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THE DEMOGRAPHY OF PLANTS

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Demography is "that branch of anthropology which treats the statistics of births, deaths and diseases etc." (Shorter Oxford English Dictionary, 3rd ed.). The etymology suggests specific relevance to man, but the word has been widely accepted into ecological literature for other species of animal and, in the absence of any obvious alternative, may be used of plant populations. Malthus (181) saw the statistical properties of populations as common to man, animals, and plants. "Through the animal and vegetable kingdoms, nature has scattered the seeds of life abroad with the most profuse and liberal hand. She has been comparatively sparing in the room and nourishment necessary to rear them. The germs of existence contained in this spot of earth, with ample food, and ample room to expand in, would fill millions of worlds in the course of a few thousand years. Necessity, that imperious all pervading law of nature, restrains them within the prescribed bounds. The race of plants and the race of animals shrink under this great restrictive law."

The study of plant demography has never gained significant momentum within the science of ecology; plant ecologists have concentrated on the physiology, structure, and taxonomy of vegetation, while largely ignoring the population phenomena that constitute the underlying flux. The reluctance of botanists to concern themselves with numbers is the more strange because there are fewer of the problems of search, capture, and estimation that bedevil demographic research with animals. A few zoologists have remarked that theories based on animal demography may be applicable to plants (e.g. 91), and some recent attempts have been made by textbook writers to relate plant demography to the core of demographic theory developed over fifty years by zoologists (160, 291, 339). In this review an attempt is made first to examine some of the theoretical bases for the development of plant demography. Then follows a survey of our current knowledge of the subject, virtually all of which has been gleaned from sources little concerned with demography per se. Given the present state of this information it is not surprising if a notable discordance can be detected between our broad principles outlined in the first section and the information surveyed in the second.

THEORETICAL CONSIDERATIONS

A science of plant demography cannot be built uncritically on the methods developed by zoologists. There are fundamental differences in the growth form of higher plants and higher animals that affect their population behavior. From the time of germination of a young seedling, growth involves the accumulation of structural units: leaves with axillary buds above ground, the individual units of the branched root structure below ground. Goethe described plant form as "a matriarchal tribe of units, each engrafted upon another" (6). The higher plant in this sense is a subpopulation in its own right, having the potential of exponential growth in the number of its parts. So fundamental is this subunitary construction that the taxonomically important elements in the specific descriptions of plants are almost wholly based on the form of the units, not the form of the whole plant. While it is taxonomically useful to describe a rabbit as having four legs, only a very few plants can be described usefully by the numbers of their leaves (*Paris, Listera, Welwitschia*).

The great plasticity of plants, contrasting so markedly with the canalized form of higher animals, occurs mainly at the level of the number of constructional units making up the subpopulation that is the "individual plant." In a demographic study a count of the number of animals present in an area may give much useful information about mass and activities; a count of the numbers of plants gives much less information because of the great variation in size and reproductive activity even of even-aged individuals (117). In many ways the closest analogy among animals to the demographic properties of plants is found in colonial Hymenoptera. In ants, termites, and bees a colonization phase when fertilized queens find new sites (equivalent to seed dispersal and establishment) is followed by the growth of a subpopulation of worker units with caste differentiation (cf leaves, petals, carpels, etc) (224, 225, 341). Chemical and visual integration within the hymenopteran colony is equivalent to the correlative inhibitions that control development within the subpopulation of buds and shoot systems of a plant. Wilson (341) discussed at length the various concepts of superorganismic integration of insect colonies that have had a significant influence on students of insect behavior since the early 1900s (e.g. 334). Darwin (65) compared compound animals to plants: "we may consider the polypi in a zoophyte, or the buds in a tree, as cases where the divison of the individual has not been completely effected. . . . Surprising as this union of separate individuals in a common stock must always appear, every tree displays the same fact, for buds must be considered as individual plants."

In plant populations (like the hymenopteran analogy) there are two levels of population behavior: the number of plants (colonies) and the number of shoot units per plant (number of members per colony). Births and deaths may occur at either level of population organization. Death may be of a whole plant or of a part: a leaf, a shoot or a main branch, a root, or a rootlet. Environmental stresses may influence both birth and death rates at either demographic level. Any general theory of plant demography that fails to take into account this population dualism is seriously incomplete. The dualism is particularly conspicuous in clone forming plants when not only does the plant develop from a single seedling as a subpopulation of parts, but some of these parts may root and eventually become severed from the original. The result is a subpopulation of wholly discrete functional units, "ramets" with the genetic identity of the single individual, the "genet" (149).

One of the major tasks of a demographer is to measure, describe, and explain changes in the numbers that compose a population. A fundamental equation of population growth is:

$$N_{t+1} = N_t + \text{Births} - \text{Deaths} + \text{Immigration} - \text{Emigration}$$

Numbers are conventionally represented by N in demographic equations and rates of change as dN/dt. Because of the subpopulation-like character of individual plants we need a more sensitive symbolism, e.g. $N\eta$, to define population size where N is the number of genets present and η is the number of base units (leaves, ramets, branches) of which each genet is composed. The value of N is relevant to the population biologist interested in genetic and evolutionary processes. The values of both N and η are relevant to the population biologist interested in production. Density stress has a profound influence on the size of individual plants, and population effects are shown not only in changes of N and η, but also in interactions between N and η. The population of subunits that form the whole plant may be recognized at a variety of levels. Ultimately the population of cells represents the most fundamental level at which population phenomena operate in both animals and plants. Classically the leaf with its axillary bud is the unit of morphology. Independent rooted shoots are convenient units for some purposes, and in grasses the "tiller," a lateral shoot usually defined as bearing 2 or more leaves, has been widely used as the unit in pasture analysis.

However, when one turns to more complex branching patterns than those that, like the grasses, essentially reiterate the growth pattern of the original genet, a certain conceptual difficulty arises in determining a meaningful unit to count. The number of shoots may be counted [as e.g. on *Acer rubrum,* (340)] and distinguished into short and long shoots. In *A. rubrum* the number of shoots per tree increased exponentially with age, slowed and reached an asymptote after 25 years, and then maintained a dynamic equilibrium between recruitment and death. In fruit trees the numbers of short and long shoots have also been counted (16, 17).

Hallé & Oldeman (108) have defined 21 architectural models of tree form based on a few simple constructional principles: continuous or articulate growth, terminally or laterally borne inflorescences, orthotropic or plagiotropic branch systems. The models define the growth behavior of young trees or saplings. Mature trees are envisaged as composed of several reiterations of the basic architectural modules (209). This approach offers a real prospect of quantifying plant structure in terms of developmentally significant modules (White, in preparation). A modular theory of plant structure, "the pipe-stem model," has been developed from the principles of allometric growth (282) that complement the ideas of Hallé & Oldeman.

Some attempts have been made to treat the parts of a plant as members of a population. The successive cohorts of tillers in grasses may show characteristic age structures (White, in preparation), and there is at least one example of a density-dependent age structure in leaves (294). The dynamics of leaf production have been studied in *Rhizophora mangle* (100), *Phaseolus viridissimus,* and *Nicotiana tabacum* (264), and of bud production in *Fraxinus americana* (99).

If the size of subunits is relatively nonplastic, measurements of individual plant weight, w, crudely approximate counts of the number of subunits and give indirect evidence for values of η. Several recent studies have shown that formal relationships between total plant weight and the weight of some specific part can be defined with some accuracy (4, 26). There are simple allometric relationships between leaf weight and both total plant weight and stem diameter (4, 155).

N and w are closely related at least in populations of single species. In dense populations of a wide variety of plant species the two processes of growth in weight of survivors and the mortality of genets proved to be closely related; this is the so-called 3/2 thinning law (344). When log mean plant weight is plotted against log density of survivors the line has a slope of 3/2. The relationship seems to have been noticed first by Tadaki (303, 304) and has been further extended by White & Harper (335). This generalization has an important bearing on the development of any general theory of plant demography in the following respects:

1. The rate of mortality of genets is directly related to the stresses caused by the pressures of population density.
2. The rate of elimination of genets is related to the rate of growth of the survivors. If the growth rate is increased (e.g. by nutrient addition) the death rate is increased.
3. In density stressed populations the frequency distribution of individual genet weight becomes strongly skewed with the passage of time, approaching log normality (159). Thus a population of even-aged individuals develops a hierarchy of size with a few dominant and a large class of suppressed genets: mortality is largely concentrated in this suppressed class (161, 335).
4. The mortality risk tends to remain constant with time, i.e. the relationship between log number of survivors and time is nearly linear (335).
5. Density-dependent mortality that is most conspicuous in the death of genets (N) is accompanied by (and probably usually preceded by) death at the subpopulation level. The phenomenon is most clearly seen in forest stands at high density, in which not only is there death of the suppressed weaklings but also accelerated death of the lower shaded branches of the survivors (340). However, in populations of *Trifolium subterraneum* (294) there was accelerated turnover of leaves at lower densities as plants grew rapidly. At high density considerably fewer leaves developed per plant and these tended to persist throughout its life.

The closest approach to a study of plant demography in which changes in N and η have been followed simultaneously has been made with deliberately sown populations of *Lolium perenne* (149). High density populations thinned as they grew with a steady rate of death of genets according to the 3/2 thinning law, but, synchronously, the death of ramets (tillers) occurred with the result that populations having initially a 30-fold range of genet densities adjusted to a constant ramet density after 20 weeks. The constant density of ramets was achieved by different numbers of surviving genets (N), depending on the sowing density; part of this adjustment was achieved by different numbers of ramets per genet (η), part by different death rates of ramets, and, where all of the ramets of a genet died, part by death of whole genets. An essentially similar process has been described in populations of *Tussilago farfara* (203).

Clonal growth is a common feature in the life of herbaceous perennials and some woody plants that may extend a population of shoots of a single genet over great distances; the phenomenon is, however, essentially similar to the extension of a population of shoots of a tree within the canopy of a forest. In both cases the subpopulation has a structure dependent on internode length and branching angles (e.g. 152) and a structural demography—the addition of new elements and the death of old.

The population phenomena of immigration and emigration have normally very limited expression at the subpopulation level with the exception of the relatively few species that form propagules from maternal tissue on an inflorescence, e.g. bulbils of some *Allium* and *Lilium* species. In these special cases the population consequences are that a single genet becomes widely distributed. Such population behavior is common in aquatic species, e.g. *Eichhornia crassipes* in the Nile (41, 96). Ramet dispersal in a variety of plants has been reviewed by van der Pijl (222).

Reproduction by seed permits the multiplication of genets, genetic variation, and dispersal. Growth at the subpopulation level allows a proven successful genotype to exploit a proven successful environment. A high intrinsic rate of natural increase may occur at either level and a plant species may be said to have two intrinsic rates of increase: (*a*) that due to seed production and (*b*) that due to the growth rate of the individual genet manifested either in size or in clonal spread. Emphasis on *a* by the investment of a high proportion of assimilates in ± precocious seed production is usually associated with colonizing ability, a ± fugitive habit, an *r* species, and a poorer competitive ability. Forms that emphasize *b* show a high proportion of assimilates going to vegetative vigor, particularly early in life, and are *K* species, with longer habitat tenure and an aggressive and often persistent habit.

Models of Continuous Population Growth

The formal equation of population growth originally proposed by Verhulst (316) and later by Pearl & Reed (212) is $\mathrm{d}N/\mathrm{d}t = rN(K - N)/K$. The elements of such population growth are illustrated by simple experiments with aquatic plants. Species of *Lemna* and *Spirodela* are ideal for such studies; *Salvinia* is also convenient but frond number is less readily counted (46).

If a frond of *Lemna* [*L. minor, L. gibba, L. (Spirodela) polyrrhiza*] is introduced into a beaker of continually renewed culture solution under controlled light and temperature, the fronds multiply by the production of daughters which in turn produce further daughters; each daughter separates from the parent. Three overlapping phases can be detected in the growth process. Phase I is a period of exponential growth expressed as fronds per frond per day [this is formally equivalent to the concepts of (*a*) *the intrinsic rate of natural increase,* which is a demographic measure of the capacity of a population to increase in numbers in an environment unstressed by crowding, and (*b*) *the relative growth rate,* used by physiologists to measure the rate of growth of an individual plant (247)]. As the fronds come to cover the beaker surface some overlapping occurs and phase I gives ways to phase II, in which the growth of the population is governed by the resource supplying the environment's power. The population growth rate is then best expressed as fronds (or *g*) per beaker per day. As growth continues the frond mat thickens and the lowermost fronds fail to receive adequate light to support growth; they become pale and die. The population now enters phase III when the number of fronds per beaker becomes stable and the birth rate of new fronds equals the death rate. Such growth curves roughly approximate the model proposed by Verhulst, with the exception of the rather long continued linear phase II. This experiment demonstrates the relevance of two major components of population behavior: *r,* the intrinsic rate of natural increase, and *K,* the environmental saturate, ceiling, or carrying capacity, which expresses the inability of the environment to support an indefinite population growth.

The growth of a population of *Lemna* fronds models the growth of a single plant that happens to fall to pieces when it is growing. The fronds are formally equivalent to the units that compose a single rooted higher plant such as a tree. The growth of *Lemna* also models a continuously growing population of organisms [cf the classic experiments of Gause (95) with paramecium]. Much of theoretical demography has been built on models of continuous growth (176, 323). Growth in the number of parts of an individual genet (η) is almost certainly best treated as a truly continuous growth process, as in the formal methods for plant growth analysis (247).

In contrast the numbers of genets do not increase in a continuous manner, but by episodes of seed production set within life cycles. This means that they may be more effectively modelled by difference equations than by continuous growth processes [e.g. (269b), for discussion see (185)].

PHENOMENOLOGY

The life cycles of flowering plants form a continuum broken for convenience into the categories of annual, biennial, and perennial. Annuals range from, e.g., *Arabidopsis thaliana* and desert annuals requiring 4–6 weeks from seed germination to first seed set, to forms where the growth cycle requires 4–6 months for completion. In turn the cycles range from winter annuals that germinate in the fall, over-winter as rosettes and set seed early in the following year, to biennials that may take a large part of the post-germination year to reach seed set (e.g. *Digitalis, Verbascum, Dipsacus*). Annuals are typically monocarpic; they die in the year in which they set seed (329), though in some cases [e.g. *Senecio vulgaris* (120)] it seems to be the onset of winter or drought that kills rather than any intrinsic reaction to having flowered.

Digitalis purpurea, a classic biennial, may flower and die in the year following germination or may persist as a small vegetative rosette under crowded or infertile conditions. It is usually monocarpic, but occasionally basal buds persist and grow after flowering to give an effective perennial habit (Oxley, in preparation). Among perennials, a useful distinction is that between those with and those without an accumulating (ageing) vegetative body. In general, the competitive advantage of height can only be gained at the expense of accumulating a perennial ageing structure and dead tissue. Perenniality by the annual renewal of parts avoids problems of senescence, giving in theory an infinite length of life but denying the attainment of dominance in a high canopy or in a deep root zone.

Life cycles may be described in a more robust manner by reference to the features that affect the potential rate of population growth (53, 94, 286). Reproductive age and reproductive frequency have profound effects on the development of populations, and the consequences of various types of fecundity schedules occupy a central role in contemporary ecological theory (53, 171, 178).

A life cycle may be described in the crude form of Figure 1. Formal analysis of variations in the structure of such a model (171) shows that *r,* the intrinsic rate of natural increase, is maximized not just by maximizing the total number of progeny produced, but by shortening *a* and advancing the precocity of *b.* Any life cycle that fails to maximize *r* must presumably reflect some sacrifice to another component of fitness. It is convenient to discuss reproductive systems in this context.

THE JUVENILE PERIOD

ANNUALS AND BIENNIALS The ideal speedy life cycle might involve a seed that germinates to expose a green flower that immediately proceeds to leave several seeds that germinate without delay. The flower would need to photosynthesize sufficiently to stock the new seeds with reserves and to support a root for the necessary mineral uptake. This ideal does not exist and what we see in the array of higher plant forms

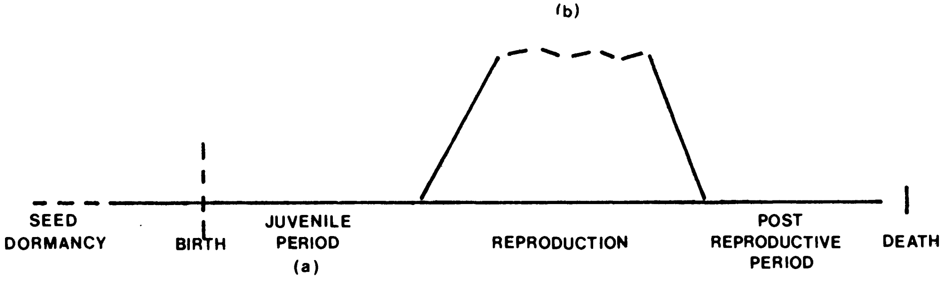

Figure 1 Generalized scheme for the development of a plant population, showing important demographic events. Germination of seeds is here equated with birth.

is a variety of compromises in which precocity of reproduction is sacrificed to the growth of a vegetative structure. The shortest time from seed to germination to first seed produced is found in annuals of deserts (333), dunes (215) and cultivated habits.

A number of annuals start flowering and set their first seed when very young and small; flowers are borne in the axils of early leaves. [Given the correct day, length, and temperature treatments, germinating seeds of the annual *Chenopodium rubrum* were induced to flower when the cotyledons had expanded and only two rudimentary leaves had formed (62).] New flowers continue to be formed as the plant grows and seed set (and dispersal) continues at an increasing rate through the growing season. Some species (e.g. many *Veronica* species; *Poa annua, Senecio vulgaris*) are well fitted to an unpredictable environment in which, if the season turns out to be short, some seed will have been produced; however, if the season turns out to be long it can be fully exploited. Such annuals have indeterminate growth systems and are not normally clocked into flowering by periodic stimuli; they are commonly weeds in the uncertain or complex rotations of horticulture. There is often no post-reproductive life and perhaps no intrinsic death process—life is cut short by the intervention of drought, the first killing frosts, or, as the environment deteriorates, the plant slowly rots away while still in the process of producing more flower buds (203).

In other annuals a relatively long period of vegetative growth precedes a rather sudden transition to the flowering and fruiting stage; this is optimal behavior in an environment of high predictability and characterizes the weeds of many arable crops in which the timing of seed release is just before harvesting, e.g. *Agrostemma githago, Avena fatua, Papaver rhoeas,* and *P. dubium.* The change from the vegetative to the reproductive phase in these species is often rigidly seasonal and timed by photoperiod (267, 276). The growth forms are commonly determinate and death follows seed set as if the act of seed production was itself lethal. Annuals with longer life cycles, e.g. winter annuals, also biennials, have a more or less long vegetative stage that changes under periodic stimuli to a flowering phase; vegetative apices are converted to a flowering condition and a "big bang" of reproduction is followed by death.

It is questionable whether the length of the juvenile period has any significant effect on the potential rate of population growth in annual species. If germination and the growth of the next generation followed immediately on seed set the length of the juvenile period would be of profound importance. In practice most annual species are rigidly seasonal in their germination. Even among annual weeds that may set seed and germinate at almost any season in the year (e.g. *Poa annua, Senecio vulgaris*) there is some uncertainty whether the populations are composed of a variety of ecotypes with different seasonal behavior or of a single type that can repeat several generations in a year. This problem warrants much further study.

In biennials at least one year of vegetative growth is made before seed is produced. Evidence from density experiments with *Digitalis purpurea* (Oxley, in preparation) show that, under stress, flowering may not occur for several years; it would appear that a minimal rosette size must be achieved before flowering. In deliberately sown populations of *Dipsacus fullonum* (Werner, personal communication) no rosettes flowered in the first year, a few flowered in the second year, and the majority in the third summer; by the fourth summer a few stragglers flowered and a few very large four year old rosettes remained which showed no signs of flowering at all. The life table data varied from field to field and there was no correlation between flowering and rosette size except that rosettes <15 cm diameter did not flower.

Theoretically, a strict biennial would be required to produce the square of the number of seeds of a comparable annual to achieve a comparable population growth rate, assuming no mortality. If the mortality risk is evenly distributed throughout life the same rule holds, but if there is a particularly high risk in the juvenile stages the annual experiences it twice in two years and the biennial only once. The biennial habit is therefore clearly favored when seedling establishment is risky, and the best return on seeds that germinate is obtained by living long and producing many seeds at the end of that life (116). If environmental hazards affect all stages of the life cycle equally, there would appear to be no special advantage in the biennial habit.

HERBACEOUS PERENNIALS The juvenile period in herbaceous perennials appears to be very variable: e.g. *Prunella vulgaris* (2 yr); *Potentilla erecta* and *Cirsium palustre* (4 yr); *Ranunculus auricomus, Chrysanthemum leucanthemum, Polygonum viviparum* (5 yr); *Ranunculus acer* (6 yr); *Trollius europaeus, Alchemilla vulgaris, Geum rivale* (8 yr). These values were obtained from field records in Finland (174), but it is probably very dangerous to generalize these values from habitat to habitat for the same species. Very early juvenile phases of perennial grasses may live many months or even years (244) without appreciable increase in size. This is called "resistance to inanition" (44, 45, 54). The same is true of dicotyledonous seedlings of woodland that may survive several months of darkness and then resume vigorous growth when suitable light conditions return (135).

The juvenile period of geophytes varies from one to at least seven years (even under ideal horticultural conditions), depending on the minimal size necessary for flowering and on the rate at which this minimal size is achieved (86). The juvenile period may last only 1 yr in *Freesia, Dahlia, Tritonia, Brodiaea,* and potato, 1–2 yr in *Gladiolus* and *Allium,* 2–3 yr in *Lilium,* 3–4 yr in *Crocus* and *Iris,* 3–5 yr in hyacinth, 4–6 yr in daffodils, 4–7 yr in tulips. In many species the growth of clones may start before flowering, but this does not seem to be correlated with the length of the juvenile period. In tulips the long juvenile period is accounted for by (*a*) large minimal bulb size for flowering, (*b*) a comparatively small annual increase in bulb weight (100–200%), (*c*) a season of bulb growth of only about 6 weeks, and (*d*) a low proportion (60%) of total plant weight in photosynthetic tissue (86). In general, species with tubers or corms reproduce more precociously than those with bulbs and storage rhizomes. The life cycles and demography of natural populations of bulbous species might be a particularly rewarding study.

Information on the length of the juvenile period and the longevity of a variety of plant species is brought together in Figure 2. Clearly herbaceous perennials show very wide variation, but the data for perennial herbs are even less reliable than the comparable data for trees and shrubs. Several of the observations quoted are essentially anecdotal and lack the precision in recording which is given for *Ananas, Anthoxanthum, Carica,* and *Guadua.* Many of the records are from quite specific

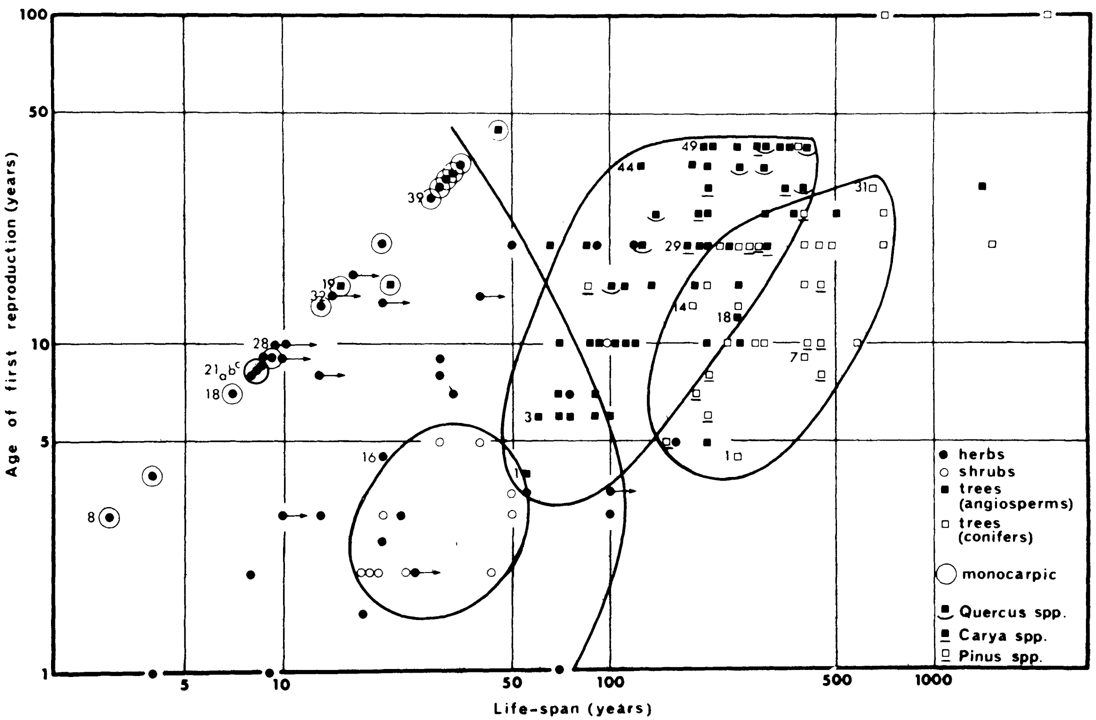

Figure 2 The relationship between prereproductive life (or juvenile period) and total life span for perennial plants. The data give the known normal life spans and not exceptional examples of great longevity. Each of four groups—perennial herbs, shrubs, coniferous trees, angiospermous trees—is separately numbered, counting cumulatively from left to right and from bottom to top of the graph; a few numbers are inserted as a guide. The names of the species are given in the Appendix, with sources indicated. The heavy lines roughly delineate each group of species.

environmental conditions in localized sites. In some cases the life span is for genets, but in most there is no distinction made between genets and ramets. In clone forming species genet life span is potentially very long (see later under longevity).

As a group, orchids are notable for their very gradual vegetative development from seed, as they require a mycorhizal association for several months or years before autotrophic tissues are formed (some species remain permanently heterotrophic or saprophytic). *Orchis ustulata* has remarkably delayed development of leaves, none being formed until it has developed a rhizome 10–15 yr old. Consequently, many orchids do not flower for many years after germination, e.g. *Listera ovata, Spiranthes spiralis,* and *Cypripedium calceolus* which require 13–16 yr growth before flowering (300). *Listera ovata* has a life span of at least 40 years (307).

WOODY PERENNIALS The length of the juvenile period for a number of woody species is given in Figure 2. These represent the period of juvenile, vegetative growth for "normal" trees, probably biased towards minimal age estimates, although a number are minimal ages for commercial seed production. There is a very general relationship between life span and the age of first reproduction, but the variation is large. Shrubs have a reasonably defined and circumscribed variation, and trees fall into two fairly distinct groups, angiosperms and conifers, the latter having earlier reproductive ages for a given length of life. Several conifers that may survive over 200 yr reproduce before age 10. Most angiosperms with a life span of over 200 yr spend at least 20 yr in the juvenile phase. The length of the juvenile phase and the longevity of the species are much more closely related in angiosperms than in conifers (the ratio is ~ 10:1 between these parameters) (note particularly the data for *Quercus* and *Carya* which illustrate this generalization). Very few hardwood trees live more than 400 yr and there are no records of trees in normal circumstances taking much more than forty years to reach reproductive age. These observations add greater precision to the general conclusions of Molisch (193): (*a*) plants with brief youth (period from germination to first seed production) have short longevity; (*b*) plants with a long youthful period generally enjoy great longevity; (*c*) a long youthful period is usually followed by a long and often very extended bearing time.

Of 57 species, hybrids, and varieties of *Pinus* observed in California (253) 55 produced ovulate cones at an average minimum age of 5.2 yr and 39 produced staminate cones at an average minimum age of 4.4 yr. Many of these data were from single individuals of a species and under the conditions of a forest genetics institute, not a commercial forest. This clearly shows that the common belief that timber tree species require 20 or more years to reach reproductive maturity does not apply to this genus. A rare example of a population study on the distribution of juvenile periods was made on *Pinus sylvestris* in Pennsylvania (97): of 1050 trees grown, 2 carried ovulate cones at age 3, 3 at age 4, 41 at age 5, 46 at age 6, 377 at age 7, and 790 at age 8. Only 199 had staminate cones by age 8, so that apparently the juvenile period for cones is shorter than for pollen. Very few data exist for tropical species (61, 197); the first recorded flowering of 50 dipterocarpous species in Malaya ranged from 17 to 36 yr and for most between 20 and 30 yr.

During the juvenile stages of development a tree commonly experiences ecological conditions markedly different from those in the mature phase. Perhaps associated with this is a frequently different morphology during the juvenile period (2, 274). Some parts of the subpopulation of a single tree may retain the juvenile characteristics while others develop into an adult and reproductive condition ["Topophysis" (193)], e.g. the adult and juvenile stages of the shrub *Hedera helix* (72). The juvenile period in *Hedera* lasts at least 10 yr (90) and (like plagiotropic shoots of *Araucaria*) the adult characters are retained permanently after vegetative propagation. The physiologic changes that occur before an adult condition is reached in woody plants are still not understood, and phrases like "maturation" or "phase change" (158) are only blankets for ignorance. The essential demographic feature of the juvenile phase is the absence of sexual reproduction. A certain minimum size may be necessary before flowering can begin (158). The first trees to flower at a given age are usually among the largest and most vigorous (275). In general, those environmental conditions (weather, soil, cultural practices) that promote vegetative growth tend to shorten the juvenile phase (130, 318). The length of the juvenile phase in apple and pear seedlings is negatively correlated with trunk diameter, and apparently genetic control of the growth rate determines when the minimum size for reproduction is reached. The length of the juvenile period is also correlated with parental characters such as the season of flowering and fruit ripening and the time from flowering to fruit maturity (319–322).

The genetic control of the length of the juvenile period has been clearly established. The period between planting and flowering in the oil palm (*Elaeis guineensis*) has been reduced by breeding from 45 to about 30 months (25). Three generations of selection for early flowering in *Betula verrucosa* reduced the juvenile period to two years (293) and precocious flowering in this species is apparently determined by a single gene (141). Precocity has obvious economic value in fruit tree culture and also in practical forestry because it increases the number of generations available for selection (263, 343).

The juvenile period can sometimes be modified by special physiologic treatment. For example, that of *Betula verrucosa* was reduced from 5–10 yr to little over a year in some plants by growing seedlings continuously under 18 hr photoperiods at 60–70°F (175); also in a remarkable experiment Pharis & Morf (218) reduced the juvenile period of *Sequoia* and *Sequoiodendron* seedlings from 20–70 yr to 8 and 12 months with gibberellin sprays. The very precocious *Cupressus arizonica* with a juvenile period of 18 months could be made more precocious (3 months) by gibberellin sprays (219). Surprisingly, juvenile periods cannot be reduced by grafting young tissue on to older stocks (72, 258).

In comparisons between species vegetative vigor is associated with late flowering. Within the species the more vegetatively vigorous individuals flower first. A generalization that describes much of the variation between species in the length of a juvenile phase is that shade intolerant, colonizing (*r*-type) species tend to have precocious reproduction associated with large seed numbers, small seeds, and high reproductive efficiency. In contrast, species that occupy later positions in forest succession and are shade tolerant have fewer and larger seeds and a long juvenile period. All available assimilates in early life are channelled into establishing canopy height and achieving competitive dominance. The fact that the length of the juvenile period is heritable presumably implies that the length to which the species has become adjusted in nature represents an adaptive response.

THE PHASE OF SEED PRODUCTION

In this section the reproductive behavior of perennial plants is discussed in relation to age-specific fecundity and to frequency. A later section will deal with comparisons of the numbers of seeds produced by different species.

It requires remarkable tenacity of purpose to collect data about the fecundity schedules of plants. The most accurate record of seed production with age may be for *Poa pratensis* (81). This is a rhizomatous species and genets were not distinguished. The records are per unit area and per panicle over a period of seven years. Seeds sown in 1961 produced plants that bore seeds two years later and subsequently underwent a "characteristic age-associated decrease" in reproductive output. Although the application of nitrogenous fertilizer increased the weight of seeds per unit area it did not arrest the drop in seed yield between 1964 and later years. This form of fecundity schedule has been observed in a number of grass species (e.g. 36). For example, the yield of seed per acre of *Bromus marginatus* declined from 1100 pounds per acre 2 yr after sowing to 414, 337, and 283 pounds in the succeeding years (292).

The most detailed studies of reproductive frequency in herbaceous perennials of grassland and woodland come from Russian authors and from the detailed studies of Tamm (305–308). *Heracleum sibiricum* has a life span of 13–15 yr, during which most individuals bloom and fruit three or four times, although a few are mono- or dicarpic. The juvenile period varies from 3–10 yr (238). The variations in flowering frequency within populations of *Anemone fasciculata* (237), *Ranunculus acer,* and *R. auricomus* (239) have also been recorded. In Tamm's (306) earlier studies of perennial dicotyledonous species the behavior of mapped individuals was followed over 15 yr, giving some indication of "on" and "off" years with respect to flowering in species like *Sanicula europaea* and *Centaurea jacea,* and also a large unpredictable element in the flowering pattern that may reflect phases of vigorous growth and later suppression by neighbors in the constantly changing pattern of the community studied.

Many species of bamboo appear to have a characteristic flowering cycle of about 1, 3, 11, 15, 30, 48, 60, or even 120 yr, when all plants from a given seedling (genet) flower simultaneously (186). However, since accurate records are rare "there is no positive basis for the generally held assumption that bamboos have in their character a flowering cycle of precise and invariable length" (186). Three groups can be recognized, (*a*) relatively small species that fruit and flower repeatedly at short intervals without genet death, (*b*) plants dying inevitably after the first and only fruiting, and (*c*) plants dying in part after flowering and renewing the dead parts.

After the juvenile period the seed output of trees tends to increase with age to an optimal age for seed bearing (315). Most trees produce their best seed crop in middle age, which may last from several decades to a century or more; seed production tends to decline as the physiologic and pathologic symptoms of over-maturity appear. The yield of acorns of several species of *Quercus* increases with age, being greatest in the 40–100 yr age classes, but declines subsequently as portions of the crown die (103). The age-specific fecundity curve of trees is only known accurately for a few species that are of commercial importance for their fruit, but even here there appear to be no examples of output throughout the entire life span. Much valuable demographic data undoubtedly lie entombed in the records of experimental stations, such as a very accurate record for the coconut (*Cocos nucifera*) (Nelliat, personal communication). Five trees planted in 1917 fruited in 1928 and were observed annually until 1968. The total accumulated seed output of these five trees was 2244, 3087, 3153, 3399, and 3708 nuts. These are probably the best recorded fecundity schedules for any plant, but they stop well short of a real decline period. Similar long term data exist for cocoa (317).

The age-specific fecundity curve has been recorded for citrus species (*C. paradisi, C. reticulata, C. sinensis*), though the information is given in "boxes per tree." Trees began to bear fruit at 3 yr of age, reaching a plateau at ∾20 yr, and maintaining or slowly decreasing the output over the next 30 or so years (271). The Mango (*Mangifera indica*) bears 15–20 fruits at 5 yr of age, 400–600 in an "on year" after 10 yr, about 1000 between 10 and 15 yr, 2500 by 20 yr, and thereafter up to 5000 a year, declining after 40 yr (285). These various commercial records are unsatisfactory in many ways, but support the generalization that following a juvenile phase the fecundity schedule of trees consists of a period of increasing production, a plateau of yield, and a subsequent steady decline in reproductive activity.

The size and age of trees are usually related, but the seed yield of individual trees is more closely linked with size than with age (158, 183, 213, 348). For example, the seed output of *Pinus taeda* correlates well with the diameter of the trees at breast height (326). A detailed study of *Pinus ponderosa* (164) showed clearly that tree diameter accounted for about 94% of the variation in annual cone production over a 10 yr period. Trees 36–40 in. diameter at breast height (dbh) averaged 446 cones per tree per crop; those 20–24 in. dbh averaged only 75. This is yet another point at which the plastic development of whole genets makes tidy demographic treatment difficult. Rabotnov's school partly solves this problem by concerning itself with the reproductive activities of size classes of individuals rather than with ages. It is, however, not a helpful solution for the population geneticist who may wish to know when individuals were recruited and how they contribute in the process of population growth and selection.

Although the nature of the root stock may not greatly affect the juvenile period, it can have profound effects on the fecundity schedule. Striking evidence comes from apple cultivars (227–229) grafted onto rootstocks with different dwarfing or vigor characteristics. Scions on vigorous rootstocks produced more fruits in the first 35 yr of life, but were distinctly less efficient in allocating energy to reproduction than dwarfing stocks. 27 yr-old trees of Lane's Prince Albert on dwarfing stocks had yielded nearly 14 times their own weight in fruit, but only 5–7 times on vigorous stocks. This suggests that vegetative vigor and high reproductive activity are not compatible (179).

The three main phases that compose the fecundity schedule of trees conceal major fluctuations and periodicities. The causes of the well-known "mast year" phenomenon are both proximal and ultimate. Ultimately, environmental conditions favor the development of large seed crops. Proximally, successful reproduction in one year is usually made at the expense of vegetative growth, and such success can only be repeated after a period of recovery. During the recovery period, reproductive output often falls to zero. Such periodic flushes of reproduction are obviously unsatisfactory in an economic crop such as fruit trees (68) and may be prevented by deliberately reducing the crop in "on" years.

Long records of the periodicity in seed production have been made for species of *Pinus, Pseudotsuga, Abies, Picea,* and *Fagus* (24, 29, 75, 89, 107, 346). Much effort and argument has been put into determining the precise environmental conditions that lead to periodicity (67, 158, 163, 168, 189, 251). Whatever the cause, it appears that the frequency of fruiting depends on the vigor of the tree (164, 189).

Studies of the periodicity of reproduction in fruit trees are particularly revealing because they indicate the extent to which trees are behaving as subpopulations of unit shoots. Young trees of *Mangifera indica* produce a regular crop of fruits each year, but after ∼10 yr cropping becomes periodic and sometimes biennial. A heavy fruit crop entails a lower production of vegetative shoots in the same year. Accordingly, the branches have few shoots on which fruit might develop the following year since inflorescences are generally borne on new shoots. Regularly bearing cultivars produce only ∼30 mature fruits annually, whereas biennially bearing cultivars produce 500–1000 (285). [Of some interest is the relation between the numbers produced by the annual and biennial bearer respectively, which is in the ratio x to x^2, the theoretical significance of which has been discussed by Cole (53) and Oxley (in preparation) for strictly annual and biennial herbs.] Such cultivars seem to be extreme examples of the principle of allocation of energy resources (120), involving the devotion in alternate years of growth materials either to seed production or to vegetative development, but little or none to both simultaneously. An extreme example of internal competition between the reproductive and vegetative parts of a tree has been reported for *Betula alleghaniensis* and *B. papyrifera.* These species developed extremely large seed crops in Ontario in 1967 resulting in dwarfed or missing foliage in the heavily seeded portions of the crop, a failure of buds to develop on terminal parts of branches, and a reduction of terminal and diameter growth. The following year there was extensive dieback (105). Problems of biennial bearing have been intensively investigated for many woody perennials of commercial importance: apple, pear, orange, plum, mango, coffee, prune (15, 58, 59, 68, 167, 194, 195, 230, 235, 236).

Other evidence that a period of great reproductive activity reduces vegetative growth (implying an internal competition for resources) comes from the inverse relationship between mast years and annual wood increment (123). The first clear-cut analysis of the correlation was that of Holmsgard (132), who showed that the annual ring width of *Fagus sylvatica* in good mast years (every six or seven years) may be only half the average ring width in unaffected years, and the reduced increment continues for an additional two years while carbohydrate reserves are replenished.

Flowering periodicity may be pronounced in tropical trees where annual fluctuations of climate are less marked than in temperate regions. Four types of nonannual periodicity can be recognized (3): (*a*) ever-flowering species producing flowers continuously during the year, (*b*) nonseasonal flowering species showing variation in flowering performance both between plants and from branch to branch, (*c*) gregariously flowering species flowering indefinitely but more or less simultaneously in all plants of a species in a given area (especially notable in bamboos), and (*d*) seasonal flowering species. Most tropical trees seem to flower at more or less regular intervals, but the pattern varies widely in different species and is commonly not annual. In a 4 acre area of forest in Malaysia some species did not flower at all over a period of 5 yr, some flowered regularly, other seasonally, and others with no apparent relationship to season (187). A study in the Panama canal zone (289) suggests that small-seeded fruits ripen rather evenly throughout the year, whereas species bearing large seeds tended to be seasonal. An analysis of 45 years of flowering records for dipterocarps shows that they tend to flower gregariously every two to five years, with up to half the individuals of a species in a stand flowering in any given year (32).

Longevity

Almost all the information about the longevity of plants is for long-lived woody perennials (especially trees) with particular concern for notably long-lived rather than normal individuals. Among angiosperms a specimen of *Adansonia digitalis* has been ascribed an age of 5150 years and *Ficus religiosa* more than 2000 years (193), but these estimates were based on comparisons of diameter growth. With these exceptions, records of trees older than 1000 years are conifers. A well-authenticated record, and the only one for a living tree, is of *Pinus aristata,* restricted to isolated stands in the southwestern United States. Several trees have been found well over 3000 years old, and one individual is ~4900 years old (63, 84). A putative age of 4000 years for *Quercus gambellii* X *turbinella* (57) was for clonal material.

The data used to construct Figure 2 mainly give the "normal" life span (at least for the tree species) rather than exceptional or record ages, e.g. although there are many records of very old *Quercus robur* individuals, even up to 1200 yr old, 400 yr might be considered a normally attainable age (193). This age is accordingly placed on the graph. The concept of "normally attainable age" is very vague. Death in plant populations occurs at all stages in life and the expectation of life for most species is very short compared to the age of the oldest individuals that are found. "Normal attainable age" is probably best regarded as that at which those few survivors that gain dominance in their habitat tend to die. The oldest individuals, because they may be very large, have an importance in plant demography which is quite different from that of old individuals in animal populations.

Length of life depends much on environmental circumstances, but there may be ecotypic variations as well. For example, the life cycle of *Trifolium pratensis* **has** been observed over many years on subalpine meadows and on flood plain meadows of USSR (242). In the former, plants may live for 20 years, beginning to flower at 5–10 years old and continuing to do so for several years. On the flood plain meadows, plants usually flower once and die within two years of germination. The data of Figure 2 are presented cautiously as a preliminary and gross level of generalization.

Techniques for determining the age of long-lived herbs are often indirect, either by extrapolation from current annual increments to the current clonal size (the data for *Nuphar lutea, Juncus squarrosus, Silene acaulis, Teucrium scorodonia*) or by morphological examination of the rhizomes. This latter method has been used extensively by Russian workers, (e.g. 121, 237, 240, 241). *Cirsium acaulon* may be aged accurately up to at least 15–20 years old by the scar left annually on the rhizome when the rosette of leaves decays; thereafter the age of clonal patches is estimated by extrapolation (221). Critical estimation of age may be made by recording the survival of marked plants in permanent quadrats; such data are very rare (e.g. 306–308) but show that herbaceous perennials have very long persistence under natural conditions and that successful seedling establishment is an infrequent or rare event. The longevity of some commercially important herbs is quite accurately known, e.g. *Carica papaya* and *Ananas comosus.* For several herbaceous species in Figure 2 life spans are given with a pointer indicating that they extend beyond the estimate the author has been able to make with confidence. Most of the species shown in this way are orchids. There is little or no ambiguity about the longevity of monocarpic species ranging from short-lived perennials, e.g. *Tragopogon orientalis* (243), to bamboo species (186). Of the herbs noted in Figure 2, *Nardus stricta* has been studied in a manner which best reveals the significant stages in the life history of a genet. The juvenile period of 6–8 yr is followed by the reproductive period of 24–30 yr and a period of senility of 5–7 yr. The plant reaches its maximum complexity and greatest number of tillers after 11–15 yr (216).

There is no obvious reason why herbaceous perennials with no ageing body should ever die. Two sets of evidence suggest that extremely old clones may occur in species like *Festuca ovina, Trifolium repens,* and *Holcus mollis* (109–112), in the fern *Pteridium aquilinum,* and in *Lycopodium* species. Estimates from the rate of clonal spread have dated *Festuca rubra* clones at at least 400 years old, possibly much older. Three hundred clones of *Pteridium aquilinum* were dated by using historical records of disturbance by fire, which seems to be necessary for the establishment of this species from spores; 167 clones were more than 220 yr old and some reached an age of 800 (204–206). Using the same techniques for 2 species that require fire for regeneration from seed, clones of *Convallaria majalis* and *Calamagrostis epigeios* were found commonly to reach 200 and some clones 400 yr old (207). Similar investigations have been made on *Carpogymnia dryopteris* and *Maianthemum bifolium* (208). Estimates have been made for the age of *Osmunda* species of more than 140 yr (157) and for *Dryopteris villarii* up to 30–40 yr (98).

Data for shrubs are less abundant than for herbs, and there is apparently less variation in longevity. Shrubs frequently live 30–50 yr (27). In addition to data shown in Figure 2, there are a few records of the longevity of shoots rather than entire plants, e.g. *Empetrum hermaphroditum* (50 yr) and other ericaceous shrubs

(10–20 yr) (27). The ageing of tundra shrubs may be confounded by false annual rings, but they and desert shrubs may attain the greatest ages amongst shrub species. *Epacris petrophila* in the alpine fjaeldmark has been recorded as being up to 100 yr old (18), and in a population of *Salix arctica* in Northeast Greenland (249) of 68 individuals, 58 were less than 60 yr old and the remainder older. Ages of 175, 210, 236 were recorded for some specimens, but these were quite rare (250).

Estimates are available for desert shrubs (283): *Larrea tridentata* may live 100 yr, *Fouquieria splendens* 60 yr, and small shrubs such as *Calliandra eriophylla, Coldenia canescens,* and *Encelia farinosa* may live for 20 yr. *Carnegiea gigantea* has a life span well over 100, perhaps as great as 175 yr and *Ferocactus wislizeni* appears to live about 130 yr.

Shoots of *Symphoricarpos occidentalis* live from 3 to 13 yr, but the rhizomes attain a much greater age (5–40 yr) (214). Genet age may be even greater. A similar situation occurs in *Vaccinium myrtillus* (85), where the maximum age attained by rhizomes was ~25 yr, and 10–15 yr by the aerial shoots. It is difficult to detect any decline or senescence in shrubs that form clones.

The most thorough documentation of longevity has been for trees, where the special interests of foresters and the ease of counting well-defined growth rings have resulted in a great number of age studies. Fowells' *Silvics of Forest Trees of the United States* (88) is a rich source of demographic information on more than 120 temperate tree species, a result of over 50 years of observations by a large number of foresters. Trees in the tropics do not produce annual growth rings and ages have only been speculated (61). The data of Figure 2 suggest that very great longevity of trees is primarily a property of conifers; there are few records of hardwood species living beyond 400 yr of age and several live less than 100 yr. However, if clonal reproduction occurs great ages may be achieved, e.g. *Populus tremuloides* var. *aurea* may be 8000 yr old (56). Dominant specimens of conifers (with the rare exception of *Pinus radiata, P. virginiana,* and *P. banksiana*) live normally for at least 200 yr and several live for over 400.

Conspicuous in Figure 2 are three monocarpic palm species; *Corypha elata* is the longest lived, and grows 40 yr before flowering (55). A specimen in Miami, Florida flowered 44 yr after seed germination, having attained a height of 24 m and a stem diameter of 82.5 cm (347). A peculiar example of reproductive exhaustion occurs in *Caryota urens,* which builds up a massive trunk 18–30 cm tall and begins to flower after about 15 yr (55, 232). The first inflorescence appears at the top, followed by others developed from axillary buds in succession from above downwards until the base of the trunk is reached and the tree dies, the whole flowering process lasting 5–7 years.

Reviews of plant longevity are given in Molisch (193) and Wangermann (327).

The Number of Seeds Produced per Plant

The immense plasticity of plants makes comparisons of seed productivity extremely difficult to interpret. An individual plant of *Papaver rhoeas* grown under stressed conditions may produce one capsule and ripen 4 seeds, but grown under high fertility may develop 400 capsules with 800–900 seeds per capsule (115). Moreover, the frequency distribution of seeds per plant in natural populations (like the frequency distribution of dry weight) is often log normal, so that the average number of seeds per plant does not represent the commonest number. Estimates are commonly based (e.g. 266) on performance in "normal" habitats, counting as many plants as are necessary to stabilize estimates of average seed output. This figure may or may not be corrected with respect to the average germination to give "the average reproductive capacity." This correcting procedure contains dangers: it estimates the number of seeds that germinate under the special conditions of a test, and we now know that different fractions of a seed population may have quite different requirements for germination (40). No seed can be safely written off as dead unless a very exhaustive range of tests has been made.

In a survey of a wide range of British species, Salisbury (266) showed that the highest seed outputs (usually more than 2×10^4 seeds per plant) were from species of intermittently available habitats (wood clearings, exposed mud, shingle banks). Values of $5–6 \times 10^3$ seeds per plant characterized permanently open, semiclosed, and closed but unshaded habitats (e.g. grasslands). Species from shaded habitats rarely produced more than $3–4 \times 10^2$ seeds per plant. In general, the species from open habitats tended to be annuals while perennials dominated the closed habitats. Very high seed outputs are characteristic of biennial species where two (or more) seasons' growth is ended by a "big bang" of seed production. The seed output of perennials is usually measured as that per flowering shoot (that is, a ramet), although a single clone (a genet) may have been represented by a population of such shoots. Moreover, in perennial species only a single year's seed output is recorded: if seed output per successful seed input had been measured and the reproductive capacity of a whole clone summed over its life, the differences in reproductive capacity might have disappeared altogether. Surveys in other areas have given similar results but suffer from the same general criticisms (102, 145, 245, 277, 297, 298).

The number of seeds produced by a plant (genet) is the product of (*a*) the number of shoots per genet, (*b*) the seasonal dry matter increment per shoot, (*c*) the proportion of the increment that is devoted to seed (reproductive efficiency), (*d*) the number of seeds per unit weight (118), (*e*) the number of seasons of life of the genet (longevity), and (*f*) the fecundity schedule. When considered in this way it appears that reproduction by seed of a genet, e.g. *Agropyron repens,* may be infinitely large. Although it produces very few seeds per shoot, the length of life of the genet is potentially infinite and individual clones are very extensive (e.g. 310).

Table 1 summarizes a mass of statistical information about woody perennials. The orders of magnitude are probably correct, but, as there is tremendous variation from year to year for many species, the estimates are rough and are based generally on good crop years and mature trees. A good crop year is defined as one with an abundance of seed on the majority of trees (11). However, reproductive capacities cannot be calculated from these data because the necessary information about longevity and fertility schedules are lacking. Certain striking points emerge: a tree of *Betula papyrifera* has a seed output of the same order per annum as has a biennial herb such as *Digitalis purpurea* in its one burst of monocarpic reproduction. *Picea*

Table 1 Number of seeds produced per mature tree in a good seed year $(\times 10^3)$

0.1–2	*Quercus alba* (33, 73), *Q. cinerea* (103), *Q. coccinea* (33), *Q. falcata* (103), *Q. marilandica* (103), *Q. petraea* (281), *Q. prinus* (103), *Q. rubra* (73), *Q. stellata* (103), *Q. velutina* (33)
2–4	*Lithocarpus densiflorus* (262), *Quercus nigra* (103)
4–15	*Abies concolor* (89), *Carya illinoensis* (88), *C. ovata* (315), *Pinus elliottii* var. *elliottii* (88), *P. monticola* (88), *P. ponderosa* (89, 164), *P. resinosa* (88)
15–50	*Chamaecyparis thyoides* (88), *Larix occidentalis* (88), *Liriodendron tulipifera* (39), *Pinus banksiana* (296), *P. lambertiana* (89), *P. taeda* (88, 223), *Pseudotsuga taxifolia* (131)
50–300	*Betula papyrifera* (345), *Larix laricina* (74), *Picea glauca* (311), *Thuja occidentalis* (88)
400	*Thuja plicata* (88)
4500	*Sequoia gigantea* (88)

glauca, Sequoia gigantea, and *Thuja* species also have extremely high annual seed output. In contrast, several *Quercus* species have a very low seed output, seldom exceeding 2000 acorns per tree per annum even in mast years (the seeds are, of course, consistently heavier than in conifers). In *Quercus,* as in many other forest tree species, high seed output depends on the trees having well developed crowns, fully exposed to sunlight; the output from a dense tree population comes mainly from those few individuals whose crown is well exposed in the canopy (107). In a seed trapping experiment made in Britain (281), and oak woodland of 120 yr-old trees at a density of 390 trees per hectare dropped only 41.3, 9.8, and 0.0 acorns per m^2 in three successive years—but of course had presumably been doing this for 100 or so years already and would continue to do so. Information about the seed production of forest trees unfortunately is usually reported on an area rather than on an individual plant basis (88), and the complicated nature of fecundity schedules obviously limits the use of statistics of this sort.

There seems to be no complete record of the total reproductive output during the lifetime of any long-lived perennial, although there are some extremely long runs of data for a few species of commercial importance: e.g. 32 yr for an apple orchard (280), 55 yr for citrus fruits (271), 18 yr for cocoa (317), and 25 yr (Manthriratua, personal communication) and 40 yr (Nelliat, personal communication) for coconuts. A more intensive examination of horticultural literature or of experimental station records would probably produce further examples.

Birth (Germination)

The formal equivalent of births in higher plants is germination. This is the time at which the embryo escapes from maternal investing tissues and acquires independence. Normally a period of rest intervenes between fertilization and germination, allowing precise seasonal adjustment of "birth." This has close analogies in animals (342), e.g. insect diapause (71). Some mangrove species lack any seasonal dormancy at the seed phase; embryo growth on the maternal plant continues unchecked during and after the dispersal process in sea or mud. This is, however, an unusual state of affairs, and it is questionable whether there are any naturally occurring species of terrestrial habitats in which a seasonal seed dormancy of some sort is completely absent. Seasonal dormancy is demographically unimportant except insofar as that any pause in the continuing cycle of development slows down the potential rate of increase of the population.

A special feature in the demography of higher plants is the longevity of seeds. Seeds of many species, deprived of appropriate conditions or stimuli for germination, may remain dormant for very long periods of time. Plant populations exist in two parts: one growing and producing more seeds, the other stored in a viable dormant state, insulated both from many of the forces of ecological succession and of natural selection.

Most observations on seed longevity have been made with artificially rather than naturally stored seeds (11, 19–21, 254). Under artificial storage conditions the rate of seed ageing is chiefly influenced by the relative humidity of the air and temperature; the life of the seed is halved (*a*) by each 1% increase in seed moisture between 5 and 14%, and (*b*) for each 5°C increase in seed temperature between 0 and 50°C (122).

Two long experimental studies have been made involving the deliberate burial of seed. In 1897, Beal buried seed of 23 different species in inverted bottles of sand at a depth of 45 cm in the field. Samples have been taken from these seeds at thirteen intervals, the most recent being 90 yr after the start of the experiment (64, 156). The species included two trees (*Quercus rubra* and *Thuja occidentalis*), a biennial (*Verbascum blattaria*), and two perennials (*Plantago lanceolata* and *Trifolium repens*); the remainder were all annuals. Seed of the trees and of five of the herbaceous species died in less than 5 yr (*Bromus secalinus, Erechtites hieracifolia, Chamaescye maculata, Agrostemma githago,* and *Trifolium repens*). Three species remained viable after 80 yr, and only *Verbascum blattaria* germinated after 90 yr. In a similar experiment, Duvel buried a group of crop and weed seeds; the longest lived seeds were of weeds native to the area (309).

Viable seeds of *Nelumbo nucifera* have been dated at 150–250 yr old (83). Naturally buried seed can sometimes be dated by radiocarbon techniques. Libby (172) reported an age of 1040 ± 210 for "ancient Manchurian lotus seeds, still fertile . . . genus Nelumbo, similar to the Indian *N. nucifera.*" Similar techniques have shown that seed of *Chenopodium album* and *Spergula arvensis* may remain viable in the soil for 1600 yr (201). The viable seed content of soil taken from under historically dated buildings, tombs, and even tomb contents generally confirms evidence from experiments that seed longevity is characteristic of annuals and particularly biennials. The optimum conditions for longevity appear to be slightly to moderately moist soil, deficient in oxygen (201).

Indirect evidence of seed longevity comes from studies of natural populations of seed in the soil (180). There are major discrepancies between the buried seed floras and the species growing in the above-ground vegetation because seed from early successional species may persist buried or dormant for decades after a different flora has developed above ground. Seeds of arable weeds can remain viable in undisturbed soil for 50–70 yr (255), although their longevity is considerably reduced by disturbance (257). Indeed, the "safest" place for some species to persist in nature may be below ground as dormant seeds.

Species may be classified according to seed longevity (82, 122). Generally, aquatic species, temperate tree species with nuts, and tropical tree species from primary forest have short-lived seeds. Even with artificial storage, the longevity of seeds of many tropical trees is measured in weeks or months rather than years, but the seeds of secondary species in tropical rain forest may persist in the soil for very long periods (on the order of a century) (252). Certainly, buried seed populations build up under tropical conditions (23, 106, 150, 302), but there is very little information about natural longevity. Seed of some tropical species in the Philippines may retain viability for periods of up to 6 yr (147). The tropical rain forest species *Pterocarpus officinalis* may retain nearly 98% viability for up to eight months when stored in the laboratory, but not under natural conditions in the forest (Moreno, in preparation).

Large seeds (e.g. nuts) tend to have short lives even on temperate trees, and some temperate trees without nuts have extremely short lives. Seed of *Salix* species have only a few days viability in nature, and among gymnosperms *Taxus* is reported to have a short seed life (122).

The class of long-lived seeds (more than 10 yr) contains grasses, sedges, rushes, and many herbaceous dicotyledons, mainly weedy species and ruderals, with very many Leguminosae. A few tree families are represented, mainly conifers, but the list is predominantly herbaceous (122). A special type of longevity is found where seed is retained in closed cones on the tree (serotiny) (52); viable seeds have been extracted from closed cones of *Pinus contorta* 75–80 years old (182).

Presumably the different seed longevities of various species represent adaptations. Certainly seed dormancy has been shown to be heritable (119) and selection can change the dormancy properties of a population (336). Information about the genetic control of longevity comes from studies of cultivars: different cultivars of six crop species showed significant differences in seed longevity under similar storage conditions (137), and the longevity of corn seed in storage has a marked heritable component with longevity tending to be dominant over short life (173). A very special case of differential longevity occurs in many species with seed polymorphism, e.g. *Dimorphotheca* in which the seed shed from a single flower head is of two types, one germinating readily in the first year and the other being delayed in germination until the next or subsequent years. Seed longevity may mean that the progeny of a single parent are represented in quite distinct generations of descendants. Buried long-lived seed populations are a memory, both of past genotypes and of past vegetation. The full impact of this phenomenon in the population genetics and demography of flowering plants has never been really examined, though it is commented upon by Antonovics (5).

In all cases, seed longevity implies that some of the potential rate of increase of population size has been sacrificed. This can be an advantage in a hazardous environment when synchronous germination puts the whole population at risk.

The dynamics of the seed population can in some sense be isolated from the rest of the life cycle. The plant is only the means by which a seed produces more seed; the seed bank has dynamic properties of its own. The parameters that affect the size of the seed bank may be modelled to calculate strategies for different theoretical environments (48–50). Given that S = number of seeds present, i.e. the size of the seed bank, Y = number of seeds produced per germinated seedling, G = the fraction of the seeds that germinate each year (the capital that is invested in germination), D = the fraction of the seed bank that decays each year (depreciation of uninvested capital), and P_i = the probabilities associated with Y_i, the relationship between the size of the seed bank in year t and its size in year $t + 1$ can be written

$$S_{t+1} = S_t - S_tG - D(S_t - S_tG) + GY_tS_t$$

Intuitively it appears that decreasing D and increasing Y increases the growth expectation of the seed bank. The model suggests in addition that if there is a high probability of successful reproduction ($P = 0.8$, $Y = 500$) the optimal strategy is for a high fraction of the seeds to germinate each year; the proportion decaying is almost irrelevant. However, if there is a high probability of low reproduction ($P = 0.8$, $Y = 5$) the rate of decay is irrelevant if most of the seeds germinate each year, but becomes very important if there is dormancy. In contrast, if there is a low probability of reproduction ($P = 0.1$, $Y = 500$ or 5) a high germination percentage is disastrous and so is a high decay rate. The models predict that there should be a strong correlation between the fraction of the seed that germinates and the fraction of the ungerminated seed that decays, and also a correlation between the fraction that does not germinate in a given year and the probability of the total or near failure of the germinating season to produce a new crop. Many of Cohen's predictions are confirmed in the reported literature but others remain to be tested. The greatest value of this elegant modelling procedure is that it brings a formal structure into thinking about the biology of seeds, a subject that had previously been studied anecdotally.

Different authors have discussed the ecologic repercussions of dormancy and germination strategies and described simple population flux models for buried seeds in the soil (60, 114, 254, 255, 272, 273). Roberts (255) collated data on the depletion of seed populations from the soil of arable land where further seed recruitment was prevented. Strikingly linear decays were obtained, the half-life increasing as soil disturbances were reduced. In regularly cultivated soil the whole seed population (20 species) had a half-life of ∼2 yr and in undisturbed soil of 6 yr. There was considerable variation between species, with *Chenopodium album* and *Thlaspi arvense* having particularly long half-lives: 53% and 48% of the seed was still viable after 6 yr in undisturbed soil (256). Seeds of grassland species may also show exponential decay patterns, with half-lives less than a year, except *Trifolium pratense* which had a half-life of three years (248).

Seeds of three *Ranunculus* species (*R. acris, R. bulbosus, R. repens*) were sown into grassland swards and their fate followed (269). There was heavy predation (20–50%) of the seed by rodents, the losses from predation being affected by the pattern of seed placement in the soil. Of the seeds that escaped predation those of

R. repens had considerable longevity so that the seed bank of this species in the soil was composed of a number of overlapping generations. In contrast, seeds of *R. bulbosus* and *R. acris* decayed or germinated rapidly so that there was scarcely any overlap of generations (268). These observations are the more interesting in view of an analysis of the population biology of these three species using a modified Leslie matrix model, showing that populations of *R. bulbosus* and *R. acris* are strongly dependent on seedling recruitment for maintaining population size, whereas *R. repens* has greater longevity of genets with clonal spread and is much less dependent on seed for maintaining the population (269).

Causes of death of buried seeds are obscure. Earthworms may digest some seeds, but allow others to pass through the digestive tract unharmed (190). The earthworm cast may be a most important means of returning buried seeds to the soil surface in a state suitable for germination.

THE SIZE AND AGE STRUCTURE OF PLANT POPULATIONS

The structure of a population of plants can be described in terms of the ages, sizes, and forms of the individuals that compose it. Commonly, there is a hierarchy of dominant, subordinate, and suppressed forms, not only represented by different species but also within the populations of each species. Even in a pure stand of a single species sown at the same time a hierarchy of size develops, particularly if there is density stress. A few individuals come to dominate the population and the size structure closely approaches a log normal distribution. Such hierarchies occur in annuals (159, 199, 202) and long-lived woody species (133, 154). The few dominant individuals contribute disproportionately to the total seed production so that the reproductive activity of the population is largely accounted for by the size frequency distribution of its members even in the absence of age effects. When different age classes contribute to the population the hierarchy is further complicated. Later arrivals tend to take a subordinate position until senescence or a catastrophe removes the larger, older members and creates space which the suppressed individuals can exploit. The age distribution of a population is therefore a poor predictor of its reproductive activity. In populations of *Digitalis purpurea* sown at low density almost all plants flower in their second year, but at high density only a few individuals flower and the remainder persist as rosettes. The reproductive behavior of the population is then a function of the density at which it was sown rather than the age of the individuals that compose it (Oxley, in preparation). This represents one critical area in which demographic procedures designed for animal populations are unsatisfactory for plants.

Rabotnov and co-workers escape from the dilemma by describing plant populations in terms of their "life states." They distinguish ten states: viable seeds in soil, seedlings, several intermediate phases, and senile plants. These states differ in their response to environmental factors and in their influence on soil microclimate. Three major groups of population are defined: (*a*) populations of invasive type that do not yet have all stages present, (*b*) populations of normal type that have all stages present, and (*c*) populations of regressive type that have lost the ability to reproduce by seed. Unlike age, the succession of life stages is reversible and senile perennial plants may revert to reproductive activity if environmental conditions change (244). Some populations disappear before ever reaching a reproductive stage. [In a census of populations of *Ranunculus acris* in permanent grassland one plot was found to have the species present at all times of the year but represented by four successive seedling invasions, each of which disappeared quickly without flowering. The four populations all overlapped in time so that an overall impression of constancy was obtained (268).]

Definitive descriptions of this form of population analysis are given by Uranov & Smirnova (314). They recognize "normal" populations in equilibrium with the environment (analogous to the stable age distributions of animal demography), and those that are relatively rapidly changing their spectrum of life stages (referred to as "successive"). The procedure allows a description of the "spectra of ontogenetic states" (313); they showed that in five grassland species (*Festuca pratensis, Phleum pratense, Dactylis glomerata, Bromus inermis, Medicago falcata*) these spectra are sensitive to small environmental changes. This type of population analysis has been applied to *Narthecium ossifragum* in Britain (299). The populations studied did not produce seed but persisted in a habitat no longer suitable for seedling development, yet the conditions were not severe enough to eradicate the population (described as "biological inertia," although in the Russian terminology it might be regarded as a population of regressive type with an age spectrum consisting only of mature or senile plants). The population structure of a wide range of species has been studied in this way by the Russian school; these species include *Galeobdolon luteum* (288), *Phleum pratense* (184), *Dactylis glomerata* (80), *Carex pilosa, Aegopodium podagraria, Scilla sibirica, Corydalis halleri, C. marschalliana, Asarum europaeum, Viola mirablis* (287), *Ranunculus acris, R. auricomus* (246, 270), *Artemisia tianschanica* (312), *Artemisia lercheana* (324), *Medicago falcata* (290). The data are very extensive and have no counterpart in western literature.

There is one important feature that distinguishes such age structures from those familiar to animal demographers, and that is that precise annual ages are seldom given since they are not usually determinable with accuracy for herbaceous plants. However, in a few instances rather precise estimates of chronological age may be made if the plant has some organ (usually a rhizome) that persists for many years without decaying and shows well-defined annual increments. The number of leaf scars on a rhizome may be a good indicator of length of life when the mean annual leaf production is known. Using such techniques of morphological examination, Rabotnov has been able to determine with some accuracy the age structure, using year classes, of a few populations of herbaceous perennials: *Anemone fasciculata, Polygonum carneum, Libanotis transcaucasia, Peucedanum pschavicum, Pedicularis condensata* (237, see 121).

Most studies of the structure of forest tree populations have also been concerned with size class contributions rather than those of age classes (e.g. 31, 166, 188a, 191, 192). There has been much interest in the ideal structure of a forest tree population that might be managed to provide sustained yield (9). This implies maintenance of a continued felling policy while maintaining an unchanging size (diameter) distribution, analogous to the sustained yield concept of fish population biologists.

Size or life stage distributions are obviously much easier to assemble than true age distributions, and indeed for those plants that leave no lasting record of age, e.g. in the form of growth rings, the only way to assemble an age distribution may be long term observation of marked individuals. Two special classes of age distribution have been defined (e.g. 160): the stationary age distribution and the stable age distribution. The former is a fixed age distribution in a population that has achieved constant size and in which birth and death rates are equal. The latter is the distribution of ages in a growing population with constant age-specific birth and death rates. Neither of these has been described for any plant population.

Within populations of annual species there may be an age structure determined by the scatter in time of germination. A few days precocity in germination time of individuals in a dense population can have major effects on vigor (and presumably chance of death and reproduction) (260). The earliest germinators are, however, often exposed to a different set of hazards from those that are recruited later. In some seasons the older part of the population may gain dominance because it has had a longer growth period, in others the age distribution is truncated because only the relatively young members escape some early catastrophe (frost, ploughing). Autumn germinating seedlings of *Papaver dubium* are usually killed by winter frost or other hazard, but if they survive, they may yield more than 90 times the number of seeds of a spring germinating seedling (8). The arable weed *Alopercurus myosuroides* has an autumn and a spring peak of germination. Autumn plants tiller vigorously and may produce 8000 seeds per successful seed sown after an overwintering juvenile period (196). Spring germinators tiller less, produce many fewer seeds, and are relatively unimportant weeds because of their lack of vigor; hence, whether ploughing is done in the autumn or spring determines the age structure of the population, its aggressiveness, and its capacity to leave seed to the next generation.

The age structure of perennial species tends to be divided sharply into two categories depending on the time of year at which observations are made. Populations of *Ranunculus acris* and *R. bulbosus* examined shortly after their seasons of germination are dominated numerically by seedlings that are lost rather quickly, profoundly changing the age structure (268). In contrast, some other perennial herbs of grassland communities very seldom produce germinated seedlings (234), although seeds are produced in abundance; germination appears to be inhibited beneath the closed sward and the young category is thus virtually absent from the age structure. It appears as though the populations of mature plants represent isolated historic episodes of seedling establishment from the past. The age structures of two perennial herbs [*Liatris aspera* (153) and *Alchemilla glomerulans* (170)] have been determined by morphological analysis of the perennating organs.

With woody plants in strongly seasonal climates there is much less difficulty in determining age structures of populations than with herbaceous plants; but there are very few records available, although annual rings of growth are usually easily counted. The age structure of a population of *Larrea tridentata,* a sclerophyllous shrub of the American deserts, was investigated by Chew & Chew (42), who estimated the ages of 463 plants in an area of 9 hectares. The frequency distribution of ages had a range of about 60 yr, but with a median age of 17 yr, so that the total distribution was strongly skewed towards the older ages.

Although the age structure of temperate tree populations can be readily determined there are surprisingly few records. A study (92) of a 12 hectare forest of virgin redwood (*Sequoia sempervirens*) revealed the following age structure based on 1263 individuals: 0–200 yr of age, 55%; 200–400 yr, 16%; 400–600 yr, 15%; 600–800 yr, 8%; 800–1000 yr, 5%; over 1000 yr, 1%. The oldest tree was 1380 yr old. This species does, however, regenerate from stumps, and the true age distribution of genets may be different. Unfortunately, the results are biased against the younger age group since no trees of less than 30 cm diameter were included, although there were apparently as many below this diameter as above it. These data have been used erroneously (28) to justify intensive lumbering (30).

Age frequency distributions have been recorded for *Picea rubens* in Maine (69) and for *Picea rubens, Abies fraseri,* and *A. balsamea* in the eastern United States (211). Trees of the overstorey varied in age by as much as 200 yr (211). The oldest tree of *Picea rubens* was 359 yr and several trees were 200–250 yr old. The oldest accurate age of *Abies fraseri* was 168 yr and for *Abies balsamea* 148 yr, so the life expectancy of both firs appears to be much less than that of spruce (211). Early stages in the development of forests of *Picea rubens* appear to be even aged and uniform. Secondary age classes begin to infiltrate as the death of upper storey trees by blow-down or other causes opens the canopy. In one area, the phase of even-aged trees lasted for ∼55 yr and the establishment of new age classes usually began before the stands were 100 yr old. "Virgin stands" represent a third stage in which the average age is ∼163 yr; there is a greater density of seedlings and a broad spectrum of age classes (1–250 yr) in these (69). Such all-aged and apparently self-perpetuating stands seem to satisfy some of the principal criteria for the definition of a climax in the sense of Clements (47), but by no means do all "virgin" forests show an uneven age distribution. Forest stands may contain quite discrete age classes or indeed even-aged trees since the life of a stand is commonly ended abruptly by catastrophes such as hurricane or fire followed by a new cycle of development from seedlings or hitherto suppressed saplings (127). 80–90% of the "virgin" conifer forests in Minnesota can apparently be traced to a post-fire origin, the oldest known stand dating back to 1595 A.D. (126). Most stands have a nearly even-aged overstorey dating closely from the last fire, with some stands containing groves or scattered trees of two or more age classes, each dating from separate fires. Only if sites regenerate slowly do they contain a mixture of tree ages (126).

An analysis of the age frequency distribution of 854 individuals of *Prunus serotina* showed that over the period 1876 to 1960 there have been four distinct periods of establishment (10). One plant dated from 1876. From 1876 to 1909 there was low and sporadic establishment, and from 1916 to 1930 a constant high level of establishment. In 1931 to 1941 numbers increased strikingly, suggesting widespread forest disturbance that may have favored this shade-tolerant species; 58% of the whole population dated from this decade. Since 1942, establishment has been sporadic: 77% of all the stems originated in the period 1916 to 1941, a period of agricultural expansion in the area. A similar picture of a population age structure determined by periods of successful establishment interspersed with unsuccessful periods was found in a study of *Salix arctica* in a small area of Greenland (249), and in *Populus* (1). Here, as in the case noted by Summerfield (299) for *Narthecium ossifragum*, the age spectrum of a population of long-lived perennials may point to extrinsic environmental controls or changes that might be otherwise undetected. This would seem to lend a heuristic value to the determination of the age composition of perennials in attempts to monitor environmental changes, though this has seldom been explicitly the object of such investigations, with the exception of the study by Uranov et al (313).

We know next to nothing about the age structure of virgin tropical forest, but demographic studies have largely destroyed the classical vision of mature temperate forest as a stable multiple-aged population. Instead, these forests usually represent stages working out the consequences of specific past episodes. Formal application of life table analysis of trees has been attempted (129) for *Abies balsamea, Pinus strobus,* and *Acer rubrum* in a predominantly pine forest that was thought to have originated from a burn about 200 yr previously. Life tables were prepared for two year-age classes but only for plants less than 25 yr old. Assuming (and the assumption may be a big one) that recruitment each year was essentially the same, life tables could be calculated. The frequency distribution of age classes was exponential, implying that the mortality risk to the individuals remained constant through time.

LIFE TABLES AND SURVIVORSHIP

The age structure of populations must be interpreted with care; a structure dominated by young individuals may represent an expanding population with a few old early colonizers and a large number of their descendants, or a stable population in which the survivorship curve is strongly concave. An excess of old individuals may mean that a population is moving to local extinction with no successful new recruits, or that the system is stable with a convex survivorship curve. Only formal actuarial analysis involving the calculation of life tables gives the full demographic story. Very few studies have been detailed enough for such tables to be calculated.

The most elegant life table analysis for annuals has been made for *Sedum smallii* and *Minuartia uniflora* (279) in natural habitats (granite outcrops, Georgia, US). This is the most complete actuarial analysis made of any plant population and is a model for future studies. Both species exhibited concave or positively skew rectangular survivorship curves (70) typical of species with extremely high mortality early in life. A few individuals that survived past seedling establishment had relatively high expectations of completing their life cycles. Mean life expectancy was low: plants of *S. smallii* survived an average of 4.4 months beyond the time at which the seed was formed; *M. unifora* had a shorter life expectancy of only 2.6 months. Formal life table analyses have also been made for natural populations of *Plantago major, Plantago media, Plantago lanceolata* (265), *Plantago major,* and *P. rugellii* (125), *Ranunculus bulbosus, R. acris,* and *R. repens* (269). The procedure is immensely laborious, involving mapping by pantograph technique at two to three week intervals through the year, matching successive maps to determine the identity of individuals, and punching computer cards recording the life and death, reproduction, etc of each individual. This is the only way in which definitive life tables can be assembled for herbaceous perennials. The time scale of the studies (2–3 yr), however, has been too short to eliminate the category of "individuals older than the period of observation." The much more extended but less frequent population census procedure adopted by Tamm (305–308) is liable to seriously underestimate juvenile categories because of the speed at which individual seedlings can appear and die.

The shape of the survivorship curve summarizes much of the information in a life table. Some of the data collected by Tamm for grassland and woodland perennials have been analyzed to determine the shapes of the survivorship curves (116). In this case, the fate of a whole starting population of a species was followed with time irrespective of its age structure (which was not known). A number of the species, for example *Sanicula europaea, Anemone hepatica,* and *Centaurea jacea,* were shown to have linear (Deevey Type II) survivorship curves (70), indicating a constant mortality risk within the population as a whole and implying that variation between years in environmental stresses was relatively unimportant. Analysis of similar mixed-age populations of *Ranunculus acris* and *R. auricomus* (239), *R. bulbosus, R. acris,* and *R. repens* (268, 269a) also revealed linear survivorship curves.

More generally useful are the survivorship curves for different cohorts of recruits to a population. Populations of the grass *Anthoxanthum odoratum* followed in this way for 6 yr (5) gave Type II survivorship curves for individual annual cohorts that were generally of parallel slope, though an occasional year's recruitment departed from the general survivorship pattern. When the survivorship curve is of the negative exponential (Type II) form, its character can conveniently be summarized as a statement of its "half-life" (116). For many grassland dicots half-lives are 0.5–2.0 yr; they appear to be longer for woodland species. Type II survivorship curves, although linear over years, commonly show seasonal periodicities in the rate of mortality. In *Ranunculus acris, R. repens,* and *R. bulbosus* the greatest mortality risk occurs when, or just before, the survivors are making maximal growth, rather than during the harshest period of the physical environment. In *Plantago major* and *P. rugellii* studied in Ontario, Canada (125) populations suffered very slight mortality in the extreme winter conditions, but death became frequent as soon as plants started into active growth. Such data strongly suggest that it is the growth of survivors that causes the elimination of the "weaker members," perhaps in a struggle for limited resources. It is particularly relevant that dense populations of annuals thinning according to the "3/2 power law" tended to have Type II survivorships (344). One conspicuous feature of the seasonal survivorship pattern in *Ranunculus* species is that the mortality risk is slight during flowering, though heavy before and after. Although flowering might be expected to weaken individuals and make them more likely to die, the temporary slowdown in vegetative growth at this time may perhaps reduce the population pressures and hence lower the rate of elimination.

Not all survivorship curves of herbaceous perennials are of the linear (Deevey Type II) form (269a). *Danthonia caespitosa,* an important grassland species in Australia, showed a Deevey Type III curve (the heaviest mortality occurring in the young stages) (338). In contrast a number of range species in southeast California are subjected to very slight mortality during early life, but it increases with age (e.g. *Trichachne californica*) (35). This is the Deevey Type I survivorship curve characteristic of human populations, Dall mountain sheep, some bird populations, and rotifers. Other species showing Type I survivorship curves are three orchids (*Dactylorchis incarnata, D. sambucina, Orchis macula*) (307); another orchid, *Listera ovata,* had a Type II curve. Amongst various populations of *Primula veris* only one showed a Type II curve and others departed quite strongly from this (308).

Departures from a Type II survivorship curve imply that part of the force of selection is concentrated at specific life cycle stages. Presumably if a specific stage in a life cycle is subjected to excessive selectional mortality it implies differential levels of adaptation at different parts of the life cycle. If there is any sense at all in the common phrase "in equilibrium with the environment" it might be that all phases of the life cycle are equally adapted and equally at risk; Type I and Type III survivorship curves imply that the selectional forces are operating on the potentially weakest links in the cycle.

Some departures from a negative exponential survivorship may, however, be explained in other ways. The rangeland grasses (35, 338) reproduce clonally, and clumps (genets or groups of genets) rather than ramets were counted as individuals. Large gaps occurred during the study period, and in an actively changing environment they may have adversely affected keeping trace of individual plants. Unless observations are made at relatively high frequency, seedling populations may be missed. A seedling may emerge and die only hours later, leaving no trace of its existence, particularly when the death is by predation or fungal decay. Population census tends, therefore, to underestimate recruitment and seedling mortality, and hence bias survivorship curves towards Type I. When attention is concentrated on the seedling phase, it becomes apparent that this is a high risk period after which populations may enter a Phase II type survivorship curve. In natural populations of *Digitalis purpurea* a steep (Deevey Type II) survivorship curve persists for the first 4–6 months of life and then changes to a new constant but lesser mortality risk for the remainder of the life cycle (Oxley, in preparation). In *Ranunculus* species a concave survivorship curve lasts for 20–30 weeks before the population acquires a linear survivorship curve and constant half life (268, 269a). The risky seedling phase is too long to be accounted for simply by the time required for metabolic adjustment from dependence on seed reserves to dependence on the separate activities of photosynthesis etc. It may be that the high risk period represents the genetic load of illadapted genotypes that are rather quickly eliminated. If this is the case, this specific risk period should be absent from apomicts, but there is no information about the survivorship curve of such species.

Ranunculus repens is the only member of the genus with clonal spread that has been studied demographically. Individual genets may spread very extensively, and the leafy rosettes of this species are ramets, whereas the similar rosettes of *R. bulbosus* are almost inevitably genets. The survivorship curve of ramets of *R. repens* has a negative exponential form from the time of their initiation as axillary buds. This illustrates the point that reproduction at the subpopulation level is commonly safer, though slower, than reproduction by seed. Calculation of the expectation of life at birth for *R. repens* ranges from 0.2–0.6 months for plants established from seed to 1.2–2.1 months for ramets. Similarly the probability of a seedling of *R. repens* surviving the spring following its birth is 0.12, whereas for a ramet the value is 0.77 (for *R. acris* the values are closely similar, 0.12 and 0.71, and for *R. bulbosus* the seedling probability is 0.42 and ramets are not produced) (269b).

Undoubtedly there are times, habitats, and species in which sudden catastrophic death profoundly affects the survivorship curve; for example, fires and hurricanes are obviously lethal calamities that may end the life of whole populations. Local trampling activities of cattle produce catastrophic destruction of seedling populations in wet pastures (268). The local extinction of populations of *Juncus acutus* as an apparent result of the most extreme frost for 70 yr in southwest Britain also represents such a catastrophe. Some plants may avoid potential extinction by flexibility in their life cycle as a response to fluctuating or unpredictable environments. Many plants exist primarily as seed populations (79, 180), or may escape by dormancy of the vegetative axes. Several species of *Delphinium* may cease vegetative growth and enter a dormant phase (for up to a decade) under unfavorable conditions, and then resume growth. Strikingly, the dormant phase may begin at any stage in the life cycle (78). However, on the whole, the presence of a species that is persistent in an area implies that it is (or has become) tolerant of the major recurrent hazards that characterize that environment; those hazards therefore are not expected to play any significant part in determining population size. The one hazard that cannot be adapted to is the over-production of descendants, and it is perhaps not surprising that the major cause of death in plant populations is the presence of too many neighbors needing the same resources at the same time.

SUMMARY

Most of this review has been concerned with the elements of birth and death in the fundamental equation of population growth. Immigration and emigration have scarcely been studied as part of any demographic analysis. Both seed dispersal and clonal spread have received detailed study but largely at the anecdotal level, dominated in the case of seed dispersal by the collection of data on maximal distances. In practice most seeds fall more or less close to the parent and seed density declines steeply with distance (266); it is very much the minority that effect new colonizations. Only in the case of animal dispersal may large-scale transfer of seeds occur to any distance, e.g. *Nucifraga caryocatactes* which carries nuts from hazel thickets (*Corylus avellana*) and buries them in localized territories within spruce forests,

often travelling 6 km to do this (301). The relationship between the seed dispersal pattern and the search range of predators may also be responsible for determining the density and spacing of successful seedling establishment.

"Decay" of seed populations includes predation, and the role of predators in seed demography is largely obscure. Seed on the parent and after dispersal is at risk to birds, small mammals (22), and bruchids (138–140), and earthworms may also digest seed of some species (190). A recent model of seed demography has taken predation into account (337) and predicted that short dormancy species can tolerate greater seed predation. It may be that many features of plant demography warrant interpretation in terms of predator action. Darwin (66) commented on the greater risk from predation associated with small crops; some of the curious features of the timing of seed production and release may be related to the advantages of over-saturating the predator's needs by producing all the seed in a very short time.

Much clarity is brought into thinking about immigration and emigration by the theoretical models of Gadgil (93), building on considerations of Cohen (49, 50) and Levins (169). Gadgil envisages the density of a population as a function of (*a*) the number and area of sites suitable for colonization, (*b*) the spatial distribution of these sites, (*c*) the carrying capacity of the sites, (*d*) the time for which the sites remain habitable, and (*e*) the dispersal characteristics of the species.

There is an important sense in which seed longevity is an alternative to seed dispersal. In a changing environment, the future of a population may be better assured by lying in wait for a favorable stage in the succession to return than by dispersing to find suitable conditions elsewhere. This is the sort of demographic problem that can readily be examined by model building. The modelling of demographic processes provides insights into population behavior that are only slowly acquired by long term field observation; models are no substitute but they serve the invaluable function of pointing to the types of field observation that are most likely to be meaningful. Stimulating examples are (48–50, 53, 93, 94, 171, 269).

This review has not been concerned with the regulation of population size, though increasing attention is now being given to the identification of factors that may determine plant numbers. Most analyses of this process have been at the level of experimental study of single species in pure populations, though some field studies have involved deliberate perturbation of population size, showing that this approach can be rewarding (37, 87, 233).

It is hard to see how any serious attempt to bring plant ecology within the hard predictive sciences can avoid much greater attention to demographic analyses. Ultimately, such analyses focus attention on the need to discover the mechanisms that control, limit, or regulate population size. The history of the demographic study of animals suggests that this phase in plant ecology will prove immensely difficult and exciting.

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Appendix

Species shown in Figure 2. Numbers correspond to the arrangement indicated in the legend of the figure. References are given in parentheses.

HERBS

1. *Anthoxanthum odoratum* (5)
2. *Dactylis glomerata* (177)
3. *Cirsium acaulon* (221)
4. *Carica papaya* (226)
5. *Atropa belladonna* (34)
6. *Sibbaldia procumbens* (51)
7. *Draba azoides* (148)
8. *Tragopogon orientalis* (243)
9. *Linum perenne* (200)
10. *Gentiana pneumonanthe* (284)
11. *Alchemilla alpina* (151)
12. *Silene acaulis* (146)
13. *Ananas comosus* (232)
14. *Nuphar lutea* (128)
15. *Barbarea vulgaris* (243)
16. *Pulsatilla vulgaris* (332)
17. *Juncus squarrosus* (330)
18. *Ophrys apifera* (300)
19. *Nardus stricta* (216)
20. *Teucrium scorodonia* (136)

21a. *Agave cantala* (232)

21b. *Agave sisalana* (232)

21c. *Furcraea gigantea* (232)

22. *Orchis mascula* (300, 307)
23. *Dactylorchis sambucina* (307)
24. *Neottia nidus-avis* (300)
25. *Agave americana* (193)
26. *Anacamptis pyramidalis* (300)
27. *Liatris aspera* (153)
28. *Cephalanthera damasonium* (300)
29. *Orchis purpurea* (259)
30. *Agave letonae* (232)
31. *Spiranthes spiralis* (331)
32. *Orchis ustulata* (300)
33. *Listera ovata* (300, 307)
34. *Cypripedium calceolus* (300)
35. *Agave fourcroydes* (232)
36. *Anemone fasciculata* (121, 237)
37. *Primula veris* (308)
38. *Polygonum carneum* (121, 237)
39. *Thamnocalamus falconeri* (186)
40. *Guadua trinii* (186)
41. *Merostachys fistulosa* (186)
42. *Chusquea abietifolia* (186)
43. *Melocanna baccifera* (186)

SHRUBS

1. *Haplopappus tenuisectus* (134)
2. *Erica tetralix* (13)
3. *Erica cinerea* (12)
4. *Helianthemum canum* (104)
5. *Potentilla fruticosa* (77)
6. *Thymus drucei* (220)
7. *Dryas octopetala* (76)
8. *Coffea arabica* (23)
9. *Calluna vulgaris* (14, 101)
10. *Dryas drummondii* (165)
11. *Purshia spp.* (198)

TREES – ANGIOSPERMS

1. *Cocos nucifera – dwarf varieties* (43)
2. *Elaeis guineensis* (124)
3. *Robinia pseudoacacia* (88)
4. *Guilielma gasipaes* (232)
5. *Eugenia caryophyllus* (231)
6. *Cocos nucifera – tall varieties* (43)
7. *Mangifera indica* (285)
8. *Areca catechu* (55, 232)
9. *Cola nitida* (231)
10. *Corylus avellana* (193)
11. *Salix nigra* (162)
12. *Sambucus nigra* (193)
13. *Alnus rubra* (88)
14. *Betula verrucosa* (193)
15. *Gleditsia triacanthos* (88)
16. *Prunus serotina* (88)
17. *Ilex aquifolium* (217)
18. *Juglans nigra* (88)
19. *Metroxylon sago* (232)
20. *Caryota urens* (232)

Trees – Angiosperms *(Continued)*

21. *Quercus palustris* (88)
22. *Betula papyrifera* (88)
23. *Tilia americana* (88)
24. *Ulmus rubra* (88)
25. *Liriodendron tulipifera* (210)
26. *Populus grandidentata* (88)
27. *Juglans cinerea* (88)
28. *Quercus velutina* (88)
29. *Carya aquatica* (88)
30. *Ulmus americana* (88)
31. *Populus deltoides* (88)
32. *Ulmus thomasii* (88)
33. *Carya illinoensis* (88)
34. *Quercus falcata* (88)
35. *Acer campestre* (143)
36. *Carya tomentosa* (88)
37. *Shorea leprosula* (61, 197)
38. *Acer pseudoplatanus* (142)
39. *Arbutus unedo* (278)
40. *Carya cordiformis* (88)
41. *Carya glabra* (88)
42. *Quercus kelloggii* (188)
43. *Balanocarpus heimeii* (61, 197)
44. *Acer saccharinum* (88)
45. *Lithocarpus densiflorus* (88)
46. *Fraxinus excelsior* (328)
47. *Quercus macrocarpa* (88)
48. *Quercus bicolor* (88)
49. *Betula lenta* (88)
50. *Betula alleghaniensis* (88)
51. *Fagus sylvatica* (193)
52. *Carya laciniosa* (88)
53. *Quercus petraea* (144)
54. *Acer saccharum* (88)
55. *Fagus grandifolia* (88)
56. *Quercus robur* (193)
57. *Corypha elata* (347)

Trees – Conifers

1. *Chamaecyparis thyoides* (88)
2. *Pinus virginiana* (295)
3. *P. sylvestris* (38)
4. *P. banksiana* (296)
5. *P. rigida* (88)
6. *P. jeffreyi* (88)
7. *Thuja occidentalis* (88)
8. *Picea mariana* (88)
9. *Juniperus virginiana* (88)
10. *J. scopulorum* (88)
11. *Pinus monticola* (88)
12. *P. contorta* (88)
13. *Pseudotsuga menziesii* (131)
14. *Larix laricina* (88)
15. *Pinus taeda* (326)
16. *P. radiata* (88)
17. *Abies balsamea* (88)
18. *Picea rubens* (88)
19. *Pinus ponderosa* (88)
20. *Picea glauca* (88)
21. *Abies lasiocarpa* (88)
22. *Pinus resinosa* (88)
23. *P. palustris* (325)
24. *Chamaecyparis lawsoniana* (88)
25. *Tsuga mertensiana* (88)
26. *Picea engelmannii* (88)
27. *P. sitchensis* (88)
28. *Sequoia sempervirens* (261)
29. *Pinus edulis* (88)
30. *Larix occidentalis* (88)
31. *Abies procera* (88)
32. *A. concolor* (88)
33. *Larix lyallii* (7)
34. *Sequoia gigantea* (88)

Literature Cited (Literature search ended July, 1973)

1. Alder, G. M., Harper, K. T. 1969. Age profiles in aspen forests of Utah and northern Arizona, *Proc. Utah Acad. Sci.* 46:166
2. Allsop, A. 1965. Heteroblastic development in cormophytes. *Encycl. Plant. Physiol.* 15(1):1172–1221
3. Alvim, P. de T. 1964. Tree growth periodicity in tropical climates. In *The Formation of Wood in Forest Trees,* ed. M. H. Zimmermann, 479–96. New York: Academic
4. Ando, T., Sakaguchim, K., Narita, T., Satoo, S. 1962. Growth analysis on the natural stands of Japanese Red Pine (*Pinus densiflora* Sieb. et Zucc.) 1. *Bull. Gov. Forest. Exp. Sta. 144,* 30 pp.
5. Antonovics, J. 1972. Population dynamics of the grass *Anthoxanthum odoratum* on a zinc mine. *J. Ecol.* 60:351–65
6. Arber, A. 1950. *The Natural Philosophy of Plant Form.* London: Cambridge Univ. Press
7. Arno, S. F., Habeck, J. R. 1972. Ecology of Alpine Larch (*Larix lyallii* Parl.) in the Pacific Northwest. *Ecol. Monogr.* 42:417–50
8. Arthur, E. A. 1969. *Variation in natural populations of Papaver dubium.* PhD thesis. Univ. Birmingham, England
9. Assmann, E. 1970. *The Principles of Forest Yield Study.* Oxford: Pergamon. 506 pp.
10. Auclair, A. N., Cottam, G. 1971. Dynamics of black cherry (*Prunus serotina* Erhr.) in Southern Wisconsin oak forests. *Ecol. Monogr.* 41:153–77
11. Baldwin, H. I. 1942. *Forest Tree Seed of the North Temperate Regions.* Waltham, Mass: Chronica Botanica
12. Bannister, P. 1965. Biological Flora of the British Isles—*Erica cinerea* L. *J. Ecol.* 53:527–42
13. Bannister, P. 1966. Biological Flora of the British Isles—*Erica tetralix* L. *J. Ecol.* 54:795–813
14. Barclay-Estrup, P., Gimingham, C. H. 1969. The description and interpretation of cyclical processes in a heath community. 1. Vegetational change in relation to the *Calluna* cycle. *J. Ecol.* 57:737–58
15. Barlow, H. W. B. 1964. An interim report on a long term experiment to assess the effect of cropping on apple tree growth. *Rep. E. Malling Res. Sta. 1963,* 84–93
16. Barlow, H. W. B. 1966. The effect of cropping on the number and kinds of shoots on four apple varieties. *Rep. E. Malling Res. Sta. 1965,* 120–24
17. Barlow, H. W. B. 1970. Some aspects of morphogenesis in fruit trees. In *Physiology of Tree Crops,* ed. L. C. Luckwill, C. V. Cutting, 25–43. New York: Academic
18. Barrow, M. D., Costin, A. B., Lake, P. 1968. Cyclical changes in an Australian fjaeldmark community. *J. Ecol.* 56: 89–96
19. Barton, L. V. 1961. *Seed preservation and longevity.* London: Lonard Hill
20. Barton, L. V. 1965. Longevity in seeds and in the propagules of fungi. *Encycl. Plant Physiol.* 15(2):1058–85
21. Barton, L. V. 1967. *Bibliography of Seeds.* New York: Columbia Univ. Press
22. Beatley, J. 1969. Dependence of desert rodents on winter annuals and precipitation. *Ecology* 50:722–24
23. Bell, C. R. 1970. Seed distribution and germination experiment. In *A tropical rain forest. A study of irradiation and ecology at El Verde, Puerto Rico,* ed. H. T. Odum, R. F. Pigeon, D-177 to D-182. Oak Ridge, Tenn.: USAEC
24. Bingham, R. T., Rehfeldt, G. E. 1970. Cone and seed yields in young Western White Pines. *USDA Forest Service Res. Pap. INT-79,* 12 pp.
25. Blaak, G. 1972. Prediction of precocity in the oil palm (*Elaeis guineensis* (Jacq.) *Euphytica* 21:22–26
26. Bleasdale, J. K. A. 1967. The relationship between the weight of a plant part and the total weight as affected by plant density. *J. Hort. Sci.* 42:51–58
27. Bliss, L. C. 1971. Arctic and alpine plant life cycles. *Ann. Rev. Ecol. Syst.* 2:405–38
28. Bosch, C. A. 1971. Redwoods: a population model. *Science* 172:345–49
29. Brender, E. V., McNab, W. H. 1972. Loblolly pine seed production in the Lower Piedmont under various harvesting methods. *J. Forest.* 70:345–49
30. Brussard, P. F., Levin, S. A., Miller, C. N., Whittaker, R. H. 1971. Redwoods: A population model debunked. *Science* 174:435–36
31. Buell, J. H. 1945. The prediction of growth in uneven-aged timber stands on the basis of diameter distribution. *Duke Univ. Sch. Forest. Bull. 11,* 70 pp.
32. Burgess, P. F. 1972. Studies on the regeneration of the hill forests of the Malay Peninsula. *Malay. Forest.* 35: 103–23

33. Burns, P. Y., Christisen, D. M., Nichols, J. M. 1954. Acorn production in the Missouri Ozarks. *Mo. Agr. Exp. Sta. Bull. 611,* 8 pp.
34. Butcher, R. W. 1947. Biological Flora of the British Isles—*Atropa belladonna. J. Ecol.* 34:345-53
35. Canfield, R. H. 1957. Reproduction and life span of some perennial grasses of southern Arizona. *J. Range Manage.* 10:199-203
36. Canode, C. L., van Keuren, R. W. 1963. Seed production characteristics of selected grass species and varieties. *Wash. Agr. Exp. Sta. Bull. 647,* 15 pp.
37. Cantlon, J. E. 1969. The stability of natural populations and their sensitivity to technology. *Diversity and stability in ecological systems. Brookhaven Symp. Biol.* 22:197-203
38. Carlisle, A., Brown, A. H. F. 1968. Biological Flora of the British Isles—*Pinus sylvestris* L. *J. Ecol.* 56:269-307
39. Carvell, K. L., Korstian, C. F. 1955. Production and dissemination of yellow poplar seed. *J. Forest.* 53:169-70
40. Cavers, P. B., Harper, J. L. 1966. Germination polymorphism in *Rumex crispus* and *R. obtusifolius. J. Ecol.* 54:367-82
41. Chadwick, M. J., Obeid, M. 1966. A comparative study of the growth of *Eichhornia crassipes,* and *Pistia stratiotes* L. in water culture. *J. Ecol.* 54:553-75
42. Chew, R. M., Chew, A. E. 1965. The primary productivity of a desert shrub (*Larrea tridentata*). *Ecol. Monogr.* 35:355-75
43. Child, R. 1964. *Coconuts.* London: Longmans
44. Chippindale, H. G. 1932. The operation of inter-specific competition in causing delayed growth of grasses. *Ann. Appl. Biol.* 19:221-42
45. Chippindale, H. G. 1948. Resistance to inanition in grass seedlings. *Nature* 161:65
46. Clatworthy, J. N., Harper, J. L. 1961. The comparative biology of closely related species living in the same area. V. Inter- and intraspecific interference within cultures of *Lemna* spp. *Salvinia natans. J. Exp. Bot.* 13:307-24
47. Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. *Publ. Carnegie Inst. Wash.* 242:1-512
48. Cohen, D. 1966. Optimising reproduction in a randomly varying environment. *J. Theor. Biol.* 12:119-29
49. Cohen, D. 1967. Optimising reproduction in a randomly varying environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. *J. Theor. Biol.* 16:1-14
50. Cohen, D. 1968. A general model of optimal reproduction in a randomly varying environment. *J. Ecol.* 56: 219-28
51. Coker, P. D. 1966. Biological Flora of the British Isles—*Sibbaldia procumbens* L. *J. Ecol.* 54:823-31
52. Coker, W. C. 1900. Vitality of pine seeds and the delayed opening of cones. *Am. Natur.* 43:677-81
53. Cole, L. C. 1954. The population consequences of life history phenomena. *Quart. Rev. Biol.* 29:103-37
54. Cooper, J. P. 1948. Resistance to 'inanition' in grass seedlings. *Nature* 161: 894-95
55. Corner, E. J. H. 1966. *The Natural History of Palms.* London: Weidenfeld & Nicholson
56. Cottam, W. P. 1954. Prevernal leafing of aspen in Utah Mountains. *J. Arnold Arboretum Harvard Univ.* 35:239-50
57. Cottam, W. P., Tucker, J. M., Drobnick, R. 1959. Some clues to Great Basin postpluvial climates provided by oak distributions. *Ecology* 40:361-77
58. Couranjou, J. 1966. Divers types d'alternance observés chez *Prunus domestica. Ann. Amelior. Plant.* 16:233-58
59. Couranjou, J. 1970. Recherches sur les causes génétiques et les méchanisms de l'alternance du prunier domestique (*Prunus domestica* L.) *Ann. Amelior. Plant.* 20:297-318
60. Courtney, A. D. 1969. Seed dormancy and field emergence in *Polygonum aviculare. J. Appl. Ecol.* 5:675-84
61. Cousens, J. E. 1965. Some reflections on the nature of Malayan lowland rain forest. *Malay. Forest.* 28:122-28
62. Cumming, B. G. 1959. Extreme sensitivity of germination and photoperiodic reaction in the genus *Chenopodium* (Tourn.) L. *Nature* 184:1044-45
63. Currey, D. R. 1965. An ancient bristlecone pine stand in Eastern Nevada. *Ecology* 46:564-66
64. Darlington, H. T. 1951. The seventy-year period for Dr. Beal's seed viability experiment. *Am. J. Bot.* 38:379-81
65. Darwin, C. 1839. *Journal of Researches into the Natural History and Geology of the countries visited during the voyage of H.M.S. Beagle round the world under the command of Capt. FitzRoy, R. N.* London: Henry Colburn

66. Darwin, C. 1859. *The Origin of Species.* London: Murray. 1st ed.
67. Daubenmire, R. 1957. A seven-year study of cone production as related to xylem layers and temperature in *Pinus ponderosa. Am. Midl. Natur.* 64:187–93
68. Davis, L. D. 1957. Flowering and alternate bearing. *Proc. Am. Soc. Hort. Sci.* 70:545–56
69. Davis, R. B. 1966. Spruce-fir forests of the coast of Maine. *Ecol. Monogr.* 36:79–94
70. Deevey, E. S. 1947. Life tables for natural populations of animals. *Quart. Rev. Biol.* 22:283–314
71. De Wilde, J. 1969. Diapause and seasonal synchronisation in the adult Colorado beetle. (*Septinotarsa decemlineata* Say). *Dormancy and Survival. Symp. Soc. Exp. Biol.* 23:263–84
72. Doorenbos, J. 1965. Juvenile and adult phases in woody plants. *Encycl. Plant. Physiol.* 15(1):1222–35
73. Downs, A. A., McQuilkin, W. E. 1944. Seed production of Southern Appalachian Oaks. *J. Forest.* 42:913–20
74. Duncan, D. P. 1954. A study of some of the factors affecting the natural regeneration of tamarack (*Larix laricina*) in Minnesota. *Ecology* 35:498–521
75. Eis, S., Garman, E. H., Ebell, L. F. 1965. Relation between cone production and diameter increment of douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl.) Lindl.), and western white pine (*Pinus monticola* Dougl.). *Can. J. Bot.* 43:1553–59
76. Elkington, T. T. 1970. Biological flora of the British Isles—*Dryas octopetala* L. *J. Ecol.* 58:887–906
77. Elkington, T. T., Woodell, S. R. J. 1963. Biological Flora of the British Isles—*Potentilla fruticosa* L. *J. Ecol.* 51:769–81
78. Epling, C., Lewis, H. 1952. Increase in the adaptive range of the genus Delphinium. *Evolution* 6:253–67
79. Epling, C., Lewis, H., Ball, F. M. 1959. The breeding group and seed storage: a study in population dynamics. *Evolution* 14:238–55
80. Ergova, V. N. 1972. The life cycle of orchard grass (*Dactylis glomerata* L.) in the flood meadows of the River Oka. *Bull. Moscow Soc. Natur.* 77(4):118–29 [Russian]
81. Evans, D. W., Canode, C. L. 1971. Influence of nitrogen fertilization, gapping and burning on seed production of Newport Kentucky Bluegrass. *Agron. J.* 63:575–80
82. Ewart, E. J. 1908. Vitality of seeds. *Proc. Roy. Soc. Victoria* 2:1–203
83. Exell, A. W. 1931. The longevity of seeds. *Gardeners Chronicle* 89:283
84. Ferguson, C. W. 1968. Bristlecone Pine: science and esthetics. *Science* 159: 839–46
85. Flower-Ellis, J. G. K. 1971. Age structure and dynamics in stands of bilberry (*Vaccinium myrtillus* L.) *Avdel. f. Skogsekol., Rapp. Upps. 9,* 108 pp.
86. Fortanier, E. J. 1973. Reviewing the length of the generation period and its shortening particularly in tulips. *Scientia Hort.* 1:107–16
87. Foster, J. 1964. *Studies on the population dynamics of the daisy, Bellis perennis.* PhD thesis. Univ. Wales
88. Fowells, H. A. 1965. *Silvics of Forest Trees of the United States. U.S. Dept. Agr. Forest Service,* Agr. Handb. No. 271, 762 pp.
89. Fowells, H. A., Schubert, G. H. 1956. Seed crops of forest trees in the pine region of California. *USDA Tech. Bull. 1150,* 48 pp.
90. Frank, H., Renner, O. 1956. Über Verjüngung bei *Hedera helix. Planta* 47: 105–14
91. Fretwell, S. D. 1972. *Populations in a Seasonal Environment.* Princeton: Princeton Univ. Press
92. Fritz, E. 1929. Some popular fallacies concerning California redwood. *Madrone* 1:221–23
93. Gadgil, M. 1971. Dispersal: Population consequences and evolution. *Ecology* 52:253–61
94. Gadgil, M., Bossert, W. H. 1970. The life historical consequences of natural selection. *Am. Natur.* 104:1–24
95. Gause, G. F. 1934. *The Struggle for Existence.* Baltimore: Waverly
96. Gay, P. A. 1960. The water hyacinth and the Sudan. *Biology of Weeds. Symp. Brit. Ecol. Soc.* 1:184–88
97. Gerhold, H. D. 1966. Selection for precocious flowering in *Pinus sylvestris. U.S. Forest Serv. Res. Pap.* NC-6, 4–7
98. Gilbert, O. L. 1970. Biological Flora of the British Isles—*Dryopteris villarii* (Bellardi) Waynar. *J. Ecol.* 58:301–13
99. Gill, A. M. 1971. The formation, growth, and fate of buds of *Fraxinus americana* L. in central Massachusetts. *Harvard Forest Paper* No. 20, 16 pp.
100. Gill, A. M., Tomlinson, P. B. 1971. Studies on the growth of red mangrove (*Rhizophora mangle* L.) 3. Phenology of the shoot. *Biotropica* 3:109–24
101. Gimingham, C. H. 1960. Biological

Flora of the British Isles—*Calluna vulgaris* (L.) Hull. *J. Ecol.* 48:455–83

102. Golubev, V. N. 1970. The dynamics of seed productivity in some species of the upland meadow steppe of the Crimean yaila. *Bull. Moscow Soc. Natur.* 75(2): 98–107 [Russian]
103. Goodrum, P. D., Reid, V. H., Boyd, C. E. 1971. Acorn yields, characteristics, and management criteria of oaks for wildlife. *J. Wildl. Manage.* 35:520–32
104. Griffiths, M. E., Proctor, M. C. F. 1956. Biological Flora of the British Isles—*Helianthemum canum* (L.) Baumg. *J. Ecol.* 44:677–82
105. Gross, H. L. 1972. Crown deterioration and reduced growth associated with excessive seed production by birch. *Can. J. Bot.* 50:2431–3437
106. Guevera, S., Gomez-Pompa, A. 1972. Seeds from surface soils in a tropical region of Veracruz, Mexico. *J. Arnold Arboretum Harvard Univ.* 53:312–35
107. Gysel, L. W. 1971. A 10-year analysis of beechnut production and use in Michigan. *J. Wildl. Manage.* 35:516–19
108. Hallé, F., Oldeman, R. A. A. 1970. *Essai sur l'Architecture et la Dynamique de Croissance des Arbres Tropicaux.* Paris: Masson
109. Harberd, D. J. 1961. Observations on population structure and longevity of *Festuca rubra* L. *New Phytol.* 60: 184–206
110. Harberd, D. J. 1962. Some observations on natural clones in *Festuca ovina* L. *New Phytol.* 61:85–100
111. Harberd, D. J. 1963. Observations on natural clones of *Trifolium repens* L. *New Phytol.* 62:198–204
112. Harberd, D. J. 1967. Observations on natural clones in *Holcus mollis. New Phytol.* 66:401–8
113. Harper, J. L. 1957. The ecological significance of dormancy and its importance in weed control. *Proc. Int. Conf. Plant. Prot. Hamburg, 4th,* 415–20
114. Harper, J. L. 1960. Factors controlling plant numbers. In *The Biology of Weeds,* ed. J. L. Harper, 119–132. Oxford: Blackwells
115. Harper, J. L. 1966. The reproductive biology of the British poppies. In *Reproductive Biology and Taxonomy of Vascular Plants,* ed. J. G. Hawkes, 26–39. Oxford: Pergamon and Botanical Society of British Isles
116. Harper, J. L. 1967. A Darwinian approach to plant ecology. *J. Ecol.* 55:247–70
117. Harper, J. L., Gajic, D. 1961. Experimental studies of the mortality and plasticity of a weed. *Weed Res.* 1:91–104
118. Harper, J. L., Lovell, P. H., Moore, K. G. 1970. The shapes and sizes of seeds. *Ann. Rev. Ecol. Syst.* 1:327–56
119. Harper, J. L., McNaughton, I. H. 1960. The inheritance of dormancy in inter- and intra-specific hybrids of *Papaver. Heredity* 15:315–20
120. Harper, J. L., Ogden, J. 1970. The reproductive strategy of higher plants. I. The concept of strategy with special reference to *Senecio vulgaris* L. *J. Ecol.* 58:681–98
121. Harper, J. L., White, J. 1971. The dynamics of plant populations. *Proc. Advan. Stud. Inst. Dyn. Numbers Pop., Oosterbeek, 1970,* 41–63
122. Harrington, J. F. 1972. Seed storage and longevity. In *Seed Biology,* ed. T. T. Kozlowski, 3:145–245. New York: Academic
123. Hartig, R. 1889. Ueber den Einfluss der Samenproduktion auf Zuwachsgrösse und Reservestoffvorrathe der Bäume. *Allg. Forst. Jagdzt.* 65:13–17
124. Hartley, C. W. S. 1967. *The Oil Palm.* London: Longmans
125. Hawthorn, W. R. 1973. *Population dynamics of two weedy perennials, Plantago major L. and P. rugelii Decue.* PhD thesis. Univ. W. Ontario, London
126. Heinselman, M. L. 1971. The natural role of fire in northern conifer forest. In *Fire in the Northern Environment—A symposium, USDA Forest Service, Pacific Northwest Forest Range. Exp. Sta.,* 61–72
127. Henry, J. D., Swan, J. M. A. 1974. Reconstructing forest history from live and dead plant material—an approach to the study of forest succession in southwestern New Hampshire. *Ecology.* In press
128. Heslop-Harrison, Y. 1955. Biological Flora of the British Isles—*Nuphar lutea* (L.) Sm. *J. Ecol.* 43:344–55
129. Hett, J. M., Loucks, O. L. 1968. Application of life-tables analyses to tree seedlings in Quetico Provincial Park, Ontario. *Forest Chron.* 44:29–32
130. Higazy, M. K. M. T. 1962. Shortening the juveniles phase for flowering. *Meded. Landbouwhogesch. Wageningen.* 62(8):1–53
131. Hoffman, J. V. 1924. The natural regeneration of Douglas Fir in the Pacific Northwest. *US Dept. Agr., Dept. Bull. 1200*
132. Homlsgaard, E. 1955. Tree-ring analyses of Danish forest trees. *Forstl. For-*

soksv. Dan. 183:1–246 [Danish, English Summ.]

133. Hozumi, K., Shinozaki, K., Tadaki, Y. 1968. Studies on the frequency distribution of the weight of individual trees in a forest stand. I. A new approach towards the analysis of the distribution function and the -3/2th power distribution. *Jap. J. Ecol.* 18:10–20
134. Humphrey, R. R. 1937. Ecology of the burroweed. *Ecology* 18:1–9
135. Hutchinson, T. C. 1967. Comparative studies of the ability of species to withstand prolonged periods of darkness. *J. Ecol.* 55:291–99
136. Hutchinson, T. C. 1968. Biological Flora of the British Isles—*Teucrium scorodonia* L. *J. Ecol.* 56:901–11
137. James, E., Bass, L. N., Clark, D. C. 1967. Varietal differences in longevity of vegetable seeds and their response to various storage conditions. *Proc. Am. Soc. Hort. Sci.* 91:521–28
138. Janzen, D. H. 1969. Seed-eaters versus seed size, number, toxicity and dispersal. *Evolution* 23:1–27
139. Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *Am. Natur.* 104:501–28
140. Janzen, D. H. 1971. Seed predation by animals. *Ann. Rev. Ecol. Syst.* 2:465–92
141. Johnsson, H. 1940. Hereditary precocious flowering in *Betula verrucosa* and *Betula pubescens. Hereditas* 35:112–14
142. Jones, E. W. 1944. Biological Flora of the British Isles—*Acer pseudoplatanus* L. *J. Ecol.* 32:220–37
143. Jones, E. W. 1944. Biological Flora of the British Isles—*Acer campestre* L. *J. Ecol.* 32:239–52
144. Jones, E. W. 1959. Biological Flora of the British Isles—*Quercus* L. *J. Ecol.* 47:169–222
145. Jones, R. M. 1968. Seed production of species in the high veld secondary succession. *J. Ecol.* 56:661–66
146. Jones, V., Richards, P. W. 1962. Biological Flora of the British Isles—*Silene acaulis. J. Ecol.* 50:475–87
147. Juliano, J. B. 1940. Viability of some Philippine weed seeds. *Phillipine Agr.* 24:313–26
148. Kay, Q. O. N., Harrison, J. 1970. Biological Flora of the British Isles—*Draba azoides* L. *J. Ecol.* 58:877–88
149. Kays, S., Harper, J. L. 1974. The regulation of plant and tiller density in a grass sward. *J. Ecol.* 62:97–105
150. Keay, R. W. J. 1960. Seeds in forest soil. *Nigerian Forest. Inform. Bull.* NS. 4
151. Kershaw, K. A. 1960. Cyclic and pattern phenomena as exhibited by *Alchemilla alpina. J. Ecol.* 48:443–53
152. Kershaw, K. A. 1964. *Quantitative and Dynamic Ecology.* London: Arnold
153. Kerster, H. W. 1968. Population age structure in the prairie forb, *Liatris aspera. BioScience* 18:430–32
154. Kitamoto, T., Shidei, T. 1972. Studies on the spatial pattern in forest trees. I. Distribution of dominant and suppressed trees in even-aged forest. *Bull. Kyoto Univ. Forests.* 43:152–61
155. Kittredge, J. 1944. Estimation of the amount of foliage of trees and shrubs. *J. Forest.* 42:905–12
156. Kivalaan, A., Bandurski, R. S. 1973. The ninety-year period for Dr. Beal's seed viability experiment. *Am. J. Bot.* 60:140–45
157. Knight, G. J. 1964. *Distribution of Osmunda cinnamomea L. and Osmunda claytoniana L. in relation to natural soil drainage.* M.F. thesis. Harvard Forest, Harvard University
158. Kozowski, T. T. 1971. *Growth and development of trees. Vol. I. Seed Germination, Ontogeny, and Shoot Growth; Vol. II. Cambial Growth, Root Growth & Reproductive Growth.* New York: Academic
159. Koyama, H., Kira, T. 1956. Intraspecific competition among higher plants. VIII. Frequency distribution of individual plant weight as affected by the interaction between plants. *J. Inst. Polytech. Osaka City Univ. Ser. D* 7:73–94
160. Krebs, C. J. 1972. *Ecology: The experimental analysis of distribution and abundance.* New York: Harper & Row
161. Kuroiwa, S. 1960. Intraspecific competition in artificial sunflower communities. *Bot. Mag. Tokyo* 73:300–9
162. Lamb, G. N. 1915. Willows: their growth, use and importance. *US Dept. Agr. Bull. 316,* 52 pp.
163. Lamb, R. C., Waters, M. P., Brender, E. V. 1973. Apparent influence of weather upon seed production of Loblolly pine. *USDA Forest Service Res. Note SE-183,* 7 pp.
164. Larson, M. M., Schubert, G. H. 1970. Cone crops of ponderosa pine in central Arizona, including the influence of Albert squirrels. *USDA Forest Service Res. Pap. RM-58,* 15 pp.
165. Lawrence, D. B., Schoenike, R. E., Quispel, A., Bond, G. 1967. The role of *Dryas drummondii* in vegetation development following ice recession at Glacier Bay, Alaska, with special reference

to its nitrogen fixation by root nodules. *J. Ecol.* 55:793–813

166. Leak, W. B. 1964. An expression of diameter distribution for unbalanced, uneven aged stands and forests. *Forest Sci.* 10:39–50
167. Lenz, F. 1967. Relationships between the vegetative and reproductive growth of Washington Navel orange cuttings (*Citrus sinensis* (L.) Osbeck) *J. Hort. Sci.* 42:31-39
168. Lester, D. T. 1967. Variation in cone production of red pine in relation to weather. *Can. J. Bot.* 45:1683–91
169. Levins, R. 1968. *Evolution in changing environments.* Princeton: Princeton Univ. Press
170. Lewis, M. C., Callaghan, T. V., Jones, G. 1972. Bipolar Botanical Project: *Arctic Research Program, phase II. IBP. Tundra Biome Report*
171. Lewontin, R. C. 1965. Selection for colonizing ability. In *The Genetics of Colonizing Species,* ed. H. G. Baker, G. L. Stebbins, 77–91. New York: Academic
172. Libby, W. F. 1951. Radiocarbon dates, II. *Science* 114:291–96
173. Lindstrom, E. W. 1942. Inheritance of seed longevity in maize inbred and hybrids. *Genetics* 27:154
174. Linkola, K. 1935. Über die Dauer und Jahresklassenverhältnisse des Jungenstadiums bei einigen Wiesenstauden. *Acta Forest. Fenn.* 42:1–56
175. Longman, K. A., Wareing, P. F. 1959. Early induction of flowering in birch seedlings. *Nature* 184:2037
176. Lotka, A. J. 1925. *Principles of Physical Biology.* Baltimore: Waverly
177. Luff, M. L. 1965. The morphology and microclimate of *Dactylis glomerata* tussocks. *J. Ecol.* 53:771–87
178. MacArthur, R. H., Wilson, E. O. 1967. *The Theory of Island Biogeography.* Princeton: Princeton Univ. Press
179. Maggs, D. H. 1963. The reduction in growth of apple trees brought about by fruiting. *J. Hort. Sci.* 38:119–29
180. Major, J., Pyott, W. T. 1966. Buried, viable seeds in two California bunchgrass sites and their bearing on the definition of a flora. *Vegetatio* 13:253–82
181. Malthus, T. R. 1798. *An Essay on the Principle of Population.* London
182. Mason, D. T. 1915. The management of lodgepole pine. *Forest. Quart.* 13: 171–82
183. Matthews, J. D. 1963. Factors affecting the production of seed by forest trees. *Forest. Abst.* 24:i–xiii
184. Matveev, A. R. 1972. The great life cycle of *Phleum pratense* L. *Bull. Moscow Soc. Natur.* 77(3):114–23 [Russian]
185. May, R. M. 1973. On relationships among various types of population models. *Am. Natur.* 107:46–57
186. McClure, F. A. 1967. *The Bamboos—a fresh perspective.* Cambridge, Mass.: Harvard Univ. Press
187. McClure, H. E. 1966. Flowering, fruiting and animals in the canopy of a tropical rain forest. *Malay. Forest.* 29:182–203
188. McDonald, P. M. 1969. Silvical characteristics of California black oak (*Quercus kelloggii* Newb.). *US Dept. Agr. Forest. Res. Pap. PSW-53*

188a. McGee, C. E., Della-Bianca, L. 1967. Diameter distributions in natural yellow-poplar stands. *US Forest Service Res. Pap. SE-25,* 7 pp.

189. McNeill, W. M. 1954. Observations of cone and seed production in plantations of Scots pine in Scotland. *Forestry* 27:122–33
190. McRill, M., Sagar, G. R. 1973. Earthworms and seeds. *Nature London* 243:482
191. Meyer, H. A. 1952. Structure, growth and drain in balanced uneven aged forests. *J. Forest.* 50:85–92
192. Meyer, J. A., Stevenson, D. D. 1949. The structure and growth of virgin beech-birch-maple-hemlock forests in northern Pennsylvania. *J. Agr. Res.* 67(12):465–84
193. Molisch, H. 1938. *The Longevity of Plants.* Transl. E. H. Fulling. New York: E. H. Fulling
194. Moss, G. I. 1971. Effect of fruit on flowering in relation to biennial bearing in sweet orange *(Citrus sinensis). J. Hort. Sci.* 46:177–84
195. Moss, G. I., Muirhead, W. A. 1971. Climatic and tree factors relating to the yield of orange trees. I. Investigations on the cultivars "Washington Navel" and "Late Valencia." *Hort. Res.* 11:3–17
196. Naylor, R. E. L. 1972. Aspects of the population dynamics of the weed *Alopecurus myosuroides* Huds. in winter cereal crops. *J. Appl. Ecol.* 9:127–39
197. Ng, F. S. P. 1966. Age at first flowering in Dipterocarps. *Malay. Forest.* 29: 290–95
198. Nord, E. C. 1965. Autecology of bitterbrush in California. *Ecol. Monogr.* 35:307–34
199. Obeid, M., Machin, D., Harper, J. L. 1967. Influence of density on plant to

plant variation in fibre flax, *Linum usitatissimum* L. *Crop Sci.* 7:471–73

200. Ockendon, D. J. 1968. Biological Flora of the British Isles—*Linum perenne* ssp. *anglicum* (Miller) Ockendon. *J. Ecol.* 56:871–82
201. Ødum, S. 1965. Germination of ancient seeds. Floristical observations and experiments with archaeologically dated soil samples. *Dan. Bot. Ark.* 24(2):1–70
202. Ogden, J. 1970. Plant population structure and productivity. *Proc. NZ Ecol. Soc.* 17:1–9
203. Ogden, J. 1974. The reproductive strategy of higher plants. II. *J. Ecol.* 62:291–324
204. Oinonen, E. 1967. Sporal regeneration of bracken (*Pteridium aquilinum* (L.) Kuhn) in Finland in the light of the dimensions and the age of its clones. *Acta Forest. Fenn.* 83(1), 96 pp.
205. Oinonen, E. 1967. The correlation between the size of Finnish bracken (*Pteridium aquilinum* (L.) Kuhn). clones and certain periods of site history. *Acta Forest. Fenn.* 83(2), 51 pp.
206. Oinonen, E. 1968. The size of *Lycopodium clavatum* L. and *L. annotinum* L. stands as compared to that of *L. complanatum* L. and *Pteridium aquilinum* (L.) Kuhn stands, the age of the tree stand and the dates of fire, on the site. *Acta Forest. Fenn.* 87, 53 pp. [Finish, English summ.]
207. Oinonen, E. 1969. The time table of vegetative spreading of the lily-of-the-valley (*Convallaria majalis* L.) and the wood small-reed (*Calamagrostis epigeios* (L.) Roth) in southern Finland. *Acta Forest. Fenn.* 97, 35 pp.
208. Oinonen, E. 1971. The time table of vegetative spread in oak fern (*Carpogymnia dryopteris* (L.) Love & Love) and May Lily (*Maianthemum bifolium* (L.) F. W. Schmidt) in southern Finland. *Acta Forest. Fenn.* 118, 37 pp.
209. Oldeman, R. A. A. 1972. *L'Architecture de la Forêt Guyanaise.* Thèse. Université des Sciences et Techniques du Languedoc
210. Olson, D. F. 1969. Silvical characteristics of yellow-poplar (*Liriodendron tulipifera* L.). *US Dept. Agric. Forest Service, Res. Paper SE-48*
211. Oosting, H. J., Billings, W. D. 1951. A comparison of virgin spruce-fir forest in the Northern and Southern Appalachian systems. *Ecology* 32:84–103
212. Pearl, R., Reed, L. J. 1920. On the rate of growth of the population of the United States since 1790 and its mathematical representation. *Proc. Nat. Acad. Sci.* 6:275–88
213. Pearson, G. A. 1912. The influence of age and condition of the tree upon seed production in Western Yellow Pine. *USDA Forest Service Circ.* 196, 11 pp.
214. Pelton, J. 1953. Studies on the life history of *Symphoricarpos occidentalis* Hook. in Minnesota. *Ecol. Monogr.* 23:17–39
215. Pemadasa, M. A. 1973. *Ecology of some sand dune species with special reference to annuals.* PhD thesis. Univ. Wales
216. Persikova, Z. I. 1959. The formation of turf beds and the life-cycle of *Nardus stricta. Bull. Moscow Soc. Natur.* 64:61–68 [Russian]
217. Peterken, G. F., Lloyd, P. S. 1967. Biological Flora of the British Isles—*Ilex aquifolium* L. *J. Ecol.* 55:841–58
218. Pharis, R. P., Morf, W. 1969. Precocious flowering of Coastal and Giant Redwood with gibberellins A_3, $A_{4/7}$ and A_{13}. *BioScience* 19:719–20
219. Pharis, R. P., Ruddot, M. D. E., Phillips, C. C., Heftman, E. 1965. Precocious flowering of Arizona Cypress with gibberellin. *Can. J. Bot.* 43:923–27
220. Pigott, C. D. 1955. Biological Flora of the British Isles—*Thymus* L. *J. Ecol.* 43:365–87
221. Pigott, C. D. 1968. Biological Flora of the British Isles—*Cirsium acaulon* (L.) Scop. *J. Ecol.* 56:597–612
222. Pijl, L. van der. 1972. *Principles of Dispersal in Higher Plants.* Berlin: Springer. 2nd ed.
223. Pomeroy, K. B. 1949. Loblolly pine seed trees: selection, fruitfulness and mortality. *USDA Forest Service Southeastern Forest. Exp. Sta. Pap. 5,* 17 pp.
224. Pontin, A. J. 1961. Population stabilization and competition between the ants *Lasius flavus* (F.) and *L. niger* (L.). *J. Anim. Ecol.* 30:47–54
225. Pontin, A. J. 1963. Further considerations of competition and the ecology of the ants *Lasius flavus* (F.) and *L. niger* (L.). *J. Anim. Ecol.* 32:565–74
226. Pope, W. T. 1930. Papaya culture in Hawaii. *US Dept. Agr. Hawaii Agr. Exp. Sta. Bull.* No. 61, 40 pp.
227. Preston, A. P. 1958. Apple rootstock studies: thirty-five years' results with Lane's Prince Albert on clonal rootstocks. *J. Hort. Sci.* 33:29–38
228. Preston, A. P. 1958. Apple rootstock studies: thirty-five years' results with Cox's Orange Pippin on clonal rootstocks. *J. Hort. Sci.* 33:194–201
229. Preston, A. P. 1959. Apple rootstock studies: thirty-five years' results with

Worcester Pearmain on clonal rootstocks. *J. Hort. Sci.* 34:32–38

230. Priestley, C. A. 1970. Some observations on the effect of cropping on the carbohydrate content in trunks of apple trees over a long period. *Rep. East Malling Res. Sta. 1969,* 121–23
231. Purseglove, J. W. 1968. *Tropical Crops: Dicotyledons.* London: Longmans
232. Purseglove, J. W. 1972. *Tropical Crops: Monocotyledons.* London: Longmans
233. Putwain, P. D., Harper, J. L. 1970. Studies in the dynamics of plant populations. III. The influence of associated species on populations of *Rumex acetosella* L. in grassland. *J. Ecol.* 58: 251–64
234. Putwain, P. D., Machin, D., Harper, J. L. 1968. Studies in the dynamics of plant populations. II. Components and regulation of a natural population of *Rumex acetosella* L. *J. Ecol.* 56: 421–31
235. Quinlan, J. D., Preston, A. P. 1968. Effects of thinning blossom and fruitlets on growth and cropping of Sunset apple. *J. Hort. Sci.* 43:373–81
236. Quinlan, J. D., Preston, A. P. 1971. The influence of shoot competition on fruit retention and cropping of apple trees. *J. Hort. Sci.* 46:525–34
237. Rabotnov, T. A. 1950. Life cycles of perennial herbage plants in meadow communities. *Proc. Komarov. Bot. Inst. Acad. Sci. USSR* Ser 3(6):7–240 [Russian]
238. Rabotnov, T. A. 1956. The life cycle of *Heracleum sibiricum* L. *Bull. Moscow Soc. Natur.* 61(2):73–81 [Russian]
239. Rabotnov, T. A. 1958. The life cycle of *Ranunculus acer* L. and *R. auricomus* L. *Bull. Moscow. Soc. Natur.* 63(6): 77–86 [Russian]
240. Rabotnov, T. A. 1960. Methods of determining the age and length of life of herbaceous plants. *Field Geobot.* 2: 249–62 [Russian]
241. Rabotnov, T. A. 1960. On the biology of *Libanotis intermedia* Rupr. *Trans. Moscow Soc. Natur.* 3:221–28 [Russian]
242. Rabotnov. T. A. 1960. Some problems in increasing the proportion of leguminous species in permanent meadows. *Proc. Int. Grassl. Congr., 8th,* 260–64
243. Rabotnov, T. A. 1964. On the biology of monocarpic perennial plants. *Bull. Moscow Soc. Natur.* 71:47–55 [Russian]
244. Rabotnov, T. A. 1969. On coenopopulations of perennial herbaceous plants in natural coenoses. *Vegetatio* 19:87–95
245. Rabotnov, T. A. 1969. Plant regeneration from seed in meadows of the USSR. *Herbage Abstr.* 39:269–77
246. Rabotnov, T. A., Saurina, N. I. 1971. The density and age composition of certain populations of *Ranunculus acris* L. and *R. auricomus* L. *Bot. Zh.* 56: 476–84 [Russian]
247. Radford, P. J. 1967. Growth analysis formulae—their use and abuse. *Crop Sci.* 7:171–75
248. Rampton, H. H., Ching, T. May 1966. Longevity and dormancy in seeds of several cool-season grasses and legumes buried in soil. *Agron. J.* 58:220–22
249. Raup, H. M. 1965. The structure and development of turf hummocks in the Mesters Vig District, Northeast Greenland. *Medd. Groenland* 166(3):1–112
250. Raup, H. M. 1971. Miscellaneous contribution on the vegetation of the Mesters Vig District, Northeast Greenland. *Medd. Groenland* 194(2):1–105
251. Rehfeldt, G. E., Stage, A. R., Bingham, R. T. 1971. Strobili development in Western White pine: periodicity, prediction and association with weather. *Forest. Sci.* 17:454–61
252. Richards, P. W. 1952. *The Tropical Rain Forest.* London: Cambridge Univ. Press
253. Righter, F. I. 1939. Early flower production among the pines. *J. Forest.* 37:935–38
254. Roberts, E. H. 1972. Dormancy: A factor affecting seed survival in the soil. In *Viability of Seeds,* ed. E. H. Roberts, 321–59. London: Chapman & Hall
255. Roberts, H. A. 1970. Viable weed seeds in cultivated soils. *Rep. Nat. Veg. Res. Sta. 1969,* 25–38
256. Roberts, H. A., Feast, P. M. 1973. Emergence and longevity of seeds of annual weeds in cultivated and undisturbed soil. *J. Appl. Ecol.* 10:133–43
257. Roberts, H. A., Dawkins, P. A. 1967. Effect of cultivation on the numbers of viable weed seeds in soil. *Weed Res.* 7:290–301
258. Robinson, L. W., Wareing, P. F. 1969. Experiments on the juvenile/adult phase change in some woody species. *New Phytol.* 68:67–68
259. Rose, F. 1948. Biological Flora of the British Isles—*Orchis purpurea* Huds. *J. Ecol.* 36:366–77
260. Ross, M. A., Harper, J. L. 1972. Occupation of biological space during seedling establishment. *J. Ecol.* 60:77–88
261. Roy, D. F. 1966. Silvical characteristics of Redwood. *US Forest Service Res. Pap. PSW-28,* 20 pp.

262. Roy, D. F. 1957. A record of tanoak acorn and seedling production in northwestern California. *US Forest Service Calif. Forest. Range. Exp. Sta. Forest. Res. Note 124,* 6 pp.
263. Rudolph, T. D. 1966. Stimulation of earlier flowering and seed production in jack pine seedlings through greenhouse and nursery culture. *US Forest Service Res. Pap. NC-6,* 80–83
264. Saeki, T. 1960. Leaf growth as influenced by dry matter production. *Bot. Mag. Tokyo* 74:70–78
265. Sagar, G. R. 1959. *The biology of some sympatric species of grassland.* D. Phil. thesis. Univ. Oxford
266. Salisbury, E. J. 1942. *The Reproductive Capacity of Plants.* London: Bell
267. Salisbury, F. B. 1963. *The Flowering Process.* Oxford: Pergamon
268. Sarukhán, J. 1971. *Studies in plant demography.* PhD thesis. Univ. Wales
269. Sarukhán, J., Harper, J. L. 1973. Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L. and *R. acris.* I. Population flux and survivorship. *J. Ecol.* 61:675–716
269a. Sarukhán, J. 1974. Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L. and *R. acris.* II. Reproductive strategies and seed population dynamics. *J. Ecol.* 62:151–77
269b. Sarukhán, J., Gadgil, M. 1974. Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L. and *R. acris* L. III. A mathematical model incorporating multiple modes of reproduction. *J. Ecol.* In press
270. Saurina, N. I. 1972. Dynamics of numbers of individuals and age spectrum in some populations of *Ranunculus acris* and *Ranunculus auricomus. Bull. Moscow Soc. Natur.* 77(5):115–20 [Russian]
271. Savage, Z. 1966. Citrus yield per tree by age. *Fla. Agr. Exp. Sta. Agr. Exten. Serv. Econ. Ser. 66–3,* 9 pp.
272. Schafer, D. E., Chilcote, D. O. 1969. Factors influencing persistence and depletion in buried seed populations. I. A model for analysis of parameters of buried seed persistence and depletion. *Crop Sci.* 9:417–19
273. Schafer, D. E., Chilcote, D. O. 1970. Factors influencing persistence and depletion in buried seed populations. II. The effects of soil temperature and moisture. *Crop. Sci.* 10:342–45
274. Schaffalitzky de Muckadell, M. 1959. Investigations on ageing of apical meristems in woody plants and its importance in silviculture. *Forstl. Forsoksv. Dan.* 25:307–455
275. Schmidtling, R. C. 1969. Reproductive maturity related to height of loblolly pine. *USDA Forest Service Res. Note SO-94*
276. Schwabe, W. W. 1971. Physiology of vegetative reproduction and flowering. In *Plant Physiology—a treatise,* ed. F. C. Steward, VIa:234–411. New York: Academic
277. Schwerzel, P. J. 1967. Seed production of some common Rhodesian weeds. *Pest Articles and News Summaries* (C) 13:215–17
278. Sealy, J. R., Webb, D. A. 1950. Biological Flora of the British Isles—*Arbutus unedo* L. *J. Ecol.* 38:223–36
279. Sharitz, R. R. 1970. *Population dynamics of two competing plant species.* PhD thesis. Univ. N. Carolina, Chapel Hill
280. Shaw, J. K. 1934. The lifetime yield of an apple orchard. *Proc. Am. Soc. Hort. Sci.* 31:35–38
281. Shaw, M. W. 1968. Factors affecting the natural regeneration of sessile oak (*Quercus petraea*) in North Wales. I. A preliminary study of acorn production, viability and losses. *J. Ecol.* 56:565–83
282. Shinozaki, K., Yoda, K., Hozumi, K., Kira, T. 1964. A quantitative analysis of plant form—the pipe model theory. I. Basic analyses; II. Further evidence of the theory and its application in forest ecology. *Jap. J. Ecol.* 14:97–105, 133–39
283. Shreve, F., Hinckley, A. L. 1937. Thirty years of change in desert vegetation. *Ecology* 18:463–78
284. Simmonds, N. W. 1945. Biological Flora of the British Isles—*Gentiana pneumonanthe. J. Ecol.* 33:295–307
285. Singh, L. B. 1960. *The Mango.* London: Leonard Hill
286. Slobodkin, L. B. 1961. *Growth and Regulation of Animal Populations.* New York: Holt, Rinehart, Winston
287. Smirnova, O. V. 1968. Number and age composition of populations of some components of the herbaceous cover of oak woods. In *Problems of morphogenesis of flowering plants and the structure of their populations,* ed. A. A. Uranov et al, 155–82. Moscow: Nauk [Russian]
288. Smirnova, O. V., Toropova, N. H. 1972. The great life cycle of *Galeobdolon luteum* Huds. *Bull. Moscow Soc. Natur.* 77(1):76–87 [Russian]
289. Smythe, N. 1970. Relationship between fruiting seasons and seed dispersal methods in a neotropical forest. *Am. Natur.* 104:25–35
290. Snagovskaja, M. S. 1966. Comparative characteristics of *Medicago falcata*

populations under different ecological conditions. *Bull. Moscow Soc. Natur.* 71:51–59 [Russian]

291. Solomon, M. E. 1969. *Population Dynamics.* London: Arnold
292. Stark, R. H., Hafenrichter, A. L., Klages, K. H. 1949. The production of seed and forage by mountain brome as influenced by nitrogen and age of stand. *Agron. J.* 63:575–80
293. Stern, K. 1966. Über den Erfolg einer über drei Generationen geführten Auslese auf frühes Blühen bei *Betula verrucosa. Silvae Genet.* 10:48–51
294. Stern, W. R. 1965. The effects of density on the performance of individual plants in subterranean clover swards. *Aust. J. Agr. Res.* 16:541–55
295. Sterrett, W. D. 1911. Scrub Pine. *US Dept. Agr. Forest Service Bull. 94,* 27 pp.
296. Sterrett, W. D. 1920. Jack Pine. *US Dept. Agr. Bull. 820,* 47 pp.
297. Stevens, O. A. 1932. The number and weight of seeds produced by weeds. *Am. J. Bot.* 19:784–94
298. Struik, G. J., Curtis, J. T. 1962. Herb distribution in an *Acer saccharum* forest. *Am. Midl. Natur.* 68:285–96
299. Summerfield, R. J. 1972. Biological inertia—an example. *J. Ecol.* 60:793–98
300. Summerhayes, V. S. 1951. *Wild Orchids of Britain.* London: Collins
301. Swanberg, P. O. 1951. Food storage, territory and song in the thick billed nutcracker. *Proc. Xth Int. Ornithol. Congr. Uppsala, June 1950,* 545–54
302. Symington, C. F. 1933. The study of secondary growth on rain forest sites in Malaya. *Malay. Forest.* 2:107–117
303. Tadaki, Y., Ogata, N., Takagi, T. 1962. Studies on production structure of forest. III. Estimation of standing crop and some analyses on productivity of young stands of *Castanopsis cuspidata. J. Jap. Forest. Soc.* 44:350–59 [Japanese, English summ.]
304. Tadaki, Y., Shidei, T. 1959. Studies on the competition of forest trees. 11. The thinning experiment on small model stand of sugi (*Cryptomeria japonica*) seedlings. *J. Jap. Forest. Soc.* 41:341–49 [Japanese, English summ.]
305. Tamm, C. O. 1948. Observations on reproduction and survival of perennial herbs. *Bot. Notis.* 3:305–21
306. Tamm, C. O. 1956. Further observations on the survival and flowering of some perennial herbs. *Oikos* 7:273–92
307. Tamm, C. O. 1972. Survival and flowering of some perennial herbs. 11. The behaviour of some orchids on permanent plots. *Oikos* 23:23–28
308. Tamm, C. O. 1972. Survival and flowering of perennial herbs. 111. The behaviour of *Primula veris* on permanent plots. *Oikos* 23:159–66
309. Toole, E. H., Brown, E. 1946. Final results of the Duvel buried seed experiment *J. Agr. Res.* 72:201–10
310. Tripathi, R. S., Harper, J. L. 1973. The comparative biology of *Agropyron repens* (L). Beauv. and *A. caninum* (L.) Beauv. 1. The growth of mixed populations established from tillers and from seeds. *J. Ecol.* 61:353–68
311. Tripp, H. A., Hedlin, A. F. 1956. An ecological study and damage appraisal of white spruce cone insects. *Forest. Chron.* 32:400–10
312. Trulevich, N. V. 1960. Composition of bushes and structure of populations of *Artemisia tianschanica* in a series of pastures. *Moscow State Pedag Inst. V. I. Lenin, Sci. Notes Fac. Natur. Sci.* 4:107–29 [Russian]
313. Uranov, A. A., Grigorieva, V. M., Egorova, V. N., Ermakova, I. M., Matveev, A. R. 1970. The variability and dynamics of age spectra in some meadow plants. In *Theoretical problems of phytocenology and biogenocenology (to the 90th birthday of V. N. Sukachev),* 194–214. Moscow: Nauk [Russian]
314. Uranov, A. A., Smirnova, O. V. 1969. Classification and basic features of the development of perennial plant populations. *Bull. Moscow Soc. Natur.* 74: 119–34 [Russian]
315. USDA Forest Service, 1948. *Woody Plant Seed Manual.* 416 pp.
316. Verhulst, P. F. 1844. Recherches mathematiques sur la loi d'accroissement de la population. *Mem. Acad. Roy. Bruxelles* 18:1–58
317. Vernon, A. J., Morris, M. G. 1964. Variability in West African peasant cocoa farms; time studies on Agodi cocoa yields. *J. Hort. Sci.* 39:241–53
318. Visser, T. 1964. Juvenile phase and growth of apple and pear seedlings. *Euphytica* 13:119–29
319. Visser, T. 1965. On the inheritance of the juvenile period in apple. *Euphytica* 14:125–34
320. Visser, T. 1967. Juvenile period and precocity of apple and pear seedlings. *Euphytica* 16:319–20
321. Visser, T. 1970. The relation between growth, juvenile period and fruiting of apple seedlings, and its use to improve breeding efficiency. *Euphytica* 19:293–302

322. Visser, T., de Vries, D. P. 1970. Precocity and productivity of propagated apple and pear seedlings as dependent on the juvenile period. *Euphytica* 19:141–44
323. Volterra, V. 1926. Variazioni fluttuazioni del numero d'individui in specie animali conviventi. *Mem. Acad. Naz. Lincei* 2:31–113
324. Vorontsova, L. I. 1967. Variation in the life cycle of builders of vegetation cover in southern semidesert as influenced by ecological conditions. In *Ontogenesis and age composition of flowering plants,* ed. A. A. Uranov, 132–54. Moscow: Nauk [Russian]
325. Wahlenberg, W. G. 1946. *Longleaf Pine.* Washington: Charles Lathrop Pack Forestry Foundation. 429 pp.
326. Wahlenberg, W. G. 1960. *Loblolly Pine.* North Carolina: Duke Univ. Sch. Forest.
327. Wangermann, E. 1965. Longevity and ageing in plants and plant organs. *Encycl. Plant. Physiol.* 15(2):1026–57
328. Wardle, P. 1961. Biological Flora of the British Isles—*Fraxinus excelsior* L. *J. Ecol.* 49:739–51
329. Wareing, P. F., Seth, A. K. 1967. Ageing and senescence in the whole plant. *Symp. Soc. Exp. Biol.* 21:543–58
330. Welch, D. 1961. The reproductive capacity of *Juncus squarrosus. New Phytol.* 65:77–86
331. Wells, T. C. E. 1967. Changes in a population of *Spiranthes spiralis* (L). Chevall at Knocking Hoe National Nature Reserve, Bedfordshire, 1962–65. *J. Ecol.* 55:83–99
332. Wells, T. C. E., Barling, D. M. 1971. Biological Flora of the British Isles—*Pulsatilla vulgaris* Mill. *J. Ecol.* 69:275–92
333. Went, F. W. 1948. Ecology of desert plants. 1. Observations on germination in the Joshua Tree National Monument, California. *Ecology* 29:242–53
334. Wheeler, W. M. 1911. The ant-colony as an organism. *J. Morph.* 22:307–25
335. White, J., Harper, J. L. 1970. Correlated changes in plant size and number in plant populations. *J. Ecol.* 58:467–85
336. Whittington, W. J. 1972. Genetic regulation of germination. In *Seed Ecology,* ed. W. Heydecker, 5–30. London: Butterworth
337. Wilcott, J. C. 1973. *A seed demography model for finding optimal strategies for desert annuals.* PhD thesis. Utah State Univ.
338. Williams, O. B. 1970. Population dynamics of two perennial grasses in Australian semi-arid grassland. *J. Ecol.* 58:869–75
339. Williamson, M. H. 1972. *The Analysis of Biological Populations.* London: Arnold
340. Wilson, B. F. 1966. Development of the shoot system of *Acer rubrum* L. *Harvard Forest Paper* 14, 21 pp.
341. Wilson, E. O. 1971. *The Insect Societies.* Cambridge, Mass.: Harvard Univ. Press
342. Wimsatt, W. A. 1969. Some interrelations of reproduction and hibernation in mammals. *Dormancy and Survival. Symp. Soc. Exp. Biol.* 23:511–49
343. Wright, J. M. 1964. Flowering age of clonal and seedling trees as a factor in choice of breeding system. *Silvae Genet.* 13:21–27
344. Yoda, K., Kira, T., Ogawa, H., Hozumi, K. 1963. Self thinning in overcrowded pure stands under cultivated and natural conditions. *J. Biol. Osaka City Univ.* 14:107–29
345. Zasada, J. C., Gregory, R. A. 1972. Paper birch seed production in the Tanana Valley, Alaska. *USDA Forest Service Res. Note PNW-177,* 7 pp.
346. Zasada, J. C., Viereck, L. A. 1970. White Spruce cone and seed production in interior Alaska, 1957–1968. *USDA Forest Service Res. Note PNW-129,* 11 pp.
347. Zimmermann, M. H. 1973. Transport problems in arborescent monocotyledons. *Quart. Rev. Biol.* 48:314–21
348. Zon, R. 1915. Seed production of Western white pine. *USDA Bull.* 210:1–15