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Chapter 8

Fungal Demography — Mushrooming Populations

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Key words: bottlenecks, epidemiology, matrix models, population growth, population size, stage structure

1. DEMOGRAPHY AND FUNGI

A sound argument could be made that a book chapter on fungal demography is premature. After all, plant demography came of age only about 20 years ago (Harper, 1977), and one would have to search extensively to find the word demography and a reference to fungi printed in the same sentence. Nonetheless, the subject does have considerable history and development under the guise of epidemiology of plant diseases. Furthermore, consideration of theories and models of population growth as they might apply to fungi, even in the absence of extensive data, may stimulate thinking about fungi in the larger context of population biology.

Demography is the study of population size and how it varies. One seeks to analyze patterns of change in population size in order to understand the cause and regulation of population change and to forecast population growth. After preliminary consideration of units of measurement and structure of fungal populations, I present several basic models of population growth and their application to fungi. This is followed by discussion of factors regulating population size and several ways in which a population's size affects its genetic structure.

2. UNITS OF POPULATION MEASUREMENT

The mycelial nature of fungi, indeterminate growth, and habit of being dispersed and immersed in the substratum certainly present problems, both theoretical and practical, in measuring the population. Most population models were built for discrete organisms that can be relatively easily counted, such as deer, thistles, and even bacteria. However, stage-based models have been successfully used for the study of clonal plants and corals, organisms that present some of the same difficulties as fungi. The problems of measuring fungal populations are not intractable.

Where thalli are more or less determinate in size and detectable, and reproduction is strictly sexual, a simple count of thalli would be appropriate for almost all kinds of demographic studies. These conditions are met, for example, in *Rhytisma* species, which cause visible infections in maple leaves from ascospores formed in spring. Lesions represent discrete genets (genetic individuals), much as do animal bodies. Asexual reproduction is apparently not a complicating factor.

In other cases, thalli are similarly determinate and discrete, but both sexual and asexual reproduction may occur. For many purposes, the genetic relatedness of mycelia is not important, so that the type of reproduction can be ignored and colonies or lesions can be simply counted. In studies where genetic structure is also an issue, however, some means of distinguishing genets, such as molecular-genetic characters, is needed.

Indeterminate growth presents another problem. The modular construction of many organisms, particularly plants, has been a subject of some concern in quantifying them and understanding their individuality. A plant can be considered a population of parts, such as leaves, shoots, and flowers, whose rates of formation and death respond sensitively to environmental conditions (Harper, 1977). For instance, a field of grass has a complex structure of genets, each of which produces stolons with multiple tillers, on each of which are multiple culms with multiple leaves. For many purposes, however, the pasture may best be considered simply as a population of leaves.

Modularity can be considered with respect to fungi as well. Indeed, by definition, a mycelium is a population of hyphae and hyphal tips. However, aside from the impracticality of following the fate of cohorts or even counting of hyphal tips, a view of the mycelium as a simple, branching system of like parts is inaccurate (Rayner, 1992; Chapter 2). Mycelia in nature may be differentiated into portions that are dedicated to combat, foraging, resource acquisition, and asexual and sexual reproduction. Nevertheless, the mycelium can grow or shrink as conditions warrant, just as the "population-like

structure of an individual plant suit it admirably to respond to stresses by varying the birth rate and death rate of its parts" (Harper, 1977).

This suggests that the size or mass of a mycelium or volume or area of substratum colonized may be a more useful quantity than the number of parts. In studies of population development of lichens and mosses, for example, grids were established and the number of quadrats colonized was used as a measure of population size (e.g., Fridrikson, 1975). Modeling of foliar diseases caused by fungi commonly uses proportion of susceptible tissue or plants that is infected, but number or area of lesions can be used too (Jeger, 1987).

Finally, indices of abundance are commonly used as a proxy for actual abundance. One of the classic studies of population ecology, the variation of lynx and hare abundance in Canada, was not based on scientific sampling of the population but on records of furs handled by the Hudson's Bay Company (see Gotelli, 1995). Harvest records are often used in studies of game and fishery populations. Similarly, a conclusion that populations of certain macrofungi have declined dramatically in Europe was supported by foray records and market records of the sale of wild mushrooms (Arnolds, 1991; Arnolds, 1995). Disease reports from a network of growers or extension agents can provide similar data for pathogens. A potential weakness of some such approaches is the assumption that the effort and strategy of the sampling were equivalent over the time period. However, in many cases no better information is available.

An index of abundance that is commonly used with fungi is a measure of propagules, including microsclerotia sieved from soil, spores trapped from air, or colony-forming units grown on selective media. In cases where mycelia do not survive during the dormant season, propagules may be the entire population for part of the year. Numbers of colonies formed after plating of soil dilutions or plant parts is a popular measure of population size (Hata and Futai, 1996; Kirchner *et al.*, 1993; Spotts and Cervantes, 1994). Although it is not proportional to biomass or activity among species, isolation frequency should be proportional to actual mass or numbers of mycelia within a species.

Populations of macrofungi are often characterized by occurrence of fruit bodies. Fruiting is indeed the intended focus of some studies, but it is often used implicitly as a proxy for actual population size. The problems with use of fruiting to characterize populations and communities of macrofungi are obvious to anyone who has collected such fungi and studied them for a few years. First, fruiting may vary tremendously and unpredictably from year to year, largely independent of variation in mycelial populations. In three years of sampling mushrooms in a birch forest in Norway, Mehus (1986) recorded annual biomass of 311, 773, and 21 kg ha^{-1}. The species recorded changed

similarly. It has been suggested that 3 to 8 years of collecting are necessary to adequately characterize populations and communities by fruiting (Hering, 1966; Vogt *et al.*, 1992). Such extreme variation apparently depends on environmental conditions that influence fruiting, but these are not well understood and probably vary among species. Second, sampling must be intensive even within one year because fruit bodies of many species are short-lived. Even when sampling every week during peak fruiting, one quarter of the fruit bodies may be missed (Watling, 1981). Third, assuming one does sample intensively and extensively enough, one still has very little idea of how fruiting is related to actual fungal biomass or numbers. If fruiting varies so greatly, it probably will not reflect trends of mycelial mass or numbers. Fourth, fruiting usually gives no information about genetic structure of populations. Each fruit body may represent a unique genet or they may all arise from a single genet.

These obvious problems have not prevented application of fruit-body sampling because the alternatives have ranged from difficult to impossible, and in some cases present similar uncertainties. Culturing is only marginally useful because many macrofungi cannot be isolated in culture or, if so, cannot be morphologically distinguished from many other fungi in that state. Molecular techniques can offer reasonable alternatives for identification and characterization of mycelia in culture and even in natural substrates, but may be difficult when many unfamiliar species are encountered. Thus, when data are based on the vagaries of fruiting, one must ask whether no data are better than potentially misleading data. However, when used over multiple years in concert with several approaches, fruitbody sampling can give consistent results.

3. AGE, STAGE, AND SIZE STRUCTURE

As discussed above, it is not imperative to recognize individuals in a population model. One can quantify biomass or proportional cover more appropriately than numbers of individuals in some cases. However, if individuals are recognized, it is possible to structure a model to account for elements of the population that vary in their demographic features.

A common type of structure is age. For example, an age-structured model of human population growth would assign appropriate fertility and mortality probabilities to the ages or age classes. This would be particularly important to accurately model the effects over time of an extraordinary, episodic change in birth rates or a major mortality event.

However, age structure may not be useful for organisms with indeterminate growth or complex life histories. It is often more useful to recognize

stages or forms of growth that differ among themselves in demographic features. Insect populations, for instance, might be modeled as eggs, larvae, pupae, and adults. The time in the stages may vary, but demographic behavior is more dependent on stage than age. Furthermore, there is no requirement that an individual follow a single path among the stages. For instance, a seed produced in one year may be in the seed bank the following year or it may have developed into a seedling. Some fungi have a "propagule bank" or pool similar to seed banks of plants, made up of sclerotia, microsclerotia, colonized bits of organic matter, or dormant spores. A flowering adult may become a nonflowering adult the following year or flower again. Similarly, a mycelium may fruit one year but not the next. In hypothetical matrix models below, four stages of the basidiomycete life cycle are used for structure.

Similarly, size class can be a structural unit, as is often done with trees. Size class may be appropriate for some fungi whose mycelia vary greatly in size. For instance, a minimum size may be necessary before fruiting can occur, or death of the mycelium may be more likely if it is small and has limited resources (see section 5, below).

4. MODELS OF POPULATION GROWTH

4.1 Simple and Theoretical Models

Simple equations that model population growth have played a large part in developing basic concepts of population biology and in illuminating fundamental factors that regulate population growth (Begon *et al.*, 1996; Gotelli, 1995).

The fundamental demographic processes in a population are birth (B), death (D), immigration (I) and emigration (E). Together they change the size (N) of a population during the time interval t to t+1 in the difference equation as follows:

$$N_{t+1} = N_t + B - D + I - E \qquad (1)$$

Highly modified forms of the difference equation that incorporated host and pathogen populations and density dependence were used in a model of anther smut of *Silene alba* (Thrall and Antonovics, 1995). Additionally, migration among populations in a metapopulation was incorporated. Migration of fungal thalli among populations is probably not common, but it may happen, for example, with animal parasites or by transportion of saprobes or plant parasites by humans with plants or soil. Migration of propagules is

common via the many dispersal mechanisms available to fungi. Assuming a closed population (without migration) and expressing the relationship as a continuous differential equation, the change in population size during a very small time interval is:

$$\frac{dN}{dt} = B - D \tag{2}$$

The numbers of births (B) and deaths (D) clearly reflect the intrinsic rate of each per individual (b and d, respectively) times the number of individuals (N). These two intrinsic rates can be combined into one intrinsic or instantaneous rate of increase, r, giving:

$$\frac{dN}{dt} = rN \quad \text{or, integrated:} \quad N_t = N_0 e^{rt} \tag{3}$$

Expression 3 is the exponential model of population growth. N_0 is the initial population size (known in plant pathology as initial inoculum), N_t is the population size at time t, and e is a constant, the base of the natural logarithm. Such exponential growth is usually short-lived. Growth is restrained by the decreasing living space and resources available as population size increases. In fact, given constant conditions, there is a limit beyond which population size cannot grow. In the logistic equation, this is expressed as K, and population growth decreases as K is approached:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \tag{4}$$

This equation was popularized in plant pathology as a model of plant disease epidemics by van der Plank (1963). In his equation, K is not a separate term because it is inherent in $x = N/K$, x being the amount of disease expressed as a proportion of the total crop available. Thus, the equation was $dx/dt = rx(1-x)$. Van der Plank's presentation was clear and enlightening, but, except for a note in the appendix of his book, did not couch the theory and mathematics of plant disease epidemiology in well-recognized demographic and population models. Thus, population aspects of plant disease epidemiology became somewhat "orphaned" from the outset. However, the application of van der Plank's model is essentially similar to those in animal and medical literature (May, 1990). Van der Plank and others applied the logistic equation successfully to many plant diseases, gaining valuable insight into the nature of epidemics and the relative effectiveness and timing of efforts at disease control (Merrill, 1967, 1968; van der Plank, 1963).

4.2 Matrix Models

A lucid introduction to matrix models can be found in Gotelli (1995) and more advanced concepts in Caswell (1989). Two important books on stage-structured populations that feature matrix models include Manly (1990), which has a full analysis, and Tuljapurkar and Caswell (1997), which presents the theory of matrix models as well as other kinds of structured-population models and their application in a variety of systems. Matrix models applied to age classes are often called Leslie matrix models. Stage-based models, in which an individual need not progress through classes on schedule or die, are often called Lefkovitch matrix models.

A matrix model, based on life tables, recognizes life stages (or ages) and the probability of transitions among stages. For example, the life stages of a hypothetical polypore may be recognized as basidiospore (*b*), primary mycelium (*p*), secondary, nonfruiting mycelium (*s*), and fruiting mycelium (*f*). At any given time *t*, the stage structure may be represented as a vector of abundances $\mathbf{n}(t)$ that gives the population size of each stage as follows:

$$\mathbf{n}(1) = \begin{pmatrix} n_b(1) = 4.5 \times 10^{13} \\ n_p(1) = 624 \\ n_s(1) = 104 \\ n_f(1) = 208 \end{pmatrix} \tag{5}$$

To develop the model further, we need to know, for the sampling interval, the probabilities of an individual changing from one stage to another, the probabilities of surviving at each stage, and the average number of basidiospores produced by a fruiting mycelium, or fertility (*F*). These are arranged in a transition matrix (**A**) as follows:

$$\mathbf{A}_{\text{polypore}} = \begin{array}{c} \\ b \\ p \\ s \\ f \end{array} \begin{array}{c} \begin{array}{cccc} b & p & s & f \end{array} \\ \begin{bmatrix} 0 & 0 & 0 & 2.16 \times 10^{11} \\ 1.37 \times 10^{-11} & 0.001 & 0 & 0 \\ 1.0 \times 10^{-11} & 0.05 & 0.61 & 0.05 \\ 0 & 0 & 0.11 & 0.94 \end{bmatrix} \end{array} \tag{6}$$

Each element in the matrix represents the transition from the stage at time *t*, represented by the column heading, to the stage at time *t*+1, represented by the row heading. The first row is the production of basidiospores, or fertility of each stage. Only fruiting mycelia do this, so all transitions are 0 in this

row except the transition *f-b*, which has the value *F* (in this example, the number of basidiospores produced by a fruiting mycelium during one sample interval). All other transitions are probabilities. For instance, in our hypothetical example, a secondary, nonfruiting mycelium has a 61% chance of survival as such to the next census (*s-s*) and an 11% chance of becoming a fruiting mycelium (*s-f*). Transitions that are impossible (or excluded from consideration in this example) are represented with a probability of 0.

The size and stage structure of the population at the next census [$\mathbf{n}(t+1)$] can be predicted by multiplying the current vector of abundances $\mathbf{n}(t)$ by the transition matrix **A**. Each element in the first row of the transition matrix is multiplied by the corresponding element of the current vector, and these are summed to give the first element in the resultant vector (number of spores in our example). The same procedure is followed for other rows to obtain new abundances for the other population stages. For example, the number of primary mycelia at time t+1 in our example is $(1.37 \cdot 10^{-11} \times 4.5 \cdot 10^{13}) + (0.001 \times 624) + (0 \times 104) + (0 \times 208) = 617$ (Table 1, first row).

Table 1. Numerical transitions among stages of a polypore population in the first year of a hypothetical polypore model.

	Sources of mycelia				
Mycelia at end of 1st yr	Basidiospores	Primary	Secondary [a]	Fruiting	Total
Primary	616	1	—	—	617
Secondary	5	31	63	10	109
Fruiting	—	—	11	196	207

[a] References to secondary mycelia refer to nonfruiting secondary mycelia.

The stage structure of the population and transition probabilities given here (Expressions 5 and 6) were developed with a typical woodland polypore in mind. Fertility is based on annual spore production of *Phellinus tremulae* (Manion, 1991, p. 109). Based on limited sampling of genets of the same fungus (Holmer *et al.*, 1994), an initial number of fruiting and nonfruiting secondary mycelia in an arbitrary stand area of one hectare and two fruitbodies per fruiting mycelium were estimated. Relative numbers of primary and secondary mycelia are unknown for most basidiomycetes, but primary mycelia are generally considered to be rare because they either die or they are likely to mate in a short time (Frankland *et al.*, 1995). In *Echinodontium tinctorium* (Indian paint fungus), however, primary mycelia outnumbered secondary mycelia by more than 3 to 1 (Etheridge and Craig, 1976). In a study of *Heterobasidion annosum*, 37-92% of mycelia isolated were homokaryotic (Garbelotto *et al.*, 1997). That fungus is unusual because secondary mycelia produce homokaryotic hyphae and some conidia are uninucleate (Hansen *et al.*, 1993), so one nucleus could be lost in wood or during isolation. Still, primary mycelia are probably more common than generally con-

sidered because they are small and not easily sampled or recognized. In this model, primary mycelia were initially set at twice the number of secondary mycelia (including those fruiting). Based on these data, transition probabilities were estimated and adjusted to result in an approximate steady state.

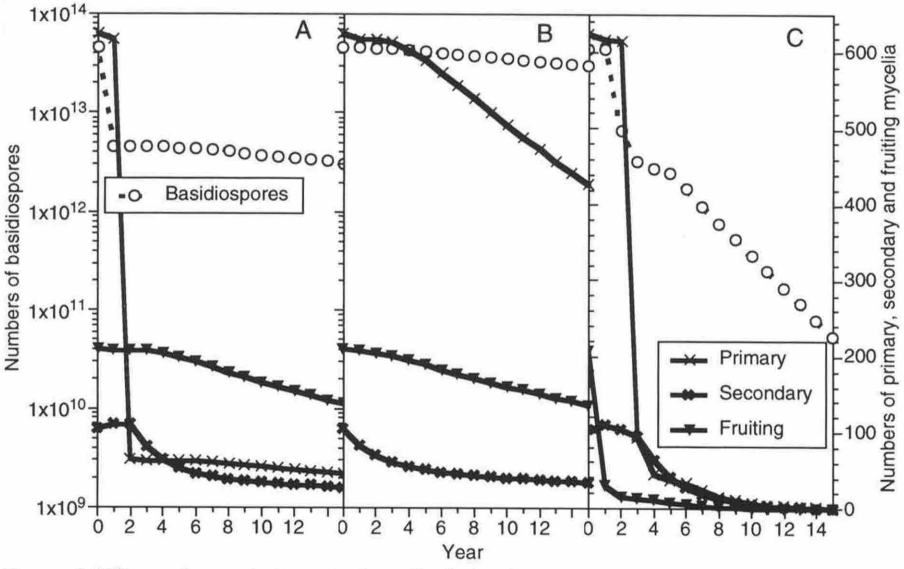

Figure 1. Effects of perturbation of a hypothetical polypore population on numbers of basidiospores (left axis) and numbers of mycelia in several stages (right axis). At year 0 the populations are identical and approximately at steady state. Shown are the effects of 90% reduction in: A) fertility (basidiospore production) of fruiting mycelia; B) probability of primary mycelium to nonfruiting, secondary mycelium (*p-s*); C) probability of fruiting mycelia surviving as such (*f-f*).

The sensitivity of the model to changes in transition probabilities was explored by permanently reducing selected matrix coefficients by 90% and observing the effect on abundances over 15 years (Fig. 1). Reducing fertility (which may simulate fruitbody predation by insects or removal by humans, or poor conditions for sporulation) caused a corresponding decrease in primary mycelia and of course basidiospores, but had much less effect on secondary and especially fruiting mycelia, stages which have much greater survivorship (Fig. 1A). Reducing the transition *b-p*, which might simulate a decrease of sites conducive to successful germination and establishment (infection courts), had a similar effect (data not shown). Reducing the transition *p-s* had a similar effect on secondary and fruiting mycelia but much less of an impact on primary, although they still were reduced by about 30% (Fig. 1B). Virtually the same effect was observed when the transition *s-f* was reduced by 90% (data not shown). The most dramatic effect on the population was observed when the transition *f-f* was reduced (Fig 1C), which

might simulate removal of trees with fruiting as a sanitation approach to disease management. In this case the population was nearly extinct in 10 years.

Because a given mycelial stage can arise from two or more other stages, it is instructive to examine the sources of the stages in the first year of the unmodified model (Table 1). Fifty-eight percent of secondary mycelia are derived from last year's secondary mycelia, 28% from primary mycelia, and a relatively small proportion from fruiting mycelia that reverted to nonfruiting, secondary mycelia. These transitions may vary greatly in importance in different species and populations, reflecting both transition probabilities and the abundances of each stage in the previous year. Populations with different stage structure and transition probabilities would likely respond differently to perturbation.

To explore this in the context of a management question, a population of a hypothetical mycorrhizal fungus was simulated. In some areas, commercial harvesting of wild mushrooms such as *Cantharellus formosus* (Pacific golden chanterelle, formerly identified as *C. cibarius*) is intensive and may negatively impact natural populations. However, mycologists' intuition and some recent empirical data suggest that such harvesting probably has little negative impact (Arnolds, 1995; Egli *et al.*, 1990; Norvell, 1995). More data are needed than presently available to develop a model that can be used to predict the effects of harvesting, but the problem is considered hypothetically here to see how sensitivity to harvesting may vary among fungi. As in the polypore population, an initial population of 208 fruiting genets in a hectare is assumed. Initial basidiospore population (5.84×10^{12}) and fertility were calculated from data of Largent and Sime (1994). The population is modeled, relative to the polypore population, with a higher probability of basidiospore establishment as primary mycelium, a larger pool of primary mycelia, and a lower proportion of secondary mycelia that fruit in any given year. Although chanterelles fruit more reliably than most, fruiting is sporadic for many mycorrhizal fungi (see section 2, above), making it more likely than in the case of a perennial polypore that a mycelium fruiting one year will not fruit the next year. Consequently, the sources of the stages are different (Table 2). The steady-state transition matrix appears as follows:

$$\mathbf{A}_{\text{mycorrhizal}} = \begin{array}{c} \\ b \\ p \\ s \\ f \end{array} \begin{array}{c} \begin{array}{cccc} b & p & s & f \end{array} \\ \begin{bmatrix} 0 & 0 & 0 & 2.8\times10^{10} \\ 1.1\times10^{-9} & 0.0001 & 0 & 0 \\ 2.5\times10^{-11} & 0.0026 & 0.46 & 0.3 \\ 0 & 0 & 0.16 & 0.68 \end{bmatrix} \end{array} \tag{7}$$

Table 2. Numerical transitions among stages of a population of a mycorrhizal fungus in the first year of a hypothetical model.

Mycelia at end of 1st yr	Sources of mycelia: Basidiospores	Primary	Secondary [a]	Fruiting	Total
Primary	6424	1	—	—	6425
Secondary	146	17	191	62	416
Fruiting	—	—	66	142	208

[a] References to secondary mycelia refer to nonfruiting secondary mycelia.

The results show that growth of this hypothetical population is more sensitive to decreasing fertility (fruitbody removal) than is the polypore population. A 90% reduction in fertility caused 92% drop in fruiting mycelia in the mycorrhizal fungus after 15 years (Fig. 2) but only 35% drop in the polypore (Fig. 1A). With estimated parameters, these models should not be taken to contradict empirical data, which suggest that intensive chanterelle harvest has little effect. Also, effects other than on fertility are conceivable, including damage to fruiting mycelia or the effects of trampling on soil (Arnolds, 1995; Egli *et al.*, 1990). However, with more accurate demographic parameters, such models offer another alternative to intuition in predicting the impacts of such perturbance. These models show that subtle differences in the stage structure and dynamics of fungal populations can greatly affect their behavior in response to perturbation.

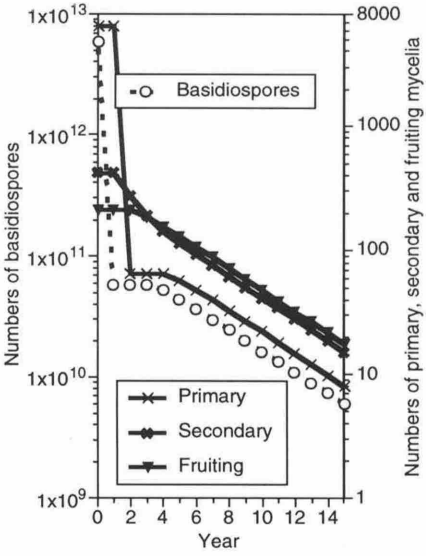

Figure 2. Effects of perturbation of a hypothetical population of a mycorrhizal fungus. At year 0 the population is at approximately steady state. After that point there is 90% reduction in fertility of fruiting mycelia (*F*), simulating the effect of heavy commercial harvest.

The left and right eigenvectors of such a matrix represent the reproductive value at each stage (the relative contribution that a typical individual of the stage will make to the next generation, taking into account life expectancy and future fertility) and stable stage distribution, respectively. They can be estimated fairly easily with a spreadsheet using the "power method" (Caswell, 1989). Alternatively various software packages such as Matlab (The Mathworks, Inc., Natick Massachussetts; available on many university mainframes) and RAMAS/stage (Applied Biomathematics, Setauket, New York) can calculate eigenvectors.

The dominant eigenvalue, which is the finite growth rate, λ (the growth rate after a stable stage distribution is reached), is also available in those procedures. In our examples, the stage distributions reflect the huge numbers of basidiospores relative to other stages (Table 3). Reproductive values of basidiospores are quite small relative to stages of most other organisms, but the reproductive value of basidiospores of the mycorrhizal fungus is greater than that of the polypore; that of primary mycelia is smaller.

Table 3. Stable stage distributions, reproductive values, and finite growth rates (right and left eigenvectors and λ = dominant eigenvalues, respectively) of the hypothetical polypore and mycorrhizal fungus matrix models. Each eigenvector is scaled to sum to 1.

	Polypore ($\lambda = 1.001$)		Mycorrhizal fungus ($\lambda = 1.000$)	
	Stable stage distribution	Reproductive values	Stable stage distribution	Reproductive values
Basidiospore	≈1	1.70×10^{-13}	≈1	6.4×10^{-12}
Primary	1.37×10^{-11}	0.011	1.1×10^{-9}	5.9×10^{-4}
Secondary [a]	2.60×10^{-12}	0.217	7.1×10^{-11}	0.228
Fruiting	4.64×10^{-12}	0.772	3.6×10^{-11}	0.771

[a] References to secondary mycelia refer to nonfruiting secondary mycelia.

An informative measure of the importance of each transition element is its elasticity. Elasticity of element a_{ij} (i and j refer to rows and columns of the matrix, respectively) is $a_{ij}v_iw_j/(\lambda<w,v>)$, where v and w are the left and right eigenvectors and $<w,v>$ is their scalar product (Caswell, 1989; DeKroon *et al.*, 1986). Elasticities give the proportional change in λ resulting from a proportional change in a_{ij}. They provide a more analytic and easily compared approach to assessing the effect of variation in elements than the process used above, varying the elements consecutively and running the model. Also, they reflect more subtle changes in matrix coefficients than those used in the sensitivity analysis above. Elasticities sum to one within a matrix and can conveniently be compared as pie charts (Fig. 3).

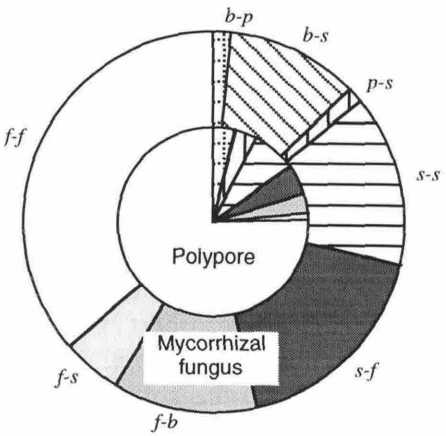

Figure 3. Elasticities of elements of transition matrices for hypothetical polypore and mycorrhizal fungus populations. Elasticities for transition p-p are very small and are not shown.

The dynamics of the polypore model are overwhelmingly dominated by the carryover of fruiting mycelia (Fig. 3). A change in this

probability would have a large proportional effect on population growth. In the model of the mycorrhizal fungus, that carryover probability is less important, and the dynamics of nonfruiting, secondary mycelia are considerably more important. Also, a change in fertility (*f-b*) would impact the mycorrhizal fungus population more than three times as much as the polypore population.

These models are largely hypothetical, and management decisions should not be based on them without more data and a broader view. They ignore, for instance, the importance of spore production in colonizing areas of newly available habitat as opposed to population maintenance. Data-gathering effort should focus on transitions with high elasticity. For some fungi, it is an open question whether data can be obtained to develop such a matrix model in realistic detail. Even when the parameters are based on sound field data, simple matrix models may not accurately forecast population numbers because they do not take into account stochasticity, density dependence and indirect effects of changes in population size. Such effects can be incorporated into more sophisticated matrix models (Caswell, 1989), which can be constructed conveniently with the software, RAMAS/stage (Ferson, 1993). Such models may verge on systems models.

4.3 Systems Models

Systems or simulation models incorporate many details of the environment and interactions to predict the development of the modeled process. They may be based on a matrix model (Bruhn and Fry, 1981), but one modified greatly to account for more factors and interactions. They usually take the form of computer programs and involve detailed inputs.

Although little work of this sort has apparently been done with nonpathogenic fungi, a number of such models have been developed for plant diseases caused by fungi. For instance, the Western Root Disease Model, a module of the Prognosis Model for Stand Development, models root diseases caused by *Armillaria* spp. and *Phellinus weirii* in coniferous forests of the western United States (Marsden *et al.*, 1993; Stage *et al.*, 1990). The user provides a detailed stand inventory, initial disease survey results, management actions, etc., and the model predicts disease development and stand yield in the future. The model incorporates spatial relationships and somatic growth from tree to tree, but apparently does not explicitly deal with fruiting, basidiospore production and the establishment of new infection foci.

In a demonstration of the model, stand and disease data from four ponderosa pine stands in New Mexico were used to simulate future stand development, the effects of diseases, and the effects of silvicultural treatments (Marsden *et al.*, 1993). In addition to Armillaria root rot, dwarf mistletoe

(*Arceuthobium vaginatum* subsp. *cryptopodum*) affected the stands. The root disease was simulated by the Western Root Disease Model; dwarf mistletoe was incorporated into the base Prognosis stand model. A typical stand had an actual inventory of 8402 trees ha^{-1} and merchantable volume of 50 m^3 ha^{-1}, 92% of which was ponderosa pine. Without disease, it was projected to reach 187 m^3 ha^{-1} in 80 years, but with the levels of dwarf mistletoe and Armillaria root disease that were measured in the stand, the model predicted that volume would increase slightly and then decrease, ending the 80-year run at 35 m^3 ha^{-1}. This impact may be overestimated because the model did not account for natural regeneration in gaps created by tree mortality.

The model predicted that silvicultural measures to reduce disease impact would be relatively ineffective. Overstory removal was simulated with and without removal of stumps. Volume at the end of the simulation was slightly less in the stand from which stumps were removed and was declining in both scenarios. My experience with the Inland Empire variant of the models (primarily northern Idaho and western Montana) in mixed conifer stands has given similar results: stump removal was usually ineffective or deleterious (unpublished). Knowledge of the disease as well as field trials, however, suggest that stump removal should reduce future disease and increase yield to some extent (Morrison *et al.*, 1988). In another stand, clearcut followed by removal of stumps down to a diameter of 13 cm appeared to have somewhat greater effect on both diseases, but the length of the simulation did not permit evaluation of the treatments at stand maturity (Marsden *et al.*, 1993).

Environmental conditions, both abiotic and biotic, certainly affect population growth of fungi. All aspects of the life cycle of many fungi are highly dependent on temperature and especially moisture, and these are commonly incorporated into simulation models and even relatively simple matrix models of many kinds of organisms. Competitors, parasites and other kinds of antagonists have been addressed also in modelling (Begon *et al.*, 1996; Caswell, 1989; Gotelli, 1995; Tuljapurkar and Caswell, 1997).

5. DENSITY DEPENDENCE

The logistic model above includes the parameter K that incorporates the net effect on population growth rates of decreased birth and increased death rates due to crowding. Similar density-dependence functions can be used in matrix and other models (Caswell, 1989). Density may affect population growth in many ways.

Although we usually associate density dependence with decreased growth at high densities, low density may also have a negative impact on

population growth. Because heterothallic fungi must meet and mate to reproduce, sexual fertility probably increases with population size up to a threshold population level. When spore production is low, the likelihood of two compatible spores settling and successfully germinating in close proximity is reduced, so a lower proportion of spores succeed in becoming reproductive mycelia. The same pattern may occur when mutualistic mycobionts are at levels too low for significant juxtaposition with their symbionts, preventing increase of both populations. This general pattern is termed the "Allee effect," first recognized in animals that hunt, avoid predators, or reproduce more efficiently in groups than individually (Allee *et al.*, 1949).

At high population levels, population growth declines due to various factors. One limiting factor that has long been recognized in plant pathology is the availability of infection courts, openings that give a pathogen access through a plant's outer structural defenses. As a population increases, a lower proportion of propagules will succeed in accessing such limited sites. Similarly, nonpathogenic fungi may require an opening created by an animal or an exogenous dispersal agent whose abundance limits population growth of the fungus.

Perhaps the most obvious and important density-dependent effect is a scarcity of suitable resources. For successful colonization, a resource must be available that provides necessary nutrients in an appropriate form. The resource must be properly conditioned (e.g., stage of decay) and, for pathogens, it must be genetically susceptible and at a susceptible stage of maturity. Although basic resources tend to be relatively predictable for plants, they are highly variable for many fungi. This variability may be modelled by stochastic or other variation in carrying capacity.

Another, more subtle way that high density can impact populations is through inefficient resource utilization. A resource unit of a given size colonized by a single or several individuals may support abundant fruiting. If the same resource unit is colonized by many small, somatically incompatible individuals, none may be able to capture sufficient territory to support normal fruiting (fertility is reduced) and decay of the resource may even be limited (Rayner *et al.*, 1984).

Just as in other organisms, this situation is probably averted in fungi in many cases by attrition, often called "self-thinning." In a sparsely colonized forest floor, for instance, leaves, twigs, rootlets, or stumps would be rapidly colonized, a process that has been termed primary resource capture (Rayner and Boddy, 1988). In such a situation, however, the stand of fungi eventually "closes," just as do stands of trees, as neighbors meet (Frankland *et al.*, 1995). At this point, aside from invading the territory of a neighbor, a mycelium's only chance for survival is to wait for new resource units to appear within its domain and quickly capture them. Fungi that do this suc-

cessfully control a sufficiently large domain that new resource units, such as leaves or dead trees, are added to it occasionally. Because the likelihood of acquiring new resource units and thus surviving is greater in a larger domain, one can predict that density-dependent mortality of genets must be very high in small size classes. Such mortality is difficult to demonstrate directly, but size distributions of genets of at least two such fungi show a high frequency in the smallest size class and a uniformly low frequency of all larger size classes (Holmer and Stenlid, 1991; Worrall, 1994). Such a structure fits the prediction that the small genets die before reaching larger size classes.

6. POPULATION SIZE AND GENETIC STRUCTURE

6.1 Bottlenecks and Genetic Drift

Local populations of fungi may fluctuate greatly in size, even in one year (Burdon, 1992). A pathogen may become established early in a growing season from very limited inoculum that survived a period with no host or immigrated, then go through a period of exponential growth, resulting in millions of individual mycelia in a few months. Perhaps only a few of those mycelia may give rise to infections in the following year. Such population dynamics may be common among fungi, especially those with short-lived mycelia. Forest succession, catastrophic disturbance, or even the death and decay of an individual plant may involve the dramatic rise and fall of populations of many associated fungi. When fungi, most notably pathogens, are transported by humans to new regions and there proliferate, they go similarly through the process of establishment from one or several individuals to a large population.

Several effects of population size have implications for genetic structure. Large populations show little deviation in frequency of neutral alleles from Hardy-Weinberg predictions. In small populations, however, such frequencies may vary greatly, such that they reach 0% or 100% and are lost or permanently fixed in the population (Burnett, 1975). This process is called genetic drift. With alleles subject to selection, a similar process operates, but it is modified by the degree of selection. In large populations, selection predominates; in small populations, drift predominates. Because of the more frequent and larger population fluctuations, ruderal fungi (which have fast growth, unstable populations, early commitment to reproduction, and utilize relatively labile substrates) probably experience genetic drift more than competitive/combative and especially stress-tolerant fungi (which tend to exhibit slow growth, stable populations, delayed commitment to reproduc-

tion, and utilize relatively recalcitrant substrates) (Burdon, 1992; Cooke and Rayner, 1984).

Genetic drift is expected in populations that decline in such a way as to randomly remove members. It is a statistical process. But if the population decline in itself is selective in nature, the process can more rapidly and directly affect corresponding allele frequencies. The population that recovers from the crash caused by such an "exclusion filter" will be very different from the preceding one with regard to the selected traits. The rapid appearance in pathogens of resistance to certain fungicides and virulence corresponding to new resistance genes in the host is related to this phenomenon.

7. CONCLUSIONS

A demographic approach may provide fresh insight into questions of fungal biology and ecology as well as pointing to areas where knowledge is lacking. Although gathering data to model fungal populations is challenging, it should be possible to make reasonable estimates of important demographic parameters for at least some fungi. Depending on the objectives, fungal populations may be measured as numbers of genets, biomass, numbers or area of lesions or colonies, or a proxy for population measurement such as numbers of colony-forming units isolated or fruit bodies collected.

The logistic equation has been widely used as a fundamental model of the epidemiology of plant diseases caused by fungi, and some diseases have been modeled in complex computer simulations, but relatively little work has gone into modelling of populations of nonpathogenic fungi. Hypothetical models of two populations show the potential utility of matrix models in illuminating features of fungal population dynamics and in considering problems of fungal management. Subtle differences in stage structure and dynamics of fungal populations may greatly affect sensitivity of the populations to perturbation.

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