The realism of models in plant demography

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CONTENTS

INTRODUCTION

This paper discusses the question of why we need to validate the realism of models used in plant demography. A model is a simplified representation of an existing or supposed reality which assists in making calculations and predictions and in formulating theories. In other words, a model mimics, as closely as possible, the relevant features of a system.

The term demography is employed in various ways by various authors to cover many uses depending on the context. Essentially, this term originates from the human sciences. Demographers are social scientists who study the dynamics of human populations (Ehrlich *et al.* 1977). They are primarily concerned with the questions of how and when birth rates change in response to social or environmental pressures. Some ecologists consider demography simply as a method to describe *how* it is, not *why* it is, and thus use demographic techniques to quantify the varying densities of plants in their areas of distribution. Others include demography within the broader field of population biology and even consider concepts of natural selection (e.g. Harper & White 1974; Harper 1977; Solbrig & Solbrig 1979; Solbrig *et al.* 1979; Blom 1987). With this approach, the principal objectives of plant demography are natality, death, immigration, emigration, and the behaviour of plants during all stages of their life cycle. These various aspects of the life cycle determine the life history of a plant. Through studies relating life-history characteristics to environmental factors, insight can be gained into the underlying processes that cause both changes in population sizes and variation in the behaviour of the members of that population. The underlying processes are linked to those environmental circumstances that may force species to adaptations brought about by natural selection. Discussions on the phenotypic determination of environmental and genetic influences on demography can be found in Bradshaw (1965), Levin (1976), Jain (1979), Blom (1983), Gottlieb (1984), Haeck & Woldendorp (1985), Lotz & Blom (1986), Schlichting (1986) and Ernst (1987). In order to understand processes as they occur in nature, a large number

of measurements are needed, and many experiments have to be carried out that test the effects of environmental factors, either separately or in combinations, on the behaviour of organisms. The development of theories and the predictions of future events are important goals for ecologists. Therefore, the construction and use of models have to be considered both as an exciting challenge and as a tool for scientists in this field of research. Although the field of ecology is only a relatively small biological discipline, there is an abundance of literature available on models. It appears that in the past each researcher constructed his own model, forgetting that model making should not be an aim in itself, but a tool to a better understanding of reality. Ecology has, as have various other branches of biology, grown top-heavy with models. Categorization of models greatly depends upon the viewpoint of the classifier and, as a consequence, many different classifications are found in the literature.

For example, Pielou (1981) tried to classify models according to their applicability and distinguished four types: models as explanations, models for forecasting, models as hypothesis generators, and models as standards of comparison. Other models have been constructed with very specific aims, such as predator–prey systems, host–parasite relationships, competition, reproduction, migration, territorial behaviour, density regulation, population growth and fitness, simple food webs, management, aquatic ecosystems, grasslands, forests, tundras, deserts, soil-litter, etc. (for descriptions of these and other models see, for example: Jeffers 1972; Maynard Smith 1974; Wiegert 1975; Van Hulst 1979; Shugart & West 1980; May 1981; Usher 1979, 1981; Pielou 1977; During & Willems 1984; Hobbs & Legg 1984; Shugart & Noble 1981; Rabonivich *et al.* 1985; Van Tongeren & Prentice 1986; De Kroon *et al.* 1987; Prentice *et al.* 1987). Many models in ecology are simulation models that can be defined as a precise description of the system to be simulated. Therefore, simulation models can also be described as descriptive models which generally use mathematical techniques. Mathematical models mimic the conditions of a system in mathematical language or formulas which are concise and can be manipulated. These models are often very complicated, and computers are therefore useful for data storing, correlation and statistics (Sitharama Iyengar 1984).

Because classification proved to be surprisingly difficult, it has been suggested that fitting a demographic model into one of the aforementioned classifications is nearly impossible. In plant demography, at least two types of models can be distinguished. One type comprises relatively simple diagrammatic models on the growth of populations (e.g. Harper 1977), and these utilize two main characteristics of a population. The first one is that the growth of a population depends on births, deaths, immigrants and emigrants. A population can be composed of different individuals of a species, as well as of the different parts or modules of one individual plant. The idea of a plant as a population of parts is important for understanding population biology at the more intricate level of groups of different individuals. The second characteristic is the organism as a life-cycle from seed to seed or to an independent functioning daughter plant born by vegetative propagation. The second type of plant demographic model consists of mathematical models constructed by the use of matrix algebra. The matrix model was first introduced to population biology by Leslie (1945, 1948), and is known as the Leslie matrix model. It summarizes the age-specific mortality and fecundity schedules of a population. A matrix based on stage rather than age is the matrix named after Lefkovitch (1965). Applications of matrix models can be found, for example, in the work of Usher (1966, 1972), Sarukhan & Gadgil (1974), Hartshorn (1975), Soane & Watkinson (1979), and Van Groenendael (1985). Matrices are designed to manipulate large sets of demographic data. These models can be

POPULATION BIOLOGY

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DEMOGRAPHIC QUESTIONS

MEASUREMENTS SAMPLING

HYPOTHESIS MODEL

TESTS VALIDATION

ACCEPTATION REJECTION REJECTION ACCEPTATION
OF HYPOTHESIS

MEASUREMENTS ADJUSTED MODEL

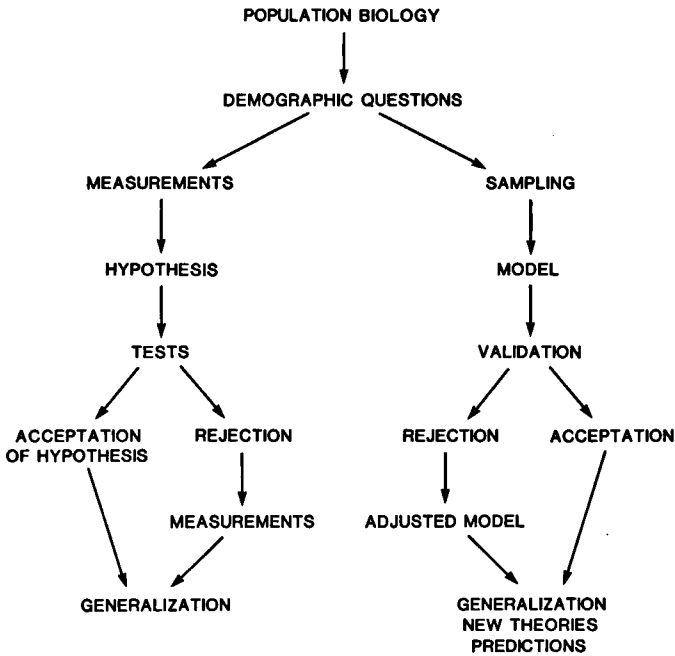GENERALIZATION GENERALIZATION
NEW THEORIES
PREDICTIONS

Fig. 1. Model building as a hypothesis generating approach.

used to describe the dynamics of organisms within a population, and to summarize life-history characteristics in order to detect strategies. Matrix models can contain static as well as dynamic information. As Caswell (1986) and Van Groenendael et al. (1988) have recently reviewed the use of matrix models in population biology, these models are not discussed in detail in this paper.

Model building in ecology forms part of the scientific method used to describe and explain nature in order to generate many valid and useful generalizations. Within the framework of scientific methodology, building a model can be compared with formulating a hypothesis (Fig. 1). A hypothesis is formulated through inductive reasoning, based on a set of data, and follows the exact statement of a scientific problem. The aims of both hypotheses and models are to give solutions, explanations or predictions with general validities, which means that they must all be verifiable through experimentation, observations, and new questions.

One inescapable property of a survey of models in plant demography is its incompleteness because of the different definitions of demography, the various classifications, and the presence of numerous models with special aims. Any further attempt to disentangle models developed by model-makers from the different approaches will only lead to a theoretical and academic discussion. To avoid further discussion on definitions and classifications, this paper will continue by presenting examples of models in demography and population biology. The realistic values of these models are given and this paper ends with a more general discussion which highlights some important questions on the realism of models in plant demography.

MODELS ON THE EARLY STAGES OF A PLANT'S LIFE CYCLE

Processes that occur during the early stages of a plant's life cycle determine, to a large extent, its life-history characteristics and its population dynamics (see Harper 1977). As a consequence, in all models attention has to be paid to seed production, dispersal, seed bank, germination, seedling survival and seedling establishment. Furthermore, some species propagate vegetatively. It is surprising that in many models these stages are, at least partly, neglected, or assumed to be constant or even zero. Few models are especially constructed to analyse these early stages. The dispersal of diaspores depends on many environmental factors and may differ per habitat and per organism. The generalizations predicted by these models are rarely to be found in the literature. Metz *et al.* (1983) discussed a model on the effects of dispersal in heterogeneous environments. Klinkhamer *et al.* (1983) analysed this model, originally developed by Kuno (1981), by means of simulation methods. In Kuno's model a comparison of non-dispersing and totally dispersing organisms shows that the expectation for population sizes is equal for both behaviours. Other simulations (Metz *et al.* 1983) proved the importance of partial dispersal, and the model predicts a low optimal dispersal fraction which is independent of the number of environmental patches: a decrease in the selective pressure towards the optimal fraction occurred with increasing number of patches. To increase the reality of this model, interactions between organisms, dormancy, delayed reproduction, movements in the soil and inaccessibility of the patches have to be included. The relationship between dispersal and so-called 'safe-sites' was described in two separate models by Green (1983) and Geritz *et al.* (1984). Green's model assumed that all seeds land in safe-sites, and it explained differences between dispersal curves by differences in safe-sites densities. The model of Geritz *et al.* (1984) demonstrated that differences in seed production and safe-site areas explain more realistically the variations in dispersal curves. However, because of the many environmental factors influencing dispersal, tests in which natural patterns are compared to models' predictions are very difficult to design, and seldom attempted. The dispersal of seeds in the field can be studied using marking methods. For example, Blom & van Heeswijk (1984) studied the fate of painted seeds in the field and found that approximately 90% of the marked seeds could be recovered after 4 weeks. Liddle *et al.* (1987) developed a simple descriptive model for studying the patterns of seed dispersal on the soil surface. Many other theoretical and mathematical models on dispersion have assumed that the transport of diaspores is a result of a succession of random movements, each with an equal chance of occurring (e.g Werner 1975a). This assumption, however, cannot be tested, whereas the relative simplicity of Liddle's model (Liddle *et al.* 1987) ensures experimental validation—in this case marked seeds were followed. Diffusion and predation were measured in the experiments and it was proved that distribution was controlled more by predation than by diffusion. The authors' attempt to construct a simple model for detecting dispersal has been very useful. It is worth investigating whether this method must be adjusted to make it applicable for predicting the dispersal of other diaspores with different morphologies and under other environmental conditions. Other important processes that influence dispersal are height and timing of release, and differences in morphology. Matlack (1987) simulated the descent of seeds and fruit of 38 anemochorous species by dropping them in still air. He found that the large differences in fall rates were dependent on interspecific variations in diaspore weight and plume area. He then experimentally changed the range of diaspore weight in some species and demonstrated that the rate of descent of the altered diaspores was controlled by weight relative to the wing or plume

area. Some species possess a wide variation in these characteristics, whereas others show a relatively low variation in plume loading and fall speed. These evolutionary constraints can be translated directly into different distribution patterns. Maynard Smith (1982) showed that evolutionary stable strategies (ESSs) in germination behaviour will evolve under natural selection. Due to genetic constraints, deviations from the ESS occur. Ellner (1985) modelled ESS-germination strategies of annual plants in a randomly varying environment. One of his goals was to identify the environmental and demographic factors that determine evolutionary stable behaviour. Many models on ESS strategies assume that the state of the population is described completely by density. In these models, however, density is averaged over the habitat; in nature, competition between neighbouring plants and changing environments over distances, even of centimetres (e.g Lotz & Spoormakers, 1988), invalidate this assumption. Another limitation is the assumed constant germination fraction. Germination behaviour varies in various ways. Within one fruit, two types of seeds with different germination characteristics can be found, as was reported by Schat (1981) in *Plantago coronopus*. Germination behaviour may differ because of the position of the seeds on the parent plant (cf. Cavers & Harper, 1966, for *Rumex* sp.). Germination heterogeneity can also be caused by the heterogeneity of the environment (Harper *et al.* 1965; Oomes & Elberse 1976). Of all the plant reproductive parameters, many authors consider seed size as the least variable (e.g. Harper *et al.* 1970). Others have demonstrated variation in seed size between and even within plants (e.g. Cavers & Steel 1984). Temme (1986) suggested that detectable genetic variation influences seed size variability. In a model in which offspring fitness is given as a function of seed size, Smith & Fretwell (1974) provided reasons for expecting offspring size to be constant. All these theories and measurements from both field and experimental conditions suggest that the incorporation of only a limited number of germination characteristics in models violates the reality.

One of the strategies in life-history traits that lowers germination risks is the occurrence of a seed bank in some species (Grime 1979). Models that incorporate dormancy are needed to explain how populations are maintained and regulated. MacDonald & Watkinson (1981) set up two models for a population of annual plants which take into account the existence of seeds that remain dormant for at least 1 year. Both models are deterministic and assume density-dependent processes in seed production and seedling self thinning. As a result, they are more realistic than models that neglect these processes. Very recently, Venable & Brown (1988) presented a model in which a spatially and temporally variable environment was considered and in which the selective interactions of dispersal, dormancy, seed bank and seed size were incorporated. Kingsolver (1986) presented a stage-transition model on the life history of *Yucca glauca* and emphasized the importance of vegetative reproduction in stabilizing the population dynamics. The rosette size of *Y. glauca* appeared to be a poor predictor of fruit set, but the capacity for vegetative reproduction depended to a large extent on the sizes of the rosettes. Because many plants have more than one mode of reproduction, the work of Kingsolver (1986) is a very valuable contribution towards the development of more realistic models in plant demography.

MODELS ON BIENNIAL PLANTS

Biennials, like annuals, have a relatively short life span, thus enabling population biologists to study the demography of these species within a limited period of time. One of

the questions asked by many authors is: has delayed flowering in biennials negative effects on the continued existence of populations? For example, using a deterministic model, Van der Meijden & Van der Waals-Kooi (1979) demonstrated that in growing populations delayed flowering has an inhibitory effect on growth, while in declining populations it is advantageous. Cohen (1968) and Venable & Lawlor (1980) showed that in widely fluctuating environments where low rates of increase and low dispersal fractions of seeds occur, delayed flowering will have a positive effect on the population growth. Klinkhamer & de Jong (1983) presented a stochastic model in which they compared a strictly biennial population with one in which delayed flowering was simulated. The conclusions to be drawn from these simulation models, in which optimal life histories were analysed, are (a) if a biennial behaves strictly as a biennial, a high density will be reached in only a few patches, whereas extinction in a large number of others must be expected and (b) if a biennial delays flowering, it will be found in many patches at lower densities. If we consider the realism of stochastic models in simulating a biennial plant population, the following remarks can be made: (i) these models assume large fluctuations in environmental conditions. (ii) the predictions depend to a large extent on the magnitude of the yearly differences in reproduction rate per flowering individual. (iii) the models consider one population of a biennial species growing in a single, isolated habitat patch. Processes such as seed dispersal and seed bank are not incorporated. Field studies are necessary to answer such questions as: how common is delayed flowering in biennials? Is it true that all individuals, indeed, die after flowering? When comparing the life histories of biennials with those of annuals and perennials, the Malthusian fitness is often used as a geometric growth rate (e.g. Hart 1977). Although valuable in the course of model development, the realism of this classical approach is limited by the assumption of a constant environment in which density-independent processes occur and a seed bank is absent. These assumptions lead to the supposition of constant population growth. De Jong *et al.* (1987) constructed a model with the more realistic assumptions of density-dependent survival and small-scale disturbances creating safe sites for establishment. Although they assume density-dependence in the very restricted sense of one seedling in one randomly created gap, a comparison of the model predictions with field data proved a better applicability than the traditional models using Malthusian fitness.

THE QUESTION OF AGE AND SIZE

Many demographic studies are based on the idea that the behaviour of plants in populations is determined by their ages (e.g. Leverich & Levin 1979; Law 1981). Other demographers believe that the sizes of individual plants are more important than age in determining life-history characteristics (e.g. Werner 1975b; Werner & Caswell 1977; Hara 1984; Klinkhamer & de Jong 1987). Kirkpatrick (1984) presented a demographic model based on size, not age. He postulated that strict age dependence is not appropriate in many cases. Size strongly affects sexual maturation, fecundity and mortality. In an attempt to understand the reality of Kirkpatrick's models, we have to consider his assumptions. In his models, all behaviour is assumed to be density independent. The sizes of individuals in a cohort remain normally distributed—a parameter based on the results of experimental studies. Unanswered remains the question in how far the experimental situation matches the distribution of sizes in the field. Moreover, it is assumed that growth, birth and mortality functions are constant in time, although the author does explain that his models can easily be changed to accommodate time dependence, which is much more realistic.

Nevertheless, numerical methods might be used to incorporate the effects of density and frequency dependence in his model, and additional information of the field situation is required.

Kawano *et al.* (1985) clearly demonstrated that size differences among plants of *Erythronium japonicum* reflect their different growth stages. Van Groenendael (1985, 1986) and van Groenendael & Slim (1988) showed that, particularly in the early life-stages of *Plantago lanceolata*, important differences in age-dependent survival and time to adulthood can be found between populations. In later life-stages, size appears to be the more important factor. Law (1983) suggested a model for the dynamics of a plant population that explicitly considers individuals classified both by age and size. Law's model is an extension of the standard matrix projection theory, and is based on the assumptions that the environment is constant from one year to the next, that reproduction occurs at one point in the year, and that all individuals start life in the same class. These assumptions, together with the fact that there is no seed dormancy involved, indicate the limitations of this model when compared with the real world. The important influence of stochastic fluctuations within the environment on the biology of populations has been ignored. Furthermore, the genetic component of life-history variation within and between populations (e.g. McGraw & Antonovics 1983a; Haeck & Woldendorp 1985; Rhebergen 1985) is not incorporated. In spite of these critical remarks, Law's model can be considered as one of the first steps to obtaining a much clearer insight into the behaviour of populations as its dynamics are determined by both the age and size characteristics of the individuals. Gross (1981) studied the relationship of both age and size on mortality, and the vegetative and generative development of four biennial species. She found that the size of the rosettes determines, to a large extent, the probabilities of flowering and dying. In general, age scarcely influences the fate of the rosettes.

Discussions on the mutual importance of size- or age-based models for predicting life-history tactics or plant strategies have provided some evidence for preferring size-based models. However, it is very clear that the relationship between age and size, and their effects on the population structure strongly depends on which species is involved. Moreover, within one species, age and size affect the life histories of different populations differently, a situation probably initiated by genetic differences or by varying abiotic or biotic environmental factors. The incorporation into models of demographic features based on size and on physiological rather than chronological age would certainly improve the realistic value of models in plant demography.

AN EXAMPLE OF A MODEL AND ITS VALIDITY

An understanding of the processes involved in the growth and maintenance of *Dupontia fisheri*, a tundra grass, enabled Lawrence *et al.* (1978) to develop a simulation model for the population processes of arctic tundra graminoids in which both chemical and physical environmental processes were integrated with population dynamical events. Using physically connected individuals as the simulation unit, the model assesses allocation patterns, reproduction, effects of grazing, population growth and spatial arrangement. This study also resulted in a general demographic model of plants with tiller systems which incorporates mentioned processes in relation to environmental factors. The plant variables include therein are innovating rhizomes, and several tillers from 1 to 5 years old, inflorescences, flowers and seeds (see Fig. 2). Ninety-five plant and environmental parameters were incorporated into the model. A number of the used values were 'educated guesses' as no
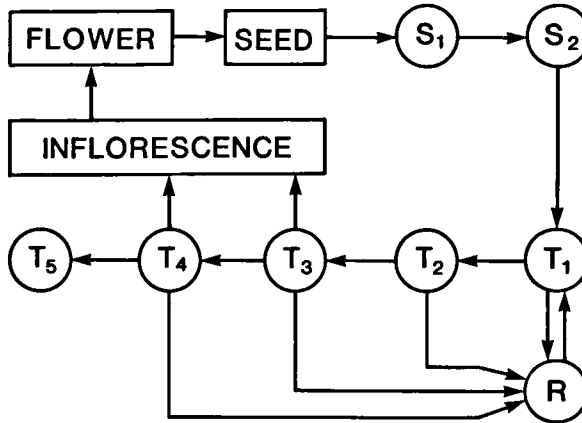
Fig. 2. Scheme variables and transfers incorporated in the model of Lawrence *et al.* (1978). R = innovating rhizomes, T1–5 = tillers from 1 to 5 years old, S1–S2 = seedling age classes.

Table 1. A comparison of simulated and observed values of some parameters in populations of *Dupontia fisheri* (data after Lawrence *et al.* 1978)

Parameters	Simulated		Observed	
	Mean	Maximum	Minimum	Maximum
Density (tillers m^{-2})	1600	2500	2000	2800
Above-ground biomass (g m^{-2})	47	82	82	102
Below-ground:above-ground ratio	1.3	13	0.9	1.6
Leaf area index	0.79	1.48	1	1.5
Flowering (%)	18		5	16.5
Non-structural carbohydrate (%)	14		20	30

quantitative data were available; most values were based on published studies, some on personally made field observations. The authors themselves validated their model by comparing results simulated with values obtained from the literature to field observations. The realism of some of these parameters is indicated in Table 1. Simulations were also performed for parameters such as germination and seedling establishment in which density-dependent influences are incorporated. Several simulations and experiments were carried out on the effects of grazing on the biomass production of tillers of different ages, age-specific mortality rates, photosynthates produced, allocation in growing plants, and the potential effects of changes in the arctic environment on the population. The work of these authors is one of the few attempts to create a model in which as many factors as possible are included in order to obtain insight into processes that determine the demography and population biology of plants. Some remarks can be made over the realism of this model. Table 1 shows that there is a reasonable agreement between simulated and observed values, which was also found for the other characteristics. Due to its complexity, however, the model cannot be easily applied—in

Table 2. Simulated and observed mean tiller weights for different age classes and the total population of *Dupontia fisheri* (Data from Lawrence *et al.* 1978). The simulations were conducted over a 20-year period and started with a tiller density of 470 per m^{-2}

Age class	Mean tiller weight (mg)		Error (%)
	Simulated	Observed	
T^0	6	25	−76
T^1	20	70	−71
T^2	71	97	−26
T^3	118	71	+66
T^4	120	67	+79
Population	67	66	+1

many sites the actual processes are unknown. Furthermore, while the simulation may reveal a general and realistic picture, it cannot be ignored that some effects of separated parameters are underestimated, while others are overestimated (see Table 2). A similar mean biomass was found for all tillers in both simulated and the real situation. However, the simulated tillers grew too slowly in the younger age classes, and continued to grow rather than to decline in the older classes. As a consequence, young plants were too small, and old plants were too large. In spite of these drawbacks, indicated by the authors themselves, the model is unique: it makes use of individuals both physically and chemically connected as the simulation unit, and it incorporates abiotic and biotic environmental factors as well as many demographic characteristics of the plants. Although the simulations should be validated further by measurements in the field, and experiments oriented towards model output, structure and parameters, this model is very valuable as a complex hypothesis for understanding the real processes in nature.

DISCUSSION

The purpose of using models in plant demography is to increase our understanding of the underlying processes that determine life-history phenomena and dynamics of populations. A model requires smaller samples, predicts future events and regenerates new theories. These aims can only be achieved when realistic models are constructed. However, many models only partly cover the behaviour of plants in the field, and some are made with very special purposes in mind. As a result, the realism of many models in understanding the system is relatively poor. To improve their realism, the results of both long-term field observations and experimental results must be involved. When deterministic models are compared with stochastic ones, it appears that often conflicting results can be found. Although most ecological models are deterministic, mathematical and computer techniques allow model-makers to construct stochastic versions with random fluctuations in the relevant parameters. The main parameters that should receive attention are summarized in Table 3. A study of the present models in plant demography raises the question: why are so many models density independent? Is it

Table 3. Main environmental-, plant- and population-parameters that need to be assimilated in order to increase the realism of models in plant demography

Environment	Plant	Population
Disturbances	Sexuality	Varying growth rate
Safe sites	Germinability	Fitness
Biotic interactions:	Seed bank	Within and between variation
animals–plant	Dispersal	Density dependency
plant–pathogens	Survival and establishment	
plant–plant	Growth	
Abiotic factors:	Vegetative propagation	
chemical, physical	Competition and stimulation	
	Age and size based behaviour	
	Genetic variation	
	Physiological processes	
	Modular structure	

just because of an increase in complexity when density-dependent mechanisms are involved, or are there reasons based on real ecological situations that force the authors of models to neglect the fact that, in the field, plants grow together and interfere with above- and below-ground parts?

We can, indeed, imagine situations in which plants grow density-independent during a certain period of time. This occurs mostly in colonizing species, or when events occur frequently, such as attacks of herbivores and abiotic disturbances (e.g. Werner 1977; Van Baalen & Prins 1983). On the contrary, most of the literature proves the existence of competition between plants growing under field conditions. Intra-specific competition due to light was, for example, demonstrated in *Lolium perenne* by Lonsdale & Watkinson (1982). Density, germination date, and spatial pattern all affected the reproductive effort of *Linum grandiflorum* (Fowler 1984). Seed size and genotype effects on seedling and adult performance, as well as on flowering and seed mass, of *Oenothera biennis* were studied in density gradients by Kromer & Gross (1987). Among five genotypes they distinguished two distinct groups in terms of their responses to increasing density. Warwick & Thompson (1987) compared five weedy biotypes of *Panicum miliaceum* under different densities. At increasing density, decreased biomass and delayed flowering was observed in all biotypes, but some of them showed greater competitive abilities than others. Higgings & Mack (1987) used a fertilized replacement series to study relationships between the diverse indices of plant performance and the competitive ability of two ecotypes of *Achillea millefolium*. Surprisingly, under high densities, plants of one of the ecotypes were taller and heavier, but exhibited no more competitive ability than plants of the other ecotype. Density dependence in *Salvia lyrata* was shown by Shaw (1987). Interspecific neighbouring effects have also been observed by many authors. For example, the effects of competition on primary plant characteristics of crop and weed species in the genus *Avena* were studied by Trenbath (1974). The effects of density on interference between individuals in species of the montane grasslands were described by Pemadasa & Amarasinghe (1982). Niche differentiation and

competition between two grassland species was demonstrated in removal experiments by Berendse (1983). Correlations between competitive effects and demographic responses have also been demonstrated in four annual plants (Goldberg & Fleetwood 1987), in plants from old-field communities (Goldberg 1987), and between plant species in a 1-year-old field community (Miller & Werner 1987).

In order to predict the effects of interference on the behaviour of neighbouring plants, many special models have been constructed. Models on density dependence in single species were, for example, developed and discussed by Gorham (1979), Watkinson (1980), Weiner (1984), and Pacala & Silander (1985). Multispecies models on competition and methods for detecting the role of self thinning on the dynamics of populations are, for example, published by Lonsdale & Watkinson (1983), Perry (1984), Symonides & Boryslawski (1986), Pacala (1986), Givnish (1986), Abrams (1987a,b), Crawley & May (1987), Firbank & Watkinson (1987), Morris (1987), Begon & Wall (1987) and Wilson (1987). Huston & Smith (1987) reviewed models and hypotheses on mechanisms such as competitive ability that causes succession. All these examples clearly demonstrate that competition for resources between individuals is an important factor that determines life-history traits in plants. In plant demography it is undoubtedly true that models that assume density independence have a poor realistic value.

Another assumption that violates the realism of many models is that of a constant environment. All ecologists know, however, that constant environments never exist in nature. Plants and other organisms alter their environments under nearly all circumstances. Furthermore, changes in climatic conditions may strongly influence the chemical and physical factors around plants. The nature of the interference between plants can be altered by different levels of nutrients in the soil. Individual plants and populations face mosaics of microsites characterized by temporal and spatial heterogeneity. Chemical changes or variations in the nutrient budget strongly influence the mineral status, growth, and reproduction of the plants concerned (e.g. Van Andel 1975; Kawano & Nagai 1986; Nagai & Kawano 1986; Tolsma *et al.* 1987; Ernst *et al.* 1987; Reekie & Bazzaz 1987; Crick & Grime 1987; Kuiters *et al.* 1987). Plants adapt to these variations in the nutrient status of the soil and life-history parameters change.

Due to different soil fertilities and moisture levels, a reallocation of the plant dry matter plants can be found, which may result in population variation (e.g. Ernst 1981, 1983; Van Andel *et al.* 1984). Further examples of responses at the vegetation level and at the population and species level to changing chemical soil conditions can be found in Van Andel *et al.* (1987). The effects of changing physical conditions on life-history parameters are strongly underestimated in models on plant demography. Compaction due to trampling has a dramatic effect on germination, seedling establishment, survival and plant growth (e.g. Liddle 1975; Blom 1978). Fluctuating anaerobic conditions resulting from flooding strongly influence growth in plants (Voesenek & Blom 1987; Talbot *et al.* 1987; Justin & Armstrong 1987; Voesenek *et al.* 1989). Waterlogging induces different responses in seed production (Van der Sman *et al.* 1988); *Rumex maritimus* appeared to be tolerant to flooding, and seed production increased under some conditions, whereas in *Chenopodium rubrum* seed production decreased significantly.

The consequences of animal and pathogen attacks on the demographic features of plants can be very severe and should be incorporated into the models. For example, Bishop & Davy (1984) showed that rabbit grazing had a significant effect on the

population regulation of *Hieracium pilosella*. Van Leeuwen (1983) found that grazing animals caused a considerable reduction in the achene production of two *Cirsium* species; predation reduces the population sizes of the species. The impact of pathogens on population biological processes in *Plantago lanceolata* was demonstrated by De Nooij (1987). She investigated the effects of pathogens on germination and seedling survival, and on the vegetative and generative stages in different populations. For example, the fungus *Phomopsis subordinaria* causes a stalk disease resulting in a dramatic reduction in the production of viable seeds. These effects differ between various host genotypes (De Nooij & van der Aa 1987). The development of special models to evaluate the effects of biotic attacks on the dynamics of plant populations and on vegetation succession emphasizes the importance of this biotic factor (e.g. Grant & French 1980; Knudsen & Hudler 1987; Byrne *et al*. 1987).

Shoot systems of plants consist of discrete construction units or modules. Ecologists interpret plant forms as being adjusted in an appropriate way to their environment (e.g. Kohyama 1987). In the sense of fitness, variation in plant form may be an adaptive response towards an optimal design. Demographic investigations of the modular structure of individual plants have emerged as a basic tool in plant population ecology (e.g. Bazzaz & Harper 1977; Lovett Doust & Lovett Doust 1987; Watkinson 1988). Differences in life-history tactics between two ecotypes have to be related to differences in modular growth (McGraw & Antonovics 1983b; Van Groenendael 1985). Demographic techniques have been used by Kotanen & Jefferies (1987) in a study of the death and birth rates of leaves and shoots in individual plants to explain differences in net primary production in grazed and ungrazed plants. Interactions between plant modules strongly influence the growth and reproduction of plants; shading and physical damage may occur when branches, leaves, or buds make mechanical contact. Computer simulations of branch interactions in trees have been developed by Honda *et al*. (1981). The adaptive architecture found in rhizomatous plants was discussed and simulated by Bell & Tomlinson (1980). We find many growth forms in a single plant community. At the present time, architectural models are relatively simple (e.g. Waller 1986). Three-dimensional arrangements of the modules of each individual plant in a population, or even in a community, should be incorporated into the model. In the future, we can expect more complex and realistic 'architectural' models. Only then can the adaptiveness of observed plant forms and their meaning for plant demography and population dynamics be fully understood.

At present we are in the phase of incomplete models on plant demography. Density effects under field conditions, influences of abiotic and biotic factors on life-history traits, and the relevance of changes in modular structures of individual plants are only being investigated partly. To construct more realistic models on plant demography, we require the persistant efforts of the true fieldworkers to collect data on the demographic features of plants. There are already excellent examples of those long-term studies and some of these can be found in the publications on the life histories of *Trillium* species (Ohara & Kawano, 1986) and of temperate woodland plants in Japan (Kawano 1985). The first examples of demographic models in which long-term field data and realistic values are incorporated are just beginning to appear in the huge amount of literature on models. Recently, Solbrig *et al*. (1988) published a density-dependent stochastic model on the demographic behaviour of the perennial herb *Viola fimbriatula*. Many of the relevant values used as simulation parameters had been empirically obtained in 5-year field study. We can only hope that more complex and realistic models on plant demography can be expected in the near future.

CONCLUSIONS

The primary roles of plant demographic models are to forecast life-history traits and strategies, to make predictions on the meaning of demographic changes on the dynamics of populations, to understand the processes in the system and to develop theories. These models should provide descriptions of demographic characteristics and both spatial and temporal dynamics of plant populations. Processes that influence these phenomena have to be incorporated in order to obtain a model that mimics the field situation realistically. In the field, the individual plant is constantly faced both with choices and with largely unpredictable abiotic as well as biotic events. Many processes are stochastic, and the more general models on plant demography should be stochastic in order to obtain more realistic values. At this moment, most models are still deterministic and designed with special purposes in mind. These models are certainly not useless, but they are only the first steps towards constructing more accurate models that involve the whole system. To increase the realism of future demographic models, density-dependent processes that occur during all stages in the life cycle of plants have to be incorporated. Long-term field observations on plants and their environment are needed. An increase in the realism of plant demographic models can also be achieved by the incorporation of physiological and genetic processes, which determine, to a large extent, the demography of individual organisms and the dynamics of plant populations. Although the need for validation may depend on the purpose for which a model was designed, validation is very useful for determining the applicability of a model. Therefore, a knowledge of processes that occur in the field is indispensable. To obtain adequate insight into these processes, appropriate experiments have to be carried out that test hypotheses obtained by descriptive field studies. These sets of data must be used to construct a model. A test of the applicability of a model is necessary; a comparison of predictions obtained from the model with randomly collected samples from the field will indicate the realism of the models. The same is true for theories revealed by models; these theories also need to be validated by field observations and experiments. Models constructed for their mathematical beauty only, or for computer employment, are useless in plant demography.

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