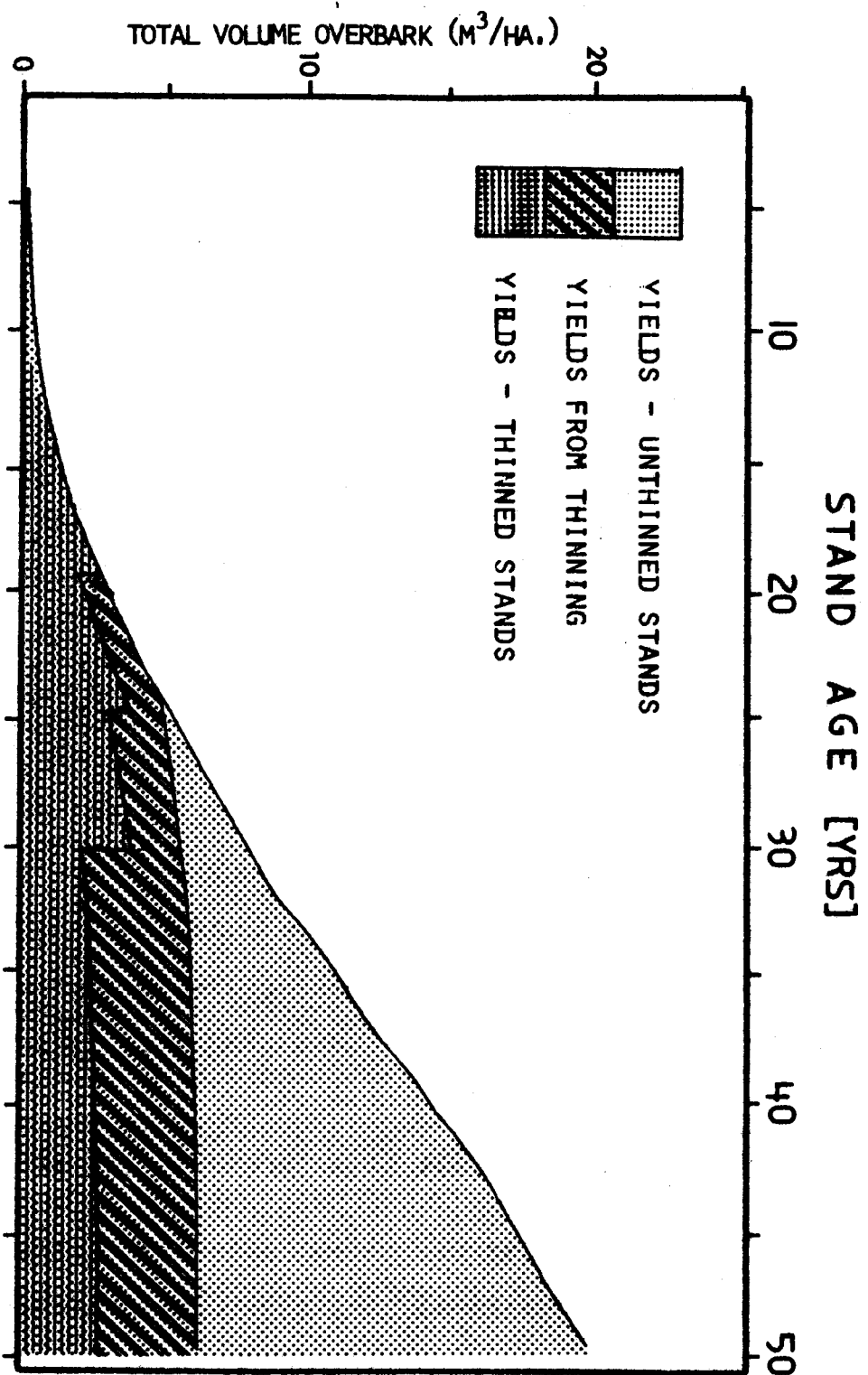


FIG. 8.21: EFFECT OF APPLYING THE 1.5D THINNING RULE ON VOLUME YIELD IN THE SIMULATED STANDS. STANDS DERIVED FROM AN INITIAL SEED-INPUT OF 30,000 SEEDS/HA. TAKEN AS AN EXAMPLE.

equivalent to 70% of the yield class of the stand, until the age of maximum m.a.i. volume is approached, at which point a lesser intensity of thinnings is applied. For the three pine species grown commercially in the U.K., thinning commences (Bradley, Christie and Johnston, p. 19) when the height of the dominants in the stand reaches 9.1 - 11.3 m. (30 - 37 ft.). The authors of the system claim that this form of management results in "near-maximum profitability under a wide range of price conditions for both pulpwood and sawtimber production" (Bradley, Christie and Johnston, p.1). This system would of necessity have to be modified, in order to reduce the costs of management in Mountain Pine Ridge. One way of producing this end result would be to increase the thinning interval. An interval of seven years was adopted in this series of simulations, with thinnings being initiated when the height of the four largest stems (excluding the seed-tree) topped 10 m. and ceasing after the stand reached 40 years. The first thinning extracted a volume equal to the annual thinning intensity, succeeding thinnings removed a volume equal to seven times this value. The yield class values for each of the seed inputs was determined by examining maximum m.a.i. volume o.b. in the unthinned mode (Fig. 8.17, Table VIII.4).

The simulated thinning regime was replicated five times for each initial seed input. The results of these runs are presented in Appendix H. Thinning begins in the 18 - 22 year interval in each case and a maximum of three further thinnings are possible

prior to the 40-yr. cutoff point. The thinned plantations described by Bradley, Christie and Johnston (op. cit.) maintain a constant basal area throughout the course of thinning. However, the simulated stands of *P. caribaea* show drastic decreases in total stem basal area in the third decade of development as a result of severe thinning, and stand recovery was retarded by further thinnings between the ages of 30 and 40 years (Fig. 8.22). Indeed, the canopy was opened up to such an extent that seedling establishment continued, albeit at a low level, to the end of the simulation (Fig. 8.23).

This destruction of stand structure was paralleled by decreases in stand yield. The mean predicted yields in terms of overbark volume, underbark volume and boardfoot volume are plotted in Figs. 8.24 - 8.26. The main stands after thinning contain only some 15% of the volume of unthinned stands. At 50 years, the volume of thinnings removed is generally of the same order of magnitude as the volume of the remnant stand (Fig. 8.24). Therefore the yield class system produces only 30% of the yields afforded by leaving stands in the unthinned mode. The reason for this unsatisfactory result is presumably the difficulty of translating a plantation-based management system to naturally regenerated stands, for at the time of the first thinning in a plantation crop, there is considerably less variation in tree size than with a stand which may still be in the regeneration phase.

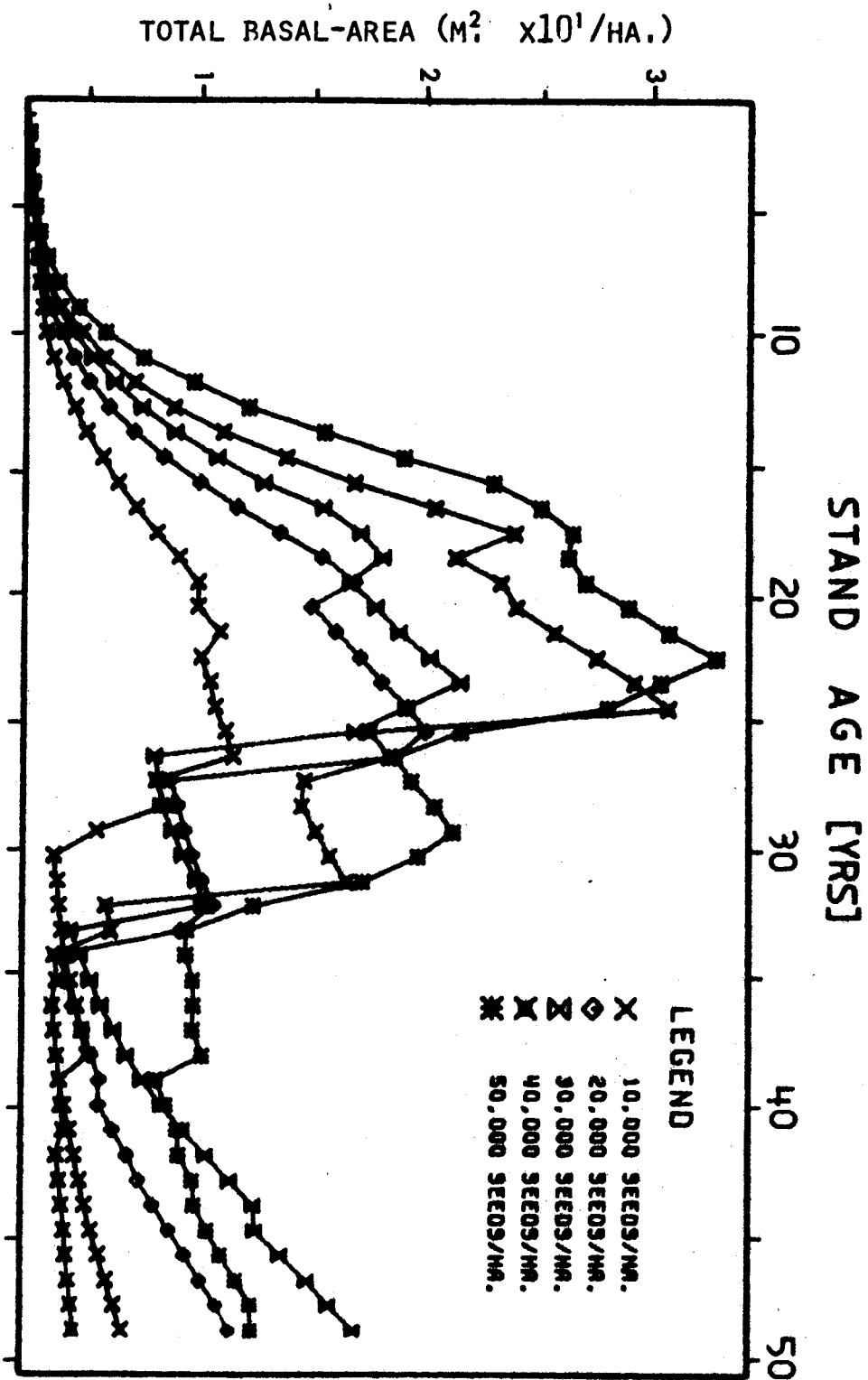


FIG. 8.22: EFFECTS OF THINNING (YIELD-CLASS SYSTEM) ON STEM BASAL-AREA.

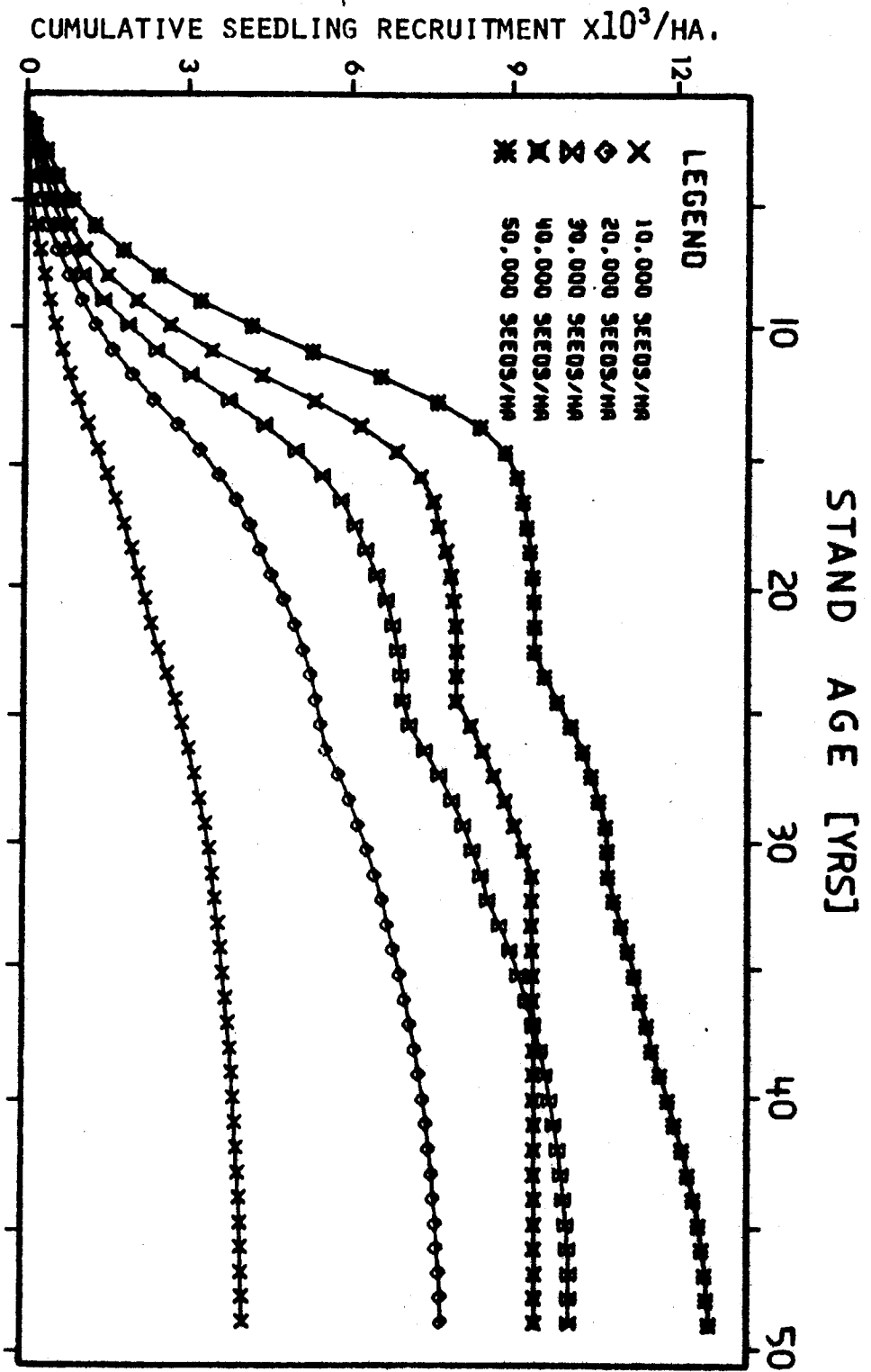


FIG. 8.23: EFFECTS OF THINNING (YIELD-CLASS SYSTEM) ON SEEDLING RECRUITMENT.

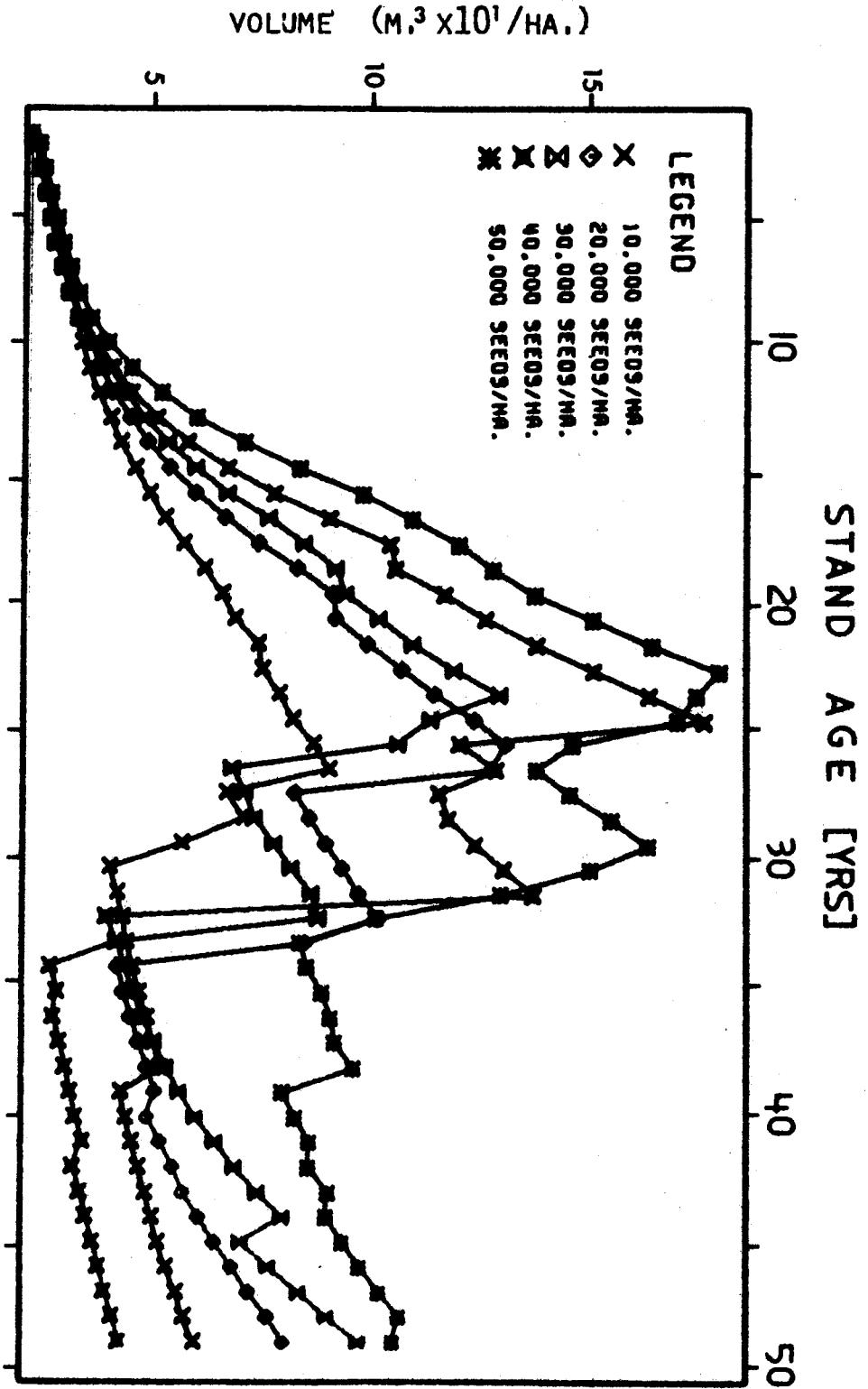


FIG. 8.24: EFFECTS OF THINNING (YIELD-CLASS SYSTEM) ON TOTAL OVERBARK VOLUME.

There are two specific reasons for the failure of the yield class system to maintain stands at a high-yielding level. In the British pine plantations the total stem basal area immediately prior to thinning is of the order of 21 sq. m./ha. (90 sq. ft./ac). In the simulated stands basal areas of this magnitude are attained in stands between 25 - 30 years of age in the less dense stands (<30,000 seeds/ha) and around 15 - 20 years in denser stands. Consequently in less dense stands, the standing crop is insufficient to maintain a high thinning intensity. In all stands the levels of current annual increment may fall below the annual thinning intensity during the third decade of stand development, thus thinning based on the yield class system eventually leads to a reduction in the standing crop.

8.4: PLANTATIONS

Although the seed-tree system will undoubtedly be the principal form of regeneration in Mountain Pine Ridge, plantations may be employed for specific purposes. Foremost among these will be the growth of superior genotypes as seed-bearers, for research purposes, and, to a lesser extent, for timber. PINUS was utilised to test the effects of various plantation spacings on tree growth and stand yield. The site index for the simulated runs was set at 15 m. (49 ft.) at 25 years, to allow comparison with the results from the seed-tree management runs. The results of the simulations, while mainly applicable to Belizean conditions, may also be employed to

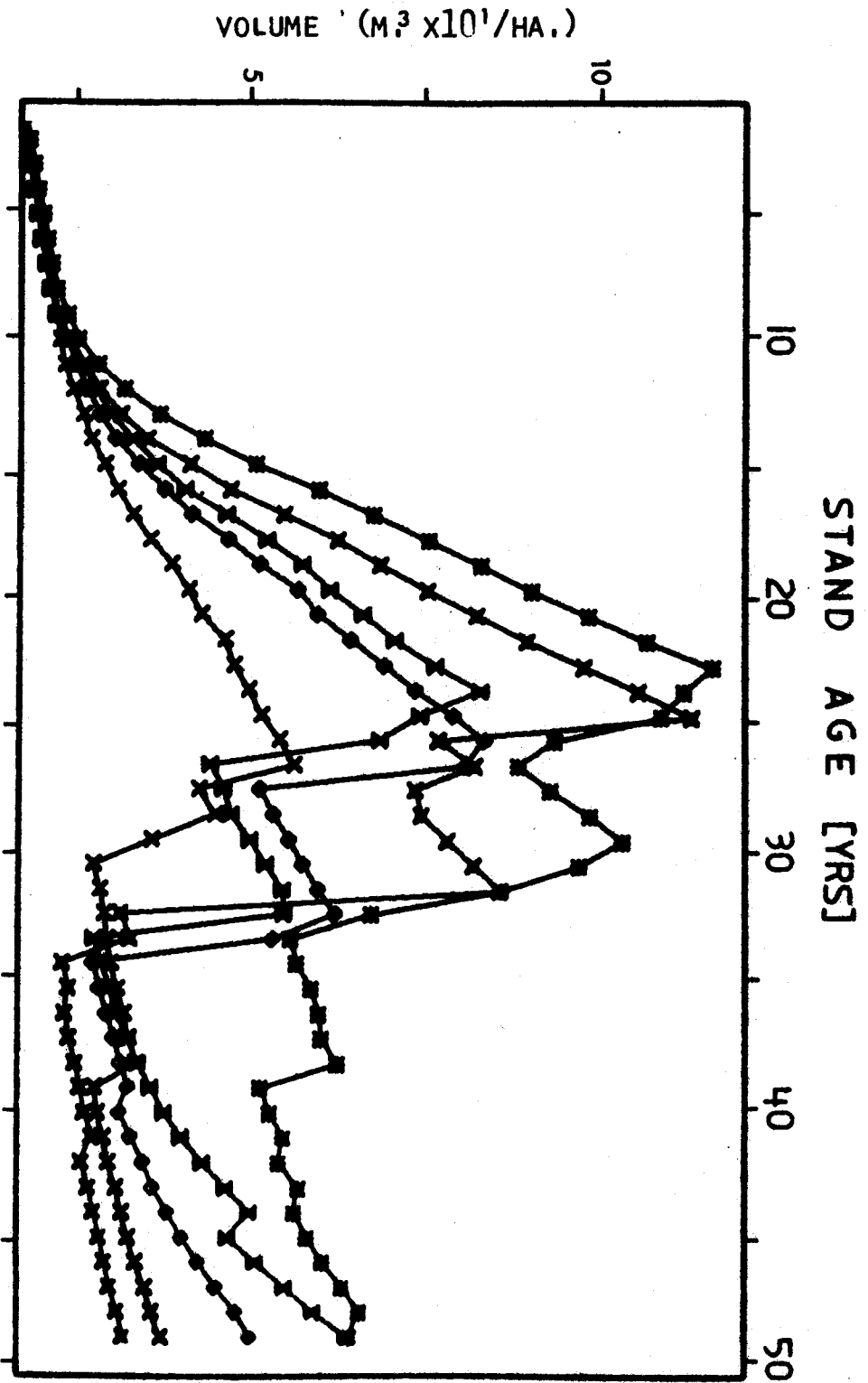


FIG. 8.25: EFFECTS OF THINNING (YIELD-CLASS SYSTEM) ON TOTAL UNDERBARK VOLUME.

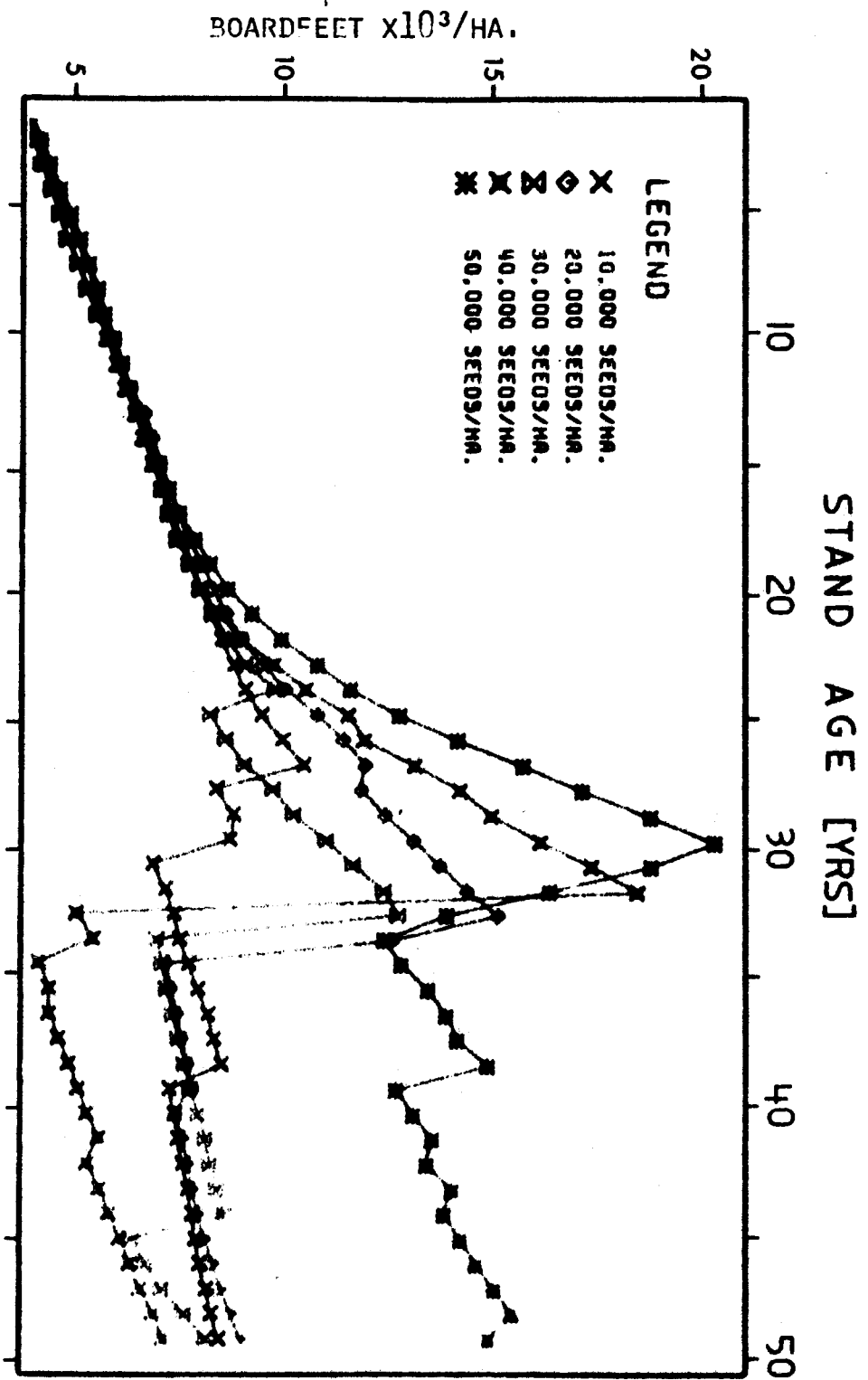


FIG. 8.2C: EFFECTS OF THINNING ON TOTAL SAWTIMBER VOLUME (YIELD-CLASS SYSTEM).

predict the yields and thinning schedules of plantations of P. caribaea of similar site-index elsewhere. Four experimental treatments were established. These consisted of running PINUS with the four initial tree spacings listed in Table VIII.5. Predicted yields from these spacings are listed in Table VIII.6. In comparison with the yields from the seed-tree regeneration system, the plantations exhibit an earlier but less rapid increment in volume (Fig. 8.27, 8.28; Appendix I). Volume increment also reaches a maximum at an earlier age. The rotation ages for saw-timber in the plantations vary from 40 - 50 years depending on the the initial planting density (Table VIII.6). The saw-timber yields in the densest plantations at the end of the rotation are therefore equivalent to that attained by the recommended seed-tree regeneration system (20 trees/ha.), but the crop is harvestable almost 20 years earlier. The predicted yields from lower planting densities are correspondingly lower. Plantings at an initial density of < 1000 stems/ha. produce yields which are somewhat less than those of the lowest simulated density of seedtrees. It seems clear therefore that plantations for saw-timber in Mountain Pine Ridge should aim for initial stockings of 1700 stems/ha. or more.

Obviously, a virtually infinite number of spacing and thinning regimes could be run on PINUS and the results employed as a guide to management practice. Until it becomes clear what the future domestic or export market demands are for pine

TABLE VIII.5: PLANTATION SPACING

| m. | Spacing | | Stem Density | |
|-----------|---------|------|--------------|-------|
| | | ft. | /ha. | /acre |
| 4.6 x 4.6 | 15 x 15 | 475 | 192 | |
| 3.6 x 3.6 | 12 x 12 | 750 | 300 | |
| 3.1 x 3.1 | 10 x 10 | 1089 | 436 | |
| 2.4 x 2.4 | 8 x 8 | 1700 | 680 | |

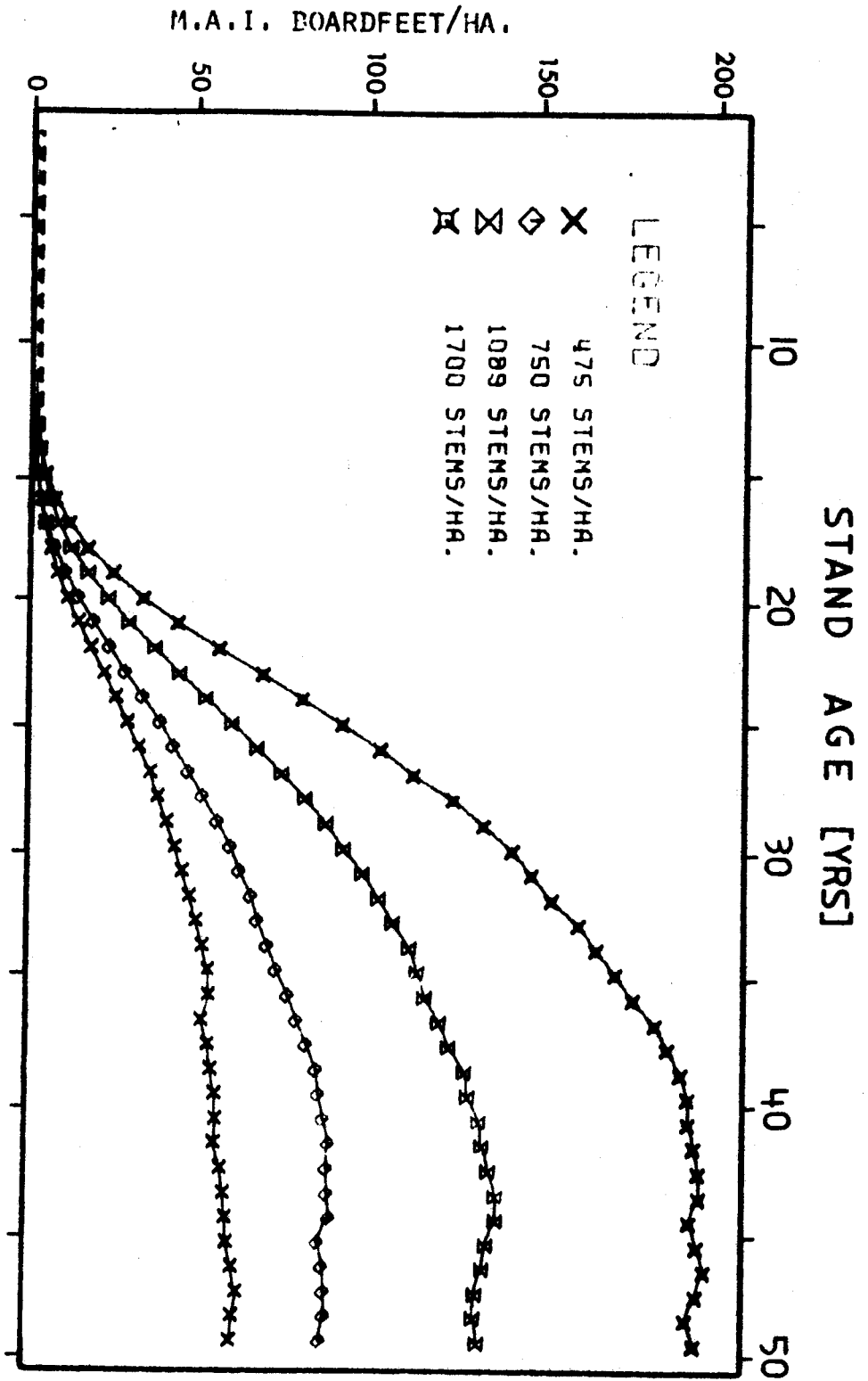


FIG. 8.27: MEAN ANNUAL INCREMENT OF SAWTIMBER VOLUME IN THE SIMULATED PLANTATIONS.

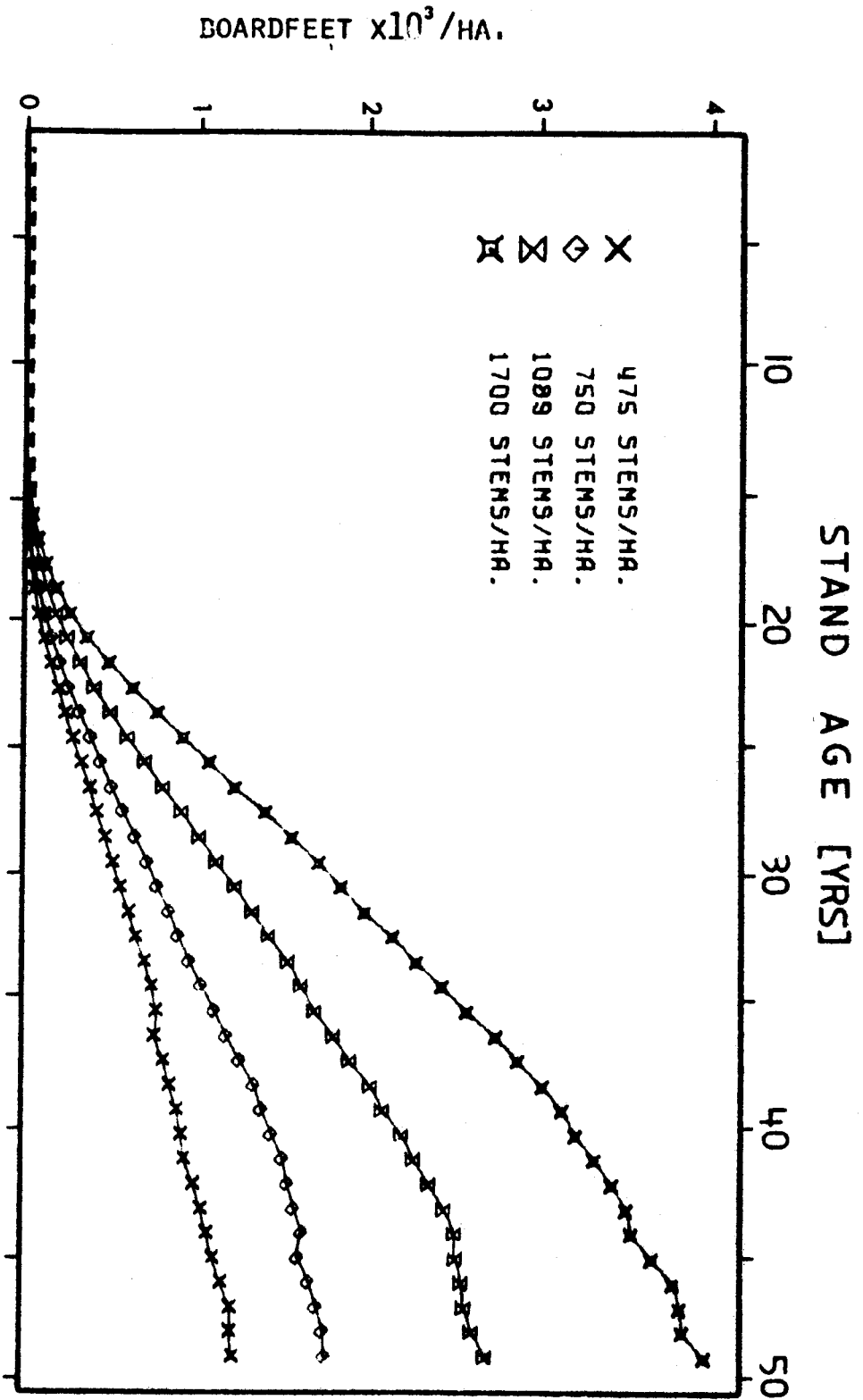


FIG. 8.28: SAWTIMBER YIELDS IN THE SIMULATED PLANTATIONS
AS A FUNCTION OF STAND AGE.

TABLE VIII.6: VOLUME INCREMENTS, ROTATION AGES AND RECOMMENDED THINNING INTENSITIES IN SIMULATED PLANTATIONS OF *P. CARIBAEA*.

| # Stems | m. ³ | Max. MAI m. ³ | MAI b/ft. | Rotation Age | Expected Yields | Annual Thinning |
|------------|-----------------|-----------------------------|--------------|-----------------|--|--------------------|
| 475 | 4.3 | 61.5 | 630 (255) | 48 | 31 (13) | 3.0 |
| 750 | 6.2 | 88.6 | 924 (374) | 42 | 45 (18) | 4.3 |
| 1080 | 9.4 | 134.3 | 427 (578) | 44 | 69 (28) | 6.6 |
| 1700 | 13.8 | 197.3 | 2052 (831) | 39 | 101 (41) | 9.7 |
| /ha. | /ha. | /ac. | ha. /ac. | Yrs. | m. ³ /ha. (ft. ³ /ac) | m. ³ /h |

products in Belize, it seems advisable simply to note a few general conclusions from these limited series of runs.

8.5: CONCLUSIONS

Three forestry management recommendations can be made. However, each recommendation should be accepted with due regard to the constraints of the model, particularly those that deal with the behaviour of stands beyond 25 years of age. Beyond this limit the model remains unvalidated and its projections are therefore tentative. With this word of caution, the specific recommendations are as follows:

- (a) PINUS indicates that regeneration of harvested stands of P. caribaea in Mountain Pine Ridge is fairly slow, and to ensure an adequate level of stocking of young pine a minimal seed input of some 20,000 seeds/ha. is required. This value can probably be achieved by retaining between 10 - 20 trees/ha. (4 - 8/ac). It is recommended that a minimum of 20 stems/ha. (8/ac) be retained to serve as seed-bearers. Even with this density of seed-trees the regeneration phase lasts for 20 years after disturbance, and maximum seedling establishment rates occur in the period between 10 and 15 years.

- (b) Given this initial level of stocking, a rotation of at least 55 years should be employed to maximize saw-timber productivity.
- (c) If thinning is practiced at all in Mountain Pine Ridge, and it may be completely unnecessary in the light of testing against the $3/2$ power law, it should only be practiced in localities where exceptional densities of seedlings occur. Even in stands over 30 years old, a light thinning may be all that is required. Severe thinnings (even those as lenient as the 1.5D rule) lead to fairly constant stand volume between 30 and 50 years, without concomitantly large thinning yields, and are not recommended, particularly as there is at present no market for thinned materials locally.
- (d) No mention has been made in the discussion so far of the role of fire as an element in the management of the pine resource, although there has been a tacit assumption in these simulations that "time-zero" represents a logging event accompanied by a controlled burn to reduce slash buildup. Such fires were utilized during the early years of logging in Mountain Pine Ridge, but there has been a moratorium on prescribed burns in Mountain Pine Ridge for almost 15 years, ever since Wolffsohn,

who originally recommended their use, found such fires difficult to contain with the equipment and manpower then available. However, the Forestry Department in Belize has recently (May, 1976), re-initiated research on the effects of prescribed burns, and such fires may well prove an acceptable silvicultural tool in the near future. Since the prime inhibitor of pine regeneration has been shown to be litter buildup, the reduction in litter mass by a control burn after logging will not only reduce the risk of wildfire, but also stimulate pine regeneration. Prescribed burning of the stand during its development may also come to play an important role in forest management in the study area. However, the current lack of data on the effects of such burns on pine regeneration has precluded the use of PINUS as a means of assessing the long-term effects of such a policy.

CHAPTER NINE: CONCLUSIONS

Pinus caribaea var. hondurensis dominates extensive areas along the Atlantic coast of Central America. Along with the other Caribbean races of the species, it has become one of the chief timber and pulp trees to be planted in the tropics and sub-tropics over the last twenty years. In its natural range, P. caribaea usually occurs in open, park-like stands generally referred to as "pine savanna." The infertile soils of the coastal and interior provenances of the Central American subspecies render the tree fairly slow-growing in its native habitat and its commercial value is therefore primarily as saw-timber; and as a source of seed for plantation development elsewhere.

In contrast, the exotic plantations of the species are found in humid coastal lowland areas, on well-drained, fairly fertile soils. In these sites it is grown on short rotations for pulp. Only in some of the older plantations at higher altitudes is sawtimber likely to be the primary product. There is therefore a strong dichotomy in the interests of forest managers in the natural and planted range of the species, and the research results generated in one situation may not be directly applicable to the other.

The population size of a plant species can be envisaged as a response to four factors: the carrying capacity of a site, the time-span for which the site remains colonizable or habitable,

the dispersibility of the species, and the spatial distribution and size of sites suitable for colonization (Gadgil, 1971). P. caribaea is a 'fire-opportunist' species capable of colonizing and surviving until reproductive maturity in sites frequently stressed by fire. However, the carrying capacity of a site exposed to a 'natural' fire regimen (recurrence interval of fire < 20 years), is low because of the high mortality rates suffered by juvenile pines during a burn.

The main thrust of forest management in the Central American stands of P. caribaea up to the present day has therefore been the containment and prevention of grass fires in an attempt to increase the carrying capacity (and therefore timber yield) of a site. In those areas in Central America in which fire protection has been adopted, regeneration of pine has increased considerably, except where over-cutting has reduced the stock of mature seed-trees. However, the exclusion of fires over several decades leads to reduced establishment of pine seedlings, and in time the competitive exclusion of P. caribaea by broadleaved species, particularly oaks, is to be expected if fire is completely excluded from the environment. It is clear therefore that the future of the pinelands of Central America, as both a timber and genetic resource, depends upon the development of management strategies aimed at conserving the pine estate. Such strategies must be based on an adequate knowledge of the ecology of the seedling phase, as population-turnover is greatest during this transition period.

This study focussed therefore on the seed and seedling dynamics of Caribbean pine in stands protected from fire for various lengths of time. The population flux during the first five years of seedling growth in all sample stands was analyzed using a static life-table. This indicated that the greatest mortality was suffered during the seed - seedling transition, and in the first year of the seedling's existence. Data on seed and seedling survivorship from a sown population of 13,600 seeds in 17 stands demonstrated that the overall small size of the established seedling-population was primarily a response to severe predation of seeds in the post-dispersal period. The magnitude of seed-predation proved to be of a fairly uniformly high intensity in all the stands sampled.

A further 20,000 seeds were sown in the same stands at the same time and at the same density as those above. The plots in which they were sown were manipulated to exclude the larger members of the seed-harvesting fauna, root competition from neighbouring trees, or root competition from the ground flora. All these experimental treatments were monitored for a period of one year. In addition, a series of laboratory and field tests were conducted on the effects of litter depth, radiation intensity, illumination, and allelopathy on seed germination and seedling survivorship.

Somewhat surprisingly, the lowest rates of seed establishment were in the youngest stands on recently disturbed

seedbeds. High incident radiation and thin litter layers (>0.5 cm. thick) led to dessication of the sandy surface soils and a subsequent inhibition of germination. Those seedlings that did germinate presumably died very soon thereafter as a result of the failure of the hypocotyl to rupture the crust that developed on these soil surfaces. Maximum rates of establishment were recorded in stands which had been undisturbed by fire or logging for 5 - 15 years.

In older stands, although germination was slightly lower than in the 5 - 15 year-old stands, the failure of pine regeneration was primarily a result of the low survivorship rates of germinated seedlings. The lower germination rate was attributed to the "perching" effects of a thick litter layer. Many of the seedlings landing on this type of substrate are unable to penetrate the litter mat and to secure a moisture supply. The low survivorship of germinated seedlings in these older stands was ascribed to the synergistic (though indirect) effects of a thick litter mat and shady forest floor conditions. It is postulated that thick litter and shade inhibit the infection of pine roots by mycobionts, on which the seedlings depend for continued growth. Uninfected seedlings, or seedlings with only a low proportion of their roots infected, are less vigorous and more open to infection by pathogenic fungi, and it is presumed (though not proven) that the low survivorship derives primarily from this cause. Seedlings in these older stands also

suffered a significantly greater degree of predation by herbivorous insects than seedlings in the 5 - 15 year age category.

The conclusions presented above are subject to a number of constraints. Although stand data were collected during the course of two field seasons, the data on seed and seedling population dynamics represent a sample period of one year because of complete failure of the seed population to germinate in the first year. The annual variability of such important variables as seed-production and seedling establishment remains unknown, and the conclusions drawn from the limited field evidence may have to be revised as further data becomes available. The high between-stand variance in the germination percentages in the control plots points to the inherent variability of stands that were grouped into particular age-classes. This variability stems probably from three causes: the small number of stands in each age-class, the environmental patchiness in each stand, and the varied history of disturbance of each stand within homogeneous age-classes. Overcoming these problems would involve a considerable increase in sample size, not only of the number of stands, but of the size and number of experimental plots within stands.

Furthermore, there is little hope for any detailed histories for the stands sampled in Mountain Pine Ridge. All have suffered from varying intensities of disturbances in the form of (usually

unrecorded) burns, logging, thinning activities, and, to a lesser extent, cone collection. The research design infers temporal dynamics of stands based upon a spatial sampling procedure, and, as with most studies in vegetation succession, the validity of the technique can only be assessed over a considerable time-period.

A simulation model was constructed to model the behaviour of mature stands. Empirical relationships derived from field sampling and experimentation were used to regulate seedling input and to model the growth and morphology of individual trees in the simulator. Growth rates of individuals and competitive interactions between individuals were simulated by employing a modified version of the JABOWA program of Botkin et al. (1970, 1972). Annual dbh increment was considered to be functionally dependent upon the degree of mutual shading of the tree crowns in the stand, and the stem volume-increment was then utilized to assess the probability of mortality of individuals. The data for this section were derived from stands of *P. taeda* and *P. elliotii* in Louisiana. The whole-model behaviour was then verified by testing its short-term growth and mortality predictions against the dynamics of real stands.

It is possible to use the model as a simple short-term (<20 years) growth and mortality predictor by employing as input data from real plots. These data would consist of a list of tree heights, dbh's and ages. They would be used to assess future

stand development, to predict mean yields, and give some indication of the variability inherent in stand dynamics. Indeed, this may well prove to be the most satisfactory use for the model.

However, in order to clarify certain problems associated with management of the pinelands of Belize, several long-term experiments were performed using the verified model. The experiments analysed the effects of various harvesting/regeneration strategies and rotation ages, and thinning regimes in pine stands of varying density. Specific recommendations from these experiments are detailed at the end of Chapter Eight. In order to produce an adequate stocking of regeneration after logging a stand, it is necessary to retain a minimum of 20 trees/ha. to act as seedbearers. Maximum mean annual increments (volumetric measure) in the simulated stands are attained 45 - 50 years after logging, and a rotation age of 60 years is therefore recommended in the study area in order to optimise saw-timber yields.

Perhaps the single most important conclusion for management practice in the pinelands of Mountain Pine Ridge consisted of the recommendations that arose from the simulation of various thinning practices. Specifically, severe thinnings, even those as lenient as the 1.5D Rule, were not recommended for silvicultural practice in the pinelands, because of the drastic deterioration of stand structure following such thinnings. The current thinning programme in Mountain Pine Ridge may well result

in considerably reduced future yields because of the reliance on such empirical rules as a guide to thinning practice. Only in young stands of exceptional density should thinnings be practiced. Future development of the model could proceed along one of two paths. The first would be to attach costs and revenues to the various management strategies, and then incorporate these into a large forest estate model. The second would be the use of the simulator as a foundation on which to build an "ecosystem" model, in which the major nutrient and energy flows are incorporated into model structure, in order to simulate the effects of such disturbances as timber harvesting, slash-burning or wildfire on nutrient reserves and fluxes.

This study has been equivalent to one pass through Forrester's nine-stage "model of a model." Undoubtedly as more data becomes available on the ecology of P. caribaea, the dynamics of early successional tree species, or the demographic strategies of pines in general, the model will require revision. A complete re-analysis of some sections may have to be undertaken, particularly areas such as density stress - mortality interactions in mature stands, and pine regeneration dynamics in very recently logged stands. Only when such data becomes available can a significant improvement be made in the predictions of the behaviour of stands of Caribbean pine.

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APPENDIX A: EXOTIC PLANTATIONS OF PINUS CARIBAEA VAR. HONDURENSIS.

| Country | Area planted up to 1970 | | Estimated rate of planting in 1975 | |
|-------------|-------------------------|--------|------------------------------------|--------|
| | ac. | ha. | ac. | ha. |
| Australia | 8,000 | 3,238 | 2,500 | 1,011 |
| Brazil | 4,000 | 1,619 | 8,000 | 3,237 |
| Fiji | 11,500 | 4,654 | 10,000 | 4,047 |
| Fr. Guiana | small | - | 500 | 203 |
| Guyana | 450 | 182 | 200 | 81 |
| India | small | - | 500 | 203 |
| Jamaica | 7,000 | 2,833 | 3,000 | 1,214 |
| Malagasy | - | - | 1,750 | 690 |
| Malaysia | small | - | 1,000 | 404 |
| Nigeria | - | - | 1,000 | 404 |
| Solomon Is. | small | - | 200 | 81 |
| S. Africa | 10,000 | 4,047 | - | - |
| Surinam | 10,000 | 4,047 | 2,470 | 1,000 |
| Tanzania | 6,700 | 2,712 | 10,000 | 4,047 |
| Trinidad | 6,000 | 2,428 | 1,000 | 404 |
| Uganda | small | - | 500 | 203 |
| Venezuela | 200 | 81 | 4,000 | 1,620 |
| Zaire | 1,500 | 607 | 2,470 | 1,000 |
| Total | 65,350 | 26,448 | 49,090 | 19,850 |

Data Source: Lamb, 1973; p.212.

APPENDIX B

I: FLORA RECORDED IN THE SAMPLE STANDS IN MOUNTAIN PINE RIDGE.

Trees and Shrubs

| | |
|--------------------------|--------------------|
| ?Aridisia spp. | Miconia albicans |
| Byrsonima crassifolia | M. argentea |
| Calliandra houstoniana | M. belizensis |
| Citharexylum caudatum | M. ciliata |
| Clethra hondurensis | M. habrolepsis |
| Clidemia deppeana | M. ibaguensis |
| C. strigillosa | M. pteropoda |
| Clusia flava | Mimosa albida |
| C. flava | M. pigra |
| Crescentia cujete | Myrica cerifera |
| Curatella americana | Psychotria spp. |
| Cyrilla racemiflora | Quercus oleoides |
| ?Eugenia (?Calypranthes) | Vismia ferruginea |
| Eupatorium oeratum | Vismia ferruginea |
| Henrietta succosa | Xylopia frutescens |
| Hypericum styphelioides | |
| H. fasciculatum | |

Subshrubs and Herbs

| | |
|-------------------------|-----------------------|
| Aeschynomene sp. | Paspalum plicatum |
| ?Ageratum | P. pulchellum |
| Andropogon tener | Panicum arenicoloides |
| A. virgatus | P. laxum |
| Bulbostylis vestita | Polygala sp. |
| Calea longipedicellata | Rhynchospora globosa |
| C. peckii | R. aff. plumosa |
| Cassia flexuosa | R. podosperma |
| Clidemia rubra | R. robusta |
| Coccocypselum hirsutum | R. rugosa |
| Dalechampia schippii | Scleria micrococca |
| Dicranopteris pectinata | Zornia reticulata |

II: LIST OF BOTANICAL AND COMMON NAMES OF PLANTS
MENTIONED IN THE TEXT

| | | |
|------------------|---|-----------------|
| Fungi: | <u>Cronartium conigenum</u> Hedge & Hunt | Cone rust |
| Gleicheniaceae: | <u>Dicranopteris pectinata</u> Underw. | Tiger-bush |
| Dennstaediaceae: | <u>Pteridium aquilinum</u> (L.) Kuhn | Bracken |
| Pinaceae: | <u>Abies balsamea</u> (L.) Mill. | Balsam fir |
| | <u>Picea glauca</u> (Moench) Voss | White spruce |
| | <u>Pinus banksiana</u> Lamb. | Jack pine |
| | <u>Pinus caribaea</u> Morelet | Caribbean pine |
| | <u>Pinus densiflora</u> Sieb. & Zucc. | Lodgepole pine |
| | <u>Pinus echinata</u> Mill. | Shortleaf pine |
| | <u>Pinus elliottii</u> Engelm. | Slash pine |
| | <u>Pinus hartwegii</u> Lindl. | |
| | <u>Pinus oocarpa</u> Scheide | Ocote |
| | <u>Pinus palustris</u> Mill. | Longleaf pine |
| | <u>Pinus pinaster</u> Ait. | Maritime pine |
| | <u>Pinus ponderosa</u> Laws. | Ponderosa pine |
| | <u>Pinus pseudostrobus</u> Lindl. | |
| | <u>Pinus radiata</u> D. Don | Monterey pine |
| | <u>Pinus resinosa</u> Ait. | Red pine |
| | <u>Pinus sylvestris</u> L. | Scots pine |
| | <u>Pinus strobus</u> L. | White pine |
| | <u>Pinus taeda</u> L. | Loblolly pine |
| | <u>Pseudotsuga menziesii</u> Franco | Douglas fir |
| | <u>Tsuga canadensis</u> (L.) Carr. | Eastern hemlock |
| | <u>Tsuga heterophylla</u> (Raf.) Sarg. | Western hemlock |
| Gramineae: | <u>Andropogon virgatus</u> Desv. | |
| Cyperaceae: | <u>Mesosetum filifolium</u> Hubbard | |
| | <u>Rhynchospora globosa</u> Roem. & Schult. | |
| | <u>Scleria bracteata</u> | Cutting grass |
| Palmae: | <u>Acoelorrhaphe wrightii</u> Wendl. | Palmetto |
| | <u>Schippia cncolor</u> Burret | Silver pimento |
| Loranthaceae: | <u>Arceuthobium</u> spp. | Dwarf mistletoe |
| Salicaceae: | <u>Populus tremuloides</u> Michx. | Quaking aspen |
| Myricaceae: | <u>Myrica</u> spp. | Teabox |
| Fagaceae: | <u>Quercus hondurensis</u> Trelease | Oak |
| | <u>Quercus oleoides</u> Sch. & Cham. | Oak |
| | <u>Quercus purulhana</u> Trelease | Oak |
| Annonaceae: | <u>Xylopia frutescens</u> | Polewood |
| Malpighiaceae: | <u>Byrsonima crassifolia</u> (L.) DC. | Crabboo |

| | | |
|------------------|---|-------------|
| Aceraceae: | <u>Acer saccharum</u> Marsh | Sugar maple |
| Dilleniaceae: | <u>Curatella americana</u> L. <u>Davilla kunthii</u> St. Hil. | Chaparro |
| Guttiferae: | <u>Clusia</u> spp. | |
| Myrtaceae: | <u>Psidium anglohondurense</u> McVaugh | |
| Melastomataceae: | <u>Clidemia rubra</u> (Aubl.) Mart. <u>Miconia albicans</u> <u>Miconia belizensis</u> Standl. | |
| Clethraceae: | <u>Clethra hondurensis</u> Britton | |
| Bignoniaceae: | <u>Tabebuia icsea</u> (Bertol.) DC. <u>Enallagma latifolia</u> (Mill.) Small | Florosul |

APPENDIX C

VEGETATION DATA FOR THE SAMPLE STANDS IN MOUNTAIN PINE RIDGE.

| Variable # | | | | | | | | | |
|------------|----|-----|-----|------|------|------|------|-----|----|
| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| 1 | 14 | 150 | 56 | 1.65 | 37.5 | 12.5 | 0.96 | 100 | 0 |
| 2 | 20 | 391 | 127 | 3.92 | 5.0 | 60.0 | 0.80 | 72 | 8 |
| 3 | 11 | 98 | 33 | 1.15 | 55.0 | 2.5 | 0.83 | 96 | 0 |
| 4 | 8 | 52 | 24 | 0.53 | 75.0 | 0.0 | 0.97 | 100 | 0 |
| 5 | 25 | 178 | 58 | 4.06 | 2.5 | 60.0 | 0.45 | 92 | 0 |
| 6 | 25 | 218 | 35 | 2.39 | 0.3 | 30.0 | 0.33 | 60 | 16 |
| 7 | 25 | 443 | 62 | 3.19 | 7.5 | 30.0 | 0.44 | 60 | 0 |
| 8 | 8 | 78 | 24 | 1.19 | 50.0 | 5.0 | 0.95 | 96 | 0 |
| 9 | 15 | 159 | 45 | 1.76 | 25.0 | 10.0 | 0.90 | 76 | 0 |
| 10 | 18 | 288 | 52 | 3.66 | 0.0 | 45.0 | 0.29 | 48 | 24 |
| 11 | 25 | 290 | 41 | 3.93 | 5.0 | 55.0 | 0.36 | 72 | 12 |
| 12 | 20 | 189 | 64 | 2.36 | 7.5 | 17.5 | 0.35 | 44 | 8 |
| 13 | 25 | 430 | 200 | 3.65 | 0.0 | 22.5 | 0.22 | 44 | 4 |
| 14 | 25 | 195 | 85 | 1.56 | 30.0 | 7.5 | 0.86 | 100 | 0 |
| 15 | 25 | 235 | 85 | 2.49 | 7.5 | 20.0 | 0.66 | 24 | 16 |
| 16 | 1 | 62 | 18 | 0.19 | 90.0 | 0.0 | 0.95 | 100 | 0 |
| 17 | 2 | 56 | 21 | 0.55 | 87.5 | 0.0 | 0.90 | 100 | 0 |

- Variable #1 = Stand #
 2 = Stand Age (yrs.)
 3 = Density of non-seedling *P. caribaea*
 (stems > 2 m. in height)
 4 = Density of seedlings of *P. caribaea*
 (stems < 2 m. in height, excluding 1st-years)
 5 = Total Pine Basal-Area (sq.cms.)
 6 = Current Annual Seed-Yield (Estimated)
 7 = Total Basal-Area of Hardwoods (sq.cms.)
 8 = Shrub Cover (%)
 9 = Grass Biomass (g/0.25 sq.m.)
 10 = Grass Cover (%)

APPENDIX D

ENVIRONMENTAL DATA FOR THE SAMPLE STANDS IN MOUNTAIN PINE RIDGE.

| Variable # | | | | | | | | | |
|------------|----|-----|-----|-------|------|------|------|-----|----|
| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| 1 | 14 | 31 | 6 | 4828 | 453 | 90 | 2.1 | 144 | 36 |
| 2 | 20 | 34 | 1 | 9770 | 1729 | 409 | 67.6 | 130 | 35 |
| 3 | 11 | 55 | 30 | 4097 | 64 | 534 | 17.3 | 89 | 39 |
| 4 | 8 | 33 | 20 | 2743 | 32 | 100 | 7.3 | 127 | 39 |
| 5 | 25 | 19 | 2 | 9752 | 2438 | 319 | 22.7 | 108 | 36 |
| 6 | 25 | 13 | 5 | 4220 | 3312 | 155 | 6.5 | 68 | 38 |
| 7 | 25 | 24 | 99 | 10531 | 3136 | 950 | 21.5 | 26 | 39 |
| 8 | 8 | 90 | 31 | 4647 | 21 | 18 | 1.6 | 120 | 29 |
| 9 | 15 | 93 | 5 | 8604 | 89 | 2764 | 13.1 | 126 | 34 |
| 10 | 18 | 94 | 7 | 18071 | 1040 | 1057 | 28.6 | 63 | 21 |
| 11 | 25 | 22 | 54 | 8975 | 8698 | 1620 | 34.3 | 44 | 16 |
| 12 | 20 | 139 | 67 | 9208 | 571 | 756 | 33.1 | 36 | 18 |
| 13 | 25 | 68 | 77 | 10409 | 5565 | 967 | 46.6 | 31 | 7 |
| 14 | 25 | 41 | 121 | 7732 | 5772 | 282 | 2.5 | 67 | 27 |
| 15 | 25 | 15 | 2 | 7897 | 4692 | 886 | 35.4 | 69 | 20 |
| 16 | 1 | 16 | 2 | 3442 | 0 | 888 | 0.0 | 5 | 3 |
| 17 | 2 | 14 | 0 | 3660 | 0 | 0 | 0.0 | 54 | 24 |

Variable #1 = Stand #

2 = Stand Age (yrs.)

3 = Mean Litter Mass (g/0.25 sq.m.)

4 = St. Deviation of Litter Mass

5 = Mean Litter Depth (cms)

6 = % Litter Depth Observations < 0.5 cms.

7 = " " " " > 3.5 cms.

8 = Median Radiation Intensity (0.0 - 1.0 Scale)

9 = % Illumination Observations > 3000 foot-candles.

10 = " " " " < 2000 " "

APPENDIX ECONVERSION CHART FOR LIGHT METER RECORDING IN F STOP
AND SHUTTER SPEEDS TO FOOTCANDLES.

ASA 64

f STOP

| 2 | 2.8 | 4 | 5.6 | 8 | 11 | 16 | FT-C. |
|------|------|------|------|------|-----|------|-------|
| 4 | 2 | 1.0 | 2.0 | 4.0 | 8.0 | 16.0 | 4 |
| 8 | 4 | 2 | 1.0 | 2.0 | 4.0 | 8.0 | 8 |
| 15 | 8 | 4 | 2 | 1.0 | 2.0 | 4.0 | 16 |
| 30 | 15 | 8 | 4 | 2 | 1.0 | 2.0 | 32 |
| 60 | 30 | 15 | 8 | 4 | 2 | 1.0 | 65 |
| 125 | 60 | 30 | 15 | 8 | 4 | 2 | 130 |
| 250 | 125 | 60 | 30 | 15 | 8 | 4 | 260 |
| 500 | 250 | 125 | 60 | 30 | 15 | 8 | 500 |
| 1000 | 500 | 250 | 125 | 60 | 30 | 15 | 1000 |
| | 1000 | 500 | 250 | 125 | 60 | 30 | 2000 |
| | | 1000 | 500 | 250 | 125 | 60 | 4000 |
| | | | 1000 | 500 | 250 | 125 | 8000 |
| | | | | 1000 | 500 | 250 | 16000 |

This table can be utilized only for light meters set to film speeds of ASA 64. The figures in the main body of the chart represent shutter speeds (4 = 1/4 of a second and 4.0 = 4 seconds). To obtain the appropriate foot-candle rating for a particular shutter speed and f stop, read down the f stop column until the requisite shutter speed is reached, then read off the the foot-candle rating on the same row of the matrix. Thus, an f stop of 8 and a shutter speed of 1/250th of a second is equivalent to a illumination of 2000 foot-candles.

```
//A276PRNT JOB (0197,G3561),PIAN UP/LOW'
//*JOBPARM PSWD=
// EXEC PGM=IEBGENER
//SYSPRINT DD SYSOUT=A
//SYSUT2 DD SYSOUT=(A,,1180),DCE=(RECFM=FBSA,LRECL=80,BLKSIZE=1120),
//   PCB=6,UCS=TN,COPIES=1
//SYSIN DD DUMMY
//SYSUT1 DD DATA
//A276TR31 JOB (1079,G2219),'3 S/TREE #1 ',MSGLEVEL=1,TIME=30,CLASS=C
//*JOBPARM PSWD=,LINES=5,CARDS=30
// EXEC FORTGCLG,REGION=200K,TIME.GO=(29,30),PARM=NOSOURCE,NOPUNCH=
//FORT.SYSIN DD *
```

```
*****
**
**          PINUS          **
**
**   A PROGRAM TO SIMULATE THE GROWTH AND POPULATION **
**   DYNAMICS OF PINUS CARIBAEA IN MANAGED AND UNMANAGED **
**   STANDS IN THE MOUNTAIN PINE RIDGE AREA OF BELIZE.  **
**
**
*****
```

```
*****
*
*   VARIABLE LISTING
*
*****
```

***** ARRAYS *****

```
NTREE = VECTOR OF TREE NUMBERS (1 - 1000)
HSEED - VECTOR OF MEAN SEEDLING HEIGHTS FOR THE FIRST 8 YRS.
SSEED = STANDARD DEVIATIONS FOR SEEDLING HEIGHTS
STRNC = VECTOR OF - CF TREES IN EACH BASAL-AREA SIZE CLASS
PECU  = VECTOR OF SEED-PRODUCTION FOR EACH SIZE-CLASS
NAGE  = VECTOR OF TREE-AGES
H     = TREE HEIGHT VECTOR
DBH   = DIAMETER AT BREST HEIGHT VECTOR
VOL   = TREE VOLUME VECTOR (CU. M.)
VINC  = ANNUAL VOLUME INCREMENT VECTOR (CU.M.)
BA    = TREE BASAL AREA (SQ.CMS.)
SLA   = - SUM OF NEEDLE AREAS FOR ALL HIGHER TREES (SQ.A.)
AL    = LIGHT LEVEL AT THE TCP OF EACH CROWN (SCALE - 0-1.0)
ELA   = ESTIMATED LEAF (NEEDLE) AREA FOR EACH TREE (SQ.M.)
CL    = CROWN LENGTH VECTOR (M.)
BASUM = VECTOR OF TOTAL BASAL AREA PER SITE PER YEAR
ALITT = AMOUNT OF LITTER (GMS./0.25 SQ.M.) PER SITE
GRASS = AMOUNT OF GRASS (GMS./0.25 SQ.M.) PER SITE
PVEC  = MORTALITY VECTOR FOR SEEDLINGS
MORT  = LIST OF DEAD TREES
BMORT = BASAL AREA OF DEAD TREES PER YEAR
ZZ    = STORAGE VECTOR IN THIN SUBROUTINE
AA    = STORAGE VECTOR IN THIN SUBROUTINE
VMORT = VOLUME OF DEAD TREES PER YEAR
VTHIN = VOLUME THINNED PER YEAR
BTHIN = BASAL-AREA THINNED PER YEAR
VSIG  = STANDARD DEVIATION OF VOLUME INCREASE PER SIZE-CLASS
VBAR  = EXPECTED VOLUME INCREASE PER SIZE CLASS
```

***** COEFFICIENTS *****

```
A0 = INTERCEPT IN MORTALITY REGRESSION EQUATION
A1 = SLOPE IN MORTALITY REGRESSION EQUATION
FMORT=A0 * EXP(-A1*VCON)
    WHERE VCON IS THE MEAN ANNUAL INCREMENT IN VOLUME
    CONVERTED TO CUBIC CENTIMETRES
```

```
FOR P. CARIBAEA A0 = 0.04467, A1 = 0.0004
```



```

VHORT (JP) =0.0
BHORT (JP) =0.0
14 BAREQ (JP) =0.0

READ (5, 27) KDATA, NT, IX
IF (KDATA.NE.1) GOTO 110
READ (5, 1) (PECU (J), J=1, 13)
READ (5, 2) (PVEC (K), K=1, 3)
READ (5, 28) A0, A1, B2, B3
READ (5, 3) D1, D2, F1, F2, F3, G1, G2
READ (5, 4) NTIME, PRINT, MAYR, IPIANT
READ (5, 6) NTHIN, NTH, MTHIN
110 CONTINUE
WRITE (6, 101)
DO 15 L=1, NT
IF (IPLANT.EQ.1) GOTO 30
READ (5, 5) DBH (L), H (L), NAGE (L)
GOTO 31
30 DBH (L) =0.0
H (L) =0.2
NAGE (L) =0
31 CONTINUE
EA (L) = ((DBH (L) /2.) **2) *J.1416
MTREE (L) =L
FP=0.40
VOL (L) = (DA (L) *0.0001) *H (L) *FP
WRITE (6, 102) H (L), DBH (L), EA (L), VOL (L), NAGE (L)
15 CONTINUE
WRITE (6, 104) NTHIN, NTH, MTHIN
IF (NTHIN-1) 20, 18, 16
18 DO 19 IK=1, MTHIN
READ (5, 9) (NFREQ (IK))
NF=NFREQ (IK)
READ (5, 103) BAREQ (NF)
19 WRITE (6, 106) NFREQ (IK), BAREQ (NF)
GOTO 20
16 DO 17 JJ=1, MTHIN
READ (5, 9) NFREQ (JJ)
NF=NFREQ (JJ)
READ (5, 194) NTREQ (NF)
17 WRITE (6, 195) NFREQ (JJ), NTREQ (NF)
WRITE (6, 105)
20 CONTINUE
CALL STAGES (NYR)
PKT=PKT+1.
MAYR=MAYR+1
CALL LEAF (SUMLA, NYR)
IF (IPLANT.EQ.1) GOTO 26
CALL BIRTH (MAYR, NYR, SUMIA)
MN=NT+1
NT=NT+NBORN (NYR)
IF (NBORN (NYR) -1) 26, 22, 23
23 CONTINUE
DO 21 JK=MN, NT
21 MTREE (JK) =JK
GOTO 26
22 MTREE (MN) =MN
26 CONTINUE
WRITE (7, 114) NYR, SEEDP (NYR), ALITT (NYR), GRASS (NYR), NBORN (NYR),
1 GERM (NYR), SLITE (NYR)
114 FORMAT (13, F7.0, 2F5.0, 14, 2F9.3)
IF (PKT.LT.PRINT) GOTO 113
WRITE (6, 111) NYR, SEEDP (NYR), ALITT (NYR), GRASS (NYR), NBORN (NYR),
1 GERM (NYR)
113 CONTINUE
KK=0
13 KK=KK+1
NAGE (KK) =NAGE (KK) +1
IF (KK.LT.NT) GOTO 13
CALL GROW (MTREE, NYR, IX, PRINT, PKT)
CALL MORTAL (MTREE, NYR, IX, PRINT, PKT)
KH=0
IF (MTHIN) 25, 25, 223
223 DO 24 I=1, MTHIN
24 IF (NYR.EQ.NFREQ (I)) KH=1

```

```

IF(KM.EQ.0)GOTO 25
CALL THIN(MTREE, NTHIN, BAREQ, STREQ, NYR, PRINT, PKT)
25 CONTINUE
IF(NT.EQ.0)GOTO 112
IF(NYR.LT.NTIME)GOTO 10
DATA DEFLT/.001/, IVAR/3/, IOPT/2/, XSCALE/10./, YSCALE/6.0/
IPOINT=NTIME
DO 998 J=1, NYR
DO 999 I=1, IVAR
999 XX(I,J)=FLOAT(J)
DATA(1,J)=SEEDP(J)
DATA(2,J)=FLCAT(NBORN(J))
DATA(3,J)=GERM(J)
IF(DATA(3,J).EQ.0.0)DATA(3,J)=DEFLT
998 CONTINUE
CALL XLIMIT(100.0)
CALL MPLOTS(XX,DATA,IPCINT,IVAR,IOPT,XSCALE,YSCALE)
DO 997 J=1, NYR
DATA(1,J)=ALITT(J)
DATA(2,J)=GRASS(J)
997 DATA(3,J)=SLITE(J)
CALL PLOT(18.0,0.0,-3)
CALL MPLOTS(XX,DATA,IPCINT,IVAR,IOPT,XSCALE,YSCALE)
DO 996 J=1, NYR
DATA(1,J)=HBS(J)
DATA(2,J)=DBS(J)
DATA(3,J)=VUB(J)
IF(DATA(3,J).EQ.0.0)DATA(3,J)=DEFLT
996 CONTINUE
CALL PLOT(18.0,0.0,-3)
CALL MPLOTS(XX,DATA,IPCINT,IVAR,IOPT,XSCALE,YSCALE)
IVAR=2
DO 995 J=1, NYR
DATA(1,J)=JLMAX(J)
995 DATA(2,J)=BASUM(J)
CALL PLOT(18.0,0.0,-3)
CALL MPLOTS(XX,DATA,IPCINT,IVAR,IOPT,XSCALE,YSCALE)
IVAR=3
DO 994 J=1, NYR
DATA(1,J)=SURV(J)
DATA(2,J)=BM(J)
DATA(3,J)=VM(J)
IF(DATA(2,J).EQ.0.0)DATA(2,J)=DEFLT
IF(DATA(3,J).LE.0.0)DATA(3,J)=0.0001
994 CONTINUE
CALL PLOT(18.0,0.0,-3)
CALL MPLOTS(XX,DATA,IPCINT,IVAR,IOPT,XSCALE,YSCALE)
1 FORMAT(13F5.1)
2 FORMAT(3F5.3)
3 FORMAT(2F8.5,5F8.4)
4 FORMAT(12,F3.0,13,I1)
5 FORMAT(2F8.3,I3)
6 FORMAT(3I2)
7 FORMAT(10I3)
8 FORMAT(2F4.2)
9 FORMAT(I3)
27 FORMAT(2I3,I6)
28 FORMAT(2F8.5,2F8.3)
101 FORMAT('1',50X,'INITIAL STAND DATA'//31X,'HEIGHT',8X,'DBH',7X,'BAS
1.AR',6X,'VOLUME',7X,'AGE'//)
102 FORMAT(32X,F4.1,8X,F4.1,7X,F5.0,7X,F6.4,7X,I3)
103 FORMAT(F6.0)
104 FORMAT(///42X,'THINNING OPTIONS FOR THIS RUN'//37X,'*****
1*****')
237X,'*',15X,'*',11X,'*',15X,'*/37X,'*',3X,'NTHIN =',12,3X,'*',2X,
3'NTH =',12,2X,'*',3X,'NTHIN =',12,3X,'*/37X,'*',15X,'*',11X,'*',
415X,'*/37X,'*****')
105 FORMAT(//51X,'NTHIN = 0 FREE RESPONSE MODEL'//58X,'= 1 THIN TREES
2WITH HIGH MORTALITY RISK'//58X,'= 2 THIN TO PRESCRIBED BASAL AREA
3PER 0.1 ACRE'//63X,'BY REMOVING TREES OF PROGRESSIVELY LARGER B=A.
4/58X,'= 3 THIN TO PRESCRIBED BASAL AREA PER 0.1 ACRE'//63X,'BY REM
5OVING TREES OF PROGRESSIVELY LARGER VOLUME'//54X,'NTH = 1 REMOVE
6TREES) 1.5 M. IN HEIGHT'//51X,'NTHIN = - OF THINNINGS REQUIRE
7'//51X,'NFREQ = YEARS IN WHICH THINNINGS REQUIRED'//50X,'BAREQ
8= PRESCRIBED BASAL AREA (SQ.CMS.)')

```

```

106 FORMAT(39X,'*',38X,'**/39X,'*',2X,'MFREQ =',I3,5X,'BAREQ =',F7.0,
1 ' SQ.CMS '/39X,'*****')
111 FORMAT('1',40X,'GROWTH DATA FOR YEAR',I4/12X,'# SEEDS =',F8.0,6X,
1LITTER WT. =',F5.0,'GMS.',6X,'GRASS WT. =',F5.0,'GMS.',6X,'# BORN
2=',I4,6X,'# GEMM. =',F5.2//
38X,'FREE #',5X,'HEIGHT',5X,'EBH',5X,'BAS.AR.',4X,'VOLUME',4X,'VOLI
4NC',3X,'CROWN',5X,'LEAF',6X,'SUM LA',5X,'LIGHT'/20X,'(M.)',5X,'(C
5S)',4X,'(SQ.CH)',4X,'(CU.H)',4X,'(CU.H)',4X,'HT. (M)',4X,'AREA',6X,
6 '(SQ.M)',5X,'LEVEL',7X,'AGE'/)
194 FORMAT(I3)
195 FORMAT(37X,'*',38X,'**/39X,'*',2X,'THIN IN YEAR',I3,2X,'TO',I5,'
1 STEMS **/39X,'*****')
112 CONTINUE
STOP
END
BLOCK DATA
COMMON /BORNA/FECU(13),STRUC(13),NAGE(1000),ALITT(50),FMAX,FMIN
COMMON /MORTA/PVEC(3),MORT(800),VMORT(50),BMORT(50),KDEAD,XADUL
COMMON /SEEDA/HSEED(9),SSEED(9),VCOEF(50),GRASS(50),SEEDP(50)
COMMON /COEFP/A0,A1,B2,B3,C1,C2,D1,D2,F1,F2,F3,G1,G2
DATA FECU/0.0,0.0,0.0,0.0,0.1,0.8,5.5,40.0,175.0,500.0,1000.,
* 2000.0,4000.0/
DATA PVEC/.92,0.93,0.93/,HSEED/0.25,0.31,0.69,0.75,0.75,1.0,1.25,
* 1.0,1.0/
DATA SSEED/0.1,0.15,0.35,0.7C,1.20,1.80,1.80,1.80,1.80/
DATA A0/0 .04467/,A1/0.0G044/,B2/126.52/,B3/1.265/
DATA VCOEF/1.0,1.0,1.0,1.0,1.0,1.0,1.0,1.0,1.0,1.0,1.0,1.0,1.0,1.0,1.0,
* ,1.0,1.25,1.40,1.60,1.75,1.87,1.99,2.10,2.20,2.29,2.38,2.48,2.5
* ,2.68,2.78,2.88,2.98,3.08,3.18,3.28,3.38,3.48,3.58,3.66,3.74,3.75
* ,3.75,3.75,3.75,3.75,3.75,3.75,3.75,3.75,3.75/
DATA D1/0.1/,D2/1.0/,F1/0.6723/,F2/0.0020/,F3/0.0014/,G1/500.0/
DATA G2/150.0/
END
SUBROUTINE STAGES(NYR)
    
```

C
C
C

SUBROUTINE TO GROUP TREES INTO SIZE=CLASSES.

```

COMMON /BORNA/FECU(13),STRUC(13),NAGE(1000),ALITT(50),FMAX,FMIN
COMMON /HDATA/H(1000),DBH(1000),VOL(1000),VINC(1000),BA(1000),WT
DO 10 M=1,13
10 STRUC(M)=0.0
J=0
11 J=J+1
IF (H(J) .GE. 1.5) GOTO 20
IF (H(J) .LT. 0.5) STRUC(1) =STRUC(1) +1.
IF (H(J) .GE. 0.5 .AND. H(J) .LT. 1.0) STRUC(2) =STRUC(2) +1.
IF (H(J) .GE. 1.0) STRUC(3) =STRUC(3) +1.
GOTO 40
20 IF (BA(J) .GE. 400.) GOTO 30
IF (BA(J) .LT. 25.) STRUC(4) =STRUC(4) +1.
IF (BA(J) .GE. 25.0 .AND. BA(J) .LT. 50.) STRUC(5) =STRUC(5) +1.
IF (BA(J) .GE. 50.0 .AND. BA(J) .LT. 100.) STRUC(6) =STRUC(6) +1.
IF (BA(J) .GE. 100.0 .AND. EA(J) .LT. 200.) STRUC(7) =STRUC(7) +1.
IF (BA(J) .GE. 200.) STRUC(8) =STRUC(8) +1.
GOTO 40
30 IF (BA(J) .LT. 600.) STRUC(9) =STRUC(9) +1.
IF (BA(J) .GE. 600.0 .AND. BA(J) .LT. 800.) STRUC(10) =STRUC(10) +1.
IF (BA(J) .GE. 800.0 .AND. EA(J) .LT. 1000.) STRUC(11) =STRUC(11) +1.
IF (BA(J) .GE. 1000.0 .AND. BA(J) .LT. 1400) STRUC(12) =STRUC(12) +1.
IF (BA(J) .GE. 1400.) STRUC(13) =STRUC(13) +1.
40 CONTINUE
IF (J .LT. NT) GOTO 11
RETURN
END
SUBROUTINE LEAF(SUMLA, NYR)
COMMON /HDATA/H(1000),DBH(1000),VOL(1000),VINC(1000),BA(1000),WT
COMMON /GROWA/SLA(1000),AL(1000),ELA(1000),CL(1000),BASUM(50)
COMMON /COEFP/A0,A1,B2,B3,C1,C2,D1,D2,F1,F2,F3,G1,G2
    
```

C
C
C

CALCULATE ESTIMATED LEAF AREA

```

BASUM(NYR)=0.0
SUMLA=0.0
I=0
19 I=I+1
    
```

```

ELA (I)=0.1
IF (H(I).LE.1.5) GOTO 20
ELA (I)=D1*BA (I)**D2
BASUM (NYR)=BASUM (NYR)+BA (I)
20 SUHLA=SUHLA+ELA (I)
IF (I.LT.NT) GOTO 19
RETURN
END
SUBROUTINE BIRTH (MAYR, NYR, SUELA)
C
C
C
SUBROUTINE TO PRODUCE NEW TREES
COMMON /BORNA/FECU (13), STRUC (13), MAGE (1000), ALITT (50), PMAX, PMIN
COMMON /HDATA/H (1000), DBH (1000), VOL (1000), VINC (1000), BA (1000), NT
COMMON /GROWA/SLA (1000), AL (1000), ELA (1000), CL (1000), BASUM (50)
COMMON /SEEDA/HSEED (9), SSEED (9), VCOEF (50), GRASS (50), SEEDP (50)
COMMON /GERMA/MBORN (50), GERH (50), SLITE (50)
COMMON /COEFF/A0, A1, B2, B3, C1, C2, D1, D2, F1, F2, F3, G1, G2
DOMT=0.0
DO 5 I=9, 13
5 DOMT=DOMT+STRUC (I)
C
C
C
CALCULATE LITTER AND GRASS WEIGHTS FOR GERMINATION EQUATION
NBORN (NYR)=0
SLITE (NYR)=EXP (-SUHLA/1720.)
GRASS (NYR)=30.47+91.0*SLITE (NYR)
IF (NYR.EQ.1) GRASS (NYR)=15.0
IF (NYR.EQ.2) GRASS (NYR)=50.0
ALITT (NYR)=(16.820+0.01337*BASUM (NYR)+2.5191*(FLOAT (MAYR))
1 +6.515*DOMT)
C
C
C
CALCULATE SEED PRODUCTION
SEED=0.0
SEEDP (NYR)=0.
DO 10 M=1, 13
IF (STRUC (M).LT.1.) GOTO 9
SEED=FECU (M)*STRUC (M)
SEEDP (NYR)=SEEDP (NYR)+SEED
9 CONTINUE
10 CONTINUE
C
C
C
CALCULATE GERMINATION
GRLT=(GRASS (NYR)*ALITT (NYR))/10000.0
IF (GRLT.LT.1.0) A=5.0
IF (GRLT.LT.1.0) S=0.8
IF (GRLT.GE.1.0) A=50.0
IF (GRLT.GE.1.0) S=3.2
BORN=SEEDP (NYR)*(5.36-(23.34*SLITE (NYR))+(209.8*SLITE (NYR)**2.)
1 -(192.06*SLITE (NYR)**3))*(A*GRLT*EXP (-GRLT*S))+0.001
NBORN=BORN*(100.0-(95.0/(1.0+EXP (4.8-0.00076*BASUM (NYR)))))/100.0
NBORN (NYR)=NBORN (NYR)+IFIX (NBORN)
IF (BORN.LT.1.) GOTO 11
GERM (NYR)=(BORN/SEEDP (NYR))*100.
GOTO 12
11 GERM (NYR)=0.0
12 CONTINUE
RETURN
END
SUBROUTINE GROW (NTREE, NYR, IX, PRINT, PKT)
C
C
C
SUBROUTINE TO GROW TREES
DIMENSION NTREE (1000)
DIMENSION HOLD (1000)
COMMON /BORNA/FECU (13), STRUC (13), MAGE (1000), ALITT (50), PMAX, PMIN
COMMON /HDATA/H (1000), DBH (1000), VOL (1000), VINC (1000), BA (1000), NT
COMMON /GROWA/SLA (1000), AL (1000), ELA (1000), CL (1000), BASUM (50)
COMMON /MORTA/PVEC (3), MORT (800), VMORT (50), BMORT (50), KZDAD, MAUUL
COMMON /SEEDA/HSEED (9), SSEED (9), VCOEF (50), GRASS (50), SEEDP (50)
COMMON /SUMMA/HBS (50), DBS (50), VUB (50), SLHAX (50), SURV (50)
COMMON /COEFF/A0, A1, B2, B3, C1, C2, D1, D2, F1, F2, F3, G1, G2
IF (NT.EQ.0) RETURN

```

```

IF(NYR.EQ.1)GOTO 11
K=0
10 K=K+1
HOLD(K)=H(K)
SLA(K)=0.0
IF(K.LT.NT)GOTO 10
11 CONTINUE
J=0
9 J=J+1
XLA=0.
IF(NYR.EQ.1)GOTO 13
KILL=0
DO 12 KL=1,KDEAD
12 IF(MTREE(J).EQ.MORT(KL))KILL=1
IF(KILL.EQ.1)GOTO 24
13 LARGE=0
I=0
14 I=I+1
IF(H(I).GT.H(J))LARGE=LARGE+1
IF(I.LT.NT)GOTO 14
C
C
C
CALCULATE CROWN LENGTH
I=0
8 I=I+1
KTT=0
IF(H(I).LE.2.0)GOTO 15
KTT=KTT+1
CL(I)=(P1-P2*(FLOAT(KTT))-P3*(FLOAT(NYR)))*H(I)
GOTO 17
15 CL(I)=0.67*H(I)
17 CONTINUE
IF(I.LT.NT)GOTO 8
C
C
C
CALCULATE THE TOTAL LEAF AREA OF ALL HIGHEN TREES
I=0
18 I=I+1
IF(H(I).LT.1.5)ELA(I)=0.1
IF(I.EQ.J)GOTO 22
IF(HOLD(I)-H(J).GE.CL(I))GOTO 21
IF(HOLD(I).GT.H(J))SLA(J)=XLA+(((HOLD(I)-H(J))/CL(I))*ELA(I))
GOTO 22
21 IF(HOLD(I).GT.H(J))SLA(J)=ELA(I)+XLA
22 XLA=SLA(J)
IF(I.LT.NT)GOTO 18
IF(SLA(J).EQ.0.0)GOTO 32
IF(SLA(J).GT.4300.)SLA(J)=4300.
AL(J)=EXP(-SLA(J)/1720.)
GOTO 33
32 AL(J)=1.0
33 CONTINUE
C
C
C
CALCULATE GROWTH OF MATURE TREES
VOLD=VOL(J)
PF=0.40
RAL=2.24*(1.-EXP(-1.136*(AL(J)-0.080)))
IF(H(J).LT.1.5)GOTO 23
IF(MAGE(J).LT.10)G=G1
IF(MAGE(J).GE.10)G=G2
CC=(137.+0.25*B2**2/B3)*(0.5*B2/B3)
DEST=G*DBH(J)*(1.0-(137.*CBH(J)+B2*DBH(J)**2-B3*DBH(J)**3)/CC)/(.27
14.+3.*B2*DBH(J)-4.*B3*DBH(J)**2)*RAL
DBLG=0.0
DSTD=0.20
CALL GAUSS(IX,DSTD,DBLG,DIALOG)
DINC=DEST*(10.0*DIALOG)
DBH(J)=DBH(J)+DINC
BA(J)=(((DBH(J)/2.)**2)*3.1416)
HEST=0.60*DINC**0.60
H(J)=H(J)+HEST
VOL(J)=(BA(J)*0.0001)*H(J)*PF
VINC(J)=VOL(J)-VOLD
GOTO 24

```


C
C
C

CALCULATE GROWTH OF SEEDLINGS (~1.5M. IN HT.)

```

23 NAGE=NAGE(J)
   HBAR=HSEED(NAGE)
   SIGH=HSEED(NAGE)/4.0
   CALL GAUSS(IX,SIGH,HBAR,T)
   H(J)=H(J)+(T*AL(J))
   IF(H(J).LT.1.5)GOTO 24
   DBH(J)=2.0
   BA(J)=((DBH(J)/2.0)**2)*3.1416)
   VOL(J)=(BA(J)*0.0001)*H(J)*FF
   VINC(J)=VOL(J)-VOLD
24 CONTINUE
   IF(J.LT.NT)GOTO 9
   NLIVE=NT
   J=0
19 J=J+1
   MB=0
   IF(KDEAD.EQ.0)GOTO 26
   DO 25 JH=1,KDEAD
25 IF(MTREE(J).EQ.MORT(JH))MB=1
   IF(MB)26,26,27
27 NLIVE=NLIVE-1
   IF(PKT.LT.PRINT)GOTO 28
   WRITE(6,3)MTREE(J)
   GOTO 28
26 IF(PKT.LT.PRINT)GOTO 28
   WRITE(6,2)MTREE(J),H(J),DBH(J),BA(J),VOL(J),VINC(J),CL(J),ELA(J),
1SLA(J),AL(J),NAGE(J)
28 CONTINUE
   IF(J.LT.NT)GOTO 19
   CONV=35.31373
   SLMAX(NYR)=0.0
   BASUM(NYR)=0.0
   DBS(NYR)=0.
   DBSH=0.
   HBS(NYR)=0.
   HBSH=0.
   NADUL=0
   VUB(NYR)=0.0
   J=0
30 J=J+1
   IF(DBH(J).LT.10.0)GOTO 29
   VUB(NYR)=VUB(NYR)+(0.00001185*DBH(J)**3.028)
29 CONTINUE
   IF(J.LT.NT)GOTO 30
   VUBPT=VUB(NYR)*CONV
   KK=0
31 KK=KK+1
   DBS(NYR)=DBS(NYR)+DBH(KK)
   HBS(NYR)=HBS(NYR)+H(KK)
   IF(DBH(KK).GT.10.)DBSH=DBSH+DBH(KK)
   IF(DBH(KK).GT.10.)HBSH=HBSH+H(KK)
   IF(DBH(KK).GT.10.)NADUL=NADUL+1
   SLMAX(NYR)=SLMAX(NYR)+ELA(KK)
   BASUM(NYR)=BASUM(NYR)+BA(KK)
   IF(KK.LT.NT)GOTO 31
   SURV(NYR)=FLOAT(NLIVE)/FLOAT(NT)*100.
   SLPT=SLMAX(NYR)/0.305**2
   BAFT=BASUM(NYR)/930.
   IF(NLIVE.EQ.0)GOTO 35
   DBS(NYR)=DBS(NYR)/NLIVE
   HBS(NYR)=HBS(NYR)/NLIVE
   IF(NADUL)35,35,34
34 DBSH=DBSH/NADUL
   HBSH=HBSH/NADUL
35 CONTINUE
   WRITE(7,115)NYR,NLIVE,SURV(NYR),HBS(NYR),DBS(NYR),SLMAX(NYR),
* BASUM(NYR),VUB(NYR)
115 FORMAT(13,I4,3F7.1,F8.2,F9.1,F10.3)
   IF(PKT.LT.PRINT)GOTO 36
   WRITE(6,4)NYR,NLIVE,SURV(NYR),NADUL,HBS(NYR),DBS(NYR),HBSH,DBSH,
1 SLMAX(NYR),SLPT,BASUM(NYR),BAFT,VUB(NYR),VUBPT
   KK=1

```

```

36 CONTINUE
2  FORMAT(10X,I3,7X,F4.1,6X,F4.1,5X,F5.0,5X,F6.4,4X,F6.5,5X,F4.1,5X,F
   14.0,6X,F7.1,5X,F6.3,7X,I3)
3  FORMAT(10X,I3,42X,'DEAD')
4  FORMAT('1'//30X,'SUMMARY STATISTICS FOR GROWTH DATA IN YEAR',I4//
   133X,'# TREES ALIVE AT START OF YEAR. =',I4/47X,'PERCENT SURVIVAL
   2=',F5.1/35X,'# ADULTS (TREES >10 CHS.DBH) =',I4/40X,'MEAN HEIGHT
   3 (ALL TREES) =',F5.1, 'H.'/43X,'MEAN DBH (ALL TREES) =',F5.1,'C
   4HS.'/33X,'MEAN HEIGHT (TREES >10CHS.DBH) =',F5.1,'H.'/36X,'MEAN
   5DBH (TREES >10CHS.DBH) =',F5.1,' CHS.'/46X,'TOTAL NEEDLE AREA =
   6 ',F7.0,' SQ.H.'/65X,'=',F7.0,' SQ.FT.'/47X,'TOTAL BASAL AREA =
   7',F7.0,' SQ.CHS.'/65X,'=',F7.2,' SQ.FT.'/42X,'EST. UNDERBARK VOLUM
   8E =',F7.3,' CU.H.'/65X,'=',F7.1,' CU.FT.'/)
   RETURN
   END
SUBROUTINE MORTAL(MTREE,NYR,IX,PRINT,PKT)

```

SUBROUTINE TO ASSIGN MORTALITY BETWEEN INDIVIDUAL TREES

```

DIMENSION MTREE (1000)
COMMON /HDATA/H(1000),DBH(1000),VOL(1000),VINC(1000),BA(1000),NI
COMMON /SEEDA/HSEED(9),SSEED(9),VCOEF(50),GRASS(50),SEEDP(50)
COMMON /BORNA/PVCU(13),STRUC(13),NAGE(1000),ALITT(50),PHAX,PHIN
COMMON /MORTA/PVEC(3),MORT(800),VMORT(50),EMORT(50),KDEAD,MADUL
COMMON /GROWA/SLA(1000),AL(1000),ELA(1000),CL(1000),BASUM(50)
COMMON /MORTB/VM(50),BH(50)
COMMON /COEFF/A0,A1,B2,B3,C1,C2,D1,D2,F1,F2,F3,G1,G2

```

INITIALISE COUNTERS

```

IF(NYR.NE.1)GOTO 8
VM(NYR)=0.
MN(NYR)=0.
DO 7 I=1,800
7 MORT(I)=0
8 K=0
KOUNT=NYR
IF(PKT.LT.PRINT)GOTO 9
WRITE(6,3)NYR
9 ID=0
N=0
99 N=N+1
MCULL =0
DO 10 JK=1,KDEAD
10 IF(MTREE(N).EQ.MORT(JK))MCULL=1
IF(MCULL.EQ.1)GOTO 100

```

TREES DIVIDED INTO JUVENILES AND ADULTS, JUVENILE MORTALITY
ASSIGNED RANDOMLY, ADULT MORTALITY BASED ON VOLUME INCREMENT

```

IF(H(N).GE.1.5)GOTO 40
CALL RANDU(IX,IY,YFL)
IX=IY
IF(H(N).GT.0.5)GOTO 20
Y1=PVEC(1)*AL(N)
IF(YFL.GT.Y1)GOTO 50
GOTO 100
20 IF(H(N).GT.1.0)GOTO 30
CALL RANDU(IX,IY,YFL)
Y2=PVEC(2)*AL(N)
IF(YFL.GT.Y2)GOTO 50
GOTO 100
30 CALL RANDU(IX,IY,YFL)
Y3=PVEC(3)*AL(N)
IF(YFL.GT.Y3)GOTO 50
GOTO 100
40 JAGE=NAGE(N)
VCON=VINC(N)*1000000.0/VCOEF(JAGE)
PNORT=A0*EXP(-A1*VCON)
CALL RANDU(IX,IY,YFL)
IX=IY
IF(YFL.GT.PNORT)GOTO 100
50 K=K+1

```

CALL SUBROUTINE TO REMOVE DEAD TREES

```

C      CALL LIST(MTREE, N, KOUNT, NYR, ID, PRINT, PKT)
      KOUNT=KOUNT+1
100 CONTINUE
      IF (N.LT.NT) GOTO 99
      VM(NYR)=VM(NYR)+VMORT(NYR)
      BM(NYR)=BM(NYR)+BMORT(NYR)
      WRITE(7,116) KDEAD,K,VMORT(NYR),BMORT(NYR),VM(NYR),BM(NYR)
116  FORMAT(2I4,F9.5,F9.0,F10.5,F11.0)
      IF (PKT.LT.PRINT) RETURN
      IF (PKT.EQ.PRINT) PKT=0.
      WRITE(6,1) NYR
      WRITE(6,2) KDEAD,K,VMORT(NYR),BMORT(NYR),VM(NYR),BM(NYR)
      1  FORMAT(//////30X,'SUMMARY STATISTICS FOR MORTALITY IN YEAR',I4//)
      2  FORMAT(40X,'CUM. # TREES DEAD=',I4/40X,'% DYING IN CURRENT YR=',I4
      1/40X,'VOLUME DEAD IN CURRENT YR=',F8.4,' CU.M.'/
      2 40X,'B.AREA DEAD IN CURRENT YR=',F8.0,' SQ.CH.'/
      3 40X,'TOTAL VOLUME DEAD=',F8.4,' CU.M.'/
      4 40X,'TOTAL B.AREA DEAD=',F8.0,' SQ.CH.')
      3  FORMAT(' ',40X,'INDIVIDUAL TREE MORTALITY FOR YEAR',I4//5X,'TREE =
      1',10X,'HEIGHT(M.)',8X,' DBH (CMS.)',6X,' BASAL AREA(SQ.CMS.)',4X,'V
      2OLUME(CU.M.)',3X,'VINC(CU.M.)'//)
      RETURN
      END
      SUBROUTINE GAUSS(IX,S,AM,V)

C      SUBROUTINE TO CALCULATE A NORMAL RANDOM NUMBER
C
      A=0.0
      DO 50I=1,12
      CALL RANDU(IX,IY,Y)
      IX=IY
50  A=A+Y
      V=(A-6.0)*S+AM
      RETURN
      END
      SUBROUTINE RANDU(IX,IY,YFL)

C      SUBROUTINE TO CALCULATE A UNIFORM RANDOM NUMBER
C
      IY=IX*65539
      IF (IY) 5,6,6
5  IY=IY+2147483647+1
      6  YFL=IY
      YFL=YFL*.4656613E-9
      RETURN
      END
      SUBROUTINE LIST(MTREE, J, KOUNT, NYR, ID, PRINT, PK)
      DIMENSION MTREE(1000)
      COMMON /BORNA/ECCU(13), STRUC(13), NAGE(1000), ALITT(50), FMAX, FMIN
      COMMON /HDATA/H(1000), DBH(1000), VOL(1000), VINC(1000), BA(1000), NT
      COMMON /GROWA/SLA(1000), AL(1000), ELA(1000), CL(1000)
      COMMON /MORTA/PVEC(3), MORT(800), VMORT(50), BMORT(50), KDEAD, MADUL
      COMMON /THINA/AA(1000), ZZ(1000), VTHIN(50), BTHIN(50), NK

C      SUBROUTINE TO REMOVE FROM THE DATA FILE TREES CULLED BY MORT
C      INPUT VARIABLES
C      MTREE = VECTOR OF TREE NUMBERS
C      J = TREE TO BE REMOVED
C      KOUNT = YR. COUNTER IN LIST
C      NYR = YR. COUNTER IN MAIN PROGRAM

      IF (KOUNT.NE.NYR) GOTO 20
      NK=0
20  CONTINUE
      IY=0
      DO 21 IZ=1, KDEAD
21  IF (MTREE(J).EQ.MORT(IZ)) IY=1
      IF (IY.EQ.1) RETURN
      IF (PK.LT.PRINT) GOTO 22
      WRITE(6,2) MTREE(J), H(J), DBH(J), BA(J), VOL(J), VINC(J)
22  IF (ID) 23, 23, 24
23  VMORT(NYR)=VMORT(NYR)+VOL(J)
      BMORT(NYR)=BMORT(NYR)+BA(J)
      GOTO 25

```

```

24 VTHIN (MYR) = VTHIN (MYR) + VOL (J)
   BTHIN (MYR) = BTHIN (MYR) + BA (J)
25 IF (H (J) .GT. 1.5) MADUL = MADUL + 1
   NK = NK + 1
   KDEAD = KDEAD + 1
   MORT (KDEAD) = MTREE (J)

```

C
C
C

SET DATA FIELDS OF DEAD TREES EQUAL TO ZERO

```

H (J) = 0.
DBH (J) = 0.0
BA (J) = 0.0
VOL (J) = 0.0
VINC (J) = 0.0
CL (J) = 0.0
ELA (J) = 0.0
NAGE (J) = 0

```

```

2 FORMAT (6X, I3, 13X, F5.2, 14X, F5.0, 17X, F5.0, 15X, F7.4, 8X, P6.5)
RETURN
END

```

```

SUBROUTINE THIN (MTREE, NTHIN, EAREQ, NTREQ, MYR, PRINT, PKT)
DIMENSION MTREE (1000), NTREQ (50), BAREQ (50)
COMMON /HDATA/ H (1000), DBH (1000), VOL (1000), VINC (1000), BA (1000), NT
COMMON /GROW/ SLA (1000), AL (1000), ELA (1000), CL (1000), BASUM (50)
COMMON /MORTA/ PVEC (3), MORT (800), VMORT (50), EMORT (50), KDEAD, MADUL
COMMON /THINA/ AA (1000), ZZ (1000), VTHIN (50), BTHIN (50), NK

```

C
C

THINNING OPTIONS

```

ID = 1
KF = 0
KOUNT = NYR
WRITE (6, 3) NYR
12 IF (NTHIN - 1) 52, 32, 40
32 IF (BASUM (MYR) .LE. BAREQ (MYR)) GOTO 52
   IHK = 0
   IJK = 1
   CALL SORT (MTREE, IHK, IJK)
   JK = 0
33 JK = JK + 1
   DO 34 I = 1, KDEAD
34 IF (AA (JK) .EQ. FLOAT (MORT (I))) LN = 1
   IF (LN .EQ. 1) GOTO 35
   BASUM (MYR) = BASUM (MYR) - AA (JK)
   IZ = IFIX (ZZ (JK))
   KOUNT = KOUNT + 1
   CALL LIST (MTREE, IZ, KOUNT, NYR, ID, PRINT, PKT)
   IF (BASUM (MYR) .LE. BAREQ (MYR)) GOTO 36
35 IF (JK .LT. NT) GOTO 33
36 IJK = 0
   CALL SORT (MTREE, IHK, IJK)
   GOTO 52

40 IF (NT .LE. NTREQ (MYR)) GOTO 52
   IHK = 0
   IJK = 1
   CALL SORT (MTREE, IHK, IJK)
   JK = 0
41 JK = JK + 1
   DO 42 I = 1, KDEAD
42 IF (ZZ (JK) .EQ. FLOAT (MORT (I))) LK = 1
   IF (LK .EQ. 1) GOTO 43
   IZ = IFIX (ZZ (JK))
   NT = NT - 1
   KOUNT = KOUNT + 1
   CALL LIST (MTREE, IZ, KOUNT, NYR, ID, PRINT, PKT)
   IF (NT .LE. NTREQ (MYR)) GOTO 44
43 IF (JK .LT. NT) GOTO 41
44 IJK = 0
   CALL SORT (MTREE, IHK, IJK)
52 CONTINUE
WRITE (6, 1) NYR
WRITE (6, 2) KDEAD, NK, VTHIN (MYR), BTHIN (MYR)
1 FORMAT (////30X, 'SUMMARY STATISTICS FOR THINNING IN YEAR', I4, //)
2 FORMAT (40X, 'SUM. # TREES DEAD =', I4, /40X, ' # THINNED IN CURRENT YR =',
I4, /40X, ' VOLUME THINNED IN CURRENT YR =', F8.4, /40X, ' BA THINNED IN CU

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```

2 FREQNT YK=, F8.0)
3 FORMAT('1',40X,'INDIVIDUAL TREES THINNED IN YEAR', I4/5X, 'TREE :
1', 10X,'HEIGHT(M.)',8X,' EBH (CMS.)',6X,'BASAL AREA(SQ.CMS.)',4X,'V
2OLUME(CU.M.)',3X,'VINC(CU.M.)'/)
RETURN
END
SUBROUTINE SORT(MTREE, IHK, IJK)
DIMENSION MTREE(1000)
COMMON /HDATA/H(1000), DBH(1000), VOL(1000), VINC(1000), BA(1000), NT
COMMON /THINA/AA(1000), ZZ(1000), VTHIN(50), BTHIN(50), NK

SUBROUTINE RANKS DATA INTO ASCENDING ORDER.

INPUT VECTOR OPTIONS SPECIFIED IN SUBROUTINE THIN.
      IHK=0 - SORT ON VARIABLE BA
      IHK=1 - SORT ON VARIABLE VINC
      IJK=0 - SORT ON VARIABLE MTREE

AA AND ZZ ARE RANKED OUTPUT VECTORS.

IF(IJK.GT.0)GOTO 40
IF(IHK.GT.0)GOTO 20
DO 10 J=1,NT
AA(J)=FLOAT(MTREE(J))
10 ZZ(J)=BA(J)
GOTO 80
20 DO 30 J=1,NT
AA(JJ)=FLOAT(MTREE(J))
30 ZZ(J)=VINC(J)
GOTO 80
40 IF(IHK.EQ.1)GOTO 60
DO 50 J=1,NT
AA(J)=BA(J)
50 ZZ(J)=FLOAT(MTREE(J))
GOTO 80
60 DO 70 J=1,NT
AA(J)=VINC(J)
70 ZZ(J)=FLOAT(MTREE(J))
80 CONTINUE
L=NT-1
DO 82 I=1,L
IL=I+1
DO 81 J=IL,NT
IF(AA(I).LE.AA(J))GOTO 81
T1=AA(I)
AA(I)=AA(J)
AA(J)=T1
NT1=ZZ(I)
ZZ(I)=ZZ(J)
ZZ(J)=NT1
81 CONTINUE
82 CONTINUE
RETURN
END
SUBROUTINE MPLOTS(XX,DATA,IPCINT,IVAR,IOPT,XSCALE,YSCALE)
INTEGER XNAME(6),YNAME(6),LAEFL(5,6),GRFNAM(6),TITLE(6)
DIMENSION DATA(5,103),XX(5,103)
DIMENSION IPOMH(20),X(53),Y(53)
C IOPT=0 NORMAL X,Y SCALE
C =1 LOG10 X AXIS
C =2 LOG10 Y AXIS
C =3 LOG10 X AND Y AXIS
IF (IPOINT .EQ. 0 .OR. IPCINT .GT. 100) GO TO 1
IF (IVAR .EQ. 0 .OR. IVAR .GT. 5) GO TO 1
IF (IOPT .GT. 3) GO TO 1
IF (XSCALE .GT. 40.0) GO TO 1
IF (YSCALE .GT. 27.0) GO TO 1
CALL PLOTS
CALL OPEN
WRITE(6,111) IPOINT,IVAR,XSCALE,YSCALE
111 FORMAT(/,' NO. OF POINTS PER GRAPH:',T28,I5,/, ' NO. OF GRAPHS: ',
1 T28,I5,/, ' LENGTH OF X AXIS: ',T28,F7.2,/,
2 ' LENGTH OF Y AXIS: ',T28,F7.2,/)
NOPT=IOPT+1
GO TO (500,901,902,903),NOPT

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900 WRITE(6,910)
GO TO 904
901 WRITE(6,911)
GO TO 904
902 WRITE(6,912)
GO TO 904
903 WRITE(6,913)
904 CONTINUE
910 FORMAT(' NORMAL X,Y AXIS')
911 FORMAT(' LOG TEN X AXIS')
912 FORMAT(' LOG TEN Y AXIS')
913 FORMAT(' LOG TEN X,Y AXIS')
READ(5,103) XNAME,YNAME,TITLE
103 FORMAT(6A4,6A4,6A4)
101 FORMAT(20A4)
WRITE(6,914) TITLE
914 FORMAT(/,' TITLE OF PLOT IS: ',6A4)
DO 10 I=1,IVAR
READ(5,102) (LABEL(I,K),K=1,6)
102 FORMAT(6A4)
WRITE(6,104) (LABEL(I,K),K=1,6)
104 FORMAT(/,3X,6A4)
10 CONTINUE
DO 11 I=1,IVAR
DO 11 J=1,IPOINT
IF (DATA(I,J) .LE. 0.0) GOTO 12
GOTO 11
12 DATA(I,J)=0.1
11 CONTINUE
ISWTCH=0
IF (IOPT .EQ. 1 .OR. IOPT .EQ. 3) ISWTCH=1
CALL RANGE(XX,IVAR,IPOINT,XSCALE,XMIN,XMAX,ISWTCH,NCYCX)
ISWTCH=0
IF (IOPT .EQ. 2 .OR. IOPT .EQ. 3) ISWTCH=1
CALL RANGE(DATA,IVAR,IPOINT,YSCALE,YMIN,YMAX,ISWTCH,NCYCY)
INDEX=0
DO 30 I=1,IVAR
ILIM=IPOINT+3
DO 40 J=1,ILIM
X(J)=XX(I,J)
40 Y(J)=DATA(I,J)
DO 50 KK=1,6
50 GRFNAM(KK)=LABEL(I,KK)
IF (INDEX .EQ. 0) CALL GRAPH(X,Y,IPOINT,2,XSCALE,YSCALE,TITLE,24,
1 XNAME,24,YNAME,24,20.0,1,3,GRFNAM,24,XMIN,XMAX,YMIN,YMAX,
2 IOPT,NCYCX,NCYCY)
IF (INDEX .NE. 0) CALL GRAPHS(X,Y,IPOINT,1,3,GRFNAM,24)
30 INDEX=1
CALL CLOSE
RETURN
1 WRITE(6,117) IPOINT,IVAR,IOPT,XSCALE,YSCALE
117 FORMAT(' CONTROL PARAMETER(S) OUT OF RANGE',/,
1 ' NO. OF POINTS PER GRAPHS: ',T28,I5,/,
* ' NO. OF GRAPHS: ',T28,I5,/,
2 ' OPTION: ',T28,I5,/,
J ' LENGTH OF X AXIS: ',T28,F10.5,/,
4 ' LENGTH OF Y AXIS: ',T28,F10.5,/,
5 ' *** JOB TERMINATED ***')
RETURN
END
SUBROUTINE RANGE(DATA,IVAR,ITIME,SCALE,WMIN,WMAX,IOPT,NCYC)
DIMENSION SCRTCH(515),DATA(5,103),OUT(515)
WMIN=DATA(1,1)
WMAX=DATA(1,1)
DO 10 I=1,IVAR
DO 20 J=1,ITIME
IF (DATA(I,J) .LT. WMIN) WMIN=DATA(I,J)
IF (DATA(I,J) .GT. WMAX) WMAX=DATA(I,J)
20 CONTINUE
10 CONTINUE
IF (IOPT .NE. 1) RETURN
WMAX=ALOG10(WMAX)
WMIN=ALOG10(WMIN)
NCYC=WMAX-WMIN+1.0
ILIM=ITIME+2

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DO 40 I=1,IVAR
DO 50 J=1,ILIM
K=(I-1)*ILIM+J
50 SCRTCH(K)=DATA(I,J)
SCRTCH(K)=SCRTCH(K-2)
SCRTCH(K-1)=SCRTCH(K-2)
40 CONTINUE
INO=ILIM*IVAR-2
CALL SCALG(SCRTCH,SCALE,INO,1,OUT,NCYC)
DO 60 I=1,IVAR
DO 70 J=1,ILIM
K=(I-1)*ILIM+J
70 DATA(I,J)=OUT(K)
DATA(I,ILIM)=OUT(INO+2)
DATA(I,ILIM-1)=OUT(INO+1)
60 CONTINUE
RETURN
END
SUBROUTINE GRAPH(XI,YI,NDI,NAX,XL,YL,TITLE,LTITLE,XNAME,LONGYN,
1 YNAME,LONGYN,TICS,NCYCLE,LINEI,GRPNAM,NAMLTH,XMIN,XMAX,YMIN,
2 YMAX,IOP,NCYC1,NCYC2)
**** SEVERAL MODIFICATIONS HAVE BEEN MADE TO A.S.J.'S ORIGINAL MO
C
C      EXTRA ENTRY POINTS
C      GRAPHS
C      HIST
C      HISTS
C      OPEN
C      CLOSE
C
C      GENERAL DESCRIPTION
C      THE SUBROUTINE PLOTS SINGLE OR SUPERIMPOSED GRAPHS AND
C      HISTOGRAMS. GRAPHS MAY BE STRAIGHT LINES OR FITTED CURVES
C      GRAPHS AND HISTOGRAMS MAY HAVE SYMBOLS OR NOT
C      CALL (OPEN) BEFORE ANY OTHER ROUTINES AND CALL (CLOSE)
C      BEFORE STOPPING.
C
C      INTEGER*4 NDI,ND,NAXIS,LONGXL,LONGYN,NCYCLE,LINEG,NAMLTH,LINEI
C      DIMENSION XI(103),YI(103),ISYM(5),
C      2 XD(2000),YD(2000),DATA(2000)
C      INTEGER*4 TITLE(6),XNAME(6),YNAME(6),GRPNAM(6)
C      LOGICAL*1 TOPEN/.FALSE./,HGRAM,ELTONE
C      DATA ISYM/004,005,012,010,011/
C
C      PWIDTH IS THE WIDTH OF THE PLOTTING PAPER IN INCHES
C      THE USER MUST CHANGE PWIDTH TO CONFORM TO THE PAPER USED
C
C      DATA PWIDTH/30.0/
C      NAXIS=NAX
C      IF(NAXIS.NE.0) GOTO 91
C      WRITE(6,94)
C      94 FORMAT(' ***** NAXIS=0 IS INVALID IN GRAPH OR HIST *****')
C      RETURN
C      PLTONE=.FALSE.
C      GOTO 95
C
C      ENTRY POINT FOR SUPERIMPOSED GRAPH
C
C      ENTRY GRAPHS(XI,YI,NDI,NCYCLE,LINEI,GRPNAM,NAMLTH)
C      NAXIS=0
C      IF(.NOT.PLTONE) GOTO 95
C      96 WRITE(6,97)
C      97 FORMAT(' ***** GRAPHS OR HISTS CALLED BEFORE EITHER GRAPH OR HIS
C      2T *****')
C      RETURN
C
C      TRANSFER GRAPH DATA TO NEW ARRAYS SO THAT ORIGINAL DATA
C      IS NOT ALTERED
C      95 DO 100 NDATA = 1,NDI
C      XD(NDATA)=XI(NDATA)
C      100 YD(NDATA)=YI(NDATA)
C      ND=NDI
C      LINEG=LINEI
C      HGRAM=.FALSE.
C      GOTO 80
C

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C          ENTRY POINT FOR THE CONSTRUCTION OF HISTOGRAMS
C
ENTRY HIST (XI,YI,NDI,WAX,XL,YL,XNAME,LONGIN,YNAME,LONGIN
2 ,TICS,NCYCLE,LINEI,GRPNAM,NAHLTH)
C
NAXIS=WAX
IF(NAXIS.EQ.0) GOTO 93
PLTONE=.FALSE.
GOTO 75
C
C          ENTRY POINT FOR SUPERIMPOSING HISTOGRAMS
ENTRY HISTS (XI,YI,NDI,NCYCLE,LINEI,GRPNAM,NAHLTH)
C
NAXIS=0
IF(PLTONE) GOTO 96
LINEG=LINEI
75
C
C          CALCULATE THE POINTS FOR THE HISTOGRAMS.
C          CALCULATE THE FIRST 2 POINTS
XD(1)=XI(1)-(XI(2)-XI(1))/2.0
YD(1)=0.0
XD(2)=XD(1)
YD(2)=YI(1)
C
C          CALCULATE THE 2*(NDI-1) INTERMEDIATE POINTS
NT=NDI-1
DO 7 IH=1,NT
IH2=2*IH+1
XD(IH2)=XI(IH)+(XI(IH+1)-XI(IH))/2.0
YD(IH2)=YI(IH)
XD(IH2+1)=XD(IH2)
YD(IH2+1)=YI(IH+1)
7
C
C          CALCULATE THE LAST 2 POINTS
ND=2*NDI+2
XD(ND-1)=XI(NDI)+(XI(NDI)-XI(NDI-1))/2.0
YD(ND-1)=YI(NDI)
XD(ND)=XD(ND-1)
YD(ND)=0.0
IF(LINEG.EQ.+2) GOTO 77
LINEG=+2
HGRAM=.TRUE.
GOTO 80
77
HGRAM=.FALSE.
80
IF(TOPEN) GOTO 81
WRITE(6,58)
58
FORMAT('1',///,' ***** OPEN MUST BE CALLED BEFORE EITHER GRAPH,GRA
2PHS,HIST,HISTS. CURRENT REQUEST SKIPPED *****')
RETURN
81
IF(NAXIS.EQ.0) GOTO 14
C
C          THE GRAPH PAGE CO-ORDINATES ARE CALCULATED AUTOMATICALLY
IF((YLREF+1.0+YL+SUNY).LE.PWIDTH) GOTO 180
IF(YL.LE.(PWIDTH-1.0)) GO TO 83
WRITE(6,82)
82
FORMAT(' - ***** Y AXIS LENGTH .GT. PAPER WIDTH *****//')
RETURN
83
CALL PLOT(XLREF+2.0,1.0-SUNY,-3)
SUNY=1.0
XLREF=0.0
YLREF=0.0
GOTO 181
C
C          SET LOCAL ORIGIN FOR NEXT PLOT
180
CALL PLOT(0.0,YLREF+1.0,-3)
SUNY=SUNY+YLREF+1.0
C
C          SAVE THE LARGEST X AXIS LENGTH IN CURRENT CROSS PAGE SET
181
IF(XL.GT.ALREF) XLREF=XL
C
C          SAVE THE YAXIS LENGTH FOR USE IN LOCATING THE NEXT ORIGIN
YLREF=YL
GOTO 2
14
I=I+1
915
IF (IOPT .NE. 1 .AND. IOPT .NE. 3) GO TO 15

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XD(ND*NCYCLE+1)=XI(ND*NCYCLE+1)
XD((ND+1)*NCYCLE+1)=XI((ND+1)*NCYCLE+1)
GO TO 916
15 XD(ND*NCYCLE+1)=XMIN
16 XD((ND+1)*NCYCLE+1)=XDELTA
916 CONTINUE
IF (IOPT.NE.2.AND.IOPT.NE.3) GO TO 17
YD(ND*NCYCLE+1)=YI(ND*NCYCLE+1)
YD((ND+1)*NCYCLE+1)=YI((ND+1)*NCYCLE+1)
GO TO 9918
17 YD(ND*NCYCLE+1)=YMIN
18 YD((ND+1)*NCYCLE+1)=YDELTA
9918 CONTINUE
IF (NAXIS.EQ.2) GOTO 29
GOTO 3
2 I=1
20 XLEG=XL+1.0
21 XLEG2=XLEG+0.5
22 YLEG=6.0
IF (NAXIS.EQ.2) GOTO 50
CALL SCALE (XD,XL,ND,NCYCLE,TICS)
CALL SCALE (YD,YL,ND,NCYCLE,TICS)
25 YMIN=YD(ND*NCYCLE+1)
26 XMIN=XD(ND*NCYCLE+1)
27 XDELTA=XD((ND+1)*NCYCLE+1)
28 YDELTA=YD((ND+1)*NCYCLE+1)
GOTO 29
C
50 XDELTA=(XMAX-XMIN)/XL
YDELTA=(YMAX-YMIN)/YL
GO TO 915
29 CALL SYMBOL (XLEG,YLEG,0.15,'LEGEND',0.0,6)
YLEG=YLEG-0.10
XNCYC=NCYCX
IF (IOPT.EQ.1.OR.IOPT.EQ.3) GOTO 930
30 CALL AXIS (0.0,0.0,XNAME,-LCNGXN,XL,0.0,XMIN,XDELTA,TICS)
GO TO 931
930 CALL LOGAXS (0.0,0.0,XNAME,-LCNGXN,XL,0.0,XMIN,+1.0,XNCYC)
931 XX=XL/4.0
YY=YL+0.5
CALL SYMBOL (XX,YY,0.15,TITLE,0.0,LTITLE)
YNCYC=NCYCY
IF (IOPT.EQ.2.OR.IOPT.EQ.3) GOTO 932
31 CALL AXIS (0.0,0.0,YNAME,LCNGYN,YL,90.0,YMIN,YDELTA,TICS)
GO TO 3
932 CALL LOGAXS (0.0,0.0,YNAME,LCNGYN,YL,90.0,YMIN,+1.0,YNCYC)
3 IF (LINEG.GT.0) GOTO 5
32 ND=-ND
33 LINEG=-LINEG
5 LINEG=LINEG-2
34 ND=IABS(ND)
CALL LINE (XD,YD,ND,NCYCLE,LINEG,ISYM(I))
IF (.NOT.HGRAM) GOTO 36
C
C HISTOGRAMS ARE INITIALLY PLOTTED WITHOUT SYMBOLS,IF
C SYMBOLS WERE REQUESTED THEN A CALL TO FLINE WITH THE
C GIVEN POINTS XI AND YI IN REVERSE ORDER AND A REQUEST
C FOR SYMBOLS ONLY IS MADE.
C
C SET UP THE ARRAY WITH REVERSE ORDER POINTS.
IH2=NDI+1
DO 250 IH=1,NDI
XD(IH)=XI(IH2-IH)
250 YD(IH)=YI(IH2-IH)
HGRAM=.FALSE.
NAXIS=0
LINEG=+1
ND=NDI
GOTO 15
36 YLEG=YLEG-0.25
IF (LINEG.EQ.0) GOTO 38
37 CALL SYMBOL (XLEG,YLEG,0.15,ISYM(I),0.0,-1)
38 CALL SYMBOL (XLEG2,YLEG,0.1,GRPHAM,0.0,NAHLTH)
RETURN
C

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```

C      ENTRY OPEN
C
59     CALL PLOTS (DATA,8000)
      TOPEN=.TRUE.
      WRITE(6,60)
      FORMAT (1H1)
60
C
C      MAKE SURE THAT THE ORIGIN IS WHERE IT SHOULD BE
      CALL PLOT(1.0,-0.5,-3)
C
C      INITIALIZE THE PAGE CO-ORDINATES
C
      XLREF=0.0
      YLREF=0.0
      SUMY=0.0
      PLTONE=.TRUE.
      RETURN
C
      ENTRY CLOSE
C
      CALL PLOT (0.0,0.0,999)
      RETURN
      END

/*
//GO.PLOTTER DD SYSOUT=(1,,4110),SPACE=(CYL,(2,1),RLSE)
//GO.SYSIN DD *
  1 3541645
    0 0 0 0 0 1 8 55 400 1750 5000100002000040000
  850 930 950
0.04467 0.00044 1.26520 1.265
0.1 1.0 0.6723 0.0020 0.0014500. 200.
50 5 00
0 00
  31.8 28.3 45
  31.8 28.3 45
      STAND AGE                GERMINATION                THREE SEEDTREES (#1)
SEED PRODUCTION
% BORN
% GERMINATION
      STAND AGE                ENVIRONMENT                THREE SEEDTREES (#1)
LITTER WT.
GRASS WT.
LIGHT LEVEL
      STAND AGE                YIELD 1                THREE SEEDTREES (#1)
MEAN HI.
MEAN DBH
VOL. UNDERBARK
      STAND AGE                YIELD 2                THREE SEEDTREES (#1)
NEEDLE AREA
SUM BA
      STAND AGE                MORTALITY                THREE SEEDTREES (#1)
SURVIVAL %
BA DEAD
VOL. DEAD
/*

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