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by

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SUMMARY

During colonisation there is generally a transition from a predominantly density-independent selection regime to a predominantly density-dependent one. If appropriate genetic variation exists in a colonising population, it is likely that genetic change will occur as population density increases. An attempt is made in this thesis to test for genetic change in colonising populations of the grass Poa annua.

It is argued that under conditions of density-independent selection, genotypes with rapid development to reproduction, short lives and high seed output are selected. But if selection is density dependent, genotypes which spread the risks of seed reproduction over a greater period of time and which reproduce vegetatively are favoured. A mathematical model is developed to predict the course of demographic and genetic change during colonisation in a population containing genetic variation for life-historical characters.

Genetic change will only occur if appropriate genetic variation exists; its presence is demonstrated between and within a set of natural populations of Poa annua. Variation between populations is shown to depend on their history of selection; density-independent selected populations are generally shorter lived, have shorter prereproductive periods, greater initial seed production and are less vigorous in their vegetative growth than their density-dependent   selected counterparts.

Genetic change under artificial conditions of density independence and dependence is tested using an artificial population synthesised from a set of natural ones. It is found that genetic differences can be observed between samples after twenty months of selection at low or high population density. Prereproductive periods

are slightly shorter and initial seed production slightly greater in density-independent selected samples than in their density-dependent selected counterparts.

As a final test of the hypothesis, the analysis of a natural colonising population of Poa annua is described. A demographic analysis of colonisation shows that population density increases very rapidly during the early stages, but that the rate of increase declines as density-dependent constraints come into operation. Survival during the early stages of life and reproduction throughout life are much reduced at high density in comparison to low density. However, a test for genetic change is not made, due to insufficient change in selection pressures.

To

my mother and father

ACKNOWLEDGEMENTS

CONTENTS

Abbreviations used in life history functions

Abbreviation	Definition	First cited
A	Transition matrix of all possible one step time transitions in a plant population (both seed and adult)	Chapter 3.2.3
AA	As A but for adult population only	Chapter 3.2.2
AS	As A but for seed population only	Chapter 3.2.1
B_t	Number of individuals born at time t(animal populations)	Chapter 3.2
b_x	Number of progeny produced per individual, between age x and x+1	Chapter 2.2
d_x	Proportion of individuals alive at age 0, dead by age x	Figure 6.8
exp(x)	Exponential of x: e^x	Chapter 3.3
gs_x	Proportion of seeds alive at age x, germinated by age x+1	Chapter 3.2.1
l_x	Proportion of adult individuals alive at age 0, alive by age x	Chapter 2.2
ls_x	Proportion of seed individuals alive at age 0, alive by age x	Chapter 3.2.1
m	Instantaneous rate of increase	Chapter 2.2
N	Population density	Chapter 3.3
$_tN$	Vector of number seed and adult individuals of all ages at time t	Chapter 3.2.3
$_tn_x$	Number of adult individuals aged x at time t	Chapter 3.2.2
$_tNA$	As $_tN$ but for adult population only	Chapter 3.2.2
$_tNS$	As $_tN$ but for seed population only	Chapter 3.2.1
$_tns_x$	Number of seeds aged x at time t	Chapter 3.2.1
p_x	Proportion of adults surviving from age x to x+1	Chapter 3.2.2
ps_x	Proportion of seeds surviving from age x to x+1	Chapter 3.2.1

Abbreviation	Definition	First cited
qs_x	Proportion of seeds alive at age x, dead by age x+1	Chapter 3.2.1
r	Intrinsic rate of natural increase (maximum value of m)	Chapter 2.2
t	time	Chapter 3.2
u	Maximum age to which a seed survives	Chapter 3.2.1
v	Maximum age to which an adult individual survives (or reproduces)	Chapter 3.2
w-1	Maximum age of innate dormancy	Chapter 3.2.1
x	Age	Chapter 2.2
λ	finite rate of increase	Chapter 3.2

CHAPTER 1.

GENERAL INTRODUCTION

Evolution can be defined as genetic change in groups of organisms (Dobzhansky 1951). Within this definition we can include changes from small transitory fluctuations in gene frequencies in populations to large scale alterations over the course of geological time.

At any level of change, evolution is essentially a theory concerning the interaction between genes and the environments in which they occur. The continuity of a gene through time is a function of its environment and the environment may be partly a function of the gene. We may take the environment to comprise the whole universe with the exception of that gene itself, in which case there are many levels at which interactions between genes and environments may be studied. But some are more profitable than others and this thesis is primarily related to the 'population environment', as the population is the unit within which genetic change is most frequently measured (Ehrlich & Raven 1969).

The study of the genetic structure of groups of organisms and their environments have emerged as two quite distinct disciplines. Firstly population genetics has arisen as the mathematical analysis of the consequences of Mendelian inheritance in groups of organisms. In theoretical studies the environment has been reduced to parameters such as selection coefficients, population size, migration rates etc. and in so doing, it has been possible to predict the outcome of a wide variety of gene/environment interactions. But values of the parameters have generally been ascertained more from introspection than observation, or if by experiment then under conditions far removed from the natural environment. Thus it may be said that

population genetics has established a set of hypotheses about genes in their environments by reducing these environments to a few simple parameters.

Secondly, the study of the environment has arisen as the largely empirical discipline of ecology. A population ecologist for example, studies population size, how it changes, the factors instrumental in its regulation; and usually he does this by observing real populations. But in so doing, he generally assumes that all individuals are genetically identical and that the population is not evolving. Hence he accepts the presence of environmental complexity, while reducing the genetic structure of the population to an artificially simple state.

However in the eyes of an evolutionary biologist, population genetics and ecology are integral components of a single process of evolution. Indeed, the fundamental assertion on which this thesis is built is that sufficient conditions for the description of evolution require both genetic and environmental parameters. It will never be possible to understand genetic change without knowledge of the interaction between genes and their environments. These are generalisations which have been made many times in the past (see for example Sammeta & Levins 1970), but it is essential that they should be made at the outset.

It has recently been argued that our understanding of evolution is almost complete, that there are but few remaining gaps in our knowledge worth investigation (Monod 1972, p 132). I would challenge this proposition by asking in what proportion of natural populations can we predict even to an order of magnitude the rate of change of gene frequencies? The answer to this must surely be that the proportion is negligible. I would suggest rather that evolution is a

hypothesis concerning the natural living world and while there is much circumstantial historical evidence to support it, we have hardly begun to test it quantitatively. How else could we explain the present controversy over the relevance of two such conflicting evolutionary mechanisms as selection and drift (Lewontin 1974)? Or how else could the co-occurrence of two viewpoints as opposed as individual and group selection be explained (Wynne-Edwards 1962, Williams 1966)?

One of the most important reasons for our present ignorance of the process of genetic change arises from our methods of studying it; it is all to easy to ask questions or to formulate hypotheses that cannot be proven incorrect under any circumstances. Arguments for evolution based on the observation that organisms are adapted to their environments, require value judgements over the meaning of 'adapted'. The fact that 'non-adapted' organisms are not found is taken as evidence for evolution but a sceptic might argue that it is really evidence for 'adaptation' having been defined in a way to include all organisms. The apparent strength of the theory in its ability to explain all observations, may in some respects be its greatest weakness.

Another foundation stone of evolutionary theory - the fossil record, purports to show us genetic changes that have occurred over the course of geological time, but more precisely tells us that there are structural dissimilarities between organisms on different geological horizons. Whether relics found on different horizons are related and whether the dissimilarities are genetic cannot unfortunately be tested (Birch & Ehrlich 1967).

It might at first seem easier to test evolutionary theory by studies of contemporary populations, in which it is possible to make more detailed analyses of the mechanisms involved. But this is not necessarily the case. Suppose we wish to test the hypothesis that

natural selection brings about genetic change in populations. We are told that natural selection is an _a posteriori_ definition (Cook 1971), that we recognise the presence of selection by observing genetic change. If this is true our hypothesis can be restated as 'genetic change brings about genetic change in populations', a theory which could not be proven incorrect under any circumstances. I would therefore contend that in the formulation of evolutionary hypotheses, great care must be taken to ensure that there are no elements of tautology. In the terminology of Popper (1968), hypotheses should be formulated in such a way as to make it conceptually possible to design an experiment which could in principle refute or falsify them.

In this thesis I want to examine the interaction between genes and their environments. I want to establish whether there are characteristic genotypic changes associated with a particular environmental change. Since I am interested in genetic change rather than genetic differences, the choice of a suitable system is not easy. Rapid genetic change can be observed only if appropriate genetic variation is present and natural selection is strong. But strong selection is most often associated with the activities of man (for example industrial melanism in insects and heavy metal tolerance in plants) and there must always remain an element of doubt in its relationship to evolution in more natural environments.

However, one kind of environmental change that is general to the evolutionary process is the change in population density associated with colonisation, since all populations must undergo periods of colonisation. Thus in this thesis I have chosen colonisation as a system which satisfies the criteria of environmental change.

The choice of a species on which to study colonisation is also critical. I have chosen to study the grass *Poa annua* L. as it has several characteristics that predispose it for this research. Firstly it is a highly successful colonist with the characteristics generally associated with weedy species (Baker 1965, Gibeault & Goetze 1972). But it is not confined to 'opportunistic' environments because it can be found as a stable component of dense pastures. However it is sufficiently short lived in many situations to allow several generations of selection during the time available for research, an important consideration in a study of genetic change. Finally evidence from a number of sources suggests that it is a genetically variable species and that this variation is of a kind that could be important during colonisation (Tutin 1957, Hovin 1957, Timm 1965, Gibeault 1971, Gibeault & Goetze 1972, Ellis 1972, Wells 1974).

The proposition examined by this thesis stated formally is that specific genetic changes occur in populations of *Poa annua* during colonisation due to changes in population density. At the outset it is necessary to identify the kind of genetic variation that should *a priori* be under selection during colonisation and the next chapter works towards this end. It reviews life-historical genetic variation and leads to a general theory of the evolution of life histories during colonisation. This is followed in Chapter 3 by a more precise formulation of the theory in the form of a mathematical model that is suitable for consideration of colonisation by *Poa annua*. But the theory only holds if certain prerequisites are satisfied in colonising populations; appropriate genetic variation must be present and selection pressures must be great enough for genetic change to be perceptible. In Chapter 4 these conditions are tested by analysis of natural populations of *Poa annua*. The next step is the analysis of

colonising populations for the presence of genetic change and I approach this problem in two ways. Firstly in Chapter 5 I look for genetic change in an artificial population in which conditions for change are optimised and secondly in Chapter 6 a natural episode of colonisation is monitored. However the latter approach is incomplete as colonisation did not proceed sufficiently far during the time available. Consequently Chapter 6 is largely concerned with in situ demography during colonisation. Finally the various ideas of the thesis are brought together in Chapter 7.

CHAPTER 2

THE EVOLUTION OF LIFE HISTORIES: A REVIEW

2.1 Introduction

It is essential to begin the study of genetic change during colonisation by defining the kind of genetic variation that is likely to be under selection. Many loci may be under selective forces completely independent of population density and to study them here would be valueless, so if it is possible to define characters that lend themselves to density-dependent selection, much wasted effort can be avoided. In the course of this chapter it should become clear that certain life-historical characters fulfil these requirements and that general theories of the way in which they change during colonisation can be formulated.

There is an important sense in which all evolution by natural selection is evolution of life histories. For example, the well known increase in the carbonaria heterozygote of the Peppered Moth (Biston betularia)can be said to have arisen from an increase in adult survival due to reduced predation on soot covered treetrunks (Kettlewell 1955). Or the evolution of tolerance to heavy metals in the grass Agrostis tenuis can be interpreted in terms of a catastrophic decline in survival of all age groups in genotypes without tolerance on contaminated soil (McNeilly & Bradshaw 1968). But life histories need not only be seen as a reflection of particular morphological and physiological factors. Each population has a typical life history arising from a host of environmental, biochemical, physiological and morphological variations. It is quite justifiable to consider this life history and its variation as a phenomenon in itself, without complete knowledge of the reasons for its presence. Such an approach is adopted in this thesis and it is assumed that components of life histories are characters in their own

right with polygenically determined variation. (For example, I shall assume that the 'clutch size' of a population is a variable with a mean and a variance to which there may be a genetic component.)

In another sense there are important differences between life histories and other characters. Although variation in most characters such as wing colour in <u>Biston betularia</u> or plant height may be related to variation in fitness, fitness must be determined independently. Life-historical characters on the other hand are in themselves components of fitness and by measuring them fitness itself is being estimated. The intimate relationship between life-historical characters and fitness has led a number of people to consider the ways in which they evolve. This has generally involved theoretical rather than empirical research, although there have been a few notable exceptions.

This chapter reviews our knowledge of life histories, how they can be measured, how they evolve and the consequences of their evolution in terms of population differentiation. These studies lead to a theory of evolution of life histories during colonisation which can be tested using <u>Poa annua</u>.

2.2 Life histories

It is possible to imagine an infinite range of life histories. Length of life could in principle vary from a few minutes to effective immortality and reproduction could be distributed through life in a very large number of ways. Reproduction might, for example, occur only once or it might occur repeatedly and in this case numbers of progeny could also vary. Furthermore, development time before the onset of reproduction could vary from individual to individual. Bearing in mind that all these factors could vary independently of one another, we can appreciate that the number of possible life histories is very large indeed.

However, it is impossible for an infinite number of life

histories to occur in a finite number of organisms, so we must accept that not all possible combinations do in fact occur. For example, no plant or animal has ever been shown to be immortal, although some are known to live for a very long time. And in general terms there are some combinations of length of life and reproduction that appear to be associated, so that all forms do not vary independently of one another. For example, a low probability of survival to maturity is often correlated with a high reproductive output (although the causal relationships here are open to question).

Despite the limitations on the number of life histories that can occur, the range observable in the plant and animal kingdoms is still formidably large. Length of life varies from a few minutes in some bacteria to thousands of years in the lichen species <u>Rhizocarpon</u> <u>geographicum</u> (Benedict 1967). Reproduction may occur only once as in the mayfly, or it may occur regularly for hundreds of years as in long lived tree and grass species. Numbers of progeny produced during reproduction can vary from the extreme conservatism of humans where even twins are unusual, to the billions of spores produced by the giant puffball. Yet if life histories of these species are moulded by natural selection, all these extremes and those that lie in between should represent optimal histories for their environments.

If we wish to compare different life histories and to examine the way in which they evolve, we first require a quantitative method by which they can be measured. This is conveniently done by determining length of life and reproductive output as functions of age in the following manner. Let us suppose that an individual is x years old (or days or months etc.); then the probability of that individual surviving from age 0 to x is described by the function l_x. A table of these probabilities over different values of x is known as a life table. Similarly b_x is a function describing number of progeny produced

between age x and x+1. Thus a life table provides a quantitative measure of length of life,and reproductive output a measure of numbers of progeny, when they are produced and the development time before onset of reproduction (prereproductive period).

Human life tables have been studied by actuaries for many years. By calculating life expectancy from these tables, they are able to set appropriate life insurance premiums. But it was not until the 1930's that life tables were constructed for populations of other species (Pearl & Miner 1935), when it was first appreciated that life expectancy was an important ecological attribute. At about the same time Fisher (1958) showed that the life table was a fundamental component of fitness of a genotype.

Pearl and Miner defined three broad categories of life tables that have become known as Type 1, Type 2 and Type 3. Type 1 arises when the probability of mortality is small up to a certain age when most individuals die; life tables of this kind often occur in laboratory populations with fixed supplies of food. Type 2 describes lives in which the probability of mortality remains constant as age increases (negative exponential); a number of species of birds have this kind of life table after reaching maturity, for example the blackbird (Lack 1943). In addition most of the rather limited number of demographic studies on plant populations have shown life tables of this form in seed populations (Roberts & Dawkins 1967) and in adult populations (Tamm 1956, Sagar 1959, Sarukhan 1971, Antonovics 1972). Type 3 occurs if the probability of mortality is very high early in life but declines with age, as would arise in plant populations where there was a small probability of seed falling in a suitable site for germination. Clearly these three types are only particular extremes within a continuum of variation and it is likely that elements of each kind would be combined in many populations. For example, Antonovics (1972)

suggested that if he had measured seed and seedling mortality, the life table of _Anthoxanthum odoratum_ would have been of Type 3 initially, changing to Type 2 in older individuals. The ideas of Pearl and Miner stimulated much research on animal demography (see for example Deevey 1947, Haldane 1953), but not until recently any studies on plant demography (Harper 1967, Harper & White 1974).

It is more difficult to make generalisations about reproduction/ age functions (b_x), since reproduction can vary in time, quantity and duration. Nevertheless certain basic distinctions can be drawn and undoubtedly the most important of these is whether reproduction occurs only once in a lifetime (semelparity) or repeatedly (iteroparity) (Cole 1954); annual and perennial plants are good examples of this distinction. In iteroparous populations we can also draw a quantitative distinction between those in which individuals reproduce for only a few years (eg. _Anthoxanthum odoratum_ Antonovics 1972) and those in which reproduction continues for many years such as long lived forest tree species. We can also distinguish between populations with different times for development before the onset of reproduction (prereproductive period); weeds such as _Senecio vulgaris_ start to produce seed within a few weeks of germination whereas several species of _Orchidaceae_ grow for many years before reproducing (eg. _Listera ovata_). It need hardly be emphasised that the number of progeny produced each time reproduction takes place (clutch size) is also an important variable between populations. Yet all these variables are succinctly summarised in the function b_x which together with l_x provides much information about life histories.

It seems intuitively reasonable that for each life history there is a corresponding population growth rate. The relationship was described formally by Lotka (1956); the l_x and b_x functions are related

to the instantaneous rate of increase (m) as follows:

$$1 = \int_0^\infty e^{-m \cdot x} \cdot l_x \cdot b_x \, dx \qquad \text{Eq. 2.1}$$

This is an implicit equation for m and it can be solved if the l_x and b_x functions are known and we assume the population to be at age stability. (Until age stability is reached m is not constant.) There is another discontinuous form of this equation which is particularly useful when considering real populations, since l_x and b_x are usually estimated at discrete points in time. It takes the form:

$$1 = \sum_0^\infty \lambda^{-x} \cdot l_x \cdot b_x \qquad \text{Eq. 2.2}$$

where, λ = finite rate of increase.

These equations can equally well be applied to units other than populations insofar as we can imagine them to have life histories. In particular, each genotype in a population has a life history that could in principle be measured and hence a corresponding rate of growth. This genotypic rate of growth is of special interest since it is the absolute fitness of the genotype and will determine its contribution to future generations (Fisher 1958). In the sections that follow we must imagine population life histories to be made up of the combined effects of all the genotypes that they contain. This will help to clarify the way in which population life histories are moulded by natural selection through the gradual fixation of genotypes with greatest rates of growth.

There is considerable confusion surrounding the use of the instantaneous rate of increase (m) (Andrewartha & Birch 1954, Hairston et al. 1970) which has never been completely resolved. This arises from the fact that l_x and b_x are often functions of density from which

it follows that m is also a function of density. Usually there is a maximal value of m at a fairly low density and in this thesis I refer to this as r (the intrinsic rate of natural increase). I will use m and r both in the context of genotypes and populations, but it should be clear from the context to which unit I am referring.

2.3 Life histories under natural selection

There is therefore a vast range of life histories observable in the plant and animal kingdoms. If we are to begin to understand this range we must study its origins by analysing life histories under natural selection within populations. And in doing this it will help to keep in mind a hypothetical organism with a life cycle that leads it to be extraordinarily fit - a kind of 'Darwinian demon'. We can imagine this organism to start reproduction immediately after birth, to produce huge numbers of offspring each time it reproduces and never to die. However unrealistic it may be, the reasons for its non-existence shed some light on variation in real life histories, since we shall see that if it did exist there could be no variation.

I have briefly mentioned that the average life history of a population can be considered as being made up of all the life histories of its component genotypes. It is clear that genotypes that live longer and/or leave more progeny gradually come to predominate and in so doing alter the population life history in the direction of the 'demonic ideal'. The 'Darwinian demon' then has the perfect life history that leads to the greatest possible instantaneous rate of increase (m) or absolute fitness. In spite of this, the ideal has never been achieved by any population. The immediate reason for this paradox is that in real life resources are limited and must be partitioned between growth, maintenance and reproduction. When these energy sinks are in competition with one another, one gains at the expense of the others and this is reflected in the life history.

Insufficient energy for maintenance leads to physiological breakdown and early death; lack of energy for reproduction results in fewer progeny and lack of energy for growth may lead to less reproduction in the future. So although the 'Darwinian demon' is the eventual goal of natural selection, in real life selection leads to a compromise life-history, the exact compromise depending on the environment and the genetic structure of the population.

We must therefore examine the life-historical compromises made by some natural populations. By making some assumptions it is also possible to predict optimal life histories in theoretical environments; the results of some of these studies are also considered.

2.3.1 Empirical studies of life-historical characters under selection

Clutch size   Some of the most elegant studies of selection on life-historical characters were carried out by Lack, making observations on clutch size in a number of bird species (reviewed in Lack 1954). It is known that there is variation in clutch size within populations of many bird species and it is suspected that there is a heritable component to this variation in some of them (Kluyver 1951). At first sight one might predict that genotypes with the largest clutch size should be selected because they leave more offspring, but Lack cited a number of cases where this was not the case. For example, he found that mortality was higher in nests with three than with two eggs in the common swift (Apus apus), to the extent that more offspring finally left the nest with the smaller clutch size (1.6 fledglings per nest as opposed to 1.4) (Lack & Lack 1951). These results were paralleled by the alpine swift (Apus melba), but in this case the optimal clutch size was three (Lack & Arn 1947). Some other species appeared to have the same mortality rates in broods of

different sizes, but the young were of different weights when they left the nest. Lack noticed in the starling (<u>Sturnus</u> <u>vulgaris</u>) that post fledgling mortality was higher in broods greater than the population mean, so that a clutch size of five was most efficient (Lack 1948).

It appears from Lack's observations that there is competition for energy between maintenance and reproduction; up to a certain point increasing clutch size increase fitness, but beyond this it leads to reduced fitness through increased mortality. Although this is most interesting, it can only be used with some caution because it depends on the assumption that there is no other genetic life-historical variation. It is not possible to make rigorous statements about fitness of different genotypes without knowledge of their complete life histories. Nonetheless Lack's results do demonstrate quite clearly the life-historical compromises that arise through selection in natural populations.

<u>Reproductive effort</u> Another interesting aspect of reproduction concerns the effort that a parent expends on behalf of its progeny. Intuitively we might predict that genotypes putting most effort into their progeny would be selected and indeed the widespread presence of parental care is convincing evidence of this. Yet there must come a point when the advantage of working harder for present offspring is outweighed by the cost to future ones, when parental survival falls below a certain value.

Reproductive effort is not easy to quantify; the most extensive studies using natural populations were those of Goodman (1974), as part of a research program on a Red Footed Booby (<u>Sula</u> <u>sula</u>) colony on the Galapagos Islands. This population represented an extreme of low reproductive effort; only one egg was laid, the egg or chick was

often abandoned and long periods would elapse before breeding was attempted again. It was therefore particularly interesting to establish the reasons preventing selection against such low reproductive effort. Goodman did this by deriving an expression to relate the benefit resulting from increased reproductive effort to the cost due to the increased mortality risks of the parents. Working from the assumption that increased effort would only be selected if the increase to present fitness was greater than the loss to future fitness, he showed that

$$a \quad > \quad a' \ (1/q - 1) \qquad\qquad \text{Eq. 2.3}$$

where,   a   =   fractional amount by which prereproductive

                             survival is increased through greater effort,

             a'   =   fractional amount by which adult survival to

                             the following year is reduced by increased effort,

             q   =   annual adult mortality rate.

This equation was specifically limited to a population of constant size. If q is small reproductive effort must be considerably increased to compensate for reduced adult survival, whereas if it is large even a small increase in effort can compensate for reduced adult survival. In <u>Sula</u> <u>sula</u> annual adult mortality was estimated to be 0.05 and greater effort would be advantageous only if it increased the success of breeding by more than nineteen times the loss in adult survival. This would be a stringent condition to satisfy and it was evidently not one that was met in this population.

Goodman's results demonstrate even more clearly than Lack's how extreme the consequences of competition for energy between different life-historical ends can be. It would be hard to imagine a population expending less energy on reproduction, yet within the limitations of the population, this is the inevitable result of natural selection.

2.3.2 Theoretical studies of life-historical characters under

selection

Although the examples of life-historical selection just

discussed are not exhaustive, empirical studies have been few and

far between and much greater attention has been paid to theoretical

research. By accepting some restrictions on age-specific survival

and reproduction functions, it is possible to predict optimal life

histories in different environments. The ways in which some of these

life-historical characters can be expected to evolve are discussed

below.

Reproductive duration We have already seen that the period of

time over which reproduction extends (semelparity and iteroparity) is

an important part of a life history. If it is assumed that populations

exist with genetic variation for reproductive duration, then it

could quite conceivably be under natural selection. The subject

was first discussed by Cole (1954); he made the observation that it

seemed strange that an individual which reproduced only once could

be at a selective advantage over those that reproduced more than once,

because the latter could produce more progeny. Yet nature is full

of examples of semelparity, so under some conditions it must be

selected. This led Cole to undertake an analysis of the conditions

and he showed that 'for an annual species the absolute gain in

intrinsic population growth which could be achieved by changing to

the perennial habit would be exactly equivalent to adding one individual

to the average litter size'. Clearly for an individual producing

many offspring, the additional requirement of one more child poses

little extra strain.

Thus the problem is reversed and it begins to look more unlikely

that iteroparity could be selected. But Cole also considered this

problem (Cole 1954) and he demonstrated that iteroparity was more

likely to be selected if the litter size was small and/or if the prereproductive period was long. He cited the example of the Redwood tree (<u>Sequoia</u>) with a prereproductive period of about a hundred years, but which produces seeds for many years subsequently. With a prereproductive period of this length, it would need a very large increase in seed output to achieve semelparity with an equivalent intrinsic rate of growth.

Cole's research demonstrates another kind of compromise that prevents the selection of the 'Darwinian demon'. When there is competition between energy for growth and reproduction, genotypes diverting more energy to growth (and hence reproduction in the future) are likely to be selected if there is a long development time before reproduction. We can therefore predict that the combination of iteroparity and short prereproductive period is unlikely to arise.

More recently Cole's result was criticised as being unrealistic because it assumed that there was no mortality during the life of the individual (Gadgil & Bossert 1970). Gadgil & Bossert said that if mortality was taken into account, an annual species would have to double its reproductive rate to achieve the same rate of growth as a perennial. Thus there would be more circumstances under which iteroparity would be at a selective advantage. But Bryant (1971) was able to prove Cole's result even when mortality was included in the calculations. Charnov & Schaffer (1973) gave a general proof of the relationship between annuals and perennials in which litter size and mortality rates were variables and concluded that:

$$B_a = B_p + P/C \qquad\qquad Eq. 2.4$$

where, B_a = number of progeny produced by an annual to achieve the same growth rate as a perennial,

B_p = number of progeny produced by a perennial each year,

C = proportion of progeny surviving to become adults,

P = proportion of adults surviving from one year to the next.

The previous results were particular cases of this equation; Cole's result was for $P = C = 1$, Bryant's result for $P = C < 1$ and Gadgil & Bossert's for the limiting case when $B_a = B_p = 1$ and $P = C$.

Charnov & Schaffer (1973) extended their proof to allow for more general semelparity and iteroparity in which the prereproductive period was a variable. They derived the equation:

$$B_i/B_s = 1 - P/\lambda \qquad\qquad \text{Eq. 2.5}$$

where, B_i = number of progeny produced by an iteroparous individual per litter,

B_s = number of progeny produced by a semelparous individual,

λ = finite rate of growth.

Prereproductive period is only important in this equation insofar as it influences λ ; we can see that iteroparity is favoured when adult survival is large and/or the population growth rate is low. Finally Goodman (1974) expressed the same result in a different form which explicitly accounted for the prereproductive period:

$$\Delta m = (P/P_i).(m')^{(a-1)/a} \qquad\qquad \text{Eq. 2.6}$$

where, Δm = increase in number of progeny necessary for an iteroparous individual to compensate for becoming semelparous,

m' = number of progeny produced by a semelparous individual,

P_i = annual survival rate of immature individuals,

a = age of first reproduction.

Prereproductive period The time period for development before the onset of reproduction was also mentioned in Section 2.2 as an important reproductive character. It is easy to see that in an expanding population, genotypes with the shortest prereproductive periods will be at a selective advantage, all other parts of the life history being the same. Yet even here there must come a point when further shortening of development time is disadvantageous, if it is achieved at the expense of growth and reproduction. It is inevitable that here too there is a compromise in the selective goal of the 'Darwinian demon'.

Little is understood of the way in which the conflict between prereproductive period and other life-historical characters is resolved. However as a by-product of some research on selection for colonising ability, Lewontin (1965) provided some interesting insights into its role. He related the effect of variation in some reproductive characters on the absolute fitness of a population in an infinite environment. His results showed that a very small reduction in development time had the same effect on fitness as a doubling of the total number of progeny. Hence if genetic variation for prereproductive period existed, it should be strongly selected. And as a corollary natural populations at equilibrium should contain little genetic variability for this character.

Senescence Our attention has hitherto been concentrated on reproductive characters, survival only being invoked to help to explain the non-existence of the 'Darwinian demon'. However, age-specific survival can equally well be considered as a metric character with polygenically-determined variation. Although immortality would be theoretically the most advantageous length of life, constraints on real populations lead to ageing, senescence and death.

The current theory of ageing is to be found in its earliest form in the work of Medawar (1957), who suggested that senescence could arise from genes with favourable effects early in life, being disadvantageous later on. Williams (1957) showed that a gene with a desirable effect at an early age could be selected even if it was undesirable later, since early ages contribute more to future generations. In the extreme case when the undesirable effect occurred after reproduction had ceased, selection would be unlikely to operate at all. The theory was placed on a formal basis by Hamilton (1966), who proved that with appropriate genetic variability senescence was the inevitable outcome of natural selection. Similar conclusions were reached more recently by Emlen (1970). Deleterious genetic effects tend to be postponed, leading old age to become a 'genetic dustbin'.

Reproductive effort This has already been discussed in connection with one of the few empirical studies on life-history evolution, but it has also been the subject of several theoretical analyses, particularly during recent years. The essence of the problem is as follows: an organism as it develops and grows is continuously faced with the choice of diverting resources to reproduction at the expense of future growth, maintenance and reproduction. What distribution of effort towards reproduction over the course of a lifetime maximises the instantaneous rate of increase? Clearly the answer to this will depend on the balance between the benefit due to immediate reproduction and the cost of less reproduction in the future. Our 'Darwinian demon' living in an environment with excess resources suffers no cost and can put an enormous amount of effort into reproduction, but all real organisms are involved in a balance between the benefits and costs.

The root of the problem is to be found in Fisher (1958, p47), but it was not until Williams (1966, p171-187) developed the ideas that they provoked much research. Williams argued that low reproductive effort should be found in species with large body size, long life and fecundity that increased with age. Furthermore he suggested that reproductive effort should increase with age, because as an individual ages its proportional contribution to future generations declines. Gadgil & Bossert (1970) formalised the arguments by developing a mathematical model in which reproduction, growth and survival were functions of effort. They then used a computer to search for age-specific effort values that maximised the instantaneous rate of increase. Their most important conclusions were firstly that in populations where reproduction was associated with heavy mortality risks, all effort should be used in a single attempt at reproduction. Thus semelparous life histories should arise as for example in the pacific salmon. Secondly, they concluded that if reproduction led to little mortality, iteroparous life histories should evolve and in these reproductive effort should increase with age.

More recent research led to some doubts about the arguments of Williams and Gadgil & Bossert. Fagen (1972) reported an example of an optimal life history in which reproductive effort declined over some ages. And Schaffer (1974a) succeeded in finding analytical solutions for optimal life histories and these did not confirm all of the results of Gadgil & Bossert. For example he found that iteroparity and decreasing reproductive effort with age could evolve instead of semelparity in some circumstances. He also demonstrated that if more realistic survival and reproduction functions were introduced there could be alternative optimal life-histories depending on the starting conditions. Schaffer (1974b) in addition extended the analysis to consider environments with random fluctuations.

In these he found that if the fluctuations acted on reproduction, selection reduced reproduction, whereas if they acted on postbreeding survival, selection increased reproduction (assuming that iteroparity was optimal in a constant environment).

Although reproductive effort is not easily quantified or estimated, it is nonetheless a very useful concept and central to the problem of life histories under natural selection. It is explicitly concerned with the compromise in allocation of resources between reproduction, growth and maintenance and is much more general than the arguments discussed earlier. It would be surprising if it did not form the basis of much theoretical and empirical research in the future.

Dormancy The ability of an organism to enter a resting phase of low metabolic activity is widespread in plants (seed dormancy) but less so in animals (diapause). At first sight it might seem unlikely that dormancy could be selected because genotypes delaying germination should have lower instantaneous rates of increase. In which case why is it so general to plant populations?

This problem was considered mathematically by Cohen (1966, 1967, 1968). He developed a model in which the yield of a seed once it germinated was a random variable depending on the environment, but in which it could remain dormant undergoing a constant rate of mortality if it did not germinate. The model was limited to annual plants, in which all parameters were independent of population density and in which mortality was not a function of seed age. Within these constraints he proved that if reproduction was usually successful, the long term population growth rate was maximised by a high proportion of seeds germinating. But if reproduction was often unsuccessful, genotypes with high rates of dormancy would be favoured, because they spread the risk of reproduction over more years (Cohen 1966).

He also extended his model to situations in which a seed could receive information from the environment about the probability that reproduction would be successful if it germinated. Genotypes to which more information was available were at an advantage, the advantage increasing as the environment became more uncertain. This led him to conclude that environmental signals most closely associated with the probability of successful reproduction should be selected and he cited a number of cases where this had occurred (Cohen 1967).

Summarising the ideas developed in this section, we can see that there is only one life history that maximises the instantaneous rate of growth and this is the life history of the 'Darwinian demon'. But this ideal is never achieved because resources are limited in the real world and are partitioned to reproduction only at the expense of maintenance and future growth and reproduction. Real life histories represent a compromise of resource allocation between different parts of life, the exact compromise depending on the population and its environment. We have seen that many different compromises are possible and we can begin to appreciate how the myriad of life histories discussed earlier can arise.

2.4 Population differentiation: the consequences of life histories under natural selection

Since the wealth of life-historical variation observable in living organisms can in principle be explained in terms of natural selection, the argument can now be extended to consider variation between populations. We need to know whether different kinds of life histories are associated with different environments, since this would shed much further light on the action of natural selection. In this section some theories of this relationship and the evidence supporting them are reviewed.

2.4.1 The theory of r and K selection

Some of the clearest patterns of life-historical variation from population to population in relation to environment are to be found in clutch size. It has for example been known for a long time that clutch size in birds increases with latitude (Moreau 1944). Lack (1947) offered an explanation for this in terms of the ability of the parents to collect food for the offspring; after the spring equinox daylength is longer the greater the latitude (in the northern hemisphere), so more time is available for food collection. If food supply limits clutch size, clutch size would therefore be expected to increase with latitude.

An analogous theory was used by Johnson & Cook (1968) to explain variation in carpel number in the buttercup Ranunculus flammula over an altitudinal gradient in the Cascade Mountains in Oregon. They found that as the period available for 'food' collection increased (measured as the frost free period) so did the clutch size. This variation was maintained when samples from different altitudes were grown together in the same environment, suggesting that the variation was genetic (but not conclusively proving it since adult rather than seed material was used).

However, there were some anomalies that Lack's theory could not explain. For example, in some groups of birds that fed their young there was no correlation between latitude and clutch size (eg. some members of the crow family) and in other groups that did not feed them there was a correlation (eg. ducks and rails). Inexplicable observations such as these led Cody (1966) to suggest an alternative and more general theory. He argued that more stable environments such as those found in the tropics required the diversion of more energy from reproduction to growth and maintenance because of increased competitive stresses. This theory explained most of Lack's observations and also generated some other testable predictions, since

latitudinal gradients were not the only gradients of environmental stability. For example, oceanic islands have more stable climates than continental areas at the same latitude and the difference increases with latitude. It could therefore be predicted that island clutch sizes would be smaller than continental ones and that the difference would increase with latitude. Cody was in fact able to cite some examples to support this prediction although even the difference between temperate islands and continents was not highly significant. In fact these results were confounded with other environmental differences as well as stability (eg. number of species, trophic complexity), with their own effects on clutch size. Another prediction from the theory was that coastal clutch sizes would be smaller than those further inland because the climate would tend to be more stable. This is in fact a well established phenomenon which was demonstrated by Lack (1947) and Johnston (1960).

The diversion of energy from reproduction to competition was not the only channel that Cody considered; he also suggested that intensity of predation was likely to control the energy available for reproduction. He stated that in those species that suffered predation, the intensity increased as the latitude decreased although he did not support this with any evidence. (A theory of this kind should be simple to test as it should affect species at different trophic positions quite differently.) However he did cite some evidence that species nesting in holes and therefore predator free had larger clutch sizes.

Cody's theory was specifically limited to variation in clutch size between populations and it was followed by a more general theory of evolution of life histories suggested by MacArthur & Wilson (1967). They were interested in the demographic properties of a successful colonist as part of a study of island biogeography. During the early stages of colonisation when population density is low, they argued

that natural selection favours genotypes with the greatest intrinsic rates of increases (r). (We can recall that r was defined in Section 2.2 as the maximum instantaneous rate of increase (m) attained before density constraints start to come into operation.) MacArthur & Wilson referred to selection at this stage of colonisation as 'r selection'. Later in colonisation at high population density when population growth is on average zero, they argued that selection would favour those genotypes able to exist at highest densities. By this they meant those genotypes for which the carrying capacity of the environment (K) was greatest and they referred to selection at this stage of colonisation as 'K selection'. (The terms 'r' and 'K' were taken from the logistic equation of population growth. The degree to which they reflect this probably unrealistic equation is unfortunate, but if they are taken to represent the density-independent and density-dependent phases of selection they are very useful indeed (Pianka 1970, 1972).)

The theory of MacArthur & Wilson was more general than the biogeographic context in which it was initially framed. All populations exist on a spectrum with density-independent and density-dependent forces delimiting the extremes. For example, populations with recent histories of colonisation may be expected to have been more subject to r selection in comparison to those that have been components of stable communities. Populations subject to catastrophic crashes and subsequent rapid increase are likely to be subject to r selection to a greater extent than K selection. Populations in more variable temperate environments could be r selected relative to those in more stable tropical environments. Populations from more variable continental climates may be r selected in comparison to those from more stable maritime ones. And within these extremes we can predict a very wide range of intermediates in which the relative strength of density-independent and density-dependent forces varies to a greater

or lesser degree.

The theory of r and K selection is particularly relevant to this thesis because the essence of colonisation is a transition from a density-independent selection regime to a density-dependent one. It is natural therefore that r and K selection should be central to the ideas developed here. Nevertheless it should not be forgotten that there are many other environmental variables which could in principle have particular life-historical consequences. Two of these variables, environmental predictability and trophic position, were discussed by Wilbur et al. (1974).

2.4.2 Life-historical consequences of r and K selection

We know from Section 2.3 that selection acts to favour genotypes with life histories leading to the greatest value of m at any population density. We now need to know what kind of life histories have the greatest values of m when $m = r$ (r selection) and when $m \sim 0$ (K selection). Bearing in mind that there is unlikely to be a single 'Darwinian demon' fittest at all densities, what different kinds of resource allocation are most likely to be favoured in these different selection regimes? What allocation of reproductive effort between reproduction, growth and maintenance is likely to maximise m at these different population densities?

It is simplest to begin by discussing the life-historical consequences of r selection. Lewontin (1965) considered this problem in some detail; he built a mathematical model of the life history of a colonist and varied some reproductive characters to determine their effect on r. If it was assumed that the colonist started reproduction when 12 days old, reached maximum reproduction when 23 days old, ceased reproduction after 55 days old and produced 5000 offspring, the following results could be shown.

A doubling of the total number of eggs had the same effect on r as reducing the prereproductive period by 2.2 days, as reducing the time to maximum reproduction by 5.5 days, as reducing the time to final reproduction by 21 days or as shifting the whole reproduction/age curve 1.55 days towards the origin. It is clear from Lewontin's results that changes in reproductive effort early in life have the greatest effects on r. In a world of limited resources, genotypes partitioning energy to reproduction early in life even at the expense of reproduction later in life are selectively favoured. There will of course be a limit to this as reproduction is unlikely ever to occur immediately after birth. Nevertheless we can expect an r selected population to have a shorter prereproductive period, a greater litter size and to be less iteroparous than its unselected neighbour.

It is less easy to predict the kinds of life histories favoured by K selection. MacArthur & Wilson (1967) argued that those genotypes that are most efficient in converting energy into progeny are selected, but it is not immediately obvious how to translate this into life-historical terms. We need to know more about the ways in which populations are limited before this problem can be approached.

In principle, population regulation can be brought about by one or more life-historical character being a decreasing function of population density. To take a simple case, suppose that survival of new-born individuals declines as density increases, to such an extent that a population would never grow beyond size K, and suppose also that mortality is negligible in reproducing age groups. In this case there would be no advantage of heavy reproductive effort early in life and it could even be disadvantageous if the environment was only periodically suitable for progeny. Natural selection would favour iteroparous genotypes in these circumstances. If there was genetic variation in survival rates of new-born individuals, selection

could also operate directly on this age class; this could arise from variation in the energy invested in each new individual. For example genotypes with greater seed weight might have greater seedling survival rates and this could compensate for parents producing fewer seeds. It might even be possible to escape from a period of heavy mortality; birds for example race through their vulnerable pre-flight development very quickly (Williams 1966, p90) and many plant species avoid the vulnerable seedling stage by vegetative reproduction. Clearly there are many life-historical ramifications of just this single mode of population regulation and by the time that other methods of regulation are considered there are very many possibilities. It will therefore be necessary to treat each form of regulation on its own merits.

It is necessary to be cautious in applying the theory of K selection because genotypes or populations may not be limited by their carrying capacities. Gill (1972) found that the carrying capacity of two species of Paramecium gave no indication of their success in competition. This led him to distinguish two kinds of competition, one consisting of a race for the available resources ('exploitative' competition) and the other consisting of direct action to prevent other individuals getting to the resources first ('inter-ference' competition) (Gill 1974). He formalised these arguments in terms of the competition coefficient of type 'j' on type 'i' (α_{ij}). If i limited itself more than it was limited by j ($\alpha_{ij} < 1$), he argued that competition was exploitative and natural selection would favour the genotypes that most efficiently converted energy into progeny (K selection). On the other hand if i was more limited by j than it was by itself ($\alpha_{ij} > 1$) then interference competition was taking place. Under these circumstances selection would favour genotypes most effective in preventing others from obtaining the resources and he called this 'α selection'. He concluded that there would be a

transition from K to α selection following the r to K transition
during colonisation.

There are likely to be life-historical consequences of α
selection adding still further to the complexities considered earlier.
Returning to the example of seedling mortality in a plant population,
K selection would occur if there was a race between seedlings for
the available light. In these circumstances genotypes providing
greater energy resources for rapid growth (eg. by greater seed
size) would be advantageous. But if genotypes arose that were able
to selectively inhibit growth of other types, selection would be
radically altered towards perfection of this interference. (However,
it is far from certain whether interference of this kind really
occurs.)

It is clear from this discussion that although we can predict
the life-historical consequences of r selection, it is much more
difficult to make generalisations about selection at high population
densities. A wide range of factors are likely to participate
in population regulation with many different selective consequences.

2.4.3 Evidence for r and K selection

Many of the predictions of r and K selection can be tested by
observations of natural populations. For example the observations
made by Cody (1966) on clutch size in birds are compatible, since his
theory was a special case of the more general theory of r and K
selection. And the characteristics of weeds described by Baker
(1965) are exactly as would be expected in species with histories
of colonisation.

However the theory has also been tested by making more direct
observations on r and K selected populations. Gadgil & Solbrig
(1972) compared three adjacent populations of dandelions (Taraxacum

<u>officinale</u>) that they assumed to be subject to differing degrees of density-dependent control. There were four genotypes present in the populations but the frequency with which they occurred varied from population to population. Genotype A which produced most seed and was competitively inferior to genotype D, was present at greatest frequency in the most disturbed population. On the other hand genotype D which produced least seed, was most frequent in the least disturbed population. The presence of the greatest seed yielder in the most disturbed population indicated the presence of r selection but the relationship between the competitive genotype and K selection was not unequivocably established. This study of dandelions was later developed in more depth by Solbrig & Simpson (1974).

Another prediction that can be made from the theory of r and K selection is that populations or species characteristic of early successional stages should divert more of their resources towards reproduction than those of climax communities. There is some evidence for this in Bradshaw (1959), who found that a disturbed population of the grass common bent (<u>Agrostis tenuis</u>) put more effort into seed production than vegetative growth in comparison to less disturbed populations. More recently this hypothesis was tested by Abrahamson & Gadgil (1973) on some goldenrod species (<u>Solidago</u>); those from more colonising environments were shown to have the greatest reproductive effort. In an analogous experiment Gaines <u>et al</u> (1974) compared four sunflower species (<u>Helianthus</u>)and obtained similar results.

It has also been possible to demonstrate the efficacy of r selection within individual populations. Linhart (1974) studying a population of <u>Veronica peregrina</u>, found that individuals towards the periphery in a less predictable environment, produced more seeds than those near the centre. These differences were shown to be genetic

and demonstrated elegantly how r selection could maintain genetic differences even in the face of considerable gene flow over a few metres.

2.5 Conclusion: life histories under natural selection during colonisation by Poa annua

We have seen that the division of resources between reproduction, growth and maintenance during the lives of individuals is liable to selection. Since reproduction entails costs in terms of future reproduction in real organisms (as opposed to a hypothetical 'Darwinian demon'), different environments are likely to favour different life histories. One pattern of environmental variation with fairly clear life-historical consequences is the pattern of population regulation. Under conditions of relative density-independent regulation, genotypes with life histories maximising r are selected, whereas in populations with strong density-dependent stresses those that maximise competitive ability are selected (r and K selection).

These ideas enable us to predict the kind of genetic change to be expected during colonisation by Poa annua. Colonisation involves a transition from a selective regime of predominantly density-independence to one of density-dependence. Therefore we can predict that genotypes with life histories that maximise r should be selected in the early stages of colonisation. The work of Lewontin (1965) suggests that these genotypes would have short prereproductive periods, high initial seed output, short lives and semelparity.

As population density increases there should be a transition towards genotypes with greatest competitive ability. It is difficult to generalise about the way competitive ability is translated into life history because it depends largely on the specific factors limiting the population. However, it is likely that the survival of seedlings would be particularly sensitive to the effects of density

in _Poa annua_. Assuming that most mortality is prereproductive, the advantage in early reproduction is lost and it could be advantageous to spread the risks of reproduction over more ages. Hence genotypes with iteroparity and greater adult survival probabilities would be selected. If diversion of more energy into seeds increased the probability of seedling survival, greater seed weight could be selected, even at the expense of fewer progeny. Finally, genotypes escaping altogether from the risky seedling stage by vegetative reproduction would be selected.

However these predictions depend critically on the presence of appropriate genetic variation. Unless there are genotypes with different life histories there can be no selection and no genetic change, a problem which is considered in detail in Chapter 4. Even the condition of genetic variation is not sufficient for genetic change because of the presence of phenotypic plasticity. (Bradshaw 1965, 1973). Most plants are able to vary their growth depending on their environment and _Poa annua_ is no exception to this (Ong _pers comm_). It is conceivable that a genotype could exist in which reproductive effort was a function of density so that fitness at both low and high density was greater than others. Such a genotype would represent a novel approach towards the 'demonic ideal' and would preclude the possibility of genetic change.

CHAPTER 3

MATHEMATICAL MODEL OF AN EPISODE OF COLONISATION

3.1 Introduction

The research described in the previous chapter, led to the formulation of a theory of genetic change during colonisation. In brief, we expect a transition from a selection regime of predominantly density independence, to one of density dependence, as population density increases. If appropriate life-historical genetic variation exists, we can expect the changing selection regime to be reflected in genetic change. But the theory as formulated, is purely verbal and needs to be stated in a more precise way, before appropriate measurements can be made on natural populations. The purpose of this chapter then,is to develop a suitable mathematical model.

There are a number of different and sometimes conflicting ends, that have to be reconciled in the construction of a model. The most important of these is the compromise that is required between biological reality and mathematical amenability (Levins 1966, Pielou 1969, Bartlett 1973). Simple models, to which elegant solutions may be found, are apt to be unrealistic. On the other hand, complex models that can account for the range of factors known to be biologically important, are frequently mathematically unwieldy and at best can often only be solved by simulation. The simplest models are usually the most far reaching and they can often stimulate much discussion about biological processes, but they are frequently difficult to test with specific examples, due to the peculiarities of different organisms. On the other hand, models directed towards specific phenomena within a limited group of organisms are easier to test, but the conclusions that can be drawn from them are of less general interest.

The model described here is a compromise between biological reality and mathematical simplicity. It is directed specifically towards a colonisation episode of Poa annua (although it could be easily modified for many other plant species), but only simple one-locus genetic variation is considered. It is deterministic and discontinuous through time, for although the process of colonisation is continuous, measurements can only be made at discrete points in time. In addition, it is an age-distributed model, because the genetic changes with which I am concerned, are intricately bound up in the life histories of the individuals.

3.2 A demographic model for plant populations

Before it is possible to construct a model of an age-distributed colonising population, it is first necessary to build a simple model, to describe the demography of plant populations. However, plant demography has until recently been a neglected subject and possesses only an embryonic mathematical framework. It is not possible to apply directly the demographic equations that have been developed by animal demographers, because plant populations have several life-historical attributes without general parallels in animal populations. For example, the much quoted equation

$$B_t = \sum_{x=0}^{v} B_{t-x} \cdot l_x \cdot b_x \qquad \text{Eq. 3.1}$$

where, B_{t-x} = number of births at time t-x,

l_x = proportional survival to age x,

b_x = number of progeny produced at age x,

v = maximum age of reproduction,

is incorrect in plant populations for several reasons. Firstly, birth is not usually the immediate outcome of reproduction - progeny are

likely to enter a prolonged resting phase as seeds, before they are born (germinate). We can expect seed populations to have their own dynamic properties, that will require special investigation. Secondly, progeny at different life-historical stages can be born by vegetative reproduction. Thirdly, because plant growth is indeterminate, a general demographic model would require the inclusion of the dynamics of the subunits of the individual. These peculiarities of plant populations have been discussed and developed in papers by Harper (1967) and Harper & White (1974). It is clear from them that the classical equations of animal demographers require extensive modification, before they can be applied to plant populations.

In this section, I derive a set of recurrence relations suitable for the prediction of numbers in an age-distributed plant population, in which seeds may undergo a period of dormancy (but without vegetative reproduction or subunit dynamics). My approach follows that of Bernardelli (1941), Lewis (1942) and Leslie (1945, 1948), with the adaptations necessary for plant populations. Some applications of Leslie's model to plant populations have already been considered by Sarukhan (1971) and Sarukhan & Gadgil (1974), and I will refer to these when necessary. For convenience, I will first consider the dynamics of seed and adult populations separately and later combine them to complete the model.

3.2.1 Seed population dynamics

It is reasonable to imagine that seed populations, like adult populations, have age distributions. We can conceive of a cohort of seeds aged 0 at time 0 ($_0ns_0$), which gradually decreases in size with increasing age. It is therefore possible to construct a life table for such a cohort, analogous to life tables of adult populations. From this the proportion of seeds that survive from age x to x+1 (ps_x)

and the proportion surviving to age x (ls_x) ($= \prod_{i=0}^{x-1} ps_i$) can be
calculated. However, there is an important difference between the
life tables of seed and adult populations, arising from the fact
that the wastage of the seed population occurs through germination
as well as mortality. Let us define the proportion of seeds alive at
time x that are dead by x+1 as qs_x; similarly, the proportion of seeds
alive at time x that have germinated by x+1, as gs_x. These two
functions will be sufficient to specify the dynamics of a cohort of
seeds.

Care must be taken to specify the relationship between ps_x, qs_x
and gs_x. Unlike adult populations, $ps_x \neq 1 - qs_x$, because germination
reduces the proportion surviving to age x+1, as well as mortality.
From the definitions of ps_x, qs_x and gs_x, it follows that:

$$ps_x = 1 - qs_x - gs_x \qquad \text{Eq. 3.2}$$

However, in the development of the model some assumptions must be
made about the distributions of germination and mortality through
time because they are continuous processes. For simplicity, I will
assume that all germination occurs before any mortality during each
time interval. But it would be possible to make a closer approximation
to reality by calculating the number of seeds that germinate from
the mean number of seeds alive averaged over the time interval.

With the functions now specified, it is possible to define a
set of recurrence relations for one-step age transitions. Letting
$_t ns_x$ be the number of seeds aged x at time t,

$$_{t+1} ns_1 = {_t ns_0} \cdot ps_0 \qquad \text{Eq. 3.3}$$

$$_{t+1} ns_2 = {_t ns_1} \cdot ps_1 \qquad \text{Eq. 3.4}$$

$$_{t+1}ns_3 \quad = \quad _t ns_2 \cdot ps_2 \qquad\qquad \text{Eq. 3.5}$$

$$\vdots$$

$$_{t+1}ns_u \quad = \quad _t ns_{u-1} \cdot ps_{u-1} \qquad\qquad \text{Eq. 3.6}$$

where, u = maximum age to which any seed survives.

Similarly, the number of seeds that germinate over the time interval t to t+1 and that survive to census time t+1 is:

$$_{t+1}n_0 \quad = \quad \sum_{x=0}^{u} \, _t ns_x \cdot gs_x \qquad\qquad \text{Eq. 3.7}$$

where, $_t n_0$ = number of seedlings at time t.

These equations can be conveniently summarised in matrix notation:

$$
\begin{bmatrix}
0 & 0 & \cdots & 0 & 0 & 0 \\
ps_0 & 0 & \cdots & 0 & 0 & 0 \\
0 & ps_1 & \cdots & 0 & 0 & 0 \\
\vdots & & & & & \\
0 & 0 & \cdots & ps_{u-1} & 0 & 0 \\
gs_0 & gs_1 & \cdots & gs_{u-1} & gs_u & 0
\end{bmatrix}
\times
\begin{bmatrix}
_t ns_0 \\
_t ns_1 \\
_t ns_2 \\
\vdots \\
_t ns_{u-1} \\
_t ns_u \\
_t n_0
\end{bmatrix}
=
\begin{bmatrix}
_{t+1}ns_0 \\
_{t+1}ns_1 \\
_{t+1}ns_2 \\
\vdots \\
_{t+1}ns_{u-1} \\
_{t+1}ns_u \\
_{t+1}n_0
\end{bmatrix}
\qquad \text{Eq. 3.8}
$$

or, $\qquad$ AS $\qquad\qquad x \; _tNS \quad = \; _{t+1}NS$

Notice that the first row of the transition matrix AS contains only zero elements, because seeds aged zero cannot arise from seeds or seedlings. This row will only contain non-zero elements, when the projection matrix contains adult age classes.

In certain circumstances it is possible to simplify transition matrix AS. If ps_x = ps and gs_x = gs for x = 0,1,2 ..... u and u is a large number, then seed age is of no importance and all seed can be included in the same category. Equation 3.8 then approximates to:

$$\begin{bmatrix} ps & 0 \\ gs & 0 \end{bmatrix} \times \begin{bmatrix} {}_t ns \\ {}_t n_0 \end{bmatrix} = \begin{bmatrix} {}_{t+1} ns \\ {}_{t+1} n_0 \end{bmatrix} \qquad \text{Eq. 3.9}$$

or $\qquad AS' \qquad \times \quad {}_t NS \qquad = \qquad {}_{t+1} NS$

where, $\quad {}_t ns \quad = \quad \sum_{x=0}^{u} {}_t ns_x$.

This modified transition matrix (AS') has been developed and used by Sarukhan (1971) and Sarukhan and Gadgil (1974).

As the assumptions of AS' are quite restricting, it is of interest to consider circumstances under which they might be satisfied. Germination of seeds depends on their dormancy patterns, of which three basic categories (innate, enforced and induced) have been defined by Harper (1957). Innate dormancy is completely endogenously determined; it is in effect the ripening period of the seed. Clearly this must be a function of age, as the proportion of seeds in a state of innate dormancy declines as seeds grow older. Hence AS' is restricted to populations without innate dormancy. Another transition matrix could be used if innate dormancy occurred:

$$\begin{bmatrix} 0 & 0 & \cdots & 0 & 0 & 0 \\ ps_0 & 0 & \cdots & 0 & 0 & 0 \\ 0 & ps_1 & \cdots & 0 & 0 & 0 \\ \vdots & & & & & \\ 0 & 0 & \cdots & ps_{w-1} & ps & 0 \\ gs_0 & gs_1 & \cdots & gs_{w-1} & gs & 0 \end{bmatrix} \times \begin{bmatrix} {}_t ns_0 \\ {}_t ns_1 \\ {}_t ns_2 \\ {}_t ns_{w-1} \\ {}_t ns \\ {}_t n_0 \end{bmatrix} = \begin{bmatrix} {}_{t+1} ns_0 \\ {}_{t+1} ns_1 \\ {}_{t+1} ns_2 \\ {}_{t+1} ns_{w-1} \\ {}_{t+1} ns \\ {}_{t+1} n_0 \end{bmatrix} \text{Eq. 3.10}$$

or, $\qquad AS'' \qquad \times \quad {}_t NS'' \quad = \quad {}_{t+1} NS''$

where, w = age by which all innate dormancy has ceased,

$\quad {}_t ns = \sum_{x=w}^{u} {}_t ns_x$ (where u is a large number).

Enforced dormancy is completely environmentally determined; given the appropriate environmental conditions germination will here occur, irrespective of seed age. Hence AS' is satisfactory under conditions of enforced dormancy. The third kind of dormancy - induced dormancy - is an interaction between endogenous and environmental factors. In this case, AS' will be satisfied only if induced dormancy acts age independently. Notice that all these arguments refer only to the gs_x function; similar arguments could also be applied to the qs_x function, but at present we know little about mortality rates when seeds are in these different physiological states. Even if mortality was independent of the kind of dormancy, ps_x would still be a function of age if gs_x was, because of the functional dependence of ps_x on gs_x (see Equation 3.2).

3.2.2 Adult population dynamics

The model of the dynamics of the adult population (i.e. the non seed population) follow with few modifications from that of Leslie (1945, 1948). Defining p_x as the proportion of individuals aged x that survive to x+1 and b_x as the number of seeds produced by an individual aged x in the time interval x to x+1, we can write a set of recurrence relations for one-step age transitions as follows:

$$_{t+1}n_1 = {_t}n_0 \cdot p_0 \qquad \text{Eq. 3.11}$$

$$_{t+1}n_2 = {_t}n_1 \cdot p_1 \qquad \text{Eq. 3.12}$$

$$\vdots$$

$$_{t+1}n_v = {_t}n_{v-1} \cdot p_{v-1} \qquad \text{Eq. 3.13}$$

where, $_t n_x$ = number of individuals aged x at time t,

v = maximum age to which any individual survives.

The number of seeds produced over the time interval t to t+1, that survive to census time t+1 is:

$$_{t+1}ns_0 = \sum_{x=0}^{v} {}_{t}n_x \cdot b_x \qquad \text{Eq. 3.14}$$

Equations 3.11 to 3.14 can be summarised in matrix notation as:

$$
\begin{bmatrix}
0 & b_0 & \cdots & b_{v-1} & b_v \\
0 & 0 & \cdots & 0 & 0 \\
0 & p_0 & \cdots & 0 & 0 \\
\vdots & & & & \\
0 & 0 & \cdots & p_{v-1} & 0
\end{bmatrix}
\times
\begin{bmatrix}
_tns_0 \\
_tn_0 \\
_tn_1 \\
\vdots \\
_tn_{v-1} \\
_tn_v
\end{bmatrix}
=
\begin{bmatrix}
_{t+1}ns_0 \\
_{t+1}n_0 \\
_{t+1}n_1 \\
\vdots \\
_{t+1}n_{v-1} \\
_{t+1}n_v
\end{bmatrix}
\quad \text{Eq. 3.15}
$$

or, $\qquad AA \qquad \times \quad _tNA \qquad = \qquad _{t+1}NA$

Transition matrix AA is a modified version of the Leslie Matrix (Leslie 1945, 1948); the second row contains only zero elements, as the matrix will later be expanded to include seed population dynamics. AA provides a realistic description of the transitions in a population of Poa annua, in so far as it is possible to ignore reproduction by vegetative means. This will be more satisfactory in relation to some populations than others (see Chapter 4). A modified Leslie Matrix including vegetative reproduction, is given by Sarukhan (1971) and Sarukhan & Gadgil (1974).

3.2.3 Synthesis of seed and adult population dynamics

It is now possible to combine the recurrence relations of the seed and adult populations in a single transition matrix (A). To do this, I will use the most general transition matrix for seed population dynamics (AS); transition matrices for particular patterns of dormancy could be used in exactly the same way. The matrix equation describing all possible one-step time transitions is as follows:

$$
\begin{bmatrix}
0 & 0 & \cdots & 0 & 0 & b_0 & b_1 & \cdots & b_{v-1} & b_v \\
ps_0 & 0 & \cdots & 0 & 0 & 0 & 0 & \cdots & 0 & 0 \\
0 & ps_1 & \cdots & 0 & 0 & 0 & 0 & \cdots & 0 & 0 \\
\vdots & & & & & & & & & \\
0 & 0 & \cdots & ps_{u-1} & 0 & 0 & 0 & \cdots & 0 & 0 \\
gs_0 & gs_1 & \cdots & gs_{u-1} & gs_u & 0 & 0 & \cdots & 0 & 0 \\
0 & 0 & \cdots & 0 & 0 & p_0 & 0 & \cdots & 0 & 0 \\
0 & 0 & \cdots & 0 & 0 & 0 & p_1 & \cdots & 0 & 0 \\
\vdots & & & & & & & & & \\
0 & 0 & \cdots & 0 & 0 & 0 & 0 & \cdots & p_{v-1} & 0
\end{bmatrix}
\times
\begin{bmatrix}
{}_t ns_0 \\ {}_t ns_1 \\ \vdots \\ {}_t ns_{u-1} \\ {}_t ns_u \\ {}_t n_0 \\ {}_t n_1 \\ \vdots \\ {}_t n_{v-1} \\ {}_t n_v
\end{bmatrix}
=
\begin{bmatrix}
{}_{t+1} ns_0 \\ {}_{t+1} ns_1 \\ \vdots \\ {}_{t+1} ns_{u-1} \\ {}_{t+1} ns_u \\ {}_{t+1} n_0 \\ {}_{t+1} n_1 \\ \vdots \\ {}_{t+1} n_{v-1} \\ {}_{t+1} n_v
\end{bmatrix}
$$

<div align="right">Eq. 3.16</div>

or, $\qquad A \quad x \quad {}_tN \quad = \quad {}_{t+1}N$

Thus, given the number of individuals in each age class at time t $({}_tN)$ and transition matrix A, we can predict the number of individuals in each age class at time t+1 $({}_{t+1}N)$. From this, an equation giving the number of individuals in each age class at any point in time can be derived:

$$ {}_tN \quad = \quad A^t \quad x \quad {}_0N \qquad\qquad \text{Eq. 3.17}$$

where, $_0N$ is a column vector of numbers in each age class at t=0. Equation 3.17 is a deterministic demographic model of a plant population. It provides a reasonable description of a plant population with any pattern of dormancy, but which experiences no vegetative reproduction. (However, it can be easily modified to introduce particular kinds of vegetative reproduction, in so far as they fit into the age classifications (Sarukhan 1971, Sarukhan & Gadgil 1974).)

Although for my purposes it is more convenient to develop a plant population model in matrix form, it should be noted by way of

conclusion, that it is possible to derive an expression analogous

to Equation 3.1 for plant populations. Taking germination as the

formal equivalent of birth, the number of adults aged exactly 0 at

exact time t is as follows:

$$_t n_0 = \sum_{x=0}^{u} \left(\sum_{i=0}^{v} {}_{t-x-i} n_0 \cdot l_i \cdot b_i \right) ls_x gs_x \qquad \text{Eq. 3.18}$$

A full derivation of this equation is given in Appendix 3.1.

3.3 Colonisation - a simple example

It will help to clarify the use of the transition matrix

developed in the previous section, by considering an example of an

episode of colonisation. Since I am primarily interested in colonisation

by Poa annua, it is first necessary to transform the transition matrix

into a form that provides a useful description of the life cycle of

Poa annua.

I have shown that the appropriate transition matrix for a seed

population depends on its pattern of dormancy, but unfortunately,

the dormancy characteristics of Poa annua are far from clear. Koch

(1968) observed short term (innate) dormancy, as did Wells (1974) while

Gibeault (1971) and Ellis (1972) found populations both with and without

dormancy. Even less is known of the role of induced dormancy. In view

of this uncertainty, I will use the simplest form of the transition

matrix, incorporating AS', which will be sufficient to demonstrate

the general principles involved.

The appropriate transition matrix for an adult population depends

on the number of age classes and distribution of reproduction. It is

clear that in populations of Poa annua there are immature non-reproducing

individuals (seedlings) and that, since reproduction is not instant-

aneous, there are two or more reproducing age classes. For reasons

that will become clear later, it is convenient to consider three

reproducing age classes (young, medium and old adults). The complete

life cycle for both seeds and adults, is summarised in Figure 3.1

together with the transition matrix that describes it. Time units

in this matrix are arbitrary, but it is realistic to suppose them

to be about eight weeks, since this is the approximate length of time

between germination and the onset of reproduction.

To follow the progress of a particular episode of colonisation,

it is necessary to estimate values for the parameters in the transition

matrix in Figure 3.1. As our knowledge of age-specific survival and

seed production, germination and survival in Poa annua is almost non -

existent, values of these parameters must be chosen intuitively. Let

us suppose that between successive times, 0.2 of the seeds remain

dormant and 0.05 germinate, the proportion of individuals that survive

from the seedling age class onwards is 0.75 and the seed production of

young, medium and old adults is 100, 200 and 100 per individual

respectively. The transition matrix then takes the form shown in

Figure 3.2. Let us also suppose that colonisation begins with 100 seeds

and no adult individuals, in which case we have defined A and N_0 and

can calculate numbers in the population at any future point in time,

using Equation 3.17. Numbers in each age class over the course of time

are shown in Figure 3.2. The graphs show that with the exception of

the very first time intervals, numbers in each age class increase.

(The decline in numbers initially arises from the time lag before

reproduction begins.) At the start of colonisation, proportions in

each age class fluctuate, but the fluctuations gradually diminish, until

proportions in each age class become constant. Rate of growth of the

population is then the finite rate of growth (see Chapter 2).

It would be unrealistic to suppose that this pattern of population

growth could be maintained indefinitely. We can expect restrictions

in growth to arise and to increase in intensity as population density

FIGURE 3.1   Idealised life cycle for <u>Poa annua</u> and transition matrix that
             describes all possible changes from time t to t+1; where,
             ps = proportion of seeds surviving from t to t+1,
             gs =   "   "   germinating "   "   " ,
             p_0 =   "   "   seedlings surviving to become young adults from t to t+1,
             p_1 =   "   "   young adults   "   "   "   medium   "   "   " " "   ,
             p_2 =   "   " medium   "   "   "   "   old   "   "   " " "   ,
             b_1 = number of seeds per plant produced by young adults from t to t+1,
             b_2 =   "   "   "   "   "   "   "   " medium   "   "   " " "   ;
             b_3 =   "   "   "   "   "   "   "   " old   "   "   " " "   .
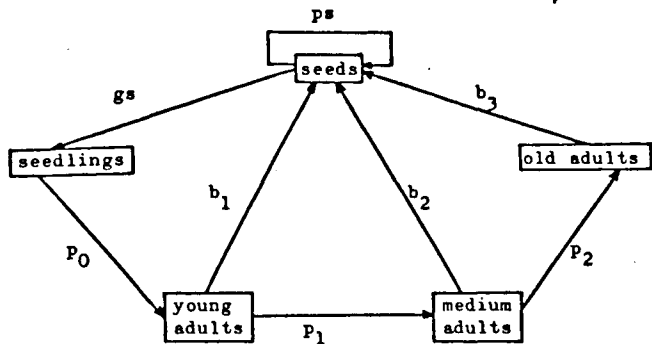
Transition matrix:

$$
\begin{bmatrix}
ps & 0 & b_1 & b_2 & b_3 \\
gs & 0 & 0 & 0 & 0 \\
0 & p_0 & 0 & 0 & 0 \\
0 & 0 & p_1 & 0 & 0 \\
0 & 0 & 0 & p_2 & 0
\end{bmatrix}
$$
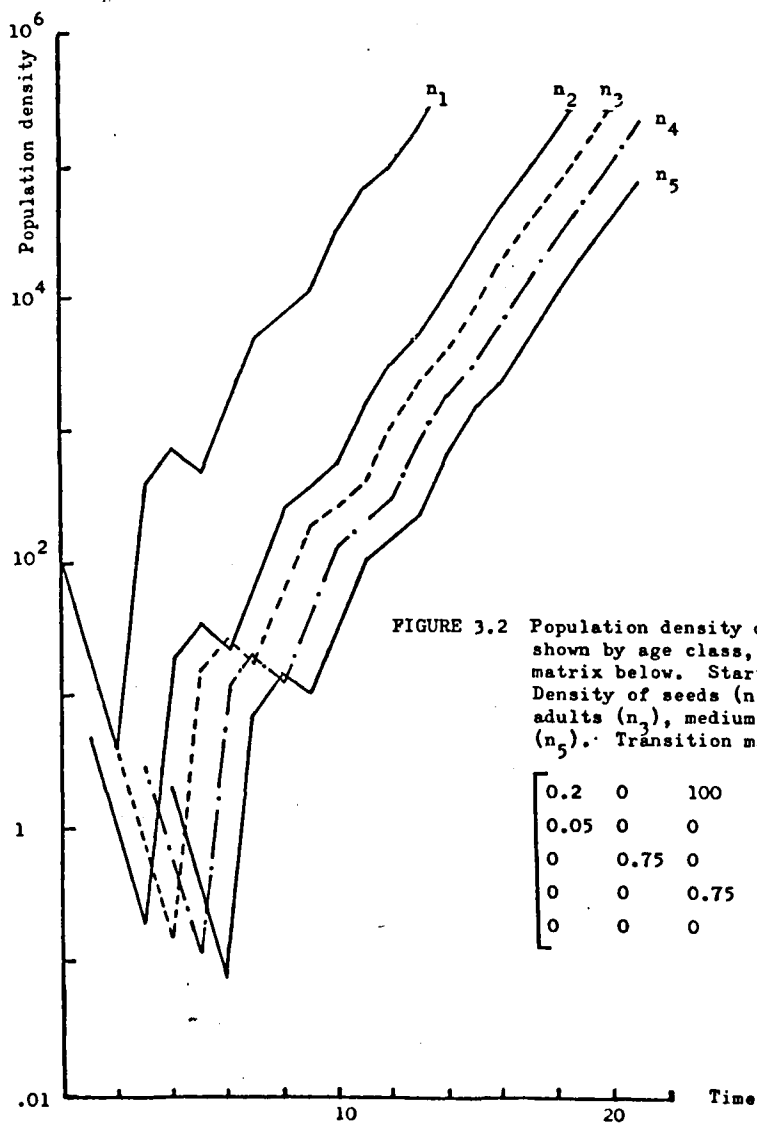
FIGURE 3.2   Population density during colonisation,
             shown by age class, calculated using transition
             matrix below. Starting density = 100 seeds.
             Density of seeds (n_1), seedlings (n_2), young
             adults (n_3), medium adults (n_4) and old adults
             (n_5). Transition matrix:

$$
\begin{bmatrix}
0.2 & 0 & 100 & 200 & 100 \\
0.05 & 0 & 0 & 0 & 0 \\
0 & 0.75 & 0 & 0 & 0 \\
0 & 0 & 0.75 & 0 & 0 \\
0 & 0 & 0 & 0.75 & 0
\end{bmatrix}
$$

increases. Reduction in rate of growth of populations is brought about by one or more life-historical parameter being a decreasing function of density. (This is with the exception of very low population densities, where successful reproduction could be an increasing function of population density. However this restriction does not apply to Poa annua, or other inbreeding plant species.) Hence, to develop further this model of colonisation, it is necessary to specify these density functions.

Unfortunately it is difficult to make general statements about age-specific survival and reproductive output as functions of density. Holiday (1960) suggested two kinds of density dependence in crop plants, one for reproductive tissue and one for vegetative tissue and he outlined a formula to relate vegetative yield per plant to density. But his formula differs substantially from that of Mead (1966), who investigated carrot yield in relation to density, and the relevance of these formulae to seed output is an open question. It is equally unclear how density influences age-specific survival. Although much research has been carried out on the effect of density on plant weight (Yoda et al. 1963, White & Harper 1970), little is known of how it effects survival. Harper & McNaughton (1962), studying five species of Papaver, found survival to be a function of population density, but patterns of mortality were quite different at different sites. It is reasonable to suppose that survival will depend on the particular environmental factors limiting the population, for example the availability of sites for germination, of light, nutrients and water and of the intensity of predation and disease (discussed by Harper et al. 1961). It is therefore difficult to make general statements about survival as a function of density. This is particularly true of Poa annua, as no such studies have ever been carried out, and is also true of seed populations of all plant species.

In animal populations on the other hand, some attempts at generalisation have been made (Pennycuick et al 1968, Pennycuick 1969, Usher 1971) and in theoretical studies logistic density dependence has been used (Anderson & King 1970, King & Anderson 1971).

Because so little is known of the effect of density on survival and reproduction in Poa annua, I will use simple exponential functions for the purpose of developing the model of colonisation. These functions are unlikely to be entirely satisfactory in real populations, but they are sufficient to demonstrate the general ideas of the model and can later be modified in the light of greater understanding of Poa annua. Suppose that the expected number of seeds produced by an individual aged x in the time interval x to x+1 is the following function of density (N):

$$b_x(N) \quad = \quad C_x \cdot \exp(c_x \cdot N) \qquad\qquad \text{Eq. 3.19}$$

where, C_x = number of seeds produced by an individual aged x in the time interval x to x+1 when population density is very low,

c_x = rate constant for x'th age class ($c_x < 0$).

Suppose also that the probability of an individual aged x surviving to be an individual aged x+1 is the following function of density:

$$p_x(N) = 1 - K_x \cdot \exp(k_x \cdot N) \quad\ \text{for } N < -\ln(K_x)/k_x \quad \text{Eq. 3.20}$$

$$p_x(N) = 0 \qquad\qquad\qquad\ \text{for } N \geqslant -\ln(K_x)/k_x$$

where K_x = proportion of individuals aged x that are dead by time x+1 when population density is very low,

k_x = rate constant for x'th age class ($k_x > 0$).

For the sake of simplicity, I will assume that of the survival probabilities, only the probability of survival from seedling to young adult is a function of density, and that survival and germination of

seeds are independent of density. It now remains to give a precise definition of density, which must also be made intuitively. It is unlikely that seeds have the same density effects as adult individuals, but the relative role of individuals of different ages is not at all clear. In this model, it is assumed that only individuals in the young, medium and old adult age classes determine density and that they do so equally. Hence

$$N = \sum_{x=1}^{3} n_x \qquad \text{Eq. 3.21}$$

Examples of age-specific survival and reproductive output functions with particular values of C_x, c_x, K_x and k_x that I will use extensively in developing the model of colonisation are given in Figures 3.3 & 3.4.

Having defined life-historical parameters as functions of population density, we can substitute them into the transition matrix and follow the progress of colonisation using Equation 3.16 iteratively. To do this it is necessary to amend the life-historical parameters after each iteration, in accordance with changing population density. Suppose that as before, colonisation begins with 100 seeds and no other individuals; the pattern of colonisation over the course of time then takes the form of Figure 3.5. Notice that,although the course of colonisation follows the previous pattern very closely (Figure 3.2) over the first ten time intervals, density constraints soon check the growth of the population. By time 16 population growth has been halted and with a series of damped oscillations, the numbers in each age class approach constant values. This model of colonisation, in which population growth becomes progressively restricted as density increases, is more realistic than the previous form of unlimited growth.

FIGURE 3.3 Proportion of seedlings surviving to become young adults (p_0) as the following function of population density (N):

$$p_0(N) = 1 - 0.25\exp(0.00005N) \quad \text{for } N < 27726$$
$$= 0 \quad \text{for } N \geq 27726$$
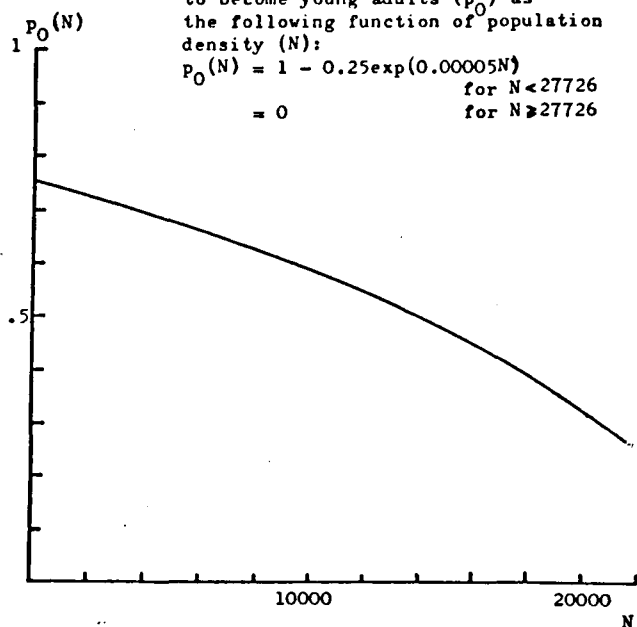
FIGURE 3.4 Age-specific seed output per plant for young (b_1), medium (b_2) and old (b_3) adults as the following functions of population density (N):

$$b_1(N) = b_3(N) = 100\exp(-0.0001N)$$
$$b_2(N) = 200\exp(-0.0001N).$$
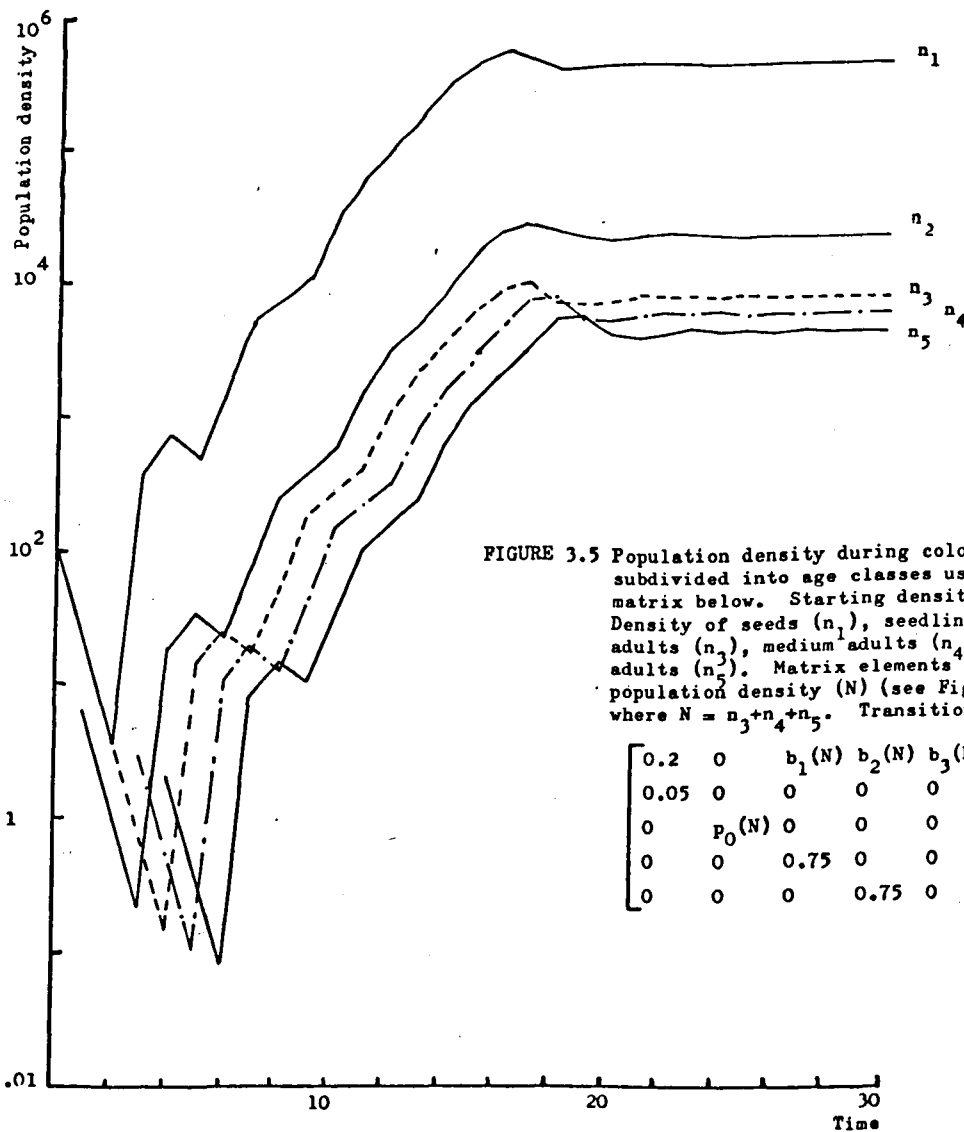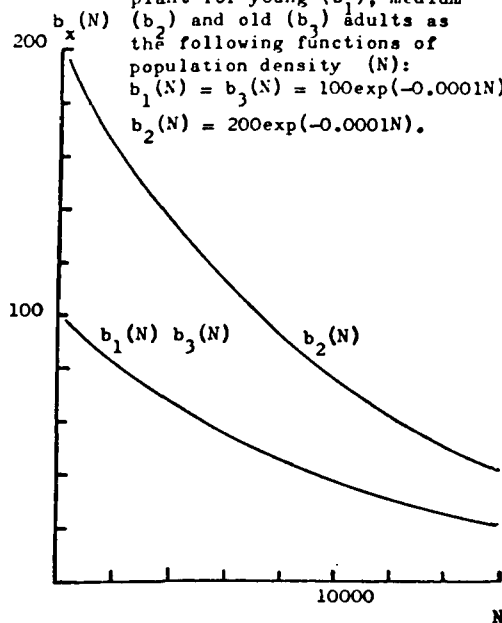
FIGURE 3.5 Population density during colonisation, subdivided into age classes using transition matrix below. Starting density = 100 seeds. Density of seeds (n_1), seedlings (n_2), young adults (n_3), medium adults (n_4) and old adults (n_5). Matrix elements are functions of population density (N) (see Figure 3.3 & 3.4), where $N = n_3 + n_4 + n_5$. Transition matrix:

$$\begin{bmatrix} 0.2 & 0 & b_1(N) & b_2(N) & b_3(N) \\ 0.05 & 0 & 0 & 0 & 0 \\ 0 & p_0(N) & 0 & 0 & 0 \\ 0 & 0 & 0.75 & 0 & 0 \\ 0 & 0 & 0 & 0.75 & 0 \end{bmatrix}$$

3.4 Colonisation with genetic life-historical variation

The model that I have described in the previous section gives a general indication of the progress of colonisation, but is deficient in a number of ways. The most serious limitation is that, being a deterministic model, it cannot accommodate the presence of variation in reproduction and survival. At a particular population density the model will predict expected age-specific survival and seed output values, but will not take into account variation around them. This is an important constraint because the presence of variation may have profound consequences on the fate of the population.

Variation can arise from a number of causes. Firstly, populations exist in environments that are heterogeneous; there is likely to be variation in the chemical and physical nature of the soil and in the microclimate around the plants. Some of these environments will be more favourable to plants than others, causing them to produce more seed or to survive for longer. Furthermore there is likely to be local variation in population density, which will also cause variation in age-specific survival and reproduction if these are functions of density. In addition, seasonality can be expected to exert an important influence on life historical characters.

However for the purpose of this model, I will ignore the presence of environmentally induced variation and consider only variation intrinsic to the plants themselves - that is genetic variation. We have seen in Chapter 2 that there are strong arguments for the existence of genetic variation in life histories and that there is evidence of it between species (Abrahamson & Gadgil 1973, Gaines et al. 1974), between populations within species (Gadgil & Solbrig 1972, Solbrig & Simpson 1974) and within populations (Linhart 1974). Some previous research has suggested that there is variation between populations of Poa annua (Tutin 1957, Hovin 1957, Timm 1965, Gibeault 1971, Gibeault & Goetze

1972, Ellis 1972, Wells 1974); they found that there were annual
and perennial populations, annual ones being characterised by short
lives, high seed production and seed dormancy and perennial ones
vice _versa_. This variation is discussed in greater detail in the
next chapter and emphasizes the central role of genetic life-historical
variation in our model of colonisation.

Ideally, we would like the model to include every genotype in a
population that has an effect on life history. Then, if the life-
history and frequency of each genotype was known and the breeding
system and mode of life-historical inheritance was understood, we
could calculate the genetic and demographic outcome of colonisation.
This would be a powerful development for several reasons. Firstly,
the requirement that natural selection should be an _a_ _posteriori_
definition (see Chapter 1) would no longer be necessary because
genotypic fitness could be estimated independently from genetic change.
Secondly, the theory would be quantitative as it would be possible
to predict not only whether genetic change occurred, but _how_ _much_
genetic change occurred. Finally, by dissecting all embracing
coefficients of selection and looking in detail at their life-
historical anatomy, much would be learnt about the causes of selection.

In reality it is likely to be difficult to construct models that
take into account all this variation. There may well be as many
genotypes as individuals in many populations, so each individual could
have different life and reproduction schedules. Hence, considerable
simplification is necessary, if the system is to be made tractable.
With this in mind I have considereda population genetically variable at
one locus only. Suppose there are two genes affecting life-history
that may occur at this locus - A and a and that A is completely dominant
to a. Suppose also that the population is diploid, so that three
possible genotypes can occur AA, Aa and aa. It is inevitable that

such a simplified model will lose much of its power, but it will nonetheless be sufficient to demonstrate some simple consequences of colonisation. An analogous model was developed by Anderson & King (1970) and King & Anderson (1971), using a different kind of density dependence.

3.4.1 Colonisation in random mating population genetically variable at one locus

The modifications required to the model of colonisation considered in section 3.3 for the inclusion of genetic variation, can be illustrated with an example. Let us suppose that genotypes AA and Aa produce more seed and have a shorter prereproductive period than aa. Suppose also that although seed output of all three genotypes is adversely affected by increasing population density, output of aa is less influenced than the others. Examples of output as functions of population density with these characteristics are illustrated in Figure 3.7. Assume also that seedling survival is a decreasing function of density in all three genotypes, but again to a lesser extent in aa. Examples of seedling survival/density functions with these characteristics are given in Figure 3.6.

Using these life-historical functions, we can construct transition matrices for each genotype analogous to the transition matrix for populations used in Section 3.3 (see Figure 3.8). The progress of colonisation can then be followed using Equation 16 iteratively. As before it is necessary to adjust age-specific survival and seed output values after each iteration where they are functions of population density. I will assume that young, medium and old adult age classes of each genotype contribute to density in direct proportion to their numbers and that as before seed and seedlings have no effect on density. It is also necessary to define the breeding system; I will assume

FIGURE 3.6 Proportion of plants surviving from seedling to young adult age class of 3 genotypes, AA ($_{AA}P_0(N)$), Aa ($_{Aa}P_0(N)$) and aa ($_{aa}P_0(N)$) as the following functions of population density (N):

$$_{AA}P_0(N) = {}_{Aa}P_0(N) = 1 - 0.25\exp(0.00005N) \quad \text{for } N < 27726$$
$$= 0 \quad \text{for } N \geqslant 27726$$

$$_{aa}P_0(N) = 1 - 0.25\exp(0.00003N) \quad \text{for } N < 46210$$
$$= 0 \quad \text{for } N \geqslant 46210.$$

$P_0(N)$
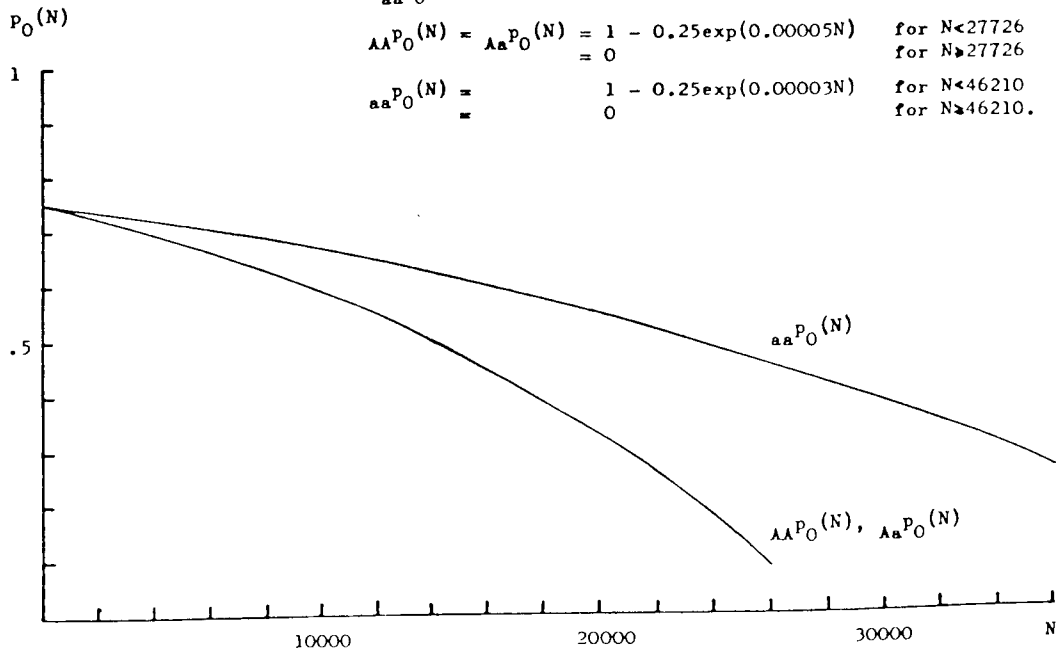
FIGURE 3.7 Age-spcific seed output per plant for young, medium and old adults of 3 genotypes, AA ($_{AA}b_1(N)$, $_{AA}b_2(N)$, $_{AA}b_3(N)$), Aa ($_{Aa}b_1(N)$, $_{Aa}b_2(N)$, $_{Aa}b_3(N)$) and aa ($_{aa}b_1(N)$, $_{aa}b_2(N)$, $_{aa}b_3(N)$) as the following functions of population density (N):

$$_{AA}b_1(N) = {}_{Aa}b_1(N) = 200\exp(-0.0001N),$$
$$_{AA}b_2(N) = {}_{Aa}b_2(N) = 100\exp(-0.0001N),$$
$$_{aa}b_2(N) = {}_{aa}b_3(N) = 100\exp(-0.00005N),$$
$$_{AA}b_3(N) = {}_{Aa}b_3(N) = {}_{aa}b_1(N) = 0.$$

$b_x(N)$
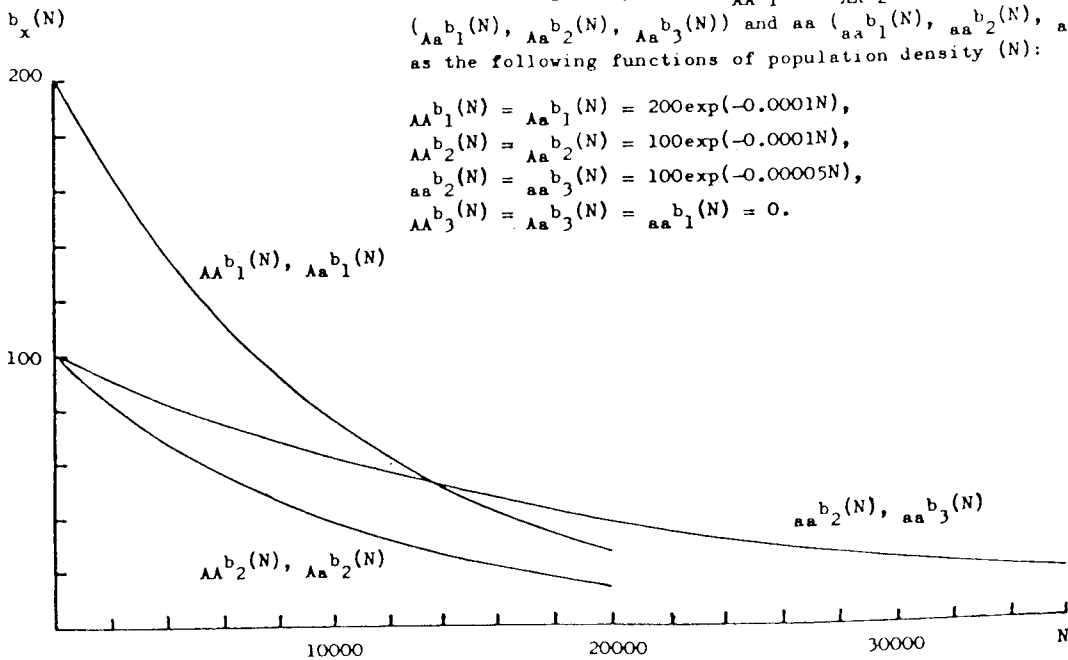
FIGURE 3.8   Population density during colonisation shown as density of
genotype AA, Aa and aa, calculated from the transition matrices
below. Population assumed to be random mating. Starting
density: 100 seeds of each genotype. Matrix elements functions
of population density, as in Figure 3.6 and 3.7. Population
density taken as the density of young, medium and old adults
irrespective of genotype.

Transition matrices:

AA=Aa:

$$\begin{bmatrix} 0.2 & 0 & {}_{AA}b_1(N) & {}_{AA}b_2(N) & 0 \\ 0.05 & 0 & 0 & 0 & 0 \\ 0 & {}_{AA}p_0(N) & 0 & 0 & 0 \\ 0 & 0 & 0.75 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

aa:

$$\begin{bmatrix} 0.2 & 0 & 0 & {}_{aa}b_2(N) & {}_{aa}b_3(N) \\ 0.05 & 0 & 0 & 0 & 0 \\ 0 & {}_{aa}p_0(N) & 0 & 0 & 0 \\ 0 & 0 & 0.75 & 0 & 0 \\ 0 & 0 & 0 & 0.75 & 0 \end{bmatrix}$$
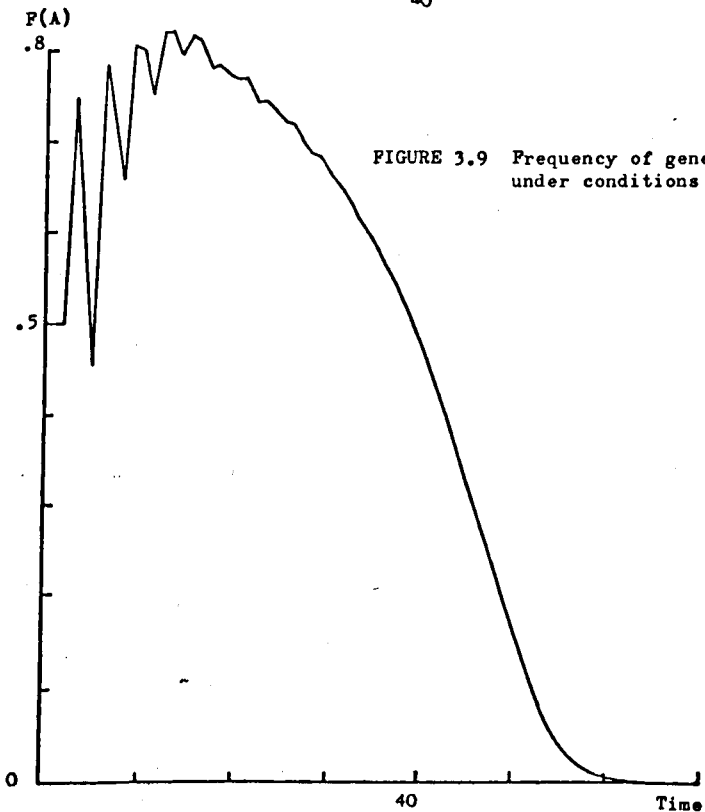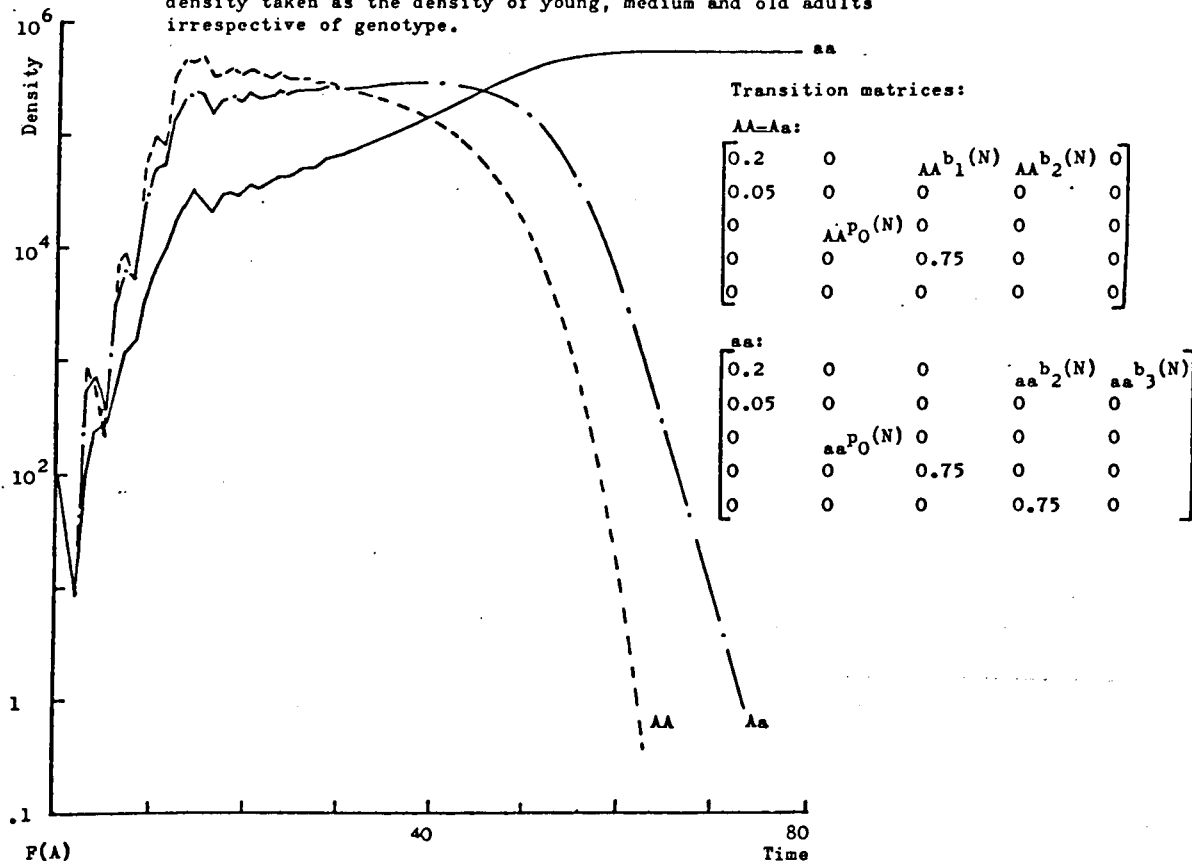
FIGURE 3.9   Frequency of gene A (F(A)) during colonisation
under conditions described in Figure 3.8.

mating to be at random with respect to age and genotype so that the
proportion of new seeds of each genotype is in Hardy Weinberg
equilibrium. Finally, I will suppose that colonisation begins with 100
seeds of each genotype.

The pattern of colonisation of genotypes AA, Aa and aa is summarised
in Figure 3.8. AA and Aa increase in numbers more quickly over the
early stages of colonisation, because their prereproductive periods are
shorter and seed output is greater than aa. (This is with the exception
of some large fluctuations in numbers over the first few iterations
arising from skewed age distributions.) However, by time 20 density
constraints on AA and Aa stop any further increase in their numbers,
whereas aa which is less adversely effected, still increases. As
numbers of aa continue to increase, survival and reproduction in AA and
Aa decrease to the point that their numbers start to decline. Eventually
AA and Aa are lost from the population and numbers of aa approach an
equilibrium value. Frequency of gene A during colonisation is given
in Figure 3.9; it rises to a peak at about the 13'th iteration and
subsequently declines. We can see from this episode of colonisation
that AA and Aa are good colonisers but poorly adapted for survival at
high density and aa <u>vice</u> <u>versa</u>.

3.4.2 Variation in breeding system, starting numbers and competitive
      interactions of different genotypes

The course of colonisation, although not the final result, will be
substantially influenced by factors apart from the life-historical
parameters in the transition matrices. For example, if the population
were completely selfing rather than forming a random mating pool, then
the number of individuals of each genotype would appear as in Figure 3.10,
all other parameters being kept the same as the previous example.

FIGURE 3.11 Population density during colonisation, shown as density of
genotype AA, Aa and aa. Conditions assumed to be identical
to those of Figure 3.8, with the exception that the starting
densities are 100 AA seeds, 10 Aa seeds and 10 aa seeds.
(Details of transition matrices in Figure 3.8.)
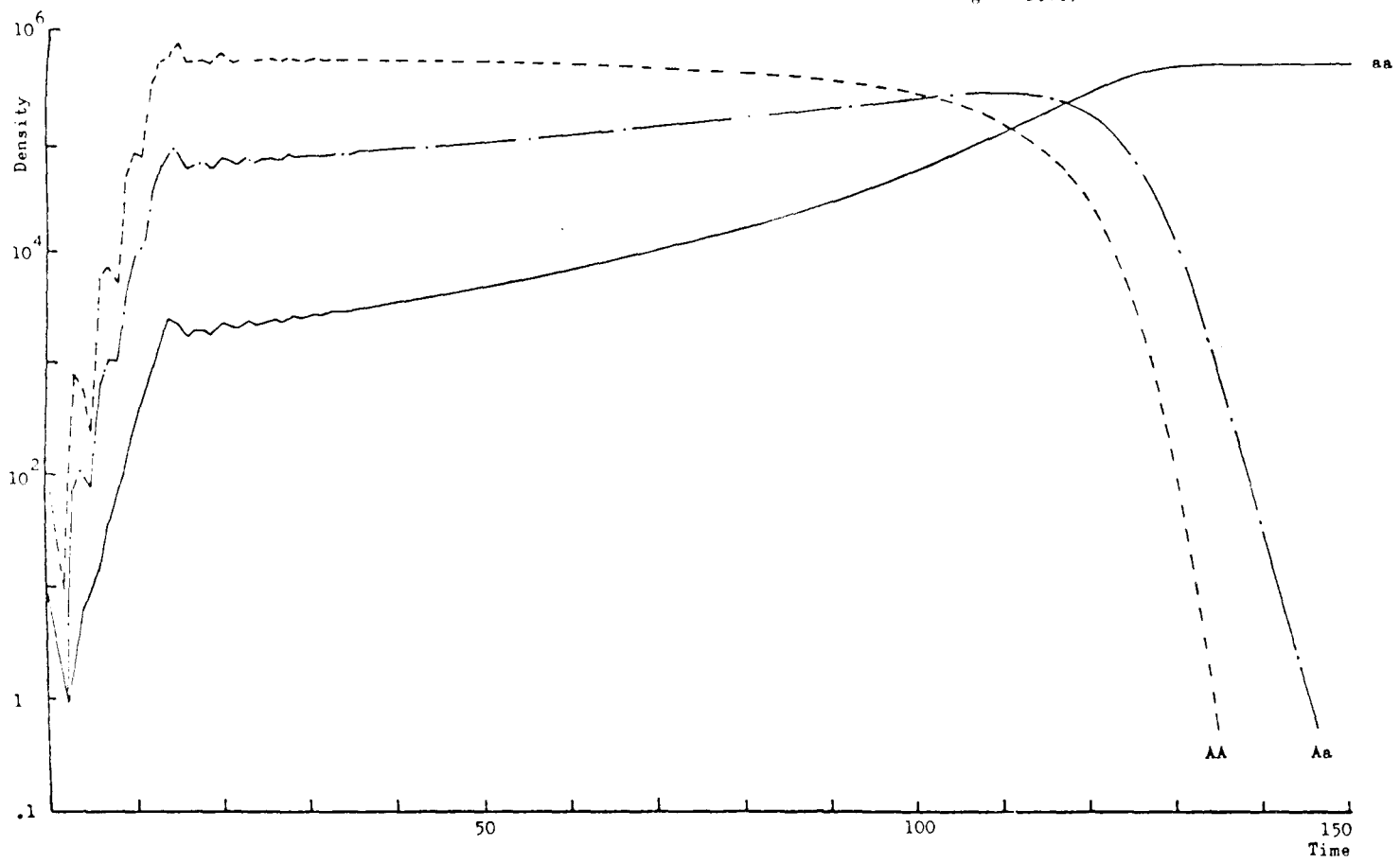
FIGURE 3.10 Population density during colonisation, shown as density of genotype AA, Aa and aa. Conditions assumed to be identical to those of Figure 3.8, with the exception that the population is completely selfing. (Details of transition matrices and starting conditions in Figure 3.8.)
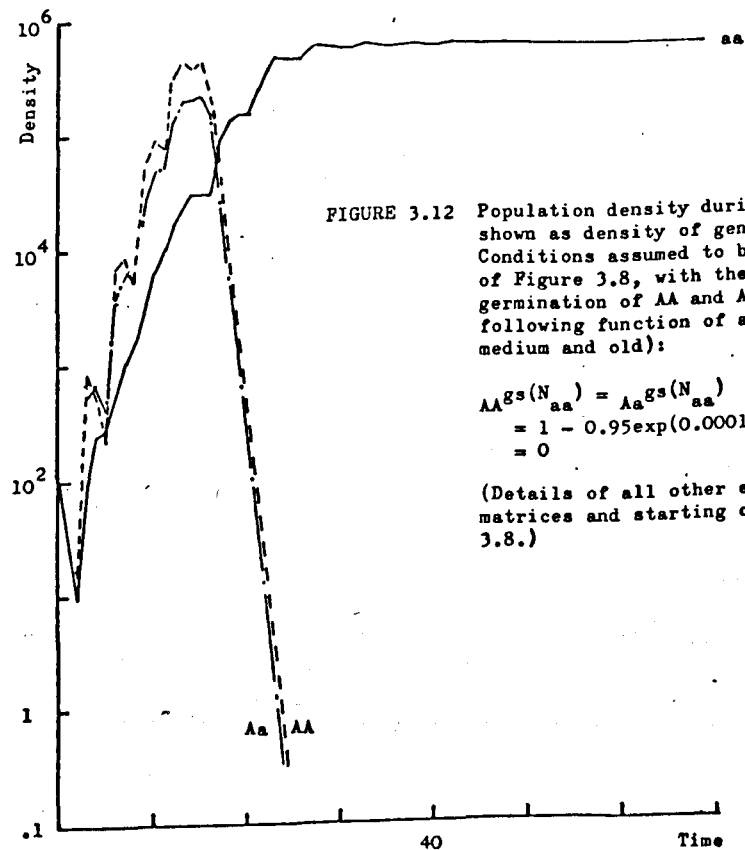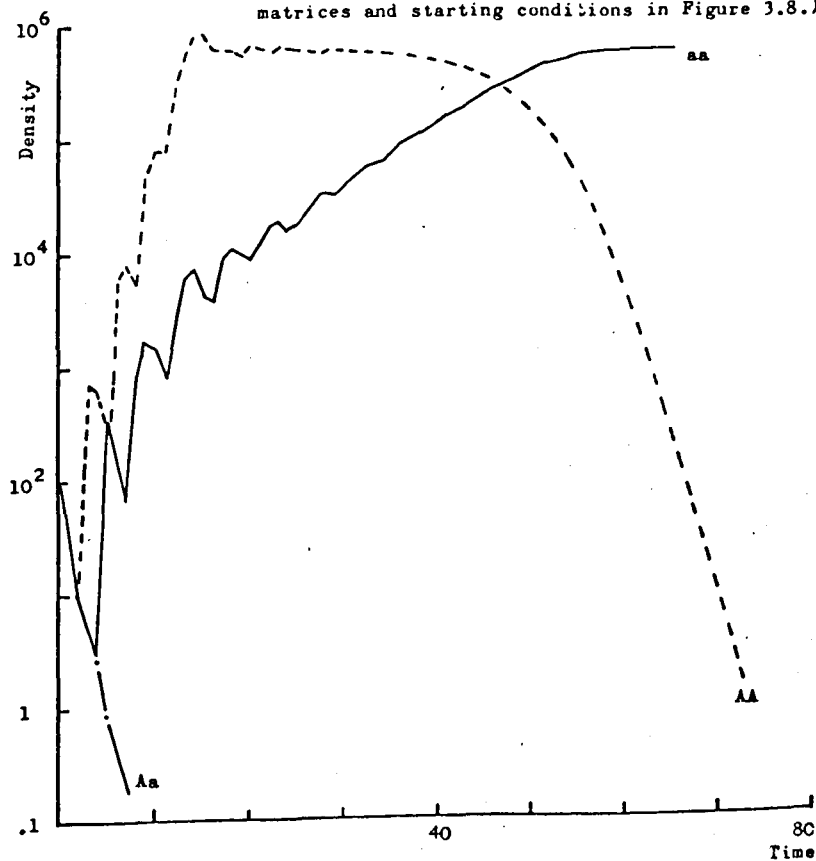
FIGURE 3.12 Population density during colonisation, shown as density of genotype AA, Aa and aa. Conditions assumed to be identical to those of Figure 3.8, with the exception that germination of AA and Aa seeds is the following function of aa adults (young, medium and old):

$$_{AA}gs(N_{aa}) = {}_{Aa}gs(N_{aa})$$
$$= 1 - 0.95\exp(0.0001N_{aa}) \quad \text{for } N_{aa} < 512$$
$$= 0 \quad \text{for } N_{aa} \geqslant 512$$

(Details of all other elements of transition matrices and starting conditions in Figure 3.8.)

Individuals of genotype Aa are of course lost rapidly from this selfing population. Those of genotype aa increase more slowly than before over the early stages of colonisation, as they are not augmented by segregation of Aa. However, the eventual outcome of colonisation is the same as before, as it takes only marginally longer for aa to be fixed. This model of colonisation is probably more relevant to Poa annua than the previous one, as there is evidence to suggest that Poa annua is generally inbreeding (Ellis 1974).

Another important factor in the pattern of colonisation is the proportion of each genotype present at the beginning. If there were only 10 Aa, 10 aa but 100 AA seeds present initially, colonisation would take the form of Figure 3.11, assuming as in Figure 3.8 that the population forms a random mating pool. It is clear that it takes aa much longer to remove AA and Aa because it starts from an initial disadvantage and is not much assisted by segregation of Aa as this has the same disadvantage as well. However the final result is the same, the only difference being that it takes much longer to achieve.

In all these calculations I have made the assumption that all individuals contribute equally to the density of the population, irrespective of their genotype. However it is quite possible that different genotypes could interact with one another to alter to different extents their age-specific survival and reproduction schedules. In these circumstances we would be considering interactive rather than exploitative competition (Gill 1974), and we would in effect be saying that the schedules were functions of the density of each genotype rather than the total density of the population. There are obviously a wide range of ways in which genotypes could interact and here I will only consider a single example. Suppose that germination of AA and Aa seeds is a decreasing function of the density of young, medium and old aa adults and that the function takes the following form:

$$_{AA}gs(N_{aa}) = 1 - 0.95 \cdot \exp(0.0001 \cdot N_{aa}) \qquad \text{Eq. 3.22}$$

$$\text{for } N_{aa} < 512$$

$$= 0 \qquad \text{for } N_{aa} \geqslant 512$$

If it is assumed that all other parts of the life history and colonisation remain as in Figure 3.8, then the pattern of growth of the population will take the form of Figure 3.12. It can be seen that the effect of this genotypic interaction is to cause a dramatic increase in the rate of loss of AA and Aa as the numbers of aa increase. Once again the eventual outcome of colonisation is unchanged.

3.5 Detection of genetic change during colonisation

In the previous section, I have shown very simply how genetic and demographic change during colonisation can be modeled. The justification for such simplification comes from practical problems of estimation, rather than mathematical difficulties. (Indeed, theoretically the only limitation on the number of genotypes is computer storage capacity for their transition matrices.) Even to model colonisation of a single genotype would require estimation of a large number of life and reproduction values over a range of densities. And populations of most species, including Poa annua, probably contain a very large number of genotypes with different life histories. The work entailed in making sufficient estimates would be so vast, that as far as I can see the model could not be developed. Little can be learnt from a model so sophisticated that the parameters it contains cannot be estimated, so it would be useless to make it genetically more complex.

With such serious difficulties over parameter estimation, one wonders how much can be learnt about genetic and demographic change during colonisation. It will help to answer this question by considering an example. Let us suppose that we are studying a real episode of

colonisation identical genetically and demographically to that of Figure 3.8, but with the constraint that the genetic structure of the population is not known. Under these conditions is it still possible to detect genetic change? One way by which we can search for genetic change is through comparison of samples taken at different stages during colonisation. Suppose the population is sampled at t=0,12,50; imagine these samples to be seed samples and suppose that they are sampled without error so that they contain the true proportions of each genotype. The seed samples can then be grown under standard conditions at a standard density to compare their life histories. If the experimental density is very low (effectively zero), mean values of each life-historical parameter for each sampling time will be as in Table 3.1. It can be seen that the proportion of medium adults surviving to be old adults is very small at time 12 but quite high by time 50 and that the number of seeds produced per young adult is high at time 12 and low by time 50. Hence we can conclude that there are life historical differences between samples taken at different stages of colonisation and that these differences must be genetic.

This example shows that ignorance of the genetic structure of a colonising population does not preclude detection of genetic change, because it is possible to use indirect methods of assessment. Nevertheless the approach to the problem is radically changed. Previously fitness of each genotype was independently determined by measurement of its life history; using these fitness values genetic change could then be quantitatively predicted. But now we can only infer the existence of genotypes with different life histories by the presence of genetically different forms at different stages of colonisation. The power of the model is drastically weakened, as it is no longer possible to predict how much genetic change can occur; yet to my knowledge there can be no alternative. And in spite of these limitations,

TABLE 3.1 Mean values of life-historical parameters for unbiased
seed samples taken at $t = 0$, 12 & 50 from colonisation
episode described in Figure 3.8. Samples grown at a
standard low density for direct comparisons.

Life-historical parameter	Time: 0	12	50
ps	0.2	0.2	0.2
gs	0.05	0.05	0.05
P_0	0.75	0.75	0.75
P_1	0.75	0.75	0.75
P_2	0.25	0.024	0.525
b_1	133	194	60
b_2	100	100	100
b_3	100	100	100

it is still worthwhile to test the hypothesis of genetic change during colonisation, because it is possible that no genetic change could occur.

There are two other points of practical importance that the example illustrates, both arising from the fact that life-historical parameters are functions of density. The first one is that care must be taken to distinguish between life-historical changes occurring in situ in the colonising population and those found when samples taken at different points in time are compared at constant density. The former contains the effects of both genetic and demographic change ('population dynamic effect' (Gadgil & Solbrig 1972)), whereas the latter contains only the effects of genetic change. In situ values of age-specific survival and seed output over the course of colonisation are given in Figures 3.13 & 3.14; most of them are quite different at t=0,12 & 50 to those in Table 3.1. The second point of practical importance is that the density at which samples are grown will have an important influence on the results obtained. For example, no differences were observed in the mean number of seeds per medium adult when they were grown at low density, whereas if samples had been grown at high density (20,000) considerable differences would have been found (21, 14 and 30 seeds per plant, at t=0, 12 & 50 respectively).

Finally, it is clear from these simulations that it is optimistic to hope to observe genetic change in the time available for this research. Assuming that a one step transition corresponds to eight weeks, only 6.5 transitions would occur per year. Bearing in mind also that estimates of life-historical characters are subject to sampling error, it is likely to be very difficult to test for genetic change. On the other hand the results obtained in this chapter depend critically on the parameter values used, which have usually been chosen intuitively. I therefore suggest that we need much more quantitative information

FIGURE 3.13 Age-specific survival during colonisation. These are values found in situ for colonisation as shown in Figure 3.8, but not divided into genotypes. Seed survival (ps), germination (gs), seedling to young adult survival (p_0), medium to old adult survival (p_2).
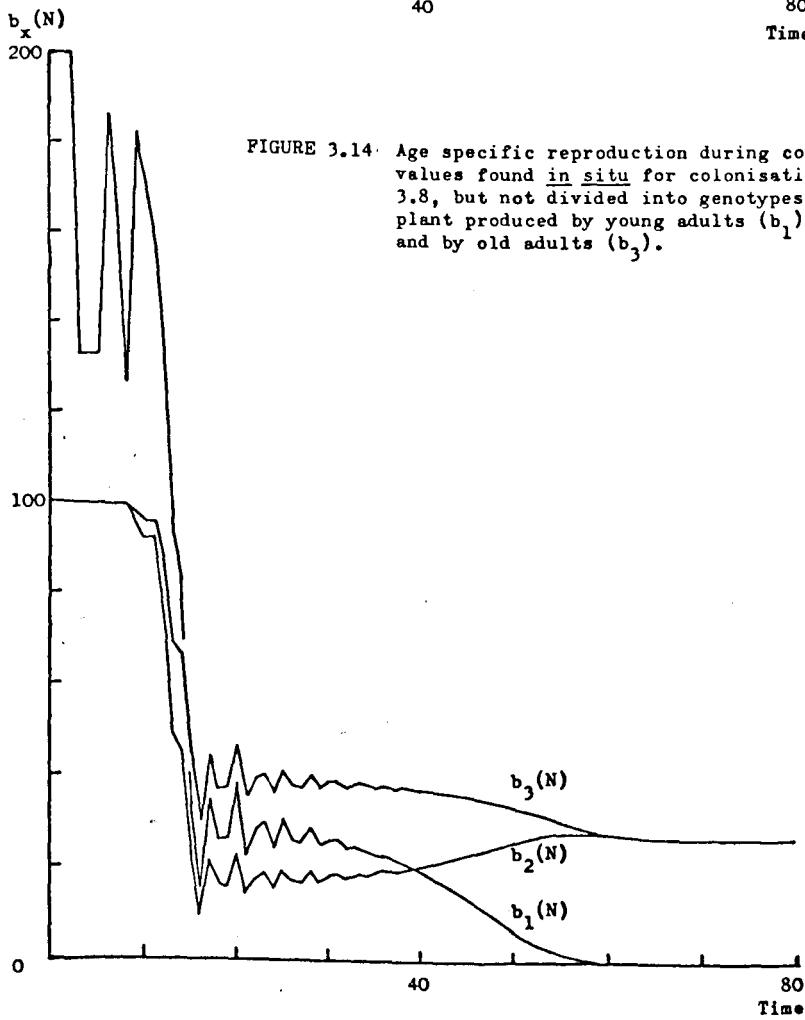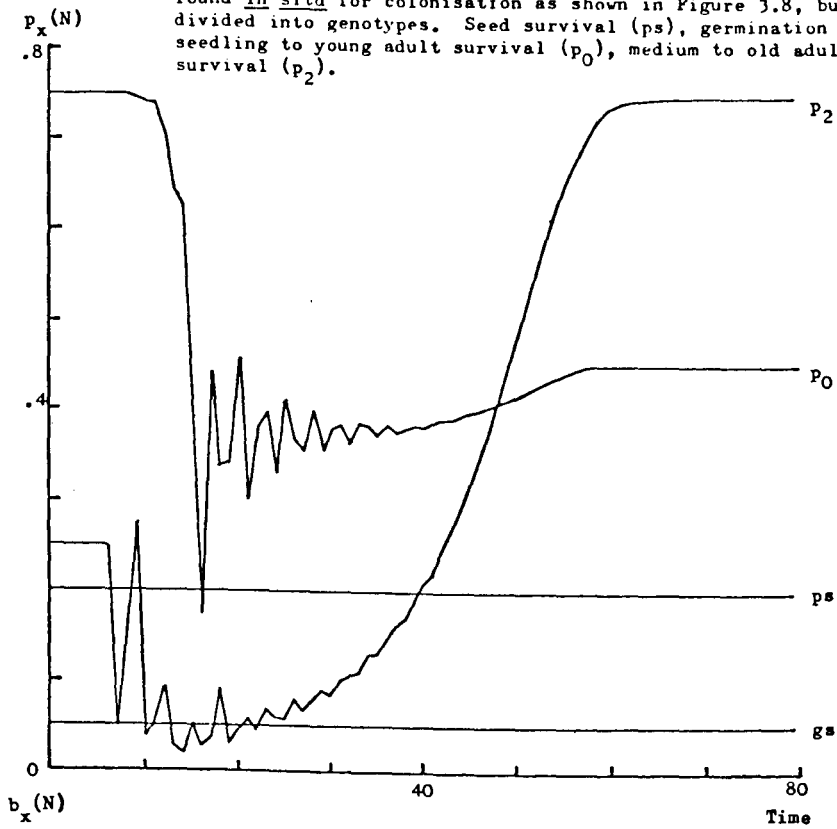
FIGURE 3.14 Age specific reproduction during colonisation. These are values found in situ for colonisation as shown in Figure 3.8, but not divided into genotypes. Number of seeds per plant produced by young adults (b_1), by medium adults (b_2) and by old adults (b_3).

about Poa annua populations, before we can predict how long should be needed to observe genetic change.

3.6 Conclusion

In this chapter I have developed a model of colonisation that states in a precise way the ideas expressed in Chapter 2. The model is suitable in particular for Poa annua and in general for plant populations with age distributions and seed dormancy but without vegetative reproduction. Ideally the model needs estimates of life and reproduction schedules of all genotypes at all population densities and a knowledge of the mode of inheritance of life-historical characters and breeding system. In this form the model would be powerful enough to deterministically predict the genetic and demographic changes during colonisation.

It should have been apparent as the model has been developed that we are continually handicapped by insufficient quantitative understanding of plant populations. Information as basic as age-specific survival and reproductive output has only been aquired for a small number of plant populations (Harper & White 1974) none of which were of Poa annua. Even less work has been attempted to establish the effect of density on these life and reproduction schedules. Such studies as have been made have been based on even aged stands (Harper & McNaughton 1962, Yoda et al. 1963), ignoring the effects of density of individuals of other ages. I doubt whether it would ever be possible to extract age-specific density effects from such experiments, even it it was supposed that all individuals contributing to density were of the same age class. And no attempts have ever been made to study genetic variation in life and reproduction schedules in plant populations, although this is fundamental to our understanding of evolution in populations (Lewontin 1974, p236).

Hence it is necessary to estimate all the parameters of the model before it can be used to predict genetic and demographic change during colonisation and Chapter 6 is directed towards this end. However it would be exceedingly difficult to do this completely for a population of normal genetic complexity, so it is necessary to seek a compromise between the theoretical ideal and practical constraints. The point of compromise that I take is to accept the impossibility of complete genetic determination of a population and to look for genetic change by indirect methods (comparing samples taken at different stages of colonisation). By doing this, the hypothesis of genetic change during colonisation can still be tested, but the predictive power of the model is lost.

CHAPTER 4

LIFE-HISTORICAL VARIATION AMONG NATURAL POPULATIONS OF POA ANNUA

4.1 Introduction

In Chapters 2 & 3, it has been shown that selection of different

forms can be expected over the course of colonisation and that

particular life-historical consequences of this selection may be

predicted. But genetic change during colonisation will only occur

if certain conditions are satisfied. These conditions are firstly,

that there should be appropriate genetic variation present, since

its absence would preclude the possibility of genetic change.

Secondly, different genotypes must be favoured, depending on the

extent to which selection is density-independent or dependent. This

condition limits the argument to populations in which there is not

a single genotype superior at all densities. But even if both of

these conditions are satisfied, it may still be impossible to observe

genetic change, if selection pressures are small. Hence the third

condition is one of empirical sufficiency (Lewontin 1974, Chapter 1);

selection pressures must be great enough for the genetic change to

be detectable.

These conditions are tested in this chapter by making observations

on natural populations of Poa annua. In the first section variation

among natural populations is analysed to determine whether the first

two conditions are satisfied. This is done by growing progeny of

samples from each population at low density as spaced plants. The

next section considers the effect of high population density on the

life histories of a small number of populations and the way in which

they interact when in competition with one another. This assists

in establishing the generality of the results in the previous section.

Finally an attempt is made to test the condition of empirical
sufficiency by comparing samples from some populations at different
stages of colonisation.

There have been several previous analyses of variation in
populations of Poa annua (Hovin 1957, Tutin 1957, Timm 1965,
Gibeault 1971, Gibeault & Goetze 1972, Ellis et al 1971, Ellis 1972,
1974, Wells 1974). Several of these have discussed the existence of
'biotypes' with different annual and perennial life histories (Hovin
1957, Tutin 1957, Timm 1965, Gibeault & Goetze 1972). In certain
cases this variation has been shown to have a genetic component
(Tutin 1957), but in others it has only been demonstrated with transplanted
adult material (Gibeault & Goetze 1972). It is known that there can
be much non-genetic variation (phenotypic plasticity Bradshaw 1965,
1973) between individuals of Poa annua (Ong pers. com.), so care must
be taken to establish the presence of genetic variation unequivocably.
Here life-historical variation in an actuarial form is analysed to
determine the extent to which it is genetically controlled.

4.2 Life-historical variation between spaced plants

4.2.1 Materials and methods

To test for the presence of genetic life-historical variation
within and between populations, samples of Poa annua were collected
from populations in North West England and North Wales. In choosing
the populations, it was crucial to distinguish those experiencing
predominantly density-independent from those experiencing predominantly
density-dependent selection. To do this quantitatively would have
required long-term observations on each population which was
impracticable in this study. Instead subjective estimates were made
based on the present distribution of individuals, the extent of
inter-plant interaction and the stresses imposed by land use. It was

also essential that the populations chosen should have been

experiencing their density-independent or dependent selection regimes

for a reasonably long period of time, so it was necessary to make an

estimate of the history of land usage of each population.

Populations were categorised in the following manner. Those

in which individuals were widely spaced, where large areas of bare

ground were present and which were likely to have been maintained

that way for some time (eg. by continuous disturbance), I took to be

experiencing predominantly density-independent selection. Examples

of such populations are those to be found in car parks, in quarries

and derelict areas; I will refer to these as opportunist populations.

On the other hand, populations in which individuals were closely

packed with individuals of their own or other species and which were

likely to have been maintained that way for some time, I took to be

experiencing predominantly density-dependent selection. Permanent

pastures and old lawns may be considered as examples of this kind of

population; I will refer to them as pasture populations. The choice

of pasture populations was further restricted by problem of ensuring

a constant history of land management, that they had not been for

example recently ploughed. To minimise this source of error, only

those populations that could not have been ploughed were sampled,

for example those on hillsides or with rock outcrops in the vicinity.

By sampling a large number of populations, it was possible to ensure

that other environmental variables such as grazing pressures, which

might have influenced life histories, were distributed and random

between opportunist and pasture environments.

28 populations were sampled, 14 from environments with

predominantly density-independent selection and 14 from ones with

predominantly density-dependent selection; details of the environment

TABLE 4.1 Description of environments of natural populations of *Poa annua*
sampled. Column 5 (Ground cover) gives a subjective estimate of
the proportion of ground covered by plants. Column 6 (Other
species) includes only those that contributed significantly to
ground cover. Column 7 (Proportion *Poa annua*) gives 3 subject-
ive rankings: low, medium or high.

Population	OS map ref.	Altitude (metres)	Site description	Ground cover (%)	Other species	Proportion Poa annua
Opportunist populations						
a Blackriggs Quarry	SD793660	250	Derelict limestone quarry 100m from population o.	60	*Deschampsia caespitosa*, *Agrostis tenuis*, *Poa pratensis*.	High
b Bargh House Track	SD817683	250	Heavily used farm track, 3m from population p.	50	*Lolium perenne*	High
c Blands Farm Car Park	SD742865	180	Small car park by river-side.	20		High
d Iron Band Car Park	NY823187	440	Small car park on high moorland; trampled and sheep grazed.	20	*Agrostis stolonifera*, *Festuca ovina*.	High
e Ashgill Head Roadside	NY807355	560	Gravel margin at edge of moorland road; sheep grazed	90	*A. stolonifera*.	Med.
f Rise Field Entrance	NY728444	430	Entrance to field; subject to trampling.	90		High
g Walvick Road-works	NY391710	200	Disturbed area at road junction, due to recent roadworks.	50	*A. stolonifera*, *Dactylis glomerata*, *Ranunculus* spp.	Low
h Tarn Hows Car Park	SD328996	200	Large heavily used car park with scattered plants near margin.	40	*F. ovina*.	High
i Ennerdale Car Park	NY109154	130	Forestry Commission car park, with plants in gravel near margin; sheep grazed.	50	*L. perenne*, *Taraxacum officinale*, *Bellis perennis*.	Med.
j Moel Arthur Track	SJ147657	370	Hillside track, trampled and sheep grazed. 20m from pop-ulation y.	40	*L. perenne*.	Med.
k Glen y Wern Field Entrance	SJ090659	30	Entrance to water meadow; heavily trampled.	20	*L. perenne*.	High
l Dyffryn Mymbyr Layby	SH696651	200	Loose roadside gravel, 30m from population z.	40	*F. ovina*.	High
m Pen y Pass Car Park	SH647556	360	Heavily used car park, with plants around perimeter; sheep grazed.	70	*L. perenne*.	High
n Travsfynydd Track	SH714361	310	At entrance to field of population aa.	80	*D. glomerata*, *T. officinale*.	High
Pasture populations						
o Blackriggs Pasture	SD792660	240	Heavily grazed limestone meadow; species rich.	100	*L. perenne*, *P. trivialis* *A. stolonifera*, *Ranunculus* spp.	Low
p Bargh House Pasture	SD817683	250	Sheep and cattle grazed limestone meadow; species rich.	100	*L. perenne*, *P. trivialis* *A. stolonifera*, *F. ovina* *Ranunculus* spp, *Trifolium*	Low
q Greenwood How Meadow	SD675894	120	Water meadow on limestone, grazed by cattle.	100	*L. perenne*, *A. tenuis*, *Trifolium* spp.	High
r White Brackens House Pasture	NY777046	210	Open pasture by riverside; closely grazed and rather trampled.	100	*L. perenne*, *A. tenuis*, *Ranunculus* spp, *Trifolium* spp.	Med.
s Well Head Pasture	NY814162	320	Hillside meadow; grazed and a little trampled.	100	*L. perenne*, *F. ovina*, *Trifolium* spp.	Med.
t Greenhills Pasture	NY839320	430	Hillside limestone pasture; lightly grazed.	100	*L. perenne*, *A. stolonifera*, *Juncus effusus*, *Ranunculus* spp.	Med.
u Knarledale Pasture			Grazed pasture at edge of moorland.	100	*A. tenuis*, *F. ovina*, *J. effusus*, *Cirsium* spp.	High
v High Shield Farm Pasture	NY768674	220	Damp, sheep grazed pasture.	100	*L. perenne*, *A. stolonifera*, *J. effusus*, *Trifolium* spp, *Cirsium* spp.	Med.
w Eltervater Moor Pasture	NY336053	150	Close grazed pasture at edge of moorland; trampled.	100	*F. ovina*, *A. tenuis*, *Pteridium aquilinum*.	Low
x Skelvith Fold Meadow	NY348027	110	Cattle grazed meadow with wet flush.	100	*A. stolonifera*, *Ranunculus*, *J. effusus*	Low
y Moel Arthur Pasture	SJ147657	370	Closely grazed pasture at edge of open hillside.	100	*F. ovina*, *A. tenuis*.	Med.
z Dyffryn Mymbyr Meadow	SH696651	200	Pasture, heavily grazed by sheep.	100	*L. perenne*, *P. trivialis* *F. ovina*, *A. stolonifera*	Med.
aa Travsfynydd Meadow	SH714361	310	Heavily grazed permanent pasture.	100	*A. tenuis*, *F. ovina*, *B. perennis*, *Luzula* spp.	Low
bb Ty Mawr Pasture	SJ156608	360	Small area of almost pure *Poa annua* on open hillside.	100	*A. tenuis*, *F. ovina*.	High

of each population are summarised in Table 4.1. Vegetative tiller samples were taken from each population at approximately 0.5 m intervals along a 10 m transect. They were transferred to an experimental field and grown to flowering. Samples of seed were collected from each tiller for experimental work; they are referred to as families in the results below. (No attempt was made to isolate tillers to prevent cross pollination as there is evidence that Poa annua is largely inbreeding (Ellis 1974). Any outcrossing would tend to reduce the differences between populations, making estimates of differences conservative.)

To test for genetic differences, 5 families were taken at random from each population and 4 seeds were taken at random from each family. Seeds were germinated on filter paper in petri dishes, the seedlings transferred to 'jiffy pots' containing John Innes No. 2 compost and laid out in a completely randomised design in a greenhouse (21.2.74). After 4 weeks the experiment was transferred to an experimental field, each individual being planted on a regular lattice about 0.5 m from its nearest neighbours. The plants were left undisturbed to enable their life histories to be measured.

Several life-historical characters were measured on each plant. Firstly, the prereproductive period taken as the time from germination to the emergence of the first inflorescence was recorded. Subsequently age-specific reproduction was estimated as the number of inflorescences produced from which all seed had fallen; this was measured at 4 week intervals and after each inflorescence had been counted it was removed to prevent it from being counted again later. Thirdly plant diameter was measured 7 months after germination to provide an indication of the amount of vegetative spread. Finally the age at death of each plant was recorded, so that age-specific survival rates could be estimated for families and populations. Death was sometimes difficult

to record because vegetative progeny developed; in these cases it was assumed to occur when there was no green tissue on the parent and the progeny appeared to be independent. Results are given here for the first 13 months of life of the plants.

The experiment was designed to be analysed by heirarchical analysis of variance so that variation in each set of data could be partitioned in two ways. Firstly to test for the presence of genetic variation, one level of nesting was used, partitioning variation between and within families (Appendix 4.1.1). Secondly to test for variation between opportunist and pasture populations, three levels of nesting were used, partitioning variation between opportunist and pasture environments, between populations within environments, between families within populations and between individuals within families (Appendix 4.1.2). However, since some plants died before others, there were different numbers of individuals in different families and it was necessary to use Satterthwaite's approximation to calculate F ratios (Sokal & Rolf 1969). There were some serious problems in carrying out analysis of variance on sets of reproductive data because many plants produced no flowers. This led to skewed distributions and heterogeneity in error variances.

4.2.2 Life-historical variation - genetic or non-genetic?

Genetic variation can be distinguished from non-genetic variation by the proportion occurring between and within families. If there is significant variation between families when compared to the variation within families, there must be a genetic component to it (as long as plants are grown from seed together in the same environment). Hence to test for the presence of genetic variation in life-historical characters here, sums of squares are partitioned between and within families.

TABLE 4.2 Results of analysis of variance between families. F ratio is the ratio of the between family mean square to the within family mean mean square. p is the probability of the null hypothesis: no significant difference between families, with n_1 numerator and n_2 denominator degrees of freedom. Analyses on reproduction characters only carried out on families without zero data.

Character	n_1	n_2	F ratio	p
Prereproductive period	139	415	10.2791	<0.001
Diameter at age 7 months	139	416	6.3670	<0.001
No. inflorescences produced when 3 months old	13	42	5.8005	<0.001
No. inflorescences produced when 4 months old	57	171	2.9468	<0.001
No. inflorescences produced when 5 months old	67	200	3.0366	<0.001
No. inflorescences produced when 6 months old	73	218	3.0200	<0.001
No. inflorescences produced when 7 months old	65	192	3.4993	<0.001
No. inflorescences produced when 8 months old	56	164	2.3065	<0.001
No. inflorescences produced when 9 months old	30	90	1.4063	>0.05

TABLE 4.3 Results of analysis of variance between opportunist and pasture environments. F ratio is the ratio of the between environment mean square to the between population within environment mean square. p is the probability of the null hypothesis: no significant difference between environments, with n_1 numerator and n_2 denominator degrees of freedom. Reproduction data transformed to square root(x+0.5).

Character	n_1	n_2	F ratio	p
Prereproductive period	1	25	32.7654	<0.001
Diameter at age 7 months	1	25	51.4476	<0.001
No. inflorescences produced when 3 months old	1	25	13.5740	<0.01
No. inflorescences produced when 4 months old	1	25	27.9324	<0.001
No. inflorescences produced when 5 months old	1	25	40.8880	<0.001
No. inflorescences produced when 6 months old	1	25	29.2276	<0.001
No. inflorescences produced when 7 months old	1	25	15.1379	<0.001
No. inflorescences produced when 8 months old	1	25	6.3075	<0.05
No. inflorescences produced when 9 months old	1	25	3.8864	>0.05

TABLE 4.4 Contingency tables of presence or absence of flowering against opportunist or pasture environment. Chisquare values calculated from the expectation that all plants have the same probability of flowering. p is the probability of this hypothesis, with 1 degree of freedom.

Character		flower	not flower	Chisquare	p
3 months old	opportunist	107	169	66.39	<0.001
	pasture	26	254		
4 months old		219	57	144.17	<0.001
		80	200		
5 months old		235	41	132.81	<0.001
		105	175		
6 months old		239	37	112.98	<0.001
		122	158		
7 months old		227	44	89.89	<0.001
		126	154		
8 months old		207	61	69.89	<0.001
		118	162		
9 months old		150	109	24.12	<0.001
		103	177		

TABLE 4.5 Results of analysis of variance between families within populations. F ratio is the ratio of between family within population mean square to the within family mean square. p is the probability of null hypothesis: no significant difference between families within populations, with n_1 numerator and n_2 denominator degrees of freedom. Reproduction data transformed to square-root(x + 0.5).

Character	n_1	n_2	F ratio	p
Prereproductive period	112	415	5.4746	<0.001
Diameter at age 7 months	112	416	3.2173	<0.001
No. inflorescences produced when 3 months old	112	416	5.5182	<0.001
No. inflorescences produced when 4 months old	112	416	6.4522	<0.001
No. inflorescences produced when 5 months old	112	416	5.2118	<0.001
No. inflorescences produced when 6 months old	112	415	4.5355	<0.001
No. inflorescences produced when 7 months old	112	409	4.2888	<0.001
No. inflorescences produced when 8 months old	112	406	3.5081	<0.001
No. inflorescences produced when 9 months old	112	396	2.8262	<0.001

F ratios and probabilities of no significant variation between families are given in Table 4.2. Prereproductive period and plant diameter being approximately normally distributed, are analysed without transformation; their F ratios are highly significant indicating a large component of genetic variation. It is rather more difficult to analyse age-specific reproduction because a considerable number of plants were not flowering at each age. Families with zero data lead to an underestimate of the error mean square and an overestimate of the significance of differences between families. However, if any families containing non-flowering individuals are excluded from the analysis, F ratios can also be calculated for reproduction characters (Table 4.2). It is clear from these F ratios that there is highly significant genetic variation between reproducing families up to 9 months after germination.

These results demonstrate the wealth of genetic variation in life-historical characters in Poa annua. They substantiate the results of previous research (Hovin 1957, Tutin 1957, Timm 1965, Gibeault 1971, Gibeault & Goetze 1972, Ellis et al 1971, Ellis 1972, 1974, Wells 1974) and place beyond question the presence of genetic variation in life-historical characters among the populations in this analysis. (It would be interesting to calculate the heritabilities of the characters measured in each population, because heritabilities of fitness characters have generally been found to be low (Falconer 1960, Chapter 10). Unfortunately this is not readily possible in Poa annua as the breeding system causes populations to depart from Hardy Weinberg equilibrium.)

4.2.3 Life-historical variation between opportunist and pasture populations

In the knowledge that genetic variation exists in life-historical characters, the analysis can be extended to study the distribution

FIGURE 4.1

Age-specific reproduction (b_x)
and survival (l_x) of opportun-
ist and pasture populations.
Age (x) in 4 week units.
Reproduction in units of nos.
of inflorescences/plant/month.
λ = finite rate of increase per
month, calculated using
data from first 11 months.

a Blackriggs Quarry
(λ=1.8258)

b Bargh House Track
(λ=1.8289)

c Blands Farm Car Park
(λ=1.8870)

d Iron Band Car Park
(λ=1.7471)

e Ashgill Head Roadside
(λ=1.8515)

f Rise Field Entrance
(λ=1.5748)

g Walwick Roadworks
(λ=1.9190)

h Tarn Hows Car Park
(λ=1.9333)

i Ennerdale Car Park
(λ=1.8439)

j Moel Arthur Track
(λ=1.8599)

k Glen y Wern Field
Entrance (λ=1.7994)

l Dyffryn Mymbyr Layby
(λ=1.9007)

m Pen y Pass Car Park
(λ=1.8561)

n Trawsfynydd Track
(λ=1.8563)

Pasture populations

o Blackriggs Pasture
(λ=1.6247)

p Bargh House Pasture
(λ=1.7672)

q Greenwood How Meadow
(λ=1.3774)

r White Brackens House
Pasture (λ=1.6833)

s Wellhead Pasture
(λ=1.5423)

t Greenhills Pasrure
(λ=1.5427)

u Knarledale Pasture
(λ=1.6139)

v High Shield Farm
Pasture (λ=1.6405)

w Elterwater Moor
Pasture (λ=1.8220)

x Skelwith Fold Meadow
(λ=1.4401)

y Moel Arthur Pasture
(λ=1.7353)

z Dyffryn Mymbyr Meadow
(λ=1.8012)

aa Trawsfynydd Meadow
(λ=1.7565)

bb Ty Mawr Pasture
(λ=1.4884)

of the variation in opportunist and pasture populations. Age-specific reproduction and survival in each population is illustrated in Figure 4.1. The graphs demonstrate certain general differences between samples from opportunist and pasture populations. Firstly, there was more reproduction in most opportunist populations; in some cases the differences were extreme (Blands Farm Car Park/ Greenwood How Meadow), but there were a few cases of overlap (Rise Field Entrance/Elterwater Moor Pasture). Secondly, there were differences in the distribution of reproduction over age, the mode for opportunist populations usually being one month earlier. Thirdly, although mortality had not begun in some populations, those in which it had were generally opportunist ones. There were also differences in the distribution of mean family prereproductive periods between opportunist and pasture families (Figure 4.2); a large proportion of opportunist families started reproduction at an early age, whereas many pasture ones did not reproduce at all during the first year. Finally there were differences in the distribution of mean plant diameters per family 7 months after germination, diameters of families from opportunist populations tending to be smaller than those from pasture ones (Figure 4.3).

Using heirarchical analysis of variance, it is possible to test the significance of differences between environments. F ratios between environments, taking the population within environment mean square as the error, confirm the differences between opportunist and pasture populations for prereproductive period and plant diameter (Table 4.3), the differences in both cases being highly significant. However there are difficulties in the analysis of age-specific reproduction because not all plants reproduced at each age and zero data leads to an underestimate of the error mean square. The problem cannot be circumvented by exclusion of zero data because there were usually many more pasture plants not flowering than opportunist ones.

FIGURE 4.2 Distribution of mean family prereproductive periods
of opportunist and pasture families. Measurements
taken at fortnightly intervals.

a Opportunist families
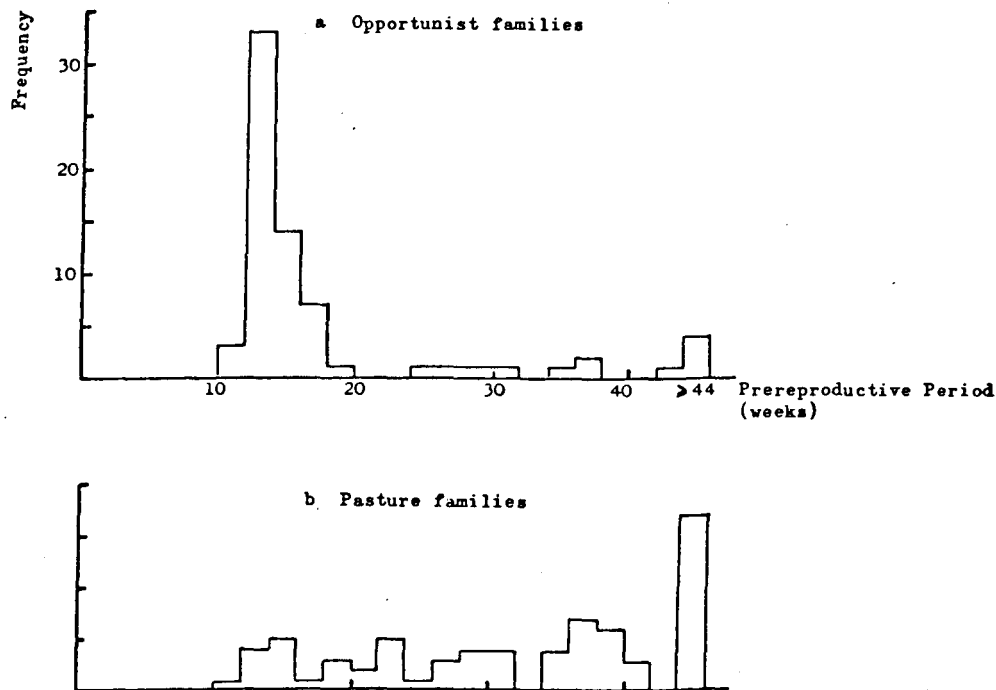
b Pasture families

FIGURE 4.3 Distribution of plant diameters 7 months after germination
for opportunist and pasture families. (Expressed as the
mean diameter for each family.)

a Opportunist families

b Pasture families
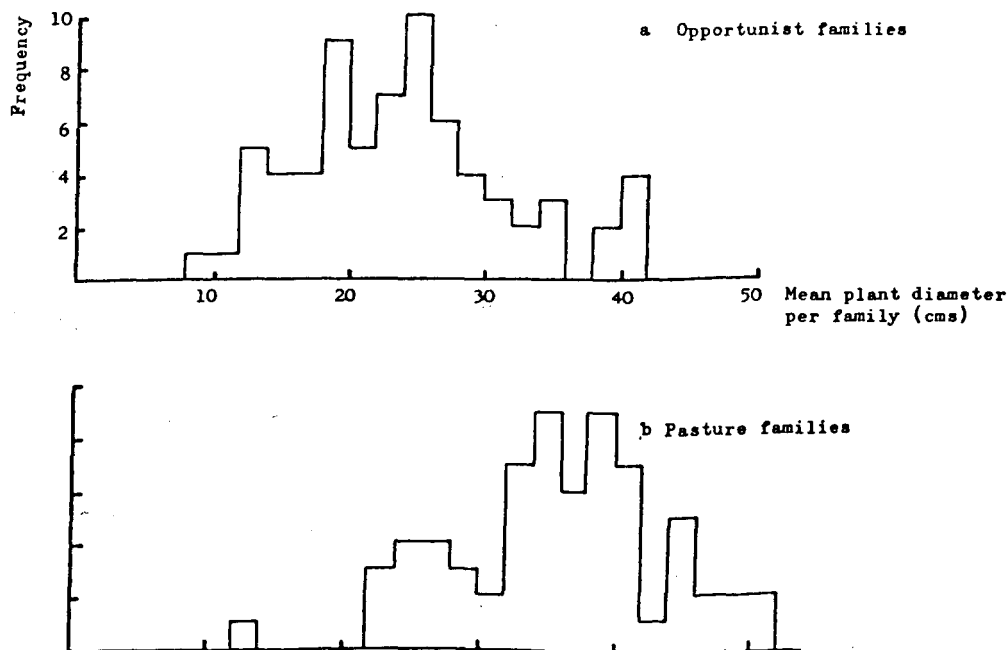
It can be argued though that since the highest level of the
heirarchy is being considered and mean values for each population
are based on about 20 plants, the means should be approximately
normally distributed, so the errors should not be serious. Working
from this argument F ratios are given for age-specific reproduction
in Table 4.3, demonstrating highly significant differences between
opportunist and pasture environments until the plants were 8 months
old. To remove any remaining doubt over differences between plants
from opportunitst and pasture environments chisquare tests can be
carried out on 2 x 2 contingency tables of presence or absence of
flowering against opportunist or pasture environment. Contingency
tables with their respective chi-square values are given in Table
4.4; they are all highly significant with one degree of freedom, so
that the null hypothesis of plants from opportunist and pasture
environments reproducing with the same probability can be rejected.

Even after removing variation between environments and between
populations within environments, there was still variation between
families within populations. Taking the mean square within families
as the error, the F ratios for each character are highly significant
(Table 4.5). This can be interpreted as genetic variation within
populations and it is variation of particular evolutionary importance
because it means that the potential for genetic change existed in
the populations. However, it is necessary to be cautious in drawing
conclusions from reproduction F ratios because the inclusion of zero
data leads to an underestimate of the within families mean square.

It is clear from these analyses that different kinds of life
histories were associated with populations from opportunist and
pasture environments. In opportunist populations prereproductive
periods were generally shorter, reproductive output greater, lives
shorter and vegetative spread less than in pasture populations. Since

only small numbers of inflorescences or none at all during the first

year (predominantly pasture plants), underwent a period of intense

reproductive activity during the spring and early summer. Thirdly,

mortality among opportunist plants was greater than pasture ones

during the spring. However, there was a period of drought in May

and June, which was associated with heavy mortality among both

opportunist and pasture plants.

4.2.4 Correlation of life-historical characters

It has become clear that there is much variation between

families in several life-historical characters. It is possible that

certain kinds of characters could be correlated with one another,

either through a common genetic basis or because selection favours

certain combinations. Hence it is interesting to calculate correlation

coefficients between each character over all families.

A matrix of product moment correlation coefficients is given

in Table 4.6. It was calculated from a data matrix of 12 life-

historical characters over 134 families that had living representatives

12 months after germination, family means being taken as data

elements. To enable prereproductive period to be included it was

necessary to assume that all plants that had not started to flower

by the end of the 12'th month, began to flower at the beginning of

the 13'th. The results show that age-specific reproduction was

strongly correlated with reproduction in the months immediately

preceding and following, but less so over greater time intervals.

For example, reproduction in 3 month old families was positively

correlated with 4 and 5 month old families, but the correlation became

less strong with reproduction at greater ages. Prereproductive

period was negatively correlated with reproduction at all ages, since

a significant proportion of the plants did not flower in the first

year. Plant diameter after 7 months was negatively correlated with

the differences were closely associated with the environments,one

is led to suspect that they could be due to natural selection. (If

the differences had been due to random genetic drift, no correlation

would have been expected with environment.) Further evidence to

support this assertion is that closely adjacent opportunist and

pasture populations were different from one another (Blackriggs

Quarry/Blackriggs Pasture, Bargh House Track/Bargh House Pasture,

Moel Arthur Track/Moel Arthur Pasture, Dyffryn Mymbyr Layby/ Dyffryn

Mymbyr Meadow, Trawsfynydd Track/ Trawsfynydd Meadow). These

differences almost inevitably occurred in the face of gene flow and

could only have been maintained by natural selection (but see Chapter

6.3).

Assuming that the differences between opportunist and pasture

environments were due to natural selection, what environmental

factors would bring about these selective pressures? There was of

course a host of environmental variables among the populations sampled,

but sufficient were sampled to put most of these at random with respect

to opportunist and pasture environments. Since the environments

were chosen to represent density-independent and density-dependent

selection regimes, I would conclude that the life-historical

differences were attributable to density-independent and dependent

selection. This conclusion is supported by the close agreement

between the differences found and those predicted under density-

independent and dependent selection in Chapter 2.5.

Although results have been quoted here up to February 1975 (t=12)

measurements of life-historical characters were continued until

June (t=16). These later results have not yet been analysed, but

they seem to show several important trends. Firstly, all plants that

did not flower at all during the first year, produced their first

inflorescences early in the spring. Secondly, the plants that produced

TABLE 4.6 Product moment correlation coefficients of life-historical characters of families of _Poa annua_, when grown at low density. The coefficients are calculated from mean values of each character per family, including only those families with living representatives 12 months after germination.

No. of inflorescences

	4 month old plants	5 month old plants	6 month old plants	7 month old plants	8 month old plants	9 month old plants	10 month old plants	11 month old plants	12 month old plants	Prereproductive period	Plant diameter 7 months
3 month old plants	.5548	.4441	.2263	.1682	.1385	-.0029	.0292	.0841	-.0298	-.4247	-.4960
4 month old plants		.8481	.6859	.4606	.4020	.2836	.1915	.2455	.0810	-.7440	-.6678
5 month old plants			.8466	.6007	.4859	.3840	.2437	.3314	.0438	-.7976	-.6938
6 month old plants				.8023	.7206	.6666	.4382	.4827	.1660	-.7883	-.5672
7 month old plants					.8230	.8013	.6030	.7086	.2281	-.6724	-.3937
8 month old plants						.8075	.7142	.7440	.2901	-.5462	-.2319
9 month old plants							.6888	.7118	.3827	-.5195	-.2312
10 month old plants								.7870	.5604	-.4206	-.0651
11 month old plants									.5502	-.4336	-.0644
12 month old plants										-.2039	.0822
Prereproductive period											.7080

No. of inflorescences

age-specific reproduction, but the strength of the correlation declined as age increased. This indicates that early reproduction was associated with little vegetative spread, which is substantiated by a positive correlation between prereproductive period and diameter.

Most sets of data used in calculating these correlations were not normally distributed so it would be misleading to attach significance levels to the coefficients. In addition, the comparisons were not independent of one another; to establish the detailed correlation structure would require partial correlation analysis. However the results are sufficient to demonstrate that short prereproductive periods were associated with high seed output in the first year and with little vegetative spread.

4.2.5 Rates of increase

It is known from Chapter 2.2 that to every life history there is an associated finite rate of growth. Using the life-historical information collected from opportunist and pasture plants, it is possible to calculate finite rates of growth of populations and families. Since the plants were grown at low density, the rates correspond to the maximal ones under the physical conditions of the experimental field (the finite equivalent of the intrinsic rate of natural increase (r)).

Finite rates of increase are calculated here using Leslie's method (Leslie 1945, 1948). This requires the life-historical data in the form of a transition matrix, the dominant eigenvalue of which is the finite rate of growth (Chapter 3.3). The way in which transition matrices for plant populations are constructed has been considered in Chapter 3.2; the particular form used here is shown in Table 4.7.

To calculate finite rates of increase, several assumptions must be made about the demographic parameters.

a   Each element of the transition matrix remains constant. Unless

this is the case, the proportion of individuals in different age

classes changes and the rate of growth changes. In reality

this assumption could never be satisfied,since both increasing

density and seasonal fluctuations would alter reproduction and

survival.

b   All plants still alive 43 weeks after germination died at the

beginning of the 44'th. This assumption must be made because

it was necessary to terminate measurements before all plants

had died.

c   Mortality occurs after reproduction in each age class. This

problem arises because reproduction and mortality were continuous

processes, but could only be measured at discrete points in time.

It does not introduce a serious error in these calculations

because mortality was small when reproduction was large.

d   There is no vegetative reproduction. This assumption is reasonable

for most opportunist plants but leads to an underestimate of

growth rates of some pasture families, which were vigorous

vegetative reproducers.

e   Reproduction, measured in the field as numbers of inflorescences,

is multiplied by a constant to convert it to numbers of viable

seeds. This constant is 79.61, calculated from the mean number

of seeds per inflorescence at low density (91.36 see Chapter 6.5.4)

and the proportion viable (0.8713 see Chapter 6.4.2). It is

doubtful if this assumption is strictly valid as there appeared

to be variation in seed output per inflorescence, associated

both with plant age and family.

f   Lacking any information on seed population dynamics, parameter

values must be chosen from other sources. It is assumed that

there was a 4 week ripening period before any germination or

TABLE 4.7 Transition matrix used for calculation of finite rates of increase of opportunist and pasture populations and families.
There are 13 age classes represented in the matrix:
age class 1 = ripening seeds aged 0 to 3 weeks inclusive,
"   "   2 = mature seeds aged 4 weeks or more,
"   "   3 = seedlings aged 0 to 3 weeks inclusive,
"   "   4 = adult individuals aged 4 to 7 weeks inclusive,
"   "   5 = adult individuals aged 8 to 11 weeks inclusive,
⋮
"   "   13 = adult individuals aged 40 to 43 weeks inclusive.
Matrix elements as defined in Chapter 3.2.

$$
\begin{bmatrix}
0 & 0 & b_0 & b_1 & b_2 & b_3 & b_4 & b_5 & b_6 & b_7 & b_8 & b_9 & b_{10} \\
ps_0 & ps & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & gs & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & p_0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & p_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & p_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & p_3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & p_4 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & p_5 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & p_6 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & p_7 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & p_8 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & p_9 & 0
\end{bmatrix}
$$

TABLE 4.8 Finite rates of increase of families from opportunist and pasture populations calculated by substituting appropriate b_x and p_x values into matrix shown in Table 4.7. (Units: per 4 week period)

Population	Family: 1	2	3	4	5
Opportunist populations					
a Blackriggs Quarry	1.7979	1.8007	1.8268	1.7243	1.9216
b Bargh House Track	1.8433	1.6828	1.8589	1.9248	1.7695
c Blands Farm Car Park	1.8534	1.7497	1.8852	1.9012	1.9808
d Iron Band Car Park	1.1171	1.2009	1.8245	1.9075	1.7396
e Ashgill Head Roadside	1.9134	1.8546	1.8261	1.8871	1.7338
f Rise Field Entrance	1.8440	0.9836	0.9836	0.9836	0.9836
g Walvick Roadworks	1.8921	1.8976	1.9412	1.9386	1.9314
h Tarn Hows Car Park	1.8240	2.0210	1.9570	1.8983	1.9247
i Ennerdale Car Park	1.8239	1.8597	1.8569	1.7963	1.8748
j Moel Arthur Track	1.8844	1.8892	1.5666	1.9550	1.8396
k Glen y Wern Field Entrance	1.4830	1.7591	1.7415	1.9010	1.8956
l Dyffryn Mymbyr Layby	1.8450	1.9800	1.9047	1.9030	1.8503
m Pen y Pass Car Park	1.8246	1.8912	1.9446	1.4214	1.9089
n Trawsfynydd Track	1.4148	1.9563	1.9647	1.9346	0.9836
Pasture populations					
o Blackriggs Pasture	1.7799	1.6305	0.9836	1.6509	1.2405
p Bargh House Pasture	0.9836	1.5986	1.9767	1.7772	1.6890
q Greenwood How Meadow	1.2008	1.0524	1.4939	1.2436	1.4436
r White Brackens House P're	1.5575	1.6851	1.7127	1.6509	1.7572
s Wellhead Pasture	1.5585	1.5929	1.6667	0.9836	1.2778
t Greenhills Pasture	1.2864	1.7115	1.6190	1.0504	1.3744
u Knarledale Pasture	1.4749	1.4427	1.5709	1.7510	1.6495
v High Shield Farm Pasture	1.5681	1.8925	0.9836	1.2760	0.9836
w Elterwater Moor Pasture	1.8445	0.9836	1.9011	1.9852	1.0485
x Skelwith Fold Meadow	0.9836	1.6809	0.9836	0.9836	0.9836
y Moel Arthur Pasture	1.7868	1.9302	1.5580	1.6048	0.9836
z Dyffryn Mymbyr Meadow	1.7007	1.9310	0.9836	1.8276	1.8490
aa Trawsfynydd Meadow	0.9836	1.9538	0.9836	1.8878	0.9836
bb Ty Mawr Pasture	1.4205	1.6476	0.9836	1.2631	1.5193

mortality occurred (ps_0=1). Subsequently seed survival is
assumed to be constant and independent of age (ps=0.9836, calculated
from a yearly decay rate of Poa annua seeds given by Roberts &
Dawkins (1967)). Germination rate is also assumed to be constant
and independent of age (gs=0.005764, calculated from yearly
germination rates given by Roberts & Dawkins (1967)).
This set of assumptions appears to be highly restrictive and one
wonders how much weight can be placed on the finite rates of increase..
In general, where information on life histories was incomplete, I
assume it to be the same for all populations whether opportunist or
pasture. So this is the most conservative approach, any differences
between populations could only be due to the characters actually
measured; differences between the finite rates of increase are the
minimum possible ones. They provide a basis for comparing different
life histories, but their relationship with the growth rates of
natural populations and families can, at best, be only approximate.

Finite rates of growth for each population are given in
Figure 4.1. These figures show, as might be expected from the
previous analyses, that finite rates of increase were generally
greater in opportunist than in pasture populations. If life-
historical measurements of all opportunist and pasture populations
are averaged, their finite rates of increase are 1.8482 and 1.6742 per
4 week period, respectively. Consequently, if there were 1000
individuals in each of these composite populations one year, there
would be 2.93×10^6 opportunist individuals and 1.02×10^6 pasture
individuals one year later (assuming individuals to be in age stable
proportions). The combined effect of shorter prereproductive period
and greater reproductive output in opportunist populations brings
about greater finite rates of increase (mortality was relatively

unimportant over the time period analysed and had only a small effect
relative to the other characters).

Despite the general differences between opportunist and pasture
populations, there were a number of exceptions; the rate of growth
of Rise Field Entrance was low in comparison to other opportunist
populations and Elterwater Moor Pasture and Dyffryn Mymbyr Meadow
were high relative to other pasture ones. But bearing in mind that,
when an opportunist population was adjacent to a pasture one, the
rate of increase of the opportunist population was always greater,
it is reasonable to assert that opportunist populations had greater
finite rates of increase than pasture ones. For example, Bargh House
Track and Pasture populations, which were sampled within 3 m of one
another, had finite rates of increase of 1.8289 and 1.7672 per month
respectively. We must not however forget the restriction that these
figures apply only to populations expanding into an infinite empty
universe; they do not necessarily represent the course of events
in natural populations.

It is equally possible to apply Leslie's method for calculating
finite rates of growth to genotypes. This rate of growth is of
particular interest as it represents the absolute fitness of the
genotype upon which its frequency in the future will depend. Although
I have no information on genotypes as such, each family in the present
analysis may be taken as an inbred line, and we can assume that as
a crude approximation, the life history of the progeny of each family
is the same as that of the parent. The rate of increase of each
family is then equivalent to its absolute fitness and we can predict its
frequency in the future. Clearly, any family with an absolute fitness
less than unity, is doomed to extinction; in fact 0.9836 is the
lowest possible absolute fitness, as it is equivalent to the survival

rate of seeds when there is no reproduction among adult individuals.
Families with absolute fitnesses greater than unity will increase in
numbers, the rate of increase depending on the magnitude of the
fitness.

Absolute fitnesses of opportunist and pasture families are
given in Table 4.8 and their distribution in Figure 4.4. Figure 4.4a
shows that the majority of opportunist families had absolute
fitnesses of 1.7 to 1.99 per 4 week period. Of the 5 families with
fitnesses less than unity, 4 came from Rise Field Entrance population,
already noted for its anomólous characteristics. A random sample of
a composite population made up of all opportunist families would
show a smaller and smaller frequency of the ones of lower fitness
over the course of time, eventually becoming dominated by one family
from Tarn Hows Car Park, with a fitness of 2.0210. On the other hand
the distribution of fitnesses among families from pasture populations
(Figure 4.4b), was quite different. Instead of being concentrated
towards the maximum values, they were dispersed over the whole range
0.9 to 1.99. There was a peak at 1.6 to 1.69 and fifteen families
had lowest possible fitness of 0.9836. Clearly selection was
operating in different ways, favouring families with greatest rates of
increase at low density in opportunist populations and in some other
as yet unexplained way in pasture ones.

Table 4.8 shows that growth rates varied not only between populations
but also between families within populations. It is not immediately
apparent how such variation could be maintained, since it is the
nature of natural selection that the most fit forms should
predominate. There are however several possible reasons for the
existence of this variation. Firstly, it is conceivable that
populations were not at equilibrium and that in the course of time
the variation would decline. Secondly, as the experimental

FIGURE 4.4 Distribution of finite rates of increase (λ) of opportunist
and pasture families.

a Opportunist families
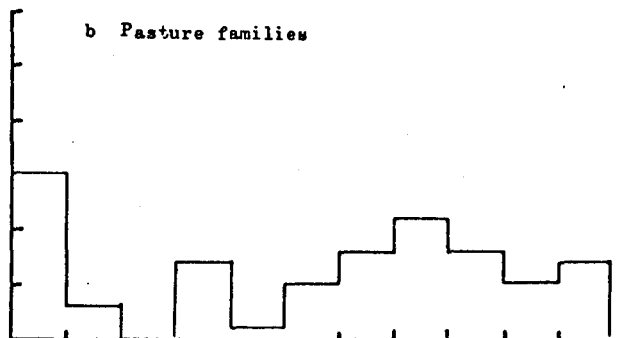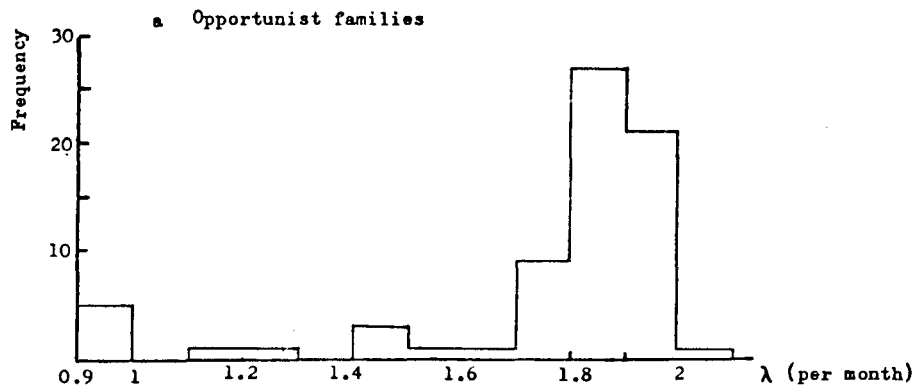
b Pasture families

environment was not identical to the natural environment, the
calculated fitnesses may be a poor indication of natural fitnesses
especially for pasture families.

Although experimental artifacts probably played a significant
role, I suspect they cannot explain the complete range of variation,
particularly between opportunist families. Environmental heterogeneity
through space within populations, arising from local variation in
the level of disturbance was likely to occur, bringing about
variation in the intensity of density-independent selection. Temporal
heterogeneity probably occurred as well, through variation in
disturbance from time to time. Together these factors could bring
about the maintenance of fitness variation, if different families had
different fitnesses at different densities. Furthermore, we know
that the degree of disturbance between adjacent populations was
variable. For example, Bargh House Track and Pasture populations
were sampled within 3 m of one another; between such populations,
it is inevitable that gene flow in the form of seeds should occur
(but see Chapter 6.3). So gene flow was probably another contributory
factor in the maintenance of variation in fitness.

It is more difficult to interpret the range of fitness observed
within pasture populations, as the experimental environment was
further removed from their natural environments. Indeed, differences
between natural and experimental environments, might account for
a significant proportion of the apparent variation in fitness.
Spatial and temporal heterogeneity within populations,could bring
about the maintenance of variation, as in the opportunist populations.
In addition, gene flow as seeds from adjacent populations, could
again be a contributory factor. This effect should have been greater
from opportunist into pasture populations than vice versa, as seed

production in opportunist populations is greater.

However, there is a further factor that I suspect to be important in contributing to the apparent variation in fitness of pasture families. It has been argued in Chapter 2.4.2 that populations experiencing strong density-dependent pressures are likely to suffer heavy seedling mortality (see also Foster 1964) and that genotypes avoiding this high risk stage would be selected (Williams 1966, p90). Hence the greater plant diameters of pasture families (Figure 4.3) could be a reflection of more vegetative reproduction by tillering. If this is the case, it is misleading to estimate fitness from seed reproduction alone; indeed the contribution of seeds to fitness could be negligible. An accurate estimate would need the inclusion of tillering capacity and the proportion of tillers to become established as new individuals.

I conclude that the finite rates of increase are useful in predicting the future of families under the idealised conditions of the environment of the experimental field being indefinitely maintained. Insofar as the natural environment of opportunist families corresponded to the experimental field, their fitnesses are predictive in those environments. But there is some doubt over the predictive capacity of fitness estimates of pasture families, due to the differences between the experimental and natural environments and the exclusion of vegetative reproduction from the estimates.

4.3 Life-historical variation between populations in competition.

So far, opportunist and pasture populations have been examined for the presence of genetic variation, when grown as spaced plants. We have seen how it is possible to calculate finite rates of increase for these populations and how these rates can be interpreted in terms of maximal growth rates of the populations. However, we know from

earlier discussions (Chapter 3.3), that life and fecundity schedules are likely to be functions of density and indeed the magnitude of the calculated rates of increase, bear witness to the necessity of this. It would be interesting to establish whether the differences found between the opportunist and pasture populations are maintained as their density increases, or whether their rates of increase change relative to one another. In addition, I suggested in Chapter 3.4.2, that life and fecundity schedules might be functions of the density of other genotypes, as well as of their own. In this section these problems are examined by growing plants from opportunist and pasture populations at high density in even aged stands, both with and without interactions with other populations.

4.3.1 Methods

Two opportunist populations (Walwick Roadworks and Dyffryn Mymbyr Layby) and two pasture populations (Knarledale Pasture and Dyffryn Mymbyr Meadow) were chosen for analysis at high density. A random sample of seed from the 5 families used in the previous section, was germinated on filter paper in petri dishes. (The seed from the families within each population was mixed.) After germination, the seedlings were planted in 8 in. plastic pots in John Innes No. 1 compost, both in pure stands of each population and also in each opportunist/pasture combination. Each treatment was replicated three times and the pots laid out in a completely randomised design in a greenhouse. The seedlings were laid out on a hexagonal matrix, 37 to each pot, so that each plant (apart from the peripheral ones) was surrounded by 6 equidistant nearest neighbours. When in competition with another population, three of these neighbours were always from that other population. This design is described by Harper (1961).
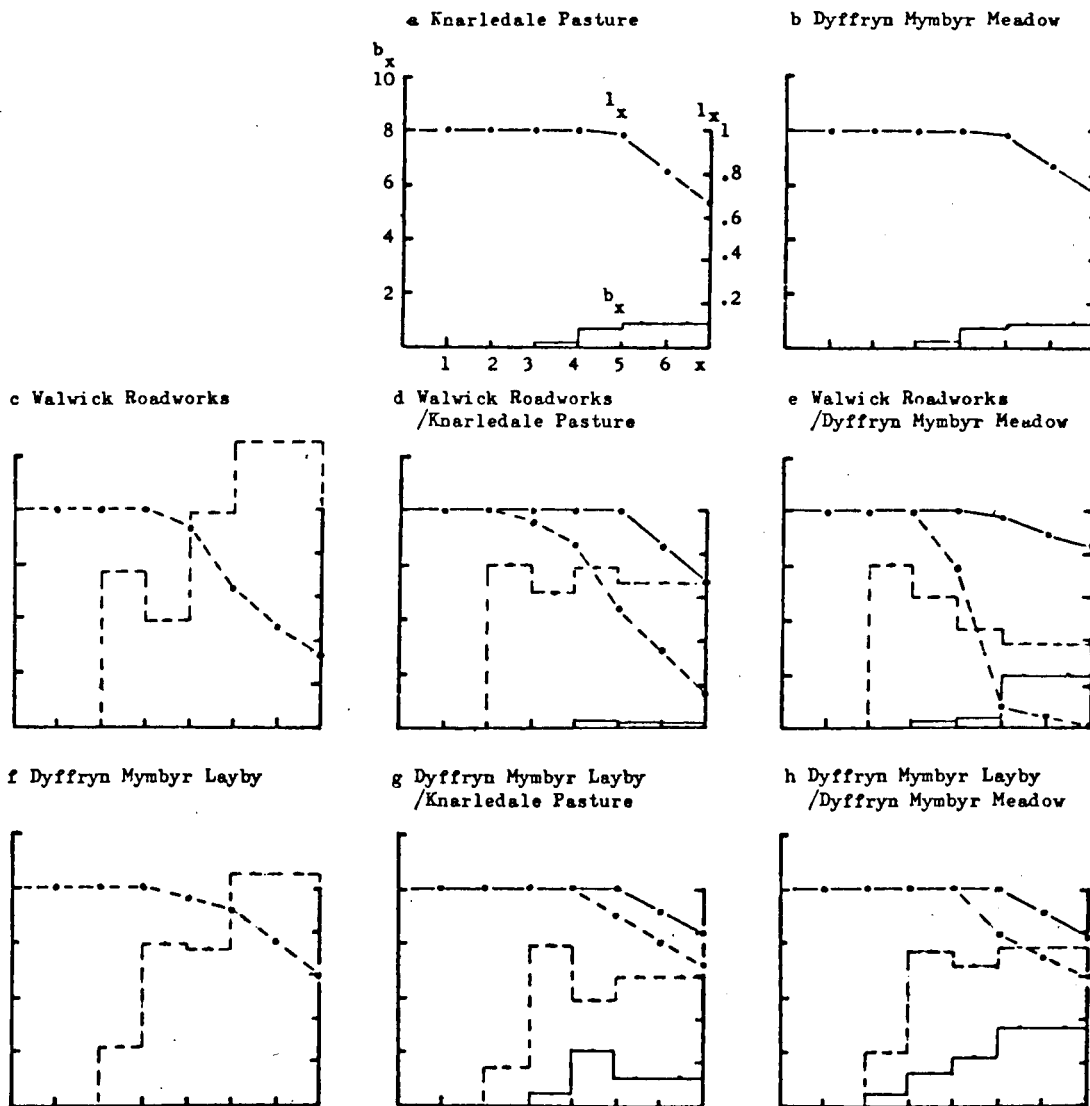
The peripheral plants were present to minimise edge effects and were not used for analysis. Characters measured were the same as those in the previous section, but measurements were terminated much sooner, due to high mortality. Not all mortality was directly attributable to high density, as some plants became infected by rust. As a result of mortality, the effective density of the plants changed over the course of the experiment, but for simplicity, any reference to density will refer to numbers at the beginning of the experiment.

Results were analysed by analysis of variance, using two different models. The first analysis tested for differences between populations from opportunist and pasture environments grown at high density as pure stands (Appendix 4.1.3). The second tested for differences in life-historical characters within populations when with different competitors (Appendix 4.1.4). It was not possible to take any measurements 6 months after germination so the 7 month numbers were divided equally between 5 and 6 month old plants in Figure 4.5 and analysed together (Tables 4.9 & 10).

4.3.2 Results and discussion

Age-specific survival and reproduction schedules of each population at high density, both in pure stands and in competition with the other populations, are summarised in Figure 4.5 (reproduction being measured in units of the number of inflorescences from which all seed had fallen). The pure stand schedules (Figure 4.5.a,b,c,f) have many similarities with the corresponding spaced plant ones (Figure 4.1.g,l,u,z.) Onset of reproduction occurred sooner in the opportunist than in the pasture populations, although the absolute time was different compared with spaced plants. Some caution should be exercised in comparison of the schedules from these experiments, as the greenhouse was a more benign environment than the experimental

FIGURE 4.5 Age-specific reproduction (b_x) and survival (l_x) of samples from 2 opportunist and 2 pasture populations. Samples grown at high density in pure stands (a,b,c,f) and in competition, using all opportunist/pasture combinations (d,e, g,h). Age (x) in 4 week units. Reproduction in units of numbers of inflorescences per plant per month. . Opportunist populations shown as discontinuous lines and pasture ones as continuous lines.

a Knarledale Pasture

b Dyffryn Mymbyr Meadow

c Walwick Roadworks

d Walwick Roadworks /Knarledale Pasture

e Walwick Roadworks /Dyffryn Mymbyr Meadow

f Dyffryn Mymbyr Layby

g Dyffryn Mymbyr Layby /Knarledale Pasture

h Dyffryn Mymbyr Layby /Dyffryn Mymbyr Meadow

field; differences in prereproductive periods could well be a reflection of this. Numbers of inflorescences were again much greater in opportunist populations than in pasture ones and mortality began sooner and was more severe in opportunist populations.

In addition, there are a number of striking dissimilarities between the high density and spaced plant schedules. In all cases there was a drastic reduction in the numbers of inflorescences at high density, in the case of Dyffryn Mymbyr Meadow, by nearly 2 orders of magnitude. This suggests that reproduction was a function of density. There was also a marked increase in mortality, but to a greater extent in opportunist populations than in pasture ones. Bearing in mind that some mortality may have been due to rust infection, it is difficult to interpret this result, but if the greater mortality was predominantly a result of high density, then it appears that age-specific survival was also a function of population density and that this function varied from population to population. Results of analysis of variance (Table 4.9) confirm that there were significant differences between populations from opportunist and pasture environments in reproductive characteristics.

It is not possible to test directly whether reproduction and survival of particular genotypes were functions of the presence of other genotypes as the samples used in this experiment were not genetically homogeneous. However, as it has already been demonstrated that samples from different populations were made of different sets of genotypes, it is safe to say that, if life-historical variation is observed when a population interacts with other populations, then this must be a reflection of the life histories of the constituent genotypes being functions of those of the other populations. To illustrate this, consider the Walwick Roadworks population, growing

TABLE 4.9 Analysis of variance of life-historical differences between opportunist and pasture populations grown at high density in pure stands. F ratio is the ratio of the between environment mean square to the between populations within environment mean square. p is the probability of null hypothesis: no difference between environments with 1 numerator and 2 denominator degrees of freedom. Data square root transformed.

Character	F ratio	p
No. inflorescences at age 3 months	57.0509	<0.05
No. inflorescences at age 4 months	48.6817	<0.05
No. inflorescences at age 5&6 months	138.7322	<0.01

TABLE 4.10 Analysis of variance of life-historical differences within opportunist and pasture populations when grown at high density with different competitors. There are 3 different treatments, each population being grown in competition with itself, and with each of the 2 populations from the other environment. F ratio is the ratio of between treatment mean square to the between replicate within treatment mean square. p is the probability of null hypothesis: no difference between treatments, with 2 numerator and 6 denominator degrees of freedom. Data square root transformed.

Character	F ratio	p
Knarledale Pasture		
No. inflorescences at age 3 months	0.8810	>0.05
No. inflorescences at age 4 months	3.8548	>0.05
No. inflorescences at age 5&6 months	1.5686	>0.05
Dyffryn Mymbyr Meadow		
No. inflorescences at age 3 months	1.3523	>0.05
No. inflorescences at age 4 months	3.9392	>0.05
No. inflorescences at age 5&6 months	1.3406	>0.05
Walwick Roadworks		
No. inflorescences at age 3 months	0.6131	>0.05
No. inflorescences at age 4 months	7.6136	<0.05
No. inflorescences at age 5&6 months	5.0865	>0.05
Dyffryn Mymbyr Layby		
No. inflorescences at age 3 months	0.7290	>0.05
No. inflorescences at age 5&6 months	3.0935	>0.05

TABLE 4.11 Competitive abilities of opportunist and pasture populations. Figures calculated as the ratio of the yield in competition (y_c) to the yield in pure stand (y_p), where

$$y_p = \sum_x l_{ii}(x) . b_{ii}(x)$$

$$y_c = \sum_x l_{ij}(x) . b_{ij}(x)$$

and where

x = age (months),

$l_{ij}(x)$ = probability of survival to exact age x in population i when in competition with population j,

$b_{ij}(x)$ = number of inflorescences produced per plant between exact ages x and x+1 in population i in competition with population j.

Population:	In competition with:			
	Walwick Roadworks	Dyffryn Mymbyr Layby	Knarledale Pasture	Dyffryn Mymbyr Meadow
Walwick Roadworks	-	-	0.6524	0.4716
Dyffryn Mymbyr Layby	-	-	0.6778	0.7760
Knarledale Pasture	0.3239	1.8780	-	-
Dyffryn Mymbyr Meadow	1.7100	3.4352	-	-

at high density in pure stand and growing in competition with samples

from Knarledale Pasture and Dyffryn Mymbyr Meadow (Figure 4.5.c,d,e).

It appears from these graphs that both survival and reproduction

were depressed when in competition with other populations, relative

to pure stand. Such variation could well reflect the fact that the

life histories of genotypes of Walwick Roadworks population were

functions of the genotypes by which they were surrounded. Analysis

of variance of life-historical differences in this population,

provide limited confirmation; reproduction by 4 month old plants

was of border-line significance (Table 4.10), but no differences

could be found in any other populations, when grown in competition.

To obtain an overall estimate of the effect of each population

on each other, the product of age-specific survival and reproduction

values for each age can be summed over all ages. (This is an

estimate of total yield per plant, in units of number of inflorescences,

which is proportional to yield in terms of number of seeds, if it

is assumed that numbers of seeds per inflorescence is constant over

populations.) Following the method of Allard and Adams (1969), yields

in competition are expressed as ratios of yields in pure stand in

Table 4.11. Notice that yield of both opportunist populations was

strongly depressed when in competition with both pasture ones, but

that yield of pasture ones was increased in competition with opportunist

ones (with the exception of the anomolous result of Knarledale

Pasture in competition with Walwick Roadworks population). This

suggests that the pasture populations were generally good competitors

and that the opportunist ones were poor competitors.

The value of this experiment is constrained by a number of

factors. On a purely practical basis, it is difficult to produce

greenhouse conditions, in which growth of Poa annua corresponds to

the growth pattern that it has in the field. Rapid shoot elongation

occurs and plants become tall and unstable, whereas in natural environments they tend to be short and compact. This limits the reliability that can be placed on extrapolations from this experiment back to field conditions. Conceptually too, this experiment is inadequate; competition experiments were initially designed for analysis of crop interactions (DeWit, 1960) that were much simpler than those of natural populations. Natural populations are not even-aged stands, with individuals on a regular lattice; they consist of individuals of many different ages and of many different genotypes, distributed in a wide range of different ways. If we are to predict the outcome of competition in natural populations, factors like these will have to be taken into account.

Even if it was possible to solve all the preceding problems, the methods used in this analysis would still be insufficient to estimate fitness in competition. This is because estimates of competitive ability have been entirely based on seed yield, vegetative reproduction being completely ignored. It is likely that reproduction by seed contributes a decreasing amount to fitness as population density increases and that vegetative reproduction contributes an increasing amount. Evidence for this stems from the observation that the probability of seedling establishment in dense swards is very small (Foster 1964) and any form of reproduction avoiding this stage of the life cycle, such as by tillering, would be highly advantageous. Ideally, an estimate of fitness would take both seed and vegetative reproduction into account and in these conditions it might become possible to predict the outcome of competition in natural populations.

4.4 Variation between populations at different stages of colonisation

We have seen that there is genetic variation both between and within populations, for life-historical characters in Poa annua. We have also seen that different genotypes are selected in populations with different histories of density-independent or dependent selection, such that characteristic differences can be observed between opportunist and pasture populations. But it still remains to be established whether it will be possible to observe genetic change over particular episodes of colonisation, that is, whether there is sufficient genetic variability and selection in natural populations for detectable genetic change to occur (the condition of empirical sufficiency). My approach to this problem is to compare populations that have been colonising for different lengths of time (analogous to Redfield 1973). This is a relatively simple task in the cities of North West England because large areas of derelict land, suitable for colonisation by Poa annua, are created in the process of slum clearance. It is often possible to establish the dates of demolition and hence the starting time of colonisation.

4.4.1 Methods

Twelve sites in Liverpool were chosen for analysis, four of them arising from demolition in August 1967, four from April 1970 and four from September 1971. Seed samples of Poa annua were collected from these sites in February 1972, so that the maximum length of time for which the populations could have been colonising were 56, 24 and 6 months respectively. The seeds were sown at two densities in John Innes No.1. compost in deep seed trays, the densities being adjusted to achieve a final growing density of 32 and 320 cm^2/plant. Each population sample at each density was replicated twice. Ten plants were chosen at random from each seed tray, for life historical

FIGURE 4.6   Cumulative reproduction of samples from 6 month old, 24 month old
and 56 month old colonising populations. Reproduction measured in
units of the number of inflorescences from which seed had started
to fall. Results given for 4 populations, each at 2 experimental
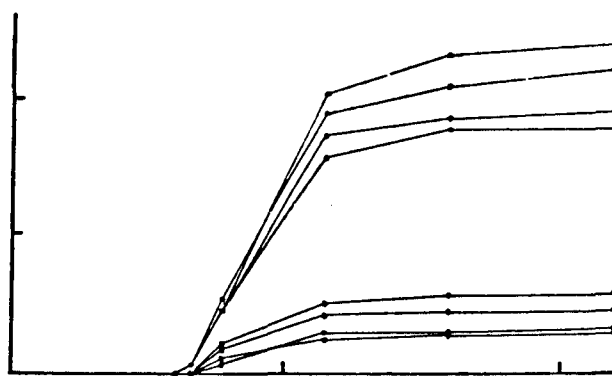growing densities. Each point is the mean of 20 plants.
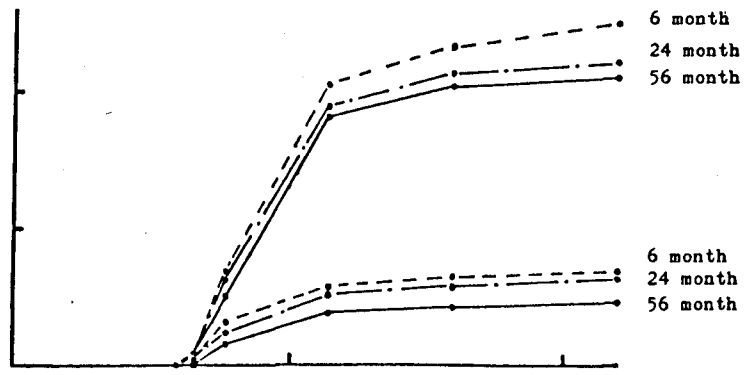
a   6 month old populations
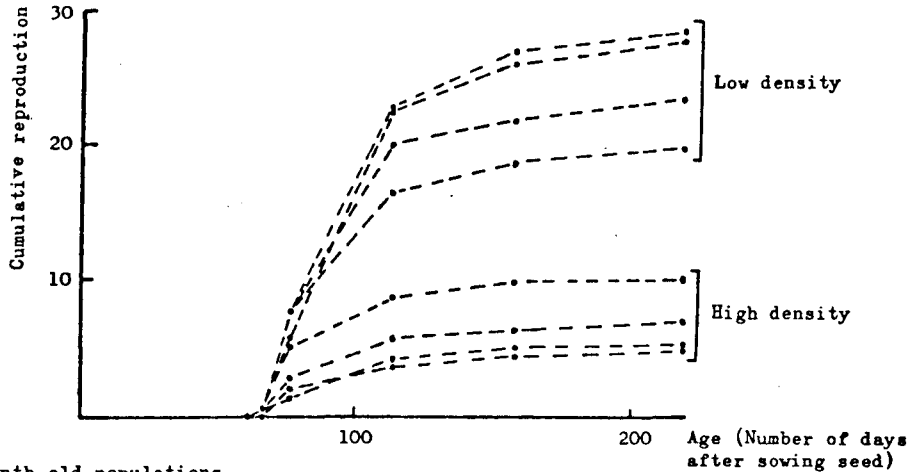
b   24 month old populations
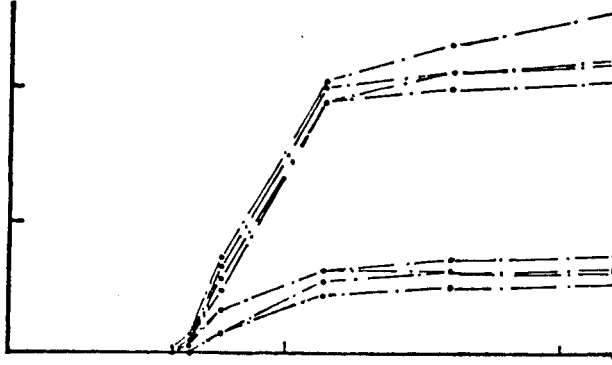
c   56 month old populations

d   Mean for populations of each age

measurements. Results were analysed by hierarchical analysis of variance, using the design described in Appendix 4.1.5.

4.4.2 Results and discussion

The cumulative number of inflorescences produced by samples of each population, over the earlier part of their lives, is summarised in Figure 4.6. It is clear that the ten fold increase in density caused a marked reduction in the number of inflorescences produced in all plants, irrespective of their origin. It is also clear that there was considerable overlap in the reproductive performance of populations at different stages of colonisation, but that, on average, there was a slight decline at both low and high density, with increasing age of the population (Figure 4.6.d). There was also a slight tendency towards delayed onset of reproduction, by about 7 days in the oldest populations. Analysis of variance confirms these observations; square root transformed, cumulative number of inflorescence data, showed highly significant density effects at all times (Table 4.12). Age of population generally did not have a significant effect, but the cumulative number of inflorescences produced up to 77 days after sowing, was of borderline significance (Table 4.13). There was no signficiant density/age of population interaction .

It is perhaps surprising that the most recent colonists should, on average, produce the greatest numbers of inflorescences, as selection for colonising ability could only start once different genotypes had reached the site. It is arguable that 6 months was sufficient time for such selection to occur, but this is unlikely as it was during the winter, over which time plant development would be relatively slow. It is more likely that selection actually occurred before the genotypes reached the sites, since there is a greater

TABLE 4.12   Analysis of variance of life-historical differences between two
experimental growing densities for populations at different stages
of colonisation. F ratio is the ratio of the between densities
mean square to the mean square of the interaction between density
and population age group. p is the probability of null hypothesis:
no difference between densities, with 1 numerator and 9 denomin-
ator degrees of freedom. Data square root transformed.

Character	F ratio	p
Inflorescences produced in first 66 days	1.6570	>0.05
Inflorescences produced in first 77 days	69.0051	<0.001
Inflorescences produced in first 114 days	834.8463	<0.001
Inflorescences produced in first 159 days	1372.2794	<0.001
Inflorescences produced in first 219 days	1318.5454	<0.001

TABLE 4.13   Analysis of variance of life-historical differences between populations
at different stages of colonisation. F ratio is the ratio of the
population age group mean square to the populations within population
age group mean square. p is the probability of the null hypothesis:
no difference between populations from different age groups, with 2
numerator and 9 denominator degrees of freedom. Data square root
transformed.

Character	F ratio	p
Inflorescences produced in first 66 days	2.4134	>0.05
Inflorescences produced in first 77 days	7.8802	<0.05
Inflorescences produced in first 114 days	2.0388 ·	>0.05
Inflorescences produced in first 159 days	2.0328	>0.05
Inflorescences produced in first 219 days	2.2862	>0.05

probability of a seed of a high seed yielding genotype reaching a
site, than a low seed yielding one. Even then, we should note that
there is considerable variation between the 6 month old populations,
possibly arising from different genotypes being present in the
'catchment area' for each site.

This experiment was deficient in a number of ways. For example,
although all the sites were broadly similar in soil conditions and
climate, there were inevitable small environmental differences from
site to site, that could mask the effects of genetic change during
colonisation. The experiment was also sensitive to the extent of
genetic variation present in the populations, on which natural
selection could act. It is conceivable that the history of opportunist
environments in Liverpool is so long, and that so few last for long
enough for high densities to build up, that there is little life-
historical genetic variation remaining in Liverpool populations of
Poa annua. This problem is accentuated by the error that was made
in taking seed samples from the populations, as this created a bias
in favour of the high seed yielding genotypes.

The cumulative effect of these deficiencies is to make it
hazardous to make firm interpretations from the results. All that can
be said is that there are slight signs of genetic differences between
populations at different stages of colonisation.

4.5 Conclusions

The results described in this Chapter have demonstrated beyond
doubt, that there is an abundance of genetic life-historical
variation in Poa annua. Hence, the first condition for genetic change
during colonisation is satisfied. Secondly, the results have shown
that different kinds of life histories are selected, depending on
the extent to which natural selection is density-independent or density-

dependent. Broadly, genotypes with a high reproductive output by seed, a short prereproductive period, a low rate of vegetative spread and a short lifespan are selected when selection is density-independent, whereas those with a low seed reproductive output, long prereproductive period, high rate of vegetative spread and long life are selected when selection is density-dependent. Hence the second condition for genetic change has been satisfied: different genotypes are favoured depending on the extent to which selection is density-independent or dependent. Thirdly, an attempt has been made to test the condition of empirical sufficiency, the results of which are not conclusive, but which show slight signs that the condition may be fulfilled. It is certainly worth continuing the investigation to examine individual populations in greater depth.

CHAPTER 5

LIFE-HISTORICAL CHANGE IN AN ARTIFICIAL POPULATION OF POA ANNUA

5.1 Introduction

We have seen that there is a wealth of genetic variation in

life-historical characters between natural populations of Poa annua

(Chapter 4). This variation is closely related to the extent to

which populations are limited by density and in general bears out

the predictions of the kinds of life histories to be expected from

density-independent and dependent selection (Chapters 2 & 3). But

a correlation between environment and life history is not a rigorous

proof of a causal relationship between selection and genetic change.

It would be much more convincing to test for genetic change within

populations that were experiencing both density-independent and dependent

selection. This approach is adopted in this chapter and the one

that follows.

We know that genetic change depends critically on the existence

of genetic variation and the intensity of selection (Chapter 1).

Here I use a system in which an attempt is made to maximise both of these

factors; genetic variation, by creating an artificial population taken

from many natural populations, and selection, by subjecting different

parts of the population to the extremes of density-independent and

dependent selection. I begin by describing the design of the

selection experiment and then consider analyses of samples selected

under different modes of population regulation for the presence of

life-historical variation. This is done with samples grown both at

low density as spaced plants and at high density under competitive

conditions.

5.2 Selection experiment

Seed was collected from a set of populations of Poa annua in

Merseyside and North Wales. Details of these populations together with the quantities of seed taken from them are summarised in Table 5.1. The populations were chosen to contain a range of modes of population regulation so that the composite population would contain appropriate life-historical variation (see Table 5.1, column 4). However, the range of populations was more limited than those of Chapter 4 (see Table 4.1), there being no representatives of the 'extreme' pasture populations. Some of the populations were sampled as seeds and the rest as tillers (see Table 5.1). Those sampled as tillers were grown to flowering in a , greenhouse and then seeds were taken from them. Seed from all the populations was thoroughly mixed to create a composite population with high genetic variability.

An experiment was designed to subject samples of the composite population to different kinds of population regulation representing different selection regimes. Four kinds of regulation were imposed on the samples.

a   Low density   In this regime population density was maintained as low as possible to minimise interactions between plants. It was the physical equivalent of a population expanding into an infinite universe and selection was predominantly independent of density. The regime was produced by sowing seeds at low density (about 40 per m^2) into a plot 5 x 5m. As population density started to increase, randomly chosen areas were treated with the weed killer 'paraquat' to create new areas at low density.

b   High density monoculture   Population density was maintained as high as possible to maximise interactions between plants and to produce a selection regime that was mainly density-dependent. Seed was sown at a density of about 4000 per m^2 into a 2 x 2m plot.

c   High density in competition with Lolium perenne   In contrast with

TABLE 5.1 Natural populations of *Poa annua* sampled to create a composite seed
population. Column 4 'disturbance' gives a subjective ranking of
each site, from 1 (population under pressures mainly independent of
density) to 4 (population under pressures mainly dependent on
density).

Population	O.S. map reference	Site description	Disturb-ance	Sample: seed or tiller	Wt. of seed harvested (gms.)
1 Abbots Moss	SJ591693	Sandy soil with little plant cover near edge of gravel pit.	1	Tiller	1.530
2 " "	"	" " " " " " " "	"	Seed	0.421
3 Bickerton	SJ506530	Grazed permanent pasture on hill-side. *Poa annua* abundant but not much flowering.	4	Seed	0.309
4 Burnhouse	SJ480707	Permanent pasture with *Poa annua* present at low frequency throughout.	4	Seed	0.509
5 Burton Barn	SJ321738	Field of *Lolium perenne* with *Poa annua* at low frequency. More abundant near field entrance.	3	Seed	0.310
6 Caldecott	SJ427525	Near entrance of hay field (previously ploughed).	2	Seed	1.128
7 Castletown	SJ432515	At edge of heavily trampled track. Subject to much disturbance.	1	Seed	0.055
8 Clotton	SJ535649	Permanent pasture with *Poa annua* at low frequency throughout.	4	Seed	1.969
9 Hermitage	SJ514747	Grazed field with some disturbance from trampling.	3	Seed	0.081
10 Liverpool, Clevedon St.	SJ362879	Derelict site with little plant cover.	1	Tiller	1.100
11 Liverpool, Newsham Park	SJ380914	Park population, under trees; regularly cut.	3	Tiller	0.985
12 Liverpool, Princes Park	SJ367881	Park population, under trees; regularly cut.	3	Tiller	5.787
13 Liverpool, W. Derby Rd.	SJ365915	Derelict site with little plant cover.	1	Tiller	4.551
14 Lower Kinner-ton	SJ348627	Grazed field; fairly disturbed especially near entrance.	2	Seed	0.715
15 Mouldesworth	SJ525711	Grazed field with some disturbance.	3	Tiller	5.230
16 Nant Gwynant	SH626511	Sheep grazed pasture on steep slope.	4	Seed	1.083
17 Norley	SJ565714	Grass bank near track.	3	Tiller	5.785
18 Pen y Pass Car Park	SH647556	Heavily used gravel car park with *Poa annua* around margin.	1	Tiller	3.885
19 Rocklands	SJ303817	At edge of track around ploughed field.	1	Seed	0.819
20 Tilston	SJ457509	At edge of grazed field	3	Seed	0.127
21 Tryfan Car Park	SH661603	Heavily used gravel car park with *Poa annua* near periphery.	1	Tiller	4.761
22 Vimbolds Trafford	SJ453733	Pasture with *Poa annua* present particularly near entrance.	3	Seed	0.794

the high-density monoculture, this selection regime introduced
the effect of population regulation with another species present.
Here seed of Poa annua was mixed in equal proportions with seed
of Lolium perenne and sown at an overall density of about 8000
seeds/m^2 in a 2 x 2m plot.

d   Natural colonisation   This regime was begun in the same way as
the low density one, seed being sown at a density of about 40/m^2
into a 5 x 5m plot. But in contrast no control was carried out
to maintain low density and population density was able to increase
unhindered. Thus starting from a predominantly density-
independent selection regime, it underwent a transition to one
that was predominantly density-dependent.

Each of these selection regimes was replicated in two plots and
laid out in a randomised design in an experimental field. About 10 m
separated each plot to minimise gene flow between them and all the
surrounding area for a distance of about 10 m was kept bare of
vegetation to prevent contamination from local populations. The plots
were regularly weeded to prevent invasion of other species. The high
density plots with L. perenne were cut at regular intervals to
prevent Poa annua from being excluded from them.

Seed was sown at the beginning of July 1972. Low density plots
were treated with paraquat in December 1972, April 1973, July 1973
and September 1973. On the first three occasions half the total area,
chosen at random, was sprayed and on the final one the complete plots
were treated. Tiller samples were collected to test for genetic
change in November 1972, April 1973, September 1973 and April 1974,
but only the final sample is considered in this chapter. Samples
were taken by collecting tillers at 5 cm intervals along randomly
chosen transects across the plots, always excluding a 0.5 m section

around the perimeter to avoid edge effects. 100 tillers were
taken from each plot, except for the ones with L. perenne, in which
there was little Poa annua; from these only 30 tillers were taken.
Tillers were planted in John Innes No. 1 compost in 3 inch pots and
grown to flowering in the greenhouse. Seed was collected from the
plants for experimental work. No attempt was made to isolate the
plants genetically from one another.

In June 1973 a sample of 100 of the initial unselected seed
population was germinated in petri dishes, and the seedlings planted
out in pots using the same technique as for the tiller samples.
The plants were grown to flowering and seed was collected from them
to enable direct comparison of the progeny of unselected seed with
progeny of selected plants.

5.3 Life-historical differences as spaced plants

To test for the presence of genetic change between plots
maintained at low and high density, it is necessary to compare
samples from them under standard conditions. We know from Chapter
3.5 that the choice of conditions will influence the results obtained,
in particular that the life-historical characters and the difference
between those from different selection regimes will be functions of
population density. Here I test for differences under conditions of
low density by growing samples as spaced plants.

5.3.1 Methods

This experiment was carried out on material sampled from the
selection experiment in April 1974. 15 of the tiller samples from
each plot (except natural colonisation plots) were chosen at random,
together with 15 unselected seeds from the composite seed population.

The progeny of each of these samples was germinated on filter paper in petri dishes during August 1974. The progeny of a single tiller or seed constitute a family in the results discussed below. After germination (20.8.74) 3 seedlings taken at random from each family were planted in John Innes No. 1 compost in 'jiffy pots'. They were laid out in a completely randomised design in a greenhouse and left to grow. When large enough (9.9.74) they were transplanted to a field plot where they were laid out at about 0.5 m intervals on a regular lattice. The randomised design was maintained and the plants were left undisturbed to develop.

Measurements of several life-historical characters were made on the plants. Firstly, the prereproductive period taken as the time from germination to the appearance of the first flower was recorded. Secondly, the number of inflorescences per plant that had been produced in the previous month (from which all seed had fallen), was recorded as a measure of age-specific reproduction. These inflorescences were then removed so that they could not be recorded in future months. The results given here are incomplete because it was only possible to follow the early part of the lives of the plants.

The experiment was designed so that each set of data could be analysed by heirarchical analysis of variance (Sokal & Rolf 1969, Chapter 10), partitioning variation between selection regimes, between plots within regimes, between families within plots and between progeny within families (Appendix 5.1.1). However the frequency distribution of some sets of data were seriously skewed and it was necessary to use less powerful chisquare tests on contingency tables of presence and absence of flowering against selection regime.

5.3.2 Results

The distribution of prereproductive periods measured at two week intervals, for unselected plants and those selected at low density, high density and in competition with L. perenne, are illustrated in Figure 5.1. The histograms show that prereproductive periods of low density selected plants tended to be slightly shorter than those of their density-dependently selected counterparts, their mean being 21.02 weeks, as opposed to 23.87 for high density, 22.76 for those in competition with L. perenne and 23.11 for unselected ones. Distributions of each group were generally bimodal, with peaks between 16 to 20 weeks and at 28 weeks. The latter mode was probably due to season; it occurred at the beginning of March during a period of increasing environmental favourability, causing truncation. It is interesting that there were differences in the relative magnitudes of the two modes between selection regimes. The majority of unselected and low density selected plants had already started to flower by the beginning of March, so their 28 week peak was small, whereas the two modes were about the same in high density plants and those selected in competition with L. perenne. This difference could reflect different proportions of the plants with vernalisation requirements.

If it is assumed that the measurements were normally distributed, it is possible to carry out analysis of variance, to establish the significance of the differences between the means of each selection regime. Results of the analysis are given in Table 5.2; differences between plots within selection regimes were pooled with variation between families within plots because the former was not significant, and the variation between selection regimes was highly significant. Since the experimental plants were grown from seed together in the same environment, this must mean that there were genetic differences

FIGURE 5.1 Distributions of prereproductive periods of plants selected under
different kinds of population regulation. Measurements taken at
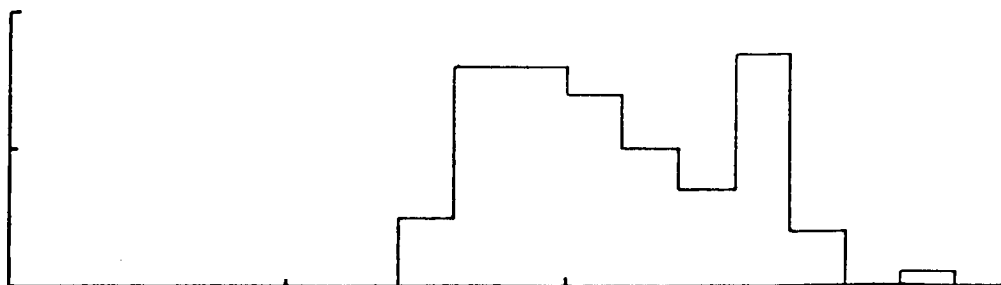fortnightly intervals.

a Low density selected plants
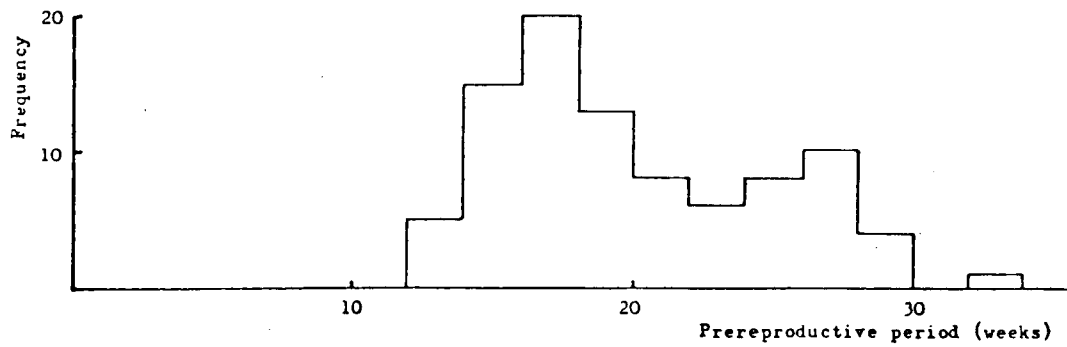
b High density selected plants
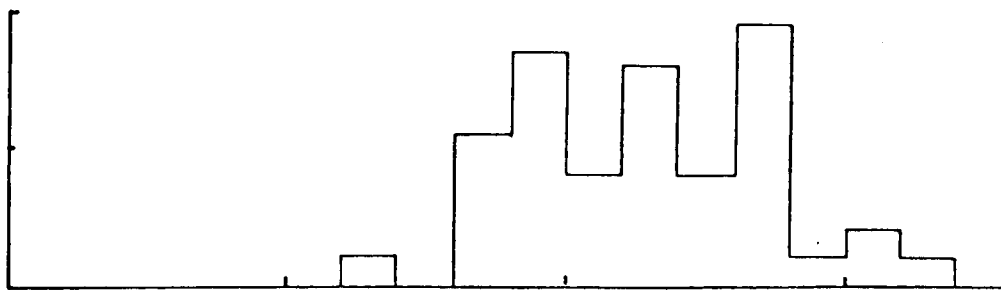
c Plants selected in competition with _Lolium_ _perenne_

d Unselected plants

between selection regimes. 'It should also be noticed that there were highly significant differences between families within selection regimes (Table 5.3). This means that there was also genetic variation within selection regimes.

The first reproduction, measured in units of numbers of inflorescences from which all seed had fallen, was observed 5 months after germination during January 1975. (As in Chapter 4, I will refer to plant age in multiples of 4 week units or 4 week months.) Frequency distributions of numbers of inflorescences per plant, produced by plants from each selection regime during month 5, are illustrated in Figure 5.2.a,b,c,d. Reproduction was observed in only 13 plants, of which 9 were low density selected, 1 was high density selected, 2 were L. perenne selected and 1 was unselected. It is clear that the majority of reproducing individuals had been selected at low density.

Reproduction increased during month 6 (Figure 5.2.e,f,g,h), being observed in 46 plants, of which 28 were low density selected, 6 high density selected, 8 selected in competition with L. perenne and 4 unselected. Once again it appears that more low density selected plants were reproducing. The differences can be tested for significance by a chisquare test on a 2 x 4 contingency table of presence or absence of flowering against selection regime. The results of this analysis are given in Table 5.4 and show that the differences were highly significant. Since any differences between selection regimes must be genetic, it can be concluded that there were genetic differences between selection regimes in the proportion of 6 month old plants reproducing.

Mean values of reproduction for each selection regime during month 6 were 0.56 inflorescences per low density selected plant, 0.12 per high density selected, 0.13 per L. perenne selected and

TABLE 5.2   Analysis of variance of life-historical differences between samples selected under different modes of population regulation (selection regimes). Two analyses are given; the first tests for the presence of differences between plots within selection regimes. The F ratio here is the ratio of the between plots within selection regime mean square to the between families within plots mean square. p_1 is the probability of null hypothesis: no difference between plots within selection regimes, with n_1 numerator and n_2 denominator degrees of freedom. The second analysis tests for differences between selection regimes. The F ratio is the ratio of the between selection regimes mean square to the between families within selection regimes mean square (if $p_1 > 0.05$) or to the between plots within selection regimes mean square (if $p_1 < 0.05$). p_2 is the probability of null hypothesis: no difference between selection regimes with n_1 numerator and n_2 denominator degrees of freedom. Age in units of 4 week months. Unselected plants excluded from analysis.

Character	Trans-formation	1 Between plots in selection regimes				2 Between selection regimes			
		F ratio	n_1	n_2	p_1	F ratio	n_1	n_2	p_2
Prereproductive period	none	2.2617	3	83	>0.05	5.3108	2	86	<0.01
No. inflorescences at age 6	$\sqrt{x}+\sqrt{x+1}$	4.1455	3	83	<0.01	2.8248	2	3	>0.05
No. inflorescences at age 7	$\sqrt{x}+\sqrt{x+1}$	0.6512	3	83	>0.05	7.0861	2	86	<0.005
No. inflorescences at age 8	none	1.6308	3	83	>0.05	0.2942	2	86	>0.05
No. inflorescences at age 9	none	1.5133	3	83	>0.05	1.3235	2	86	>0.05

TABLE 5.3   Analysis of variance of life-historical differences between families within selection regimes. F ratio is the ratio of between families within selection regimes mean square to the within families mean square (if $p_1 > 0.05$ in Table 5.2), or the ratio of between families within plots mean square to the within families mean square (if $p_1 < 0.05$ in Table 5.2). p is the probability of null hypothesis: no difference between families within selection regimes (if $p_1 > 0.05$ in Table 5.2), or the null hypothesis: no difference between families within plots (if $p_1 < 0.05$ in Table 5.2). Age in units of 4 week months. Unselected plants excluded from analysis.

| Character	Trans-formation	F ratio	n_1	n_2	p
Prereproductive period	none	2.5778	87	179	<0.001
No. inflorescences at age 6	$\sqrt{x}+\sqrt{x+1}$	1.3854	84	179	>0.05
No. inflorescences at age 7	$\sqrt{x}+\sqrt{x+1}$	1.9508	87	179	<0.001
No. inflorescences at age 8	none	3.0230	87	179	<0.001
No. inflorescences at age 9	none	2.9445	87	179	<0.001

TABLE 5.4   Contingency tables of presence or absence of flowering against selection regime. Chisquare values calculated from the expectation that all plants irrespective of selection regime have the same probability of flowering. p is the probability of null hypothesis: all plants irrespective of selection regime have the same probability of flowering, with 3 degrees of freedom.

Character	Contingency table			Chisquare	p
		flower	not-flower		
No. inflorescences at age 6 months	low density	28	62	27.54	<0.001
	high density	6	83		
	L. perenne	8	82		
	unselected	4	41		
No. inflorescences at age 7 months		47	43	20.06	<0.001
		23	66		
		24	66		
		11	34		
No. inflorescences at age 8 months		80	10	2.22	>0.05
		74	15		
		77	13		
		36	9		

0.27 per unselected plant. It is difficult to test the significance of differences between selection regimes by analysis of variance, because the large proportion of zero data leads to a very skewed distribution. The data does not support the hypothesis of a Poisson distribution; a chisquare test for goodness of fit gives highly significant departures. However there are some a priori arguments to support the hypothesis of a Poisson distribution, since early in life there are many possible sites for inflorescence production (tillers), each with a small probability of producing an inflorescence. Assuming the existence of an underlying Poisson distribution and transforming each element of data (x) to $\sqrt{x}$ + $\sqrt{x+1}$, analysis of variance can be carried out. Results are given in Table 5.2; variation between plots within selection regimes was highly significant (so it could not be pooled with variation between families within plots) and variation between selection regimes was not significant. Hence, there is no reason to suppose that there were genetic differences in mean reproductive output between selection regimes during month 6. In addition, Table 5.3 shows that there were no significant differences between families within plots for this character.

Reproduction continued to increase during month 7 (Figure 5.2.i, j,k,l); 105 plants produced seed, of which 47 were low density selected, 23 high density selected, 24 selected in competition with L. perenne and 11 unselected. As before, it appears that a greater proportion of low density selected plants were reproducing, an impression that is confirmed by a chisquare test on a contingency table of presence or absence of flowering against selection regime (Table 5.4). The results establish that there were highly significant genetic differences between selection regimes in proportions of plants reproducing.

FIGURE 5.2 Distributions of reproduction (b_x) of plants selected under different kinds of population regulation. Distributions given over a series of ages (x=5,6,7,8,9). Reproduction measured in units of numbers of inflorescences per plant per month. Note changes in scale of x axis in month 8 (b_8) and month 9 (b_9).
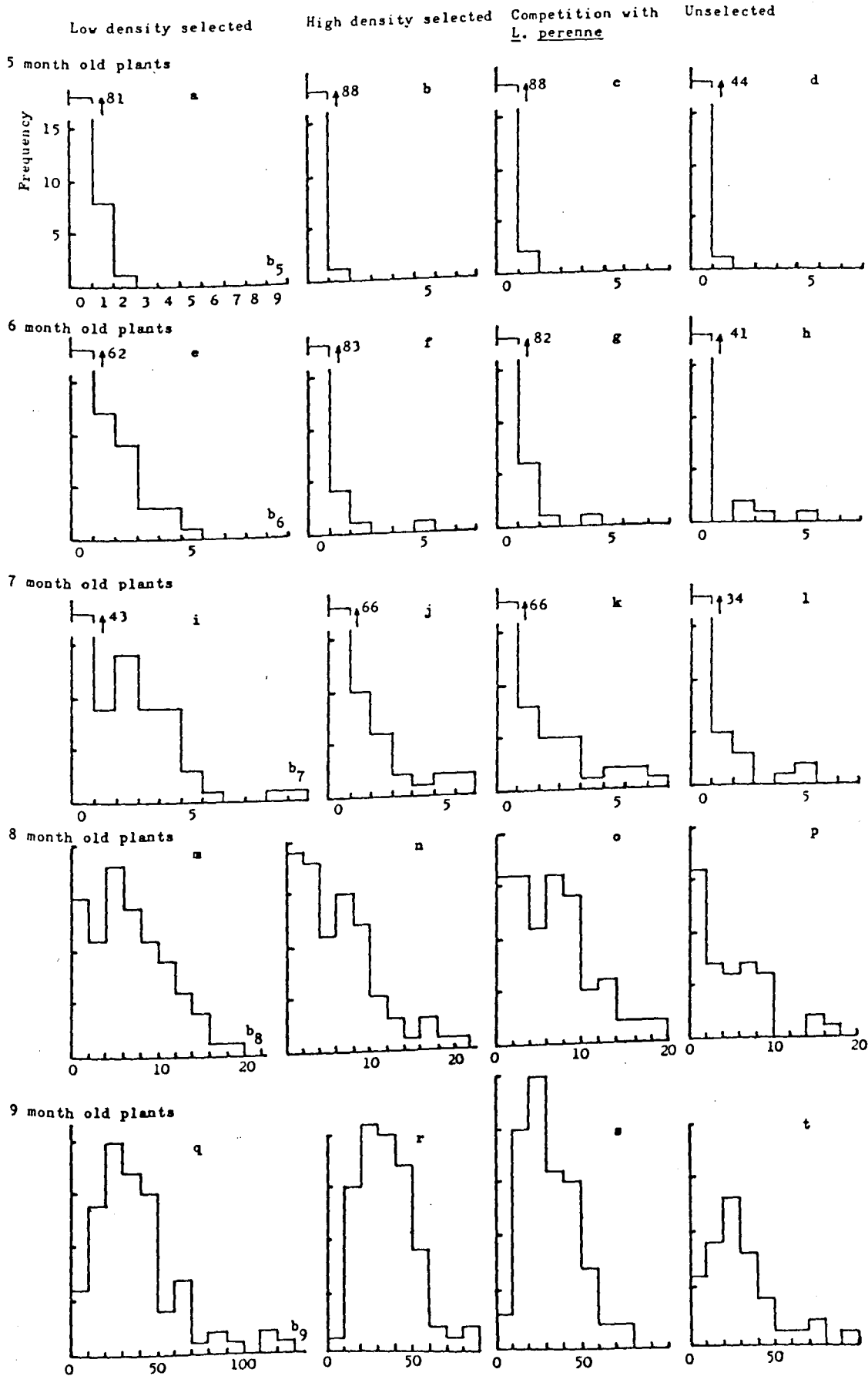
Mean reproductive output values during month 7 were 1.56 inflorescences per low density selection plant, 0.61 per high density, 0.73 per L. perenne selected and 0.56 per unselected plant. Assuming as before the existence of an underlying Poisson distribution, analysis of variance can be carried out to test the significance of differences between selection regimes. Table 5.2 shows that differences between plots within selection regimes were not significant and differences between selection regimes were highly significant. Thus it can be concluded that there were genetic differences in reproductive output during month 7 by plants from different selection regimes. It is also clear from Table 5.3 that there were highly significant genetic differences between families within selection regimes.

During month 8 reproduction was much more extensive than before (Figure 5.2.m,n,o,p). Only 47 out of a total of 314 plants were recorded as still not reproducing; of these, 10 were low density selected, 15 high density selected, 13 L. perenne selected and 9 unselected. These figures do not give the impression that there were differences between selection regimes in the proportions reproducing. The results of a chisquare test on a contingency table of presence or absence of flowering against selection regime (Table 5.4), confirm this impression.

Mean values of reproduction for each selection regime during month 8 were, 6.21 inflorescences per low density selected plant, 5.50 per high density, 5.99 per plant selected in competition with L. perenne and 3.84 per unselected plant. To test the significance of differences between selection regimes, analysis of variance can be carried out on untransformed data, there being so few plants with zero values. Table 5.2 shows that there were no significant differences between plots within selection regimes and neither were there significant differences between selection regimes. Hence it

can be concluded that there were no genetic differences between
selection regimes in reproductive output in month 8. However, it
is clear from Table 5.3 that there were highly significant genetic
differences between families within selection regimes.

In month 9 all plants were reproducing (Figure 5.2.q,r,s,t).
Mean numbers of inflorescences per plant were, 37.09 per low density
selected plant, 33.15 per high density, 31.06 per plant selected
in competition with L. perenne and 27.8 per unselected plant.
Analysis of variance on untransformed data (Table 5.2) shows no
significant differences between plots within selection regimes and
no significant differences between selection regimes. Thus, like
the previous month, there is no evidence for genetic differences
between selection regimes in reproduction during month 9. But Table
5.3 shows that there were highly significant genetic differences
between families within selection regimes.

Bearing in mind that the assumptions made about the underlying
frequency distributions of inflorescence data are open to question,
it is interesting to apply a nonparametric test to the data.
Compare first the mean number of inflorescences produced by low
density selected plants with that of high density selected ones,
over the age range 5 to 9 months inclusive. If each pair of means
were samples from the same frequency distribution, the probability
of the low density mean being greater than the high density one
would be 0.5 each month. Therefore the probability of the low
density mean being greater each month over a period of 5 months,
if both means were from the same frequency distribution each month,
is 0.031, as opposed to the alternative hypothesis that the low
density means were greater. This lends some further weight to the
hypothesis that reproduction was greater in low density selected
plants than in high density selected ones. A similar argument can

be used to compare reproduction between low density selected plants
and those selected in competition with L. perenne, from which the
same conclusion follows.

5.3.3 Discussion

The results have shown that there were some small but significant
differences between the progeny of samples taken from the different
selection regimes. In particular, prereproductive periods of plants
from low density plots were shorter than those from high density
plots or unselected ones. Closely related to this, we find that a
greater proportion of low density selected plants were producing seed
in the sixth and seventh month after germination. It is more
difficult to compare the amount of reproduction of samples from different
selection regimes, due to the skewed distribution of data. Analysis
of variance on transformed data suggested the existence of differences
particularly early in life, but there is some doubt about the validity
of the calculations with such skewed data. Nevertheless, Scheffé
(1959, p345) argued that such errors should not be serious in this
kind of analysis of variance.

Since all the plants analysed were grown from seed together
in the same environment, any difference between plants from
different selection regimes must have been genetic. In principle
there are three ways in which genetic differences between plots
could arise; firstly it is possible that there were genetic differences
in the seed samples used to establish each selection plot, due to
sampling error of the composite seed population. Low density plots
would have been particularly subject to this as they were established
with no more than about 1000 seeds. Secondly, genetic differences
could have arisen from random genetic drift during the course of the
experiment. The third possibility, the most important one in this
context, is that genetic change was brought about by natural selection.

These three causes of genetic differences would lead to different patterns of genetic differentiation. Random genetic drift would bring about genetic differences between plots irrespective of selection regime. Sampling error from the composite seed population would have the same effect, but would be greater in the plots established from small numbers of seeds. Only if natural selection was occurring could genetic change be associated with selection regime. Since significant differences were found between plots within selection regimes in only one character, random effects can generally be discounted as a source of genetic differentiation. Hence in most cases, genetic differences must have arisen from differences in the form of natural selection occurring under different modes of population regulation.

Generally it appears that life histories of samples from high density monoculture and L. perenne selection regimes were similar and that the biggest differences were between these and the low density selection regime. Thus it seems that the largest differences were attributable to the effects of density-independent selection and density-dependent selection, the precise form of density-dependent selection being unimportant. The direction of divergence from the unselected population showed no consistent patterns. The distribution of prereproductive periods of unselected plants was similar to that of the low density selected ones, whereas their mean reproduction values were closer to high density and L. perenne selected ones. There were probably elements of directional selection from the unselected plants irrespective of selection regime; unselected plants appeared to be smaller than all the others, which could be a reflection of reduced grazing pressures under these experimental conditions.

The differences found between density-independently selected plants and density-dependently selected ones agrees well with those expected from theoretical considerations (Chapter 2 & 3) and those found between natural populations (Chapter 4). The differences were smaller than those between opportunist and pasture populations, but this is to be expected from the relatively short period of time over which they had been experiencing selection. Furthermore the differences were confined to the earliest parts of life; this is also to be expected, since the earlier in life a character occurs, the more strongly it can be selected (Hamilton 1966). However, we should bear in mind that this conclusion could be confounded by the fact that it was only possible to follow the early part of the lives of the plants.

Finally it should be noted that there was significant genetic variation between families within selection regimes. This variation was also genetic and implies that genetic differentiation might have continued further, had it been possible to continue the selection experiment for longer. It is possible that there was also some genetic variation present within families to contribute still further towards genetic change, but the generally inbreeding system of Poa annua, suggests that the contribution of this would be relatively small.

5.4 Life-historical differences under competition

We have seen that genetic differences can be observed between samples previously selected at different densities when grown at low density. However, the detection of genetic differences depends in part on the density at which the samples are grown, since life-historical characters are in general functions of population density.

It is therefore useful to compare samples from different selection regimes at high density to find out if differences are still observable. Here I describe the results of a competition experiment in which samples from two selection regimes were grown at high density on their own and in competition.

5.4.1 Methods

It was practicable to compare only two of the selection regimes under competitive conditions and low density and high density with L. perenne were chosen for this purpose. A random sample of 30 seeds per tiller was collected from 15 tillers from each plot (the same 15 that were used for the spaced plant comparison). The seed from each plot was mixed giving a composite sample to compare with other plots. Seeds were germinated on filter paper in petri dishes and then planted out in John Innes No. 1 compost in 6 inch plastic pots (14.11.74). Seedlings were planted both as monocultures containing progeny from one plot only and also as each low density and L. perenne competition combination. Thus there were 8 treatments; low density plot 1, low density 2, L. perenne competition 1, L. perenne competition 2, low density 1/L. perenne competition 1, low density 1/ L. perenne competition 2, low density 2/L. perenne competition 1, low density 2/L. perenne competition 2. Each treatment was replicated three times. Seedlings were laid out on a hexagonal matrix in each pot, 19 to each pot. In pots with samples from both low and high density plots, seedlings were arranged so that the 6 nearest neighbours to each individual contained equal numbers of each type (apart from individuals around the periphery) (Harper 1961). Hence pots containing samples from different selection regimes, were made up of 11 seedlings of one and 8 of the other, identified by pins with coded heads. The pots were laid out in a completely randomised design on a bench in a greenhouse.
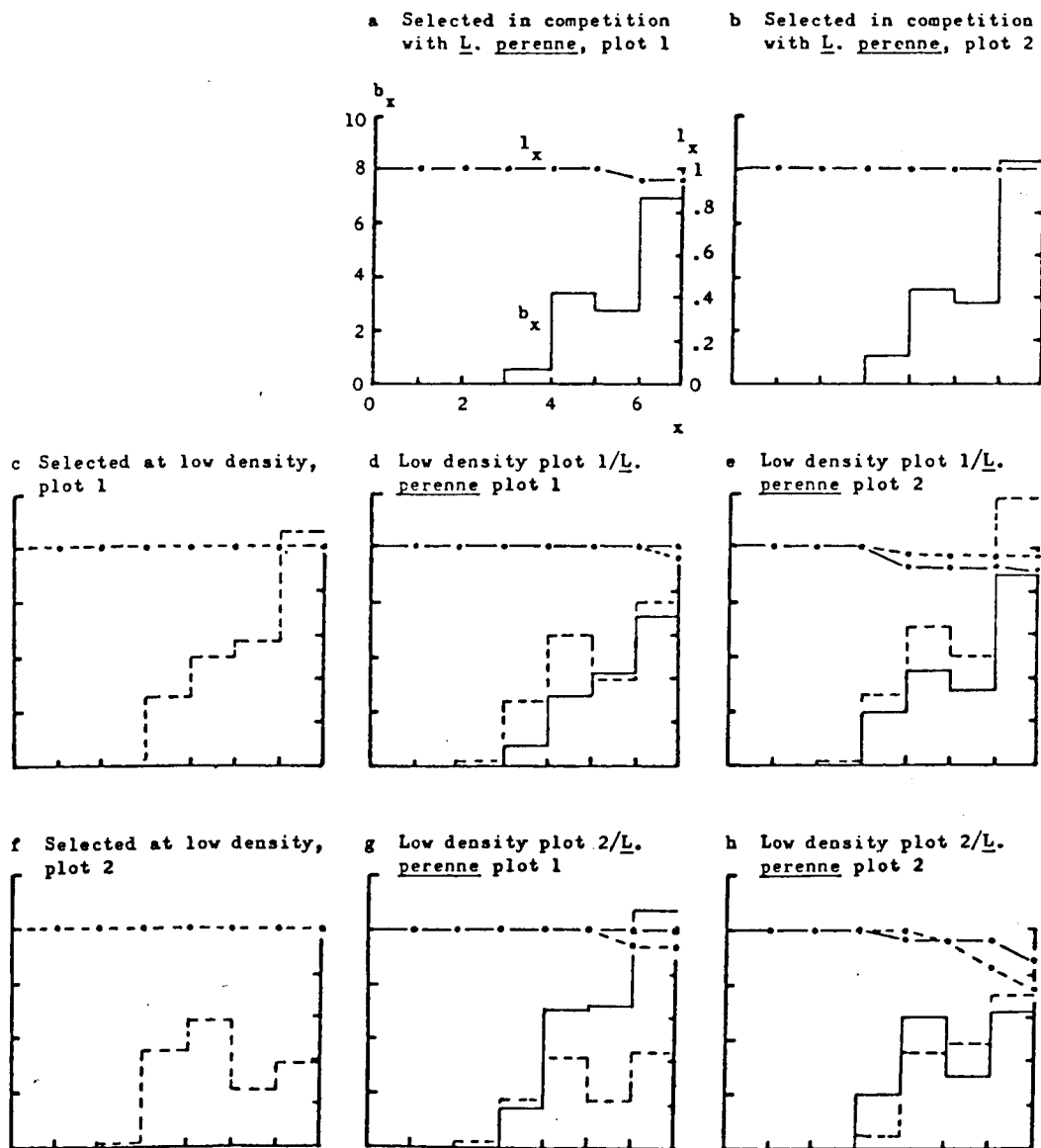
As the plants developed, measurements of age-specific survival and reproduction were taken at 4 week intervals. Death was defined as the time when no green tissue was observable; reproduction was measured in units of the number of inflorescences from which all seed had fallen in the preceding month. After being counted each inflorescence was removed so that it could not be counted again in subsequent months.

Results were analysed by heirarchical analysis of variance (Sokal & Rolf 1969, Chap. 10). The data used for the analysis were means of 8 plants from each plot per pot; in those pots which contained more than 8 plants from a plot, 8 randomly chosen plants were used (the same 8 being used for measurements in different months). Two different analyses were carried out; the first was on the monoculture pots, to determine whether there were significant differences in life-historical characters at high density, without competition between selection regimes. In this analysis variation was partitioned between selection regimes, between plots within selection regimes and between pots within plots (Appendix 5.1.2). The second analysis was on pots containing plants from both low and high density plots, to establish if there was any variation in life-historical characters within plants from each plot when grown with different neighbours. In this analysis variation was partitioned between treatments (3 categories: neighbours from the same plot and neighbours from the 2 plots of the other selection regime) and between pots within treatments (Appendix 5.1.3).

5.4.2 Results and discussion

Life histories of low density selected plants and those selected in competition with L. perenne, when grown at high density as monocultures and also in competition with one another, are illustrated

FIGURE 5.3 Age-specific reproduction (b$_x$) and survival (l$_x$) of samples from plots
selected at low density and from plots selected in competition with
Lolium perenne. Samples grown at high density in pure stands (a,b,c,f)
and in competition, using all low density plot/L. perenne competition
plot combinations (d,e,g,h). Age (x) measured in units of 4 week months.
Reproduction measured in units of numbers of inflorescences per plant
per month. Low density selected plants shown as discontinuous lines,
and plants selected in competition with L. perenne, as continuous lines.

a Selected in competition with L. perenne, plot 1

b Selected in competition with L. perenne, plot 2

c Selected at low density, plot 1

d Low density plot 1/L. perenne plot 1

e Low density plot 1/L. perenne plot 2

f Selected at low density, plot 2

g Low density plot 2/L. perenne plot 1

h Low density plot 2/L. perenne plot 2

in Figure 5.3. There do not appear to be any consistent differences between samples from the two different selection regimes when grown as monocultures (Figure 5.3.a,b,c,f). Differences between low density selected plots for reproductive characters were greater than differences between selection regimes, particularly in 5 and 6 month old individuals. Survival rates of all plants were high, so there were no visible differences between selection regimes for this character. The absence of differences is confirmed by analysis of variance (Table 5.5); there were no significant differences in reproduction between selection regimes in months 3, 4, 5 or 6 after germination.

Lack of consistent patterns of life-historical differences are also apparent when plants from one selection regime were grown with those of the other (Figure 5.3.d,e,g,h). There was variation in monthly rates of reproduction, but it does not appear to have been attributable to particular combinations of selection regimes. Mortality was marginally higher when samples from different plots were in competition, but the differences were small and again showed no consistent patterns. The lack of difference in age-specific reproduction for plants from each plot when growing in competition with those from the other selection regime is confirmed by analysis of variance (Table 5.6). No significant differences could be found in reproduction during months 3,4,5 or 6.

It is clear from these results that there were no genetic differences observable between plants selected at low density and in competition with L. perenne under these experimental conditions. Whether this was due to life histories of different genotypes tending to be alike at high density (we know that there was genetic variation present between selection regimes from the previous section) or

TABLE 5.5 Analysis of variance of life-historical differences between samples from low density selected plots and from <u>Lolium perenne</u> competition plots, grown at high density as pure stands. F ratio is the ratio of the between selection regimes mean square to the between plots within selection regimes mean square. p is the probability of null hypothesis: no difference between selection regimes, with 1 numerator and 2 denominator degrees of freedom. Each element of data (x) transformed to $\sqrt{x} + \sqrt{x+1}$.

Character	F ratio	p
No. inflorescences at age 3 months	11.7488	>0.05
No. inflorescences at age 4 months	3.9459	>0.05
No. inflorescences at age 5 months	0.1347	>0.05
No. inflorescences at age 6 months	0.4231	>0.05

TABLE 5.6 Analysis of variance of life-historical differences within samples from low density selected plots and from <u>Lolium perenne</u> competition plots, when grown at high density with different competitors. There are 3 treatments, each sample being grown in competition with itself, and with the two samples from plots of the other selection regime. F ratio is the ratio of between treatments mean square to the between replicates within treatments mean square. p is the probability of null hypothesis: no difference between treatments, with 2 numerator and 6 denominator degrees of freedom. Each element of data (x) transformed to $\sqrt{x} + \sqrt{x+1}$.

Character	F ratio	p
<u>Low density selected, plot 1</u>		
No. inflorescences at age 3 months	0.0514	>0.05
No. inflorescences at age 4 months	0.6177	>0.05
No. inflorescences at age 5 months	1.0059	>0.05
No. inflorescences at age 6 months	2.6177	>0.05
<u>Low density selected, plot 2</u>		
No. inflorescences at age 3 months	0.4425	>0.05
No. inflorescences at age 4 months	2.1648	>0.05
No. inflorescences at age 5 months	1.0338	>0.05
No. inflorescences at age 6 months	0.6933	>0.05
<u>L. perenne selected, plot 1</u>		
No. inflorescences at age 3 months	1.0386	>0.05
No. inflorescences at age 4 months	2.6970	>0.05
No. inflorescences at age 5 months	0.3876	>0.05
No. inflorescences at age 6 months	0.2619	>0.05
<u>L. perenne selected, plot 2</u>		
No. inflorescences at age 3 months	0.6572	>0.05
No. inflorescences at age 4 months	0.0016	>0.05
No. inflorescences at age 5 months	0.5057	>0.05
No. inflorescences at age 6 months	0.2920	>0.05

whether differences were present but masked by experimental error, is an open question. The experiment was defficient for the same reasons as the analogous competition experiment in Chapter 4.3.2, but here the problems were particularly critical because if there were differences they would be small. An experiment with much more replication would be necessary to test satisfactorily for differences between selection regimes.

5.5 Conclusions

In this chapter an attempt has been made to determine whether genetic change of the kind outlined in earlier chapters can be brought about by subjecting a population to different modes of regulation. It has been done under conditions intended to maximise genetic change, by starting with an artificially variable population and attempting to subject it to the extremes of density-independent and density-dependent selection. We have seen that genetic differences between samples of different selection regimes are indeed observable 20 months after starting selection, if progeny of the samples are grown together as spaced plants. However no differences could be found, when progeny of the samples were grown at high density. But further work would be necessary to reduce the errors of the competition experiment which could have masked any genetic differences.

The differences observed between samples from different selection regimes when grown together at low density were small but significant and they were exactly those expected from a priori considerations. Broadly, prereproductive periods were shorter and monthly reproductive rates greater in plants selected at low density than in those selected at high density and the differences declined as age increased. Thus the results provide direct evidence for the selective forces that brought about genetic differences between

opportunist and pasture populations described in Chapter 4.

Hitherto these differences have been attributed to the mode of population regulation on the basis of correlation with environment, but we now have more direct and rigorous evidence of the causal relationship.

The creation of genetic differences within a single population when subjected to different modes of regulation, provides some justification for the analysis of a colonising population for genetic change (Chapter 6). However, we should not forget that the differences found were small even under conditions that should have maximised the rate of genetic change. It is most unlikely that genetic change would be greater in a natural colonising population, and if there was only limited appropriate genetic variation, genetic change could be much smaller.

CHAPTER 6

THE ANALYSIS OF A COLONISING POPULATION OF POA ANNUA

6.1 Introduction

The earlier chapters of this thesis have laid the foundations for the analysis of genetic change during colonisation. We have seen that there is a wealth of genetic life-historical variation present in many populations of Poa annua and that the kinds of life histories selected are closely related with the mode of population regulation (Chapter 4). It has also been shown that under optimal conditions for genetic change, life-historical changes could be observed within a population in two years (Chapter 5).

It is now possible to undertake an intensive analysis of a single episode of colonisation, to estimate the parameters of the mathematical model developed in Chapter 3. We can recall from Chapter 3 that ideally this analysis should consist of complete life-historical specification of each genotype since this would enable the theory to be tested quantitatively. But I argued that such an analysis would be impracticable because it would be very difficult to make all the appropriate estimates. Instead it is necessary to seek a compromise which accepts the impracticability of complete genetic categorisation of the population and tests the hypothesis of genetic change indirectly.

The approach to the problem used here falls into two parts. Firstly, it is essential to quantify the process of colonisation, to estimate the changes in population density, the proportion of individuals of different ages and their life histories in situ. This is done by an intensive demographic analysis of the colonisation process. Secondly, to detect the presence of genetic change and to relate it to colonisation, it is necessary to compare samples taken

at different points in time under standardised conditions. However, in the time available, colonisation did not proceed far enough for density-dependent selection to come into full force (as was suggested in Chapter 3.5), so the test for genetic change has not been carried out. Consequently this chapter is largely concerned with the former approach, the demographic analysis of colonisation.

Only a few formal demographic analyses have ever been made on plant populations, despite the fact that in many ways plants are particularly suitable for this kind of research. Current interest in plant demography stems largely from Harper (1967) who pointed out the advantages and disadvantages of plants for such research. Prior to 1967 work was limited to some studies by Tamm (1948, 1956) on herbaceous perennials and by Sagar (1959) on Plantago lanceolata. Since then there has been a slight increase in interest in plant demography. Sharitz (1970) published an account of the demography of two competing desert annual species; Hawthorn (1973) gave an account of the dynamics of two weedy perennials; Antonovics (1972) published an actuarial analysis of a population of the grass Anthoxanthum odoratum on a waste tip of a zinc mine. Finally a very careful and intensive analysis of three species of buttercup (Ranunculus) was made by Sarukhan (1971, 1974) (see also Sarukhan & Harper 1973, Sarukhan & Gadgil 1974).

All these studies have been concerned with populations which to a first approximation could be taken to be in steady state. However, the emphasis in this study is quite different since it is the process of demographic change that is of prime importance here. Furthermore the demographic measurements are taken for more than descriptive purposes, since ultimately they are fitness components of all the genotypes in the population.

Demography is in essence concerned with the way numbers change in populations and all possible changes are conveniently summarised in the following equation:

$$N_{t+1} = N_t + I - E + B - D \qquad \text{Eq. 6.1}$$

where,

N_{t+1} = number of individuals at time t+1,

N_t = number of individuals at time t,

I = number of immigrants between t and t+1,

E = number of emigrants " " " " ,

B = number of individuals born between t and t+1,

D = number of individuals that die between t and t+1.

It is clear from this equation that a demographic description of a population is only complete if migration is estimated, as well as births and deaths within the population. Hence this chapter is divided into sections firstly on migration and secondly on birth/death processes internal to the population. The latter part is further divided into sections on the dynamics of seed and adult populations, since these require different analytical techniques.

6.2 Site of colonisation

A site was prepared for colonisation at Liverpool University Botanic Gardens during December 1972. It was crucial that the site should be in an area where gene flow would bring in genetic variability for life-historical characters and the position of the site was chosen with this in mind. The simplest way of ensuring such variability was to choose an area in which populations had been experiencing both density-independent and density-dependent forces for some time. But more gene flow could be expected from areas where regulation was predominantly density-independent (discussed in Chapter 4.2.5) so it was particularly important that the immediate vicinity of the site should be experiencing density-dependent regulation. Hence the site

was constructed in the centre of a lawn, which contained Poa annua subject to strong density-dependent stresses. But the lawn was surrounded by borders and tracks that also contained Poa annua and these populations were subject to stresses relatively independent of density. The area cleared for colonisation was approximately 20x20 m, with a 2 m margin around the periphery which was kept bare of plants, to prevent vegetative spread on to the site.

It was also essential that the site should be constructed with material containing as little Poa annua as possible; unsterilised soil for example would have been unsuitable, as it would have contained a large seed population. For this reason the site was prepared using rubble created during the demolition of houses; this material contained very little Poa annua immediately after demolition and was a typical substrate for colonisation in Liverpool (the 12 colonising populations from Liverpool discussed in Chapter 4.4 were all growing on it). The site was covered to a depth of about 0.3 m with coarse rubble over which a layer of 0.05 m of finely crushed rubble was placed. During the construction care was taken to prevent contamination of the site with soil from the vicinity.

To provide a base line for the colonisation episode it was necessary to estimate the initial density of Poa annua. There were no adult plants on the site at this time so it was only necessary to make an estimate the density of seeds. This could not be done directly, but it was practicable to count seeds that germinated. Accordingly, seven 1 x 1 m quadrats were laid out in random positions, covered to prevent contamination from other seed and left for five months to allow germination. At the end of this time the mean number of plants that had germinated per m^2 was 2.9. This is of course an estimate of the density of seeds that germinated in the

first five months rather than an estimate of the seeds present at the start of colonisation. Nevertheless it is sufficient to show that unless seed dormancy was very high, the density of Poa annua was low at the beginning.

The site was left as undisturbed as possible for a period of two years to allow colonisation by Poa annua to take place. The main source of disturbance came from periodic weeding of other species that also started to colonise; weeding was necessary to ensure maximum precision of the experimental techniques described in Section 6.5.1.

6.3 Migration

Three kinds of migration can be distinguished in plant populations arising from movement of pollen, seeds and vegetative propagules. Our understanding of pollen migration has been extensively developed, largely because of its evolutionary implications; see for example Bateman (1947), Griffiths (1950), Colwell (1951), Levin & Kerster (1968), Bradshaw (1972) and Gleaves (1973). It seems that pollen distribution in space from a point origin is leptokurtic, most travelling only a very short distance but a little travelling a long way.

Seed migration is less well understood and less amenable to generalisation due to the diversity of seed morphology. Large heavy seeds are not dispersed at all without assistance from external sources, whereas small light seeds adapted for wind dispersal could travel long distances. Quantitative information on distances travelled by seed is scarce, the most widely quoted results being those of Levin & Kerster (1968) on Phlox; they found the mean distance of seed from parents to be 1.1 m. In addition Sheldon & Burrows (1973) calculated maximum dispersal distances of 18 species of Compositae and found that no seed travelled more than 2 m when the wind speed was 5km/hr.

Even less is known of the role of vegetative reproduction in migration but like seeds we can expect it to be a function of the nature of the propagules. For example the small propagules of Polygonum viviparum probably have a distribution akin to seeds, whereas the dispersal pattern of grass tillers is completely different. Vegetative spread by grass clones was considered by Harberd (1962, 1967) and from his figures it is possible to calculate a mean rate of radial spread for Festuca ovina of 0.003m/year, clearly a very low rate of dispersal.

In the present analysis of colonisation, pollen migration can be excluded as a significant factor, because it has only indirect effects on population density, and its genetic effects are small since Poa annua is mainly selfing (Ellis 1974). Vegetative migration can also be excluded because the experiment was designed to prevent it from occurring. Hence the only important source of input and output from the population was in the form of seeds, and this section is confined to measurement of migration of seed to and from the colonising population.

6.3.1 Immigration

During the first 5 months immigration rates were tested in situ in the colonising population. 29 seed trays (seed tray area .0763m^2) containing sterilised crushed rubble were placed at regular intervals across the site one month after it had been prepared. During the next 4 months the trays were regularly examined for the presence of seedlings but none were observed at any time. (By June 1973 the earliest colonists had started to produce seed, so it was necessary to terminate the experiment). Like the estimate of seed density at the start of colonisation, this result contains the bias of including

only those seeds that germinate, but unless there were very high dormancy rates in immigrant seed, it suggests that immigration was negligible.

To follow the pattern of immigration subsequently, a long term migration experiment was set up in the vicinity of the site of colonisation. It consisted of two plots each 5 x 5 m, kept clear of vegetation at all times, with seed trays containing crushed rubble regularly spaced across them. The rubble was initially sterilised and all seedlings that appeared were recorded and removed over a period of 12 months starting from March 1973. Mean numbers of seedlings recorded at each position over the plots are given in Figure 6.1. These results show that there was considerable variation from position to position in the mean monthly germination rate, perhaps arising from non-uniform distribution of Poa annua in the surrounding lawn. But superimposed on this there were slight signs of smaller numbers further away from the periphery, so that the mean monthly germination rate in seed trays over 2 m from all margins was about $10/m^2$.

Bearing in mind that there was a 2 m margin around the colonising population, these results suggest that the proportion of seedlings from immigrant seed was very small except for the earliest stages of colonisation. Again we must assume that dormancy was not high before this result can be related to the seed population demography. But this limitation is not serious in the demography of the adult population as seedlings were the youngest age class recorded. It is the conceptual limitations and the difficulties of applying statistical tests that are the most serious problems of this experiment.

FIGURE 6.1 Monthly germination rates of Poa annua at different positions on an area of bare ground 5x5m, surrounded by a lawn containing Poa annua. The germination rates are proportional to the immigration rates of seed to each position. Values given are averages over 1 year for 2 similar areas. Units: /month/m^2. Edge of lawn shown by discontinuous line.

78.6	32.8	13.1	0	32.8
26.2	13.1	0	32.7	26.2
792.7	78.6	9.8	6.6	190
52.4	19.7	19.7	19.7	39.3
32.8	19.7	19.7	6.6	65.5

6.3.2 Emigration

It was impracticable to estimate rates of emigration from the colonising population directly because of the likelihood of contamination from other populations. Instead an experiment was set up to determine the distribution of germinating seedlings around an individual plant under conditions that minimised contamination. This was done by planting a seed-producing adult in an area of bare ground about 30 x 30 m. Around this individual, seed trays containing sterilised John Innes No. 1 compost were dug into the ground (so that the sterilised soil surface was flush with the rest of the soil) at 1 m intervals up to 5 m along 4 axes.

Numbers of seedlings in each seed tray were recorded and the results are summarised in Figure 6.2.a. This figure shows that the overwhelming majority of the seedlings were recorded within 0.5 m of the adult. It is reasonable to assume that the distribution of seedlings was the same as that of the seeds, so we can conclude that most seeds moved less than 0.5 m from the parent. The results also show a marked disparity between movement in different directions from the parent; this is a reflection of a strong prevailing wind in the direction indicated in Figure 6.2.b. Like the immigration experiments no estimates of error can be made so the generality of this result is not known. But it does confirm subjective impressions from many other plants in this study, which were observed to have a dense ring of seedlings around their perimeter, rapidly decreasing in density further from the circumference.

6.3.3 Discussion

In spite of the limitations of the migration experiments, the evidence suggests that the majority of migration by seed in _Poa annua_ occurs over very small distances. This has important bearings on the

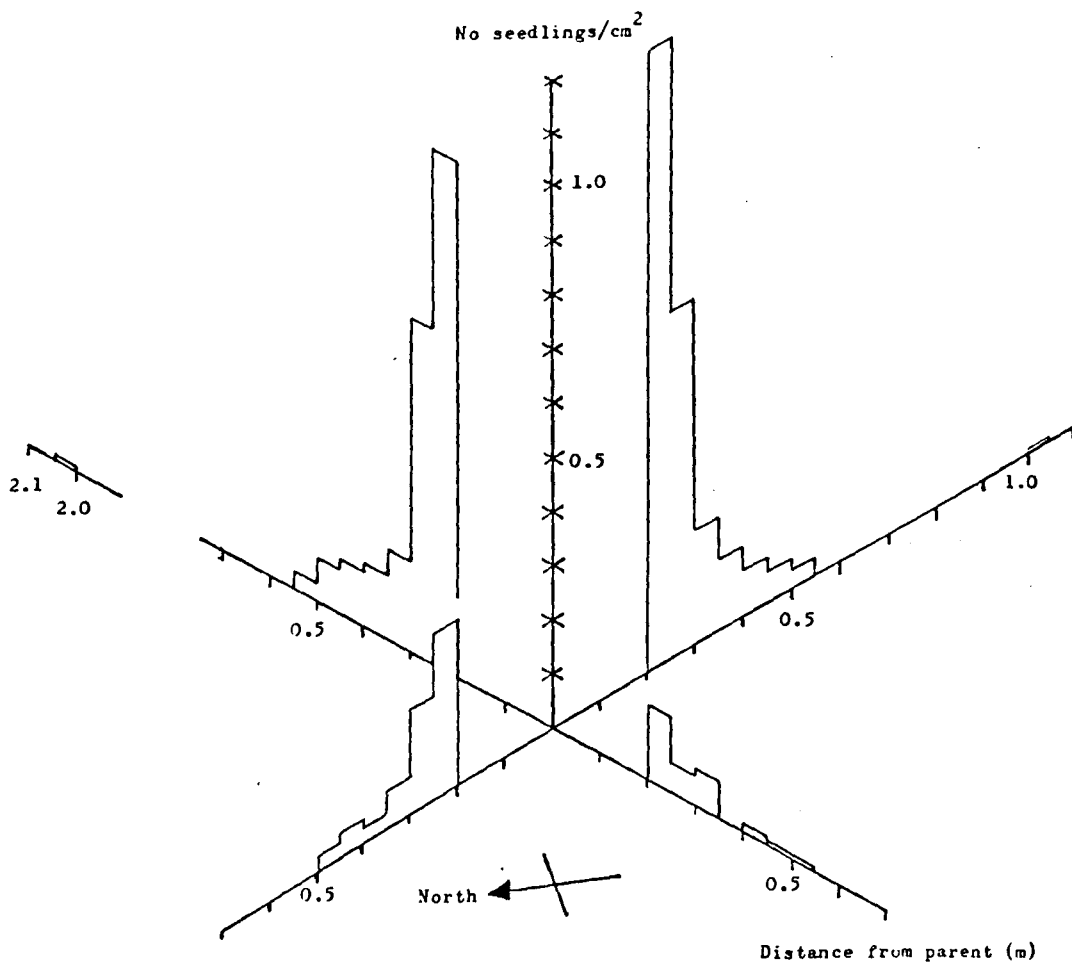FIGURE 6.2.a   Distribution of seedlings along 4 axes around
a parent plant.

FIGURE 6.2.b   Frequency x intensity of wind over a 20° arc around each
axis shown in Figure 6.2.a. Measurements taken daily
at 10.00am at weather station 100m from experiment, over
a 5 month period during which it was in progress.
Intensity measured on Beaufort scale. Arrows indicate
the direction towards which the wind was blowing.
(Data by courtesy of the Director, University of Liverpool
Botanic Gardens.)
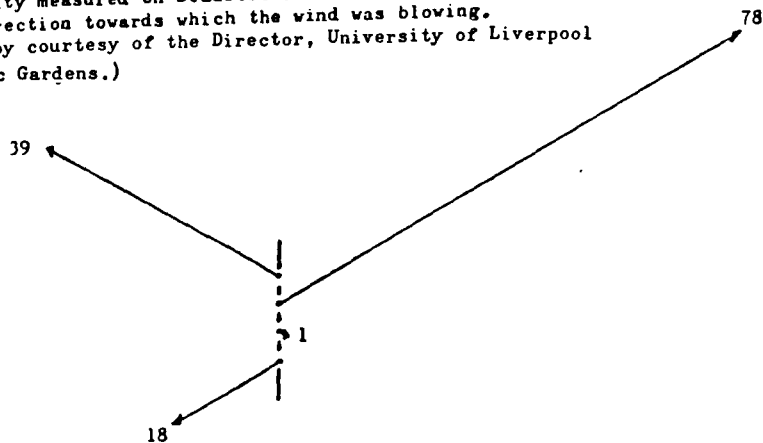
demography of colonisation since it means that for practical purposes migration can be eliminated as a factor influencing population density. With the exception of the earliest stages of colonisation, immigration can be expected to be negligible in comparison to births within the population.

The results also have important bearings on the influx of genetic variability to the population, since this is also likely to be negligible after the earliest stages of colonisation. Hence the possibilities for genetic change depend almost exclusively on the genetic variation present at the start of colonisation and a small amount of migration in the first few months. After this the population is closed to outside influences.

The distances travelled by seed can also be expected to have fundamental effects on processes taking place within the colonising population. Most of the seed produced by the first colonists should fall in their immediate neighbourhood and local patches of high density are likely to be quickly established. We can predict a period of considerable heterogeneity in population density that will only gradually decline as occasional further dispersed individuals start to fill in the gaps. This in turn can be expected to affect the transition from density-independent to density-dependent selection. After a short initial period of predominantly density-independent selection a period of considerable heterogeneity of selection pressure will follow, from which in the course of time, a predominantly density-dependent selection regime will emerge. Naturally this should influence the course of genetic change during colonisation, selection encouraging the maintenance of polymorphism while heterogeneity of population density persists.

The levels of migration also suggest that some of the conclusions

of Chapter 4 may not be strictly valid. For example, life-historical genetic variation within populations might not be attributable to gene flow from adjacent populations with different selection regimes, but due to very localised variation in population density. Nevertheless the migration rates estimated here could be unrealistically low for natural populations, since precautions were taken to ensure minimal disturbance by people and animals.

6.4 Seed population demography

In Chapter 3.2 it was shown that the turnover of seeds was an integral part of the demography of plant populations, so to describe fully the demography of colonisation by Poa annua it is necessary to make appropriate measurements on the seed population. The demographic parameters that need to be estimated were outlined in Chapter 3.2.1; they consist of the age-specific mortality rate (qs_x) and the age-specific germination rate (gs_x) for successive cohorts of seed. In this section some preliminary attempts to estimate these parameters are described.

The procedure used for estimating qs_x is complicated by the problem of distinguishing living from dead seed since it appears to be impossible to do this without destroying the seed. Instead of following the life of an individual cohort of seed, it is necessary to follow the lives of a set of replicates of the cohort so that they can be analysed at different ages. Without this information it is also not possible to estimate gs_x since the rate of germination at age x cannot be determined without knowing the proportional survival to age x.

Because so much work is required to estimate qs_x and gs_x for a single cohort of seeds, it was impracticable to follow the lives of successive cohorts and the results described here are for one

cohort only. This means that the results cannot contribute significantly to the demographic description of colonisation; at best they can only crystalise the problems of determining the dynamics of seed populations.

6.4.1 Methods

A random sample of inflorescences was placed in muslin bags on 25.7.74 and left _in situ_ in the colonising population. Two weeks later when all the seed was fully developed, the bags and seed were removed. At this stage the number of seeds per inflorescence was counted, for an estimate of seed production used in section 6.5. The seeds from all the inflorescences were mixed and 24 random samples of about 50 seeds were taken. Each sample was placed in a small nylon bag, with a mesh size large enough to permit unrestricted seedling development, but small enough to prevent loss of seeds. The nylon bags were held in 35 mm plastic slide frames and laid out in a randomised design in crushed rubble in the colonising population. At 4 week intervals numbers of seedlings in each sample were recorded and the seedlings removed. In addition the seeds from 3 bags were taken for destructive analysis, to determine seed mortality. Initially seed viability was tested using 2:3:5-triphenyl tetrazolium chloride, but subsequently I found it to be as accurate and faster to test by direct observation. (Those in which the contents of the seed were intact and healthy were invariably alive, whereas those in the process of decomposition were dead.)

Using this technique it was not possible to estimate values for qs_x directly but some assessment of age-specific mortality could nevertheless be made. If some seeds die as a cohort grows older there should be a greater proportion of dead seeds in samples of older seeds than in younger ones (where the number of dead seeds is expressed as a proportion of the number of seeds of age 0). It is

TABLE 6.1 Mortality rates in a cohort of seed, expressed as a function of age.
Rates calculated as the proportion of seeds viable at age 0, which
were dead when harvested. Seeds harvested in groups of 3 replicates
at 4 week intervals.

Replicate	Age (units: 4 week months)							
	1	2	3	4	5	6	7	8
1	.2930	.3826	.3826	.2475	.4276	.2066	.3752	.2984
2	.2295	.2311	.2984	.3676	.2926	.2811	.3587	.1435
3	.3673	.1248	.2669	.3443	.2930	.2701	.3601	.2745

TABLE 6.2 Germination rate (gs_x) as a function of age (x), calculated as the
proportion of viable seeds at age x which had germinated by x+1.
Number of viable seeds at age 0, calculated as the total number of
seeds multiplied by an estimate of proportional viability immediately
after seed fall. Number of seeds viable at all subsequent ages
calculated using the additional weighting of the proportional
viability averaged over all subsequent ages.

Sample	Age (units: 4 week months)							
	0	1	2	3	4	5	6	7
1	.2066	.3713	.0557	0	.2321	0	0	.0729
2	0	.4431	.0495	.0512	0	.1822	0	0
3	0	.2491	.2666	0	0	0	0	.2029
4	0	.2518	0	0	0	0	0	
5	.0956	.3770	0	0	0	0	0	
6	0	.1604	0	0	.3522	.0560	0	
7	.0459	.5145	.0536	0	0	0		
8	.3279	.5466	.1041	0	0	0		
9	.1125	.6869	.1467	0	.4089	0		
10	.0675	.3785	0	0	0			
11	.1800	.5870	0	0	.2333			
12	.1465	.4079	.1143	.0620	.0841			
13	.2701	.3851	.0907	.1002				
14	.0230	.1340	0	0				
15	0	.2618	0	.0401				
16	.0956	.1859	0					
17	.0459	.0686	.0369					
18	.6139	.2448	0					
19	.1196	.1548						
20	0	.4341						
21	.1996	.9904						
22	.3663							
23	.1148							
24	.2295							

therefore possible to test for the presence of mortality by comparing the proportions of dead seeds in samples of different ages. Since it is convenient to express the number of seeds dead by each age as a proportion of the number of viable seeds at age zero, an estimate was also made of viability of newly ripened seeds.

6.4.2   Results and discussion

The proportion of seeds viable immediately after ripening was estimated as 0.8713. The proportion of seeds dead by each age are listed in Table 6.1 and the average proportions shown are graphically in Figure 6.3. These are proportions of the viable seeds at age 0; they show that there were always more dead seeds in older samples than in samples aged 0, but that there is little sign of increasing proportion over the age range 1 to 7 months. This impression is confirmed by analysis of variance on arcsin transformed data (details of transformation in Bartlett 1947); the F ratio between sampling ages is 1.042, which with 7 numerator and 16 denominator degrees of freedom is not significant. The discrepancy between viability of seed aged 0 and seed aged 1 month or more, suggests the existence of heavy mortality during the first month.

Because there was no sign of greater mortality in older seed samples, it can be concluded that all values for qs_x were zero over the age range tested. This result is at first sight surprising, but on reflection it is as might be expected, considering the sample sizes used and the duration of the experiment. Previous research has shown low rates of mortality in seed of <u>Poa annua</u>; from the data of Roberts and Dawkins (1967), it is possible to calculate an approximate four weekly rate of 0.016. A much more sensitive and long-term experiment would be required to estimate rates of this order of magnitude.

FIGURE 6.3 Mortality rate up to age x; this is calculated as the proportion of
seeds that were viable at x=0 which were recorded as dead at age x.
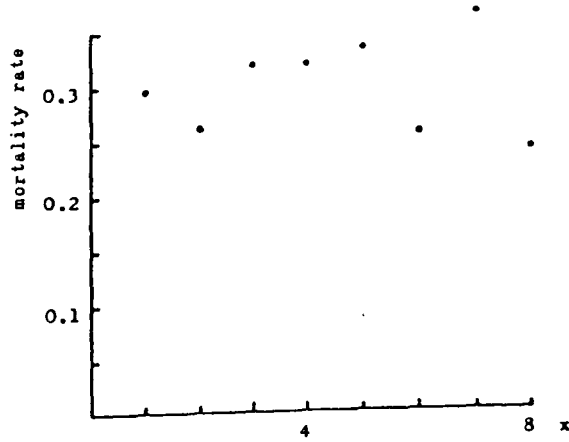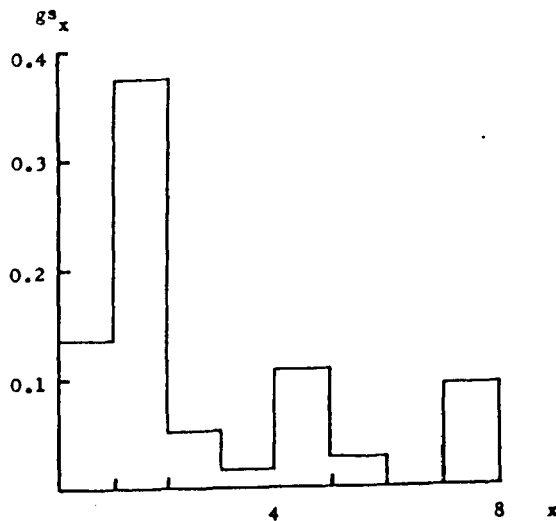Age (x) measured in units of 4 week months.

FIGURE 6.4 Germination rate (gs$_x$) as a function of age (x), calculated as the
proportion of viable seeds at age x that germinated by x+1. Age
(x) measured in units of 4 week months.

Before values for gs_x can be estimated, it is necessary to
calculate the numbers of viable seeds in each bag at the start of
each age interval. During the first month, I have taken the
viability estimate of newly ripened seed to estimate the number of
viable seeds. Subsequently, as there is no evidence of increasing
mortality from age 1 to 7 months, I have used the additional weighting
of the proportion seeds viable averaged over ages 1 to 7 months (0.7014).
Proportions of seeds germinating over successive age intervals can
then be calculated as the ratio of the number germinating to the
number alive at the beginning of the age interval. Values of these
proportions are listed in Table 6.2; the number of samples of each
age varied since destructive samples were taken to estimate mortality
during the experiment. Average proportions germinating over each age
interval are illustrated in Figure 6.4.

The values estimated for gs_x suggest that there was some
variation in the age-specific germination rate; germination rose to
a peak in seed aged 1 month and declined thereafter. By transforming
the proportions in Table 6.2 to arcsin, analysis of variance can be
carried out to test the significance of differences between ages.
The F ratio is 14.876 with 7 numerator and 100 denominator degrees
of freedom. This result tends to substantiate the presence of age-
specific variation, but the exact probability is ambiguous due to
heterogeneity of error variances arising from data elements with
value 0.

The presence of age-specific variation in germination rate does
not necessarily mean that germination was a function of age because
there were many other environmental variables associated with time
that could influence germination. It is conceivable that there might
be no causal connection at all between seed age and germination.
I have already argued that the relationship between age and
germination depends on the physiological state of the seed (Chapter

3.2.1). If dormancy is innate, germination is completely age
dependent; if it is enforced it is completely age independent;
if it is induced there may be a complex interaction between age
and germination. I suspect that here innate dormancy was important
over the first 1 or 2 months but that subsequently enforced and
induced dormancy became more important.

The values of qs_x and gs_x estimated here are of little help
in developing a general understanding of the dynamics of colonisation.
There are several reasons for this. Firstly, it was only feasible
to follow the life of a single cohort of seed; it is unlikely that
gs_x would be the same for other cohorts since it is probably in
part environmentally determined. Seasonality can be expected to
exert a strong influence over germination and the effects of this
could only be determined by analysis of successive cohorts. It is
also possible that population density might influence qs_x and gs_x;
to determine the effects of this would require analysis of cohorts
of seed throughout the whole period of colonisation. Finally, to
obtain any reliable information at all on qs_x would require a much
more sensitive experimental design. Unless non-destructive methods
for determining seed viability can be found, it will be very
difficult to obtain this information.

6.5 Adult population demography

In principle it is much more straightforward to estimate the
parameters necessary to describe the dynamics of adult populations.
The information required is firstly the numbers of seedlings
recruited in successive cohorts, secondly the proportions that
survive to each age (l_x) and thirdly the numbers of seeds per plant
produced over successive age intervals (b_x) (see Chapter 3.2). All
three sets of parameters can be estimated without disturbing a

population and consequently the entire process can be followed
in situ . However, in this population it was impracticable to
follow the life of every plant, so the results discussed here are
based on a random sample. Hence the results should be considered
as estimates of parametric values for the whole population.

6.5.1 Methods

30 permanent quadrats (0.5 x 0.5 m) were placed in random
positions in the area of colonisation before the first colonists had
appeared. These quadrats provided a basic sampling area within
which lives of plants could be followed. Each plant in each quadrat
could be unambiguously identified by x and y coordinates relative
to the quadrat, so that the course of its life could be determined.
Records were made photographically using a Pentacon camera on a
frame slotted rigidly into each permanent quadrat. Data was
retrieved from the photographs by projecting them on to a projection
table. The screen of this table was graduated to enable plant
coordinates to be read to an accuracy of about 1 mm.

Using this method the length of life of each plant could be
estimated as the period from its recruitment to the last time when
any green tissue could be observed. Plants were visible as seedlings,
so recruitment occurred very soon after germination. However, seed
output presented greater problems of estimation because it was not
feasible to measure the number of seeds per plant directly. Instead
nunbers of inflorescences per plant were counted and an independent
estimate was made of the number of seeds per inflorescence (see
Section 6.4.1). Each inflorescence was recorded after seed had
started to fall and at the same time it was marked with a small
piece of wire to prevent it from being recorded again. This

introduced an error because seed fall was not instantaneous, but the magnitude of the error is not known. No measurements were made of vegetative reproduction because, out of more than three thousand plants recorded, there was only one that showed any signs of it. Measurements on the population were made at 4 week intervals from the time of site preparation to December 1974. For convenience each time unit referred to here is equivalent to a four week month.

After the earliest stages of colonisation, numbers of plants became so great that it was no longer possible to record them all. At this stage (t = 7) a random sample of 10 of the 30 quadrats was made and from this time onwards new recruits were only recorded in these quadrats. But even this was insufficient to bring the numbers within manageable proportions and it was necessary to subsample within the quadrats. Random transects were taken across each quadrat to keep numbers of plants less than about 300 per quadrat (although the numbers of course fluctuated from time to time). Hence the area of each transect was a function of population density and varied from quadrat to quadrat. Readjustments were made to transect sizes on two occasions: August 1973 (t = 8) and July 1974 (t = 19).

A further problem arose as a result of increasing population density; it became impossible to identify plants on the basis of their position alone. Seedlings on a number of occasions appeared within about 1 mm of one another and photographic analysis alone could not identify them unambiguously. This difficulty was resolved by placing a small plastic ring over each seedling as it appeared. These rings were colour coded to distinguish recruits from different months.

Population density, age-specific survival and age-specific reproduction were calculated from the photographic data using the

TABLE 6.3 Number of plants per m^2 in a series of monthly cohorts during colonisation. Row headed sample size refers to the total number of seedlings recorded in all quadrats.

Time of cohort recruitment

	3	4	5	6	7	8
Sample size	56	57	75	55	47	252
Age 0	7.72	7.86	10.34	7.59	252.36	1331.86
1	6.07	7.45	9.79	6.21	216.41	730.65
2	6.07	7.31	9.52	5.38	176.42	543.43
3	5.93	7.31	9.24	4.69	135.98	417.21
4	5.93	7.17	7.86	4.41	109.60	365.57
5	5.24	6.34	7.17	3.31	109.60	300.02
6	4.83	5.93	4.69	2.90	91.84	250.59
7	4.41	4.41	2.76	2.21	91.84	228.89
8	3.45	2.90	2.48	2.07	70.89	227.35
9	2.76	2.48	2.34	2.07	69.27	212.24
10	2.34	2.34	2.21	1.79	61.42	182.97
11	2.21	2.21	2.07	1.65	56.49	162.34
12	1.93	2.21	2.07	1.24	56.49	127.66
13	1.79	1.79	1.24	0.83	56.49	95.48
14	1.66	1.66	1.24	0.55	39.12	75.42
15	1.66	1.24	0.97	0.41	24.26	60.75
16	0.97	0.97	0.97	0.41	24.26	59.99
17	0.83	0.69	0.41	0.41	24.26	47.20
18	0.55	0.28	0.41	0.41	24.26	
19	0.14	0.14	0.28	0.00		
20	0.00	0.14	0.28			
21	0.00	0.00				

	9	10	11	12	13	14
Sample size	403	310	225	92	48	37
Age 0	1625.96	1045.29	830.73	307.04	243.32	151.30
1	1335.59	734.22	602.74	220.31	164.74	144.47
2	989.79	635.41	511.17	182.38	121.20	118.18
3	808.64	534.49	444.76	144.19	104.48	118.18
4	705.17	492.39	388.70	108.93	97.00	113.25
5	632.76	358.06	355.30	88.79	80.00	108.31
6	547.13	301.16	331.72	68.41	60.59	78.95
7	508.13	293.39	292.92	66.52	60.59	68.32
8	472.14	259.89	270.05	66.52	47.81	53.50
9	434.73	237.61	213.96	51.19	25.50	53.50
10	374.87	218.00	178.39	43.95	25.10	45.90
11	254.97	184.01	149.00	34.43	25.10	14.07
12	189.02	148.79	132.77	21.65	10.64	
13	168.08	132.62	101.87	21.65		
14	150.12	125.79	88.69			
15	116.04	102.07				
16	108.80					

	15	16	17	18	19	20
Sample size	116	467	154	67	40	58
Age 0	449.03	1543.96	549.60	250.11	217.84	358.72
1	376.55	1214.20	435.25	222.99	184.97	331.26
2	326.03	954.66	402.88	172.03	143.28	302.70
3	295.98	894.04	391.07	152.03	94.65	265.99
4	270.72	775.67	353.11	82.84	66.72	253.20
5	250.29	703.79	311.14	79.04	63.47	217.39
6	229.17	568.62	257.82	39.25	46.76	
7	210.71	496.76	212.83	33.55		
8	169.07	447.24	157.30			
9	163.48	380.09				
10	82.95					

	21	22	23	24	25
Sample size	339	261	110	51	42
Age 0	1710.02	1258.23	547.91	276.31	222.86
1	1488.10	971.18	432.79	184.55	
2	1361.07	719.09	308.62		
3	1131.73	520.70			
4	906.49				

Liverpool University 1906s Computer. Where different sample areas
were used, numbers in each quadrat were converted to a density per
m^2 so that the mean density over all quadrats could be calculated.

6.5.2 Population density

The number of individuals in each cohort and of each age within
each cohort are given in Table 6.3. Consider first the monthly
recruitment of seedlings over the course of colonisation, summarised
in Figure 6.5. Over the first 2 months no recruits were observed in
any quadrats but by April 1973 (t=3) they were first recorded at a
density of about 8 per m^2. This was a density rather greater than
would have been expected from germination of seeds present at t=0
(see Section 6.2), and slightly lower than would have been expected
from immigration for distances of 2 m (see Section 6.3.1). Since
most of the quadrats were more than 2 m from the lawn surrounding
the population, it is reasonable to expect a rather lower rate of
germination from immigrant seed. Thus it appears that immigrant
seed contributed significantly to recruitment over the first few months
of colonisation. This low rate of recruitment was maintained until
August (t=7) although there was a slight increase during June (t=5).

In August recruitment increased very rapidly and there were
more than 30 times as many seedlings as in July. The density of
seedlings continued to increase up to October (t=9) when the density
was 1626 per m^2. However after this monthly recruitment started to
decline at an approximately exponential rate, reaching a trough in
February 1974 (t=14) of 151 per m^2. During the spring recruitment
started to increase again, reaching a new peak in April (t=16) of
1514 seedlings per m^2, but subsequently declining during May, June
and July (t=17,18,19). A trough of recruitment was recorded in July

FIGURE 6.5 Monthly recruitment of seedlings into colonising population.
The x axis is time, measured in units of 4 week months.
Histogram begins in 4th month (t=3), because until then no
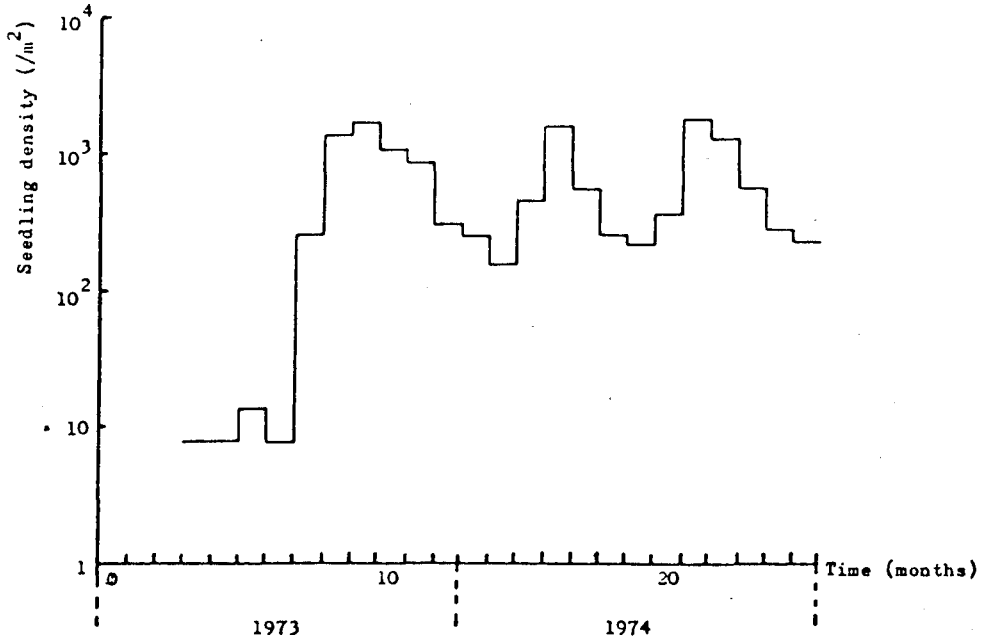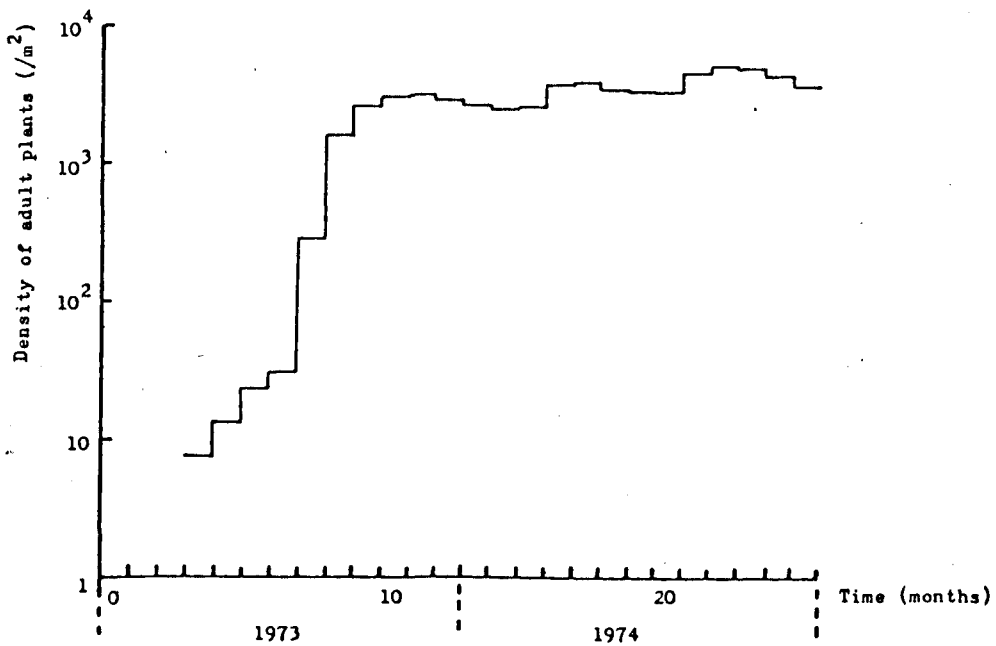recruits were recorded.

FIGURE 6.6 Density of adult plants (ie non-seed population) during
colonisation. Time is measured in units of 4 week months.
Histogram begins in 4th month (t=3), because until then
no recruits were recorded.

of 218 seedlings per m^2 after which numbers started to increase again.
The greatest monthly recruitment of any stage during colonisation
was recorded in September 1974 (t=21) (1710 seedlings per m^2) and
after this numbers again declined until December (t=25), which was
the last month when records were made.

It appears from these figures that the greatest increase
occurred in a three month period during late summer and early autumn
of the first year, during which recruitment density increased by
more than 120 fold. After this recruitment fluctuated, being greatest
in spring and autumn and lowest in summer and winter. Superimposed
on these oscillations there were still slight signs of increasing
recruitment, the greatest density at any stage of colonisation being
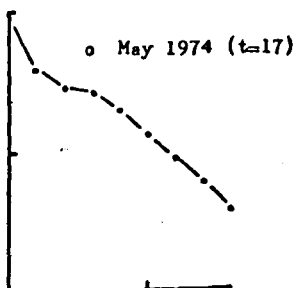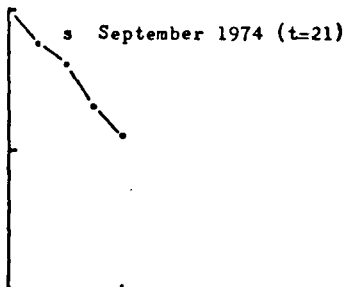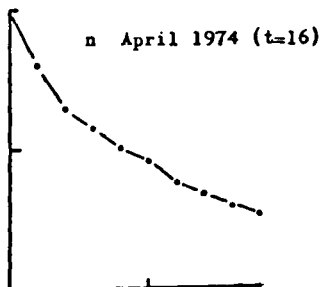in September 1974 (t=21).

The total density of adult individuals present during colonisation
gives a similar impression (Figure 6.6). There was a massive increase
in population density over the first autumn, followed by fluctuations
in density with peaks in the spring and autumn. However the
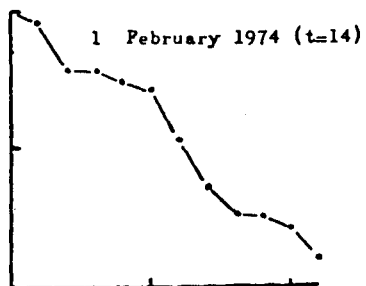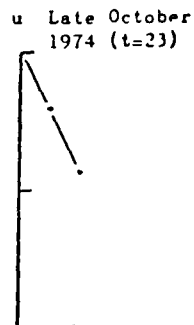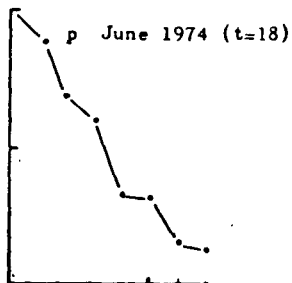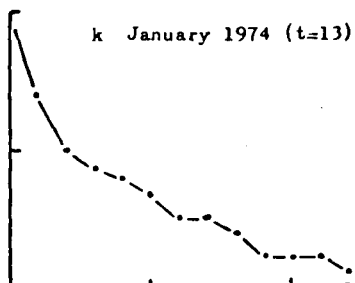fluctuations were much smaller than those of the seedlings (Figure
6.5), since each burst of recruitment was spread over individuals
of increasing age in the following months. It is also clear that
colonisation was not complete since on average the population was
still growing during 1974.

6.5.3 Life tables

Life tables of a series of cohorts recruited at monthly intervals
during colonisation are illustrated in Figure 6.7. To begin with
the first cohort recruited in April 1973 (t=3) (Figure 6.7.a), it
appears that the seedling stage was a period of relatively high
risk with only about 77% survival over the first month. After this
there was little mortality until the autumn (x=5) when survival

FIGURE 6.7 Age-specific survival (l$_x$) of a series of cohorts recruited at
monthly intervals (4 week months) during colonisation. Age (x)
measured in units of 4 week months. t is time, measured from
January 1973.

k   January 1974 (t=13)

p   June 1974 (t=18)

u   Late October
    1974 (t=23)

l   February 1974 (t=14)

q   July 1974 (t=19)

v   November 1974
    (t=24)

m   March 1974 (t=15)

r   August 1974 (t=20)

n   April 1974 (t=16)

s   September 1974 (t=21)

o   May 1974 (t=17)

t   Early October 1974 (t=22)
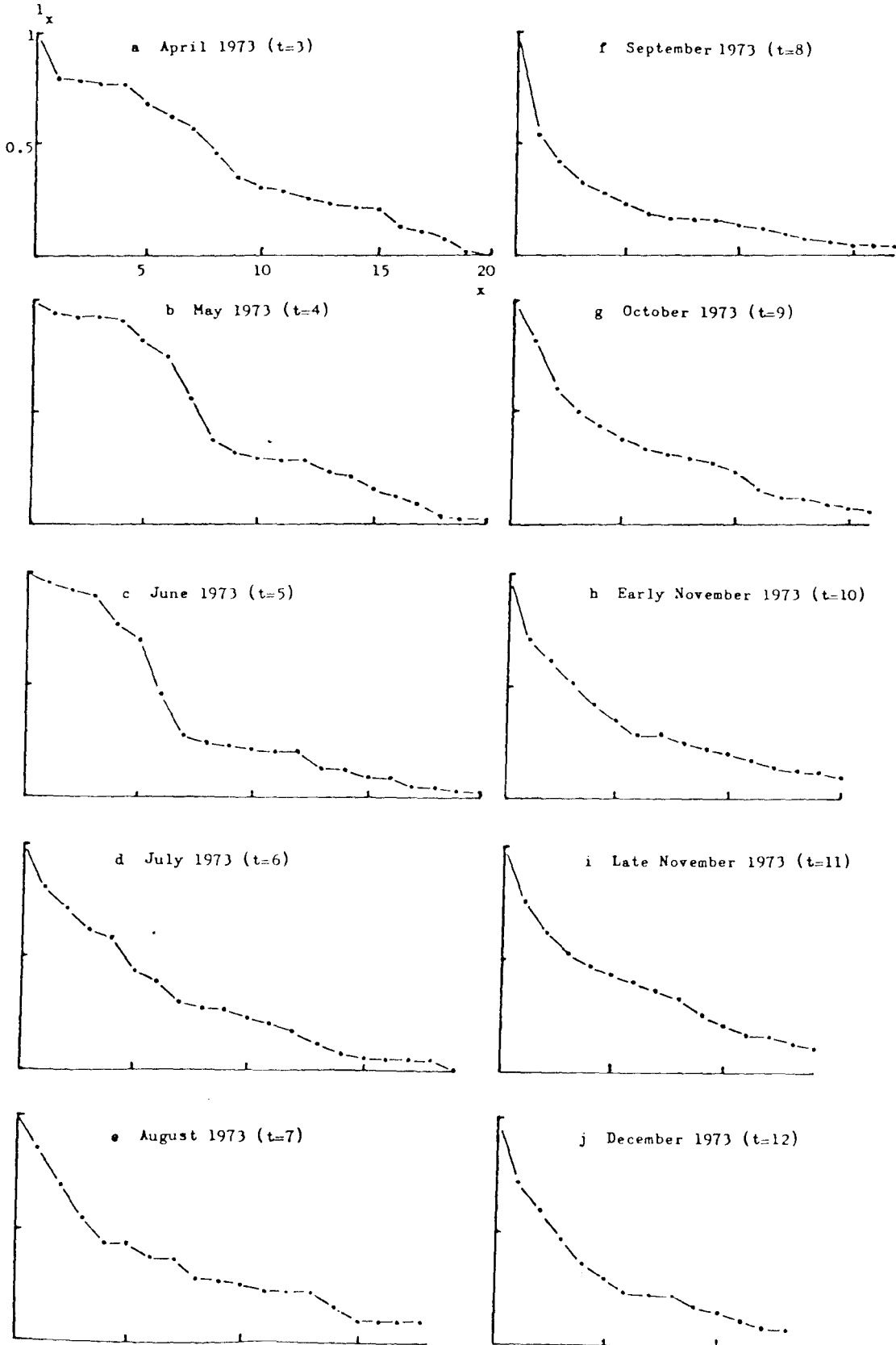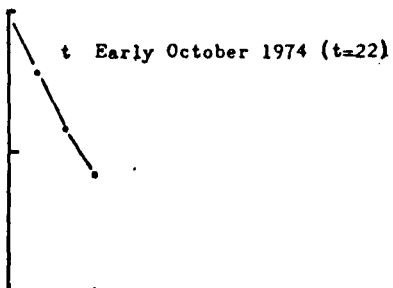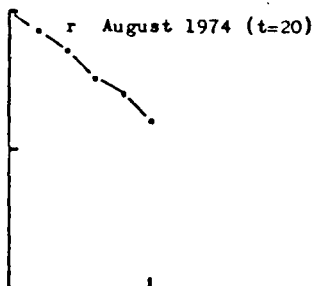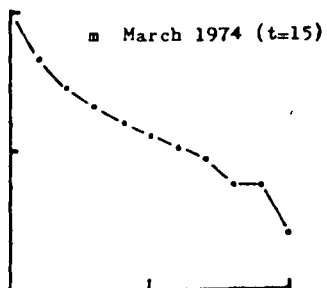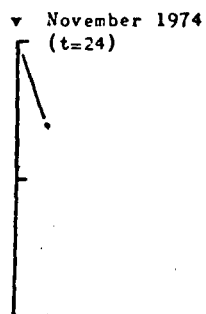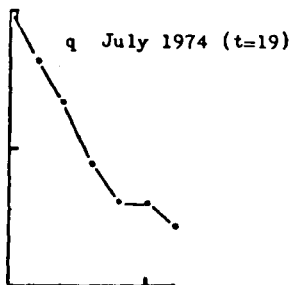
began to decrease again. However, by the end of the winter and
beginning of spring, those still surviving were subject to very
little mortality (x=10 to 15). During the summer, mortality again
increased and by late October 1974 (x=20) no survivors were left. A
similar kind of life table occurred for recruits in May and June 1973
(Figure 6.7.b&c), although in these seedling mortality was lower;
there was little mortality during the summer, it rose to a peak
in autumn, was very low during late winter and increased again in the
early summer 1974.

However, by the time of the July 1973 recruits, the life table
begins to look radically different (Figure 6.7.d). Seedling mortality
was again higher and there was no period of high survival over the
remainder of the summer. Instead the rate of mortality increased
steadily until late in the winter when it decreased again. Like the
earlier recruits, mortality increased again during the summer of 1974.
Survival of August and September 1973 recruits (Figure 6.7.e&f) was
similar, although mortality was even greater in the youngest age
classes. This kind of life table appears to have been maintained in
all subsequent cohorts, although in two of them (February and August
1974, Figure 6.7.l&r) early survival was rather higher.

It appears from this series of life tables that there was a
transition from Type 1 (mortality increasing with age) to Type 2
(constant mortality rates at all ages) and in certain cases Type 3
(mortality rate declining with age). (For further discussion of these
kinds of life tables see Chapter 2.3) The transition is closely
correlated with population density, high rates of survival in younger
age groups generally being recorded when density was low. This
effect is seen quite clearly when survival over the first 2 months
after recruitment is correlated with the logarithm of the total
population density at the time of recruitment. Figure 6.8 shows the

FIGURE 6.8 Correlation between proportional mortality up to exact age 2 months
$(1 - l_2 = d_2)$ and logarithm of population density (N), for the first
11 cohorts during colonisation. Density taken as the number of
plants/m^2 present at the time of cohort recruitment, irrespective
of their age. Population density at t=3 assumed to be 1 plant/m^2.
(Product moment correlation coefficient = 0.7306)

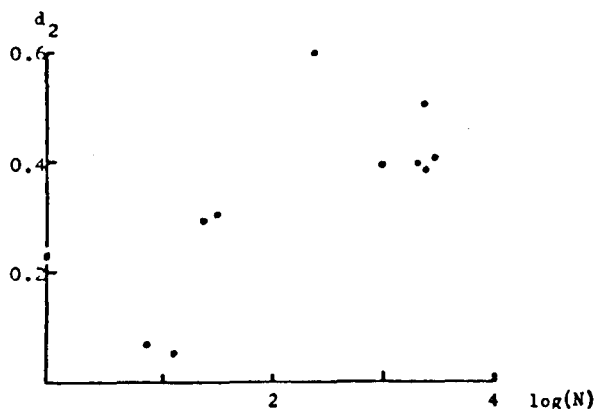FIGURE 6.9 Age-specific survival (l_x) of plants from the 2 quadrats with highest
densities and the 2 with lowest densities during autumn 1973. Plants
recruited during September, October, early November and late
November included, to increase sample size in low density quadrats
(low density sample size = 11 plants, high density sample size = 449
plants). Age (x) measured in units of 4 week months.
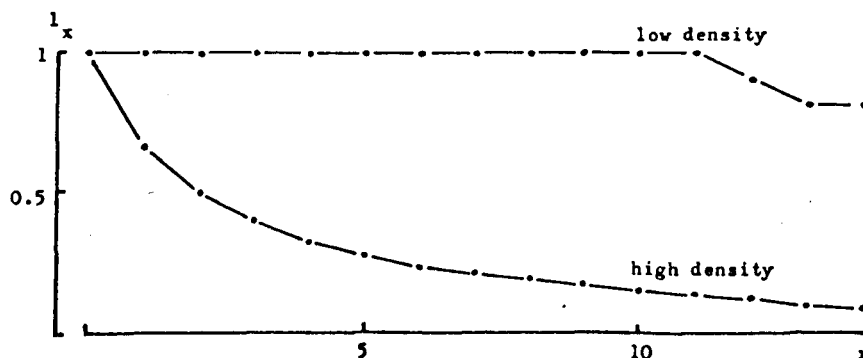
distribution of these variables over the first 11 cohorts, for which
the product-moment correlation coefficient is 0.7306. Assuming that
the variables are normally distributed, the probability of no
correlation is less than 5%.

However, this correlation by no means proves that survival was
a function of population density; firstly, there was considerable
variation in survival of cohorts from February 1974 onwards, although
population density was high throughout this period. Secondly, it is
quite conceivable that survival could have been a function of another
time-related variable apart from population density (eg. season).
Despite this,it is possible to demonstrate unequivocably that
population density had a direct effect on survival. This can be
done by comparing survival of individuals at different densities but
at the same point in time,in which case any effects of time-related
variables are eliminated. Figure 6.9 shows the life tables of
recruits into the 2 quadrats at highest density and the 2 at lowest
density during the autumn of 1973. The differences between these two
life tables are so clear that they hardly need to be discussed;
survival at low density was much greater than at high density,
particularly among younger age groups.

It is still far from clear why there was so much variability
between cohorts in mortality over the first 2 months of life after
January 1974 (t=13). If the trends had been the same as over the
first 11 cohorts, mortality would have been expected to rise still
further, yet over the spring and summer it was much lower. It might
be argued that survival was a function of season such that mortality
was greater in the autumn and winter. But this would be in direct
contrast with other studies of plant demography where mortality risks
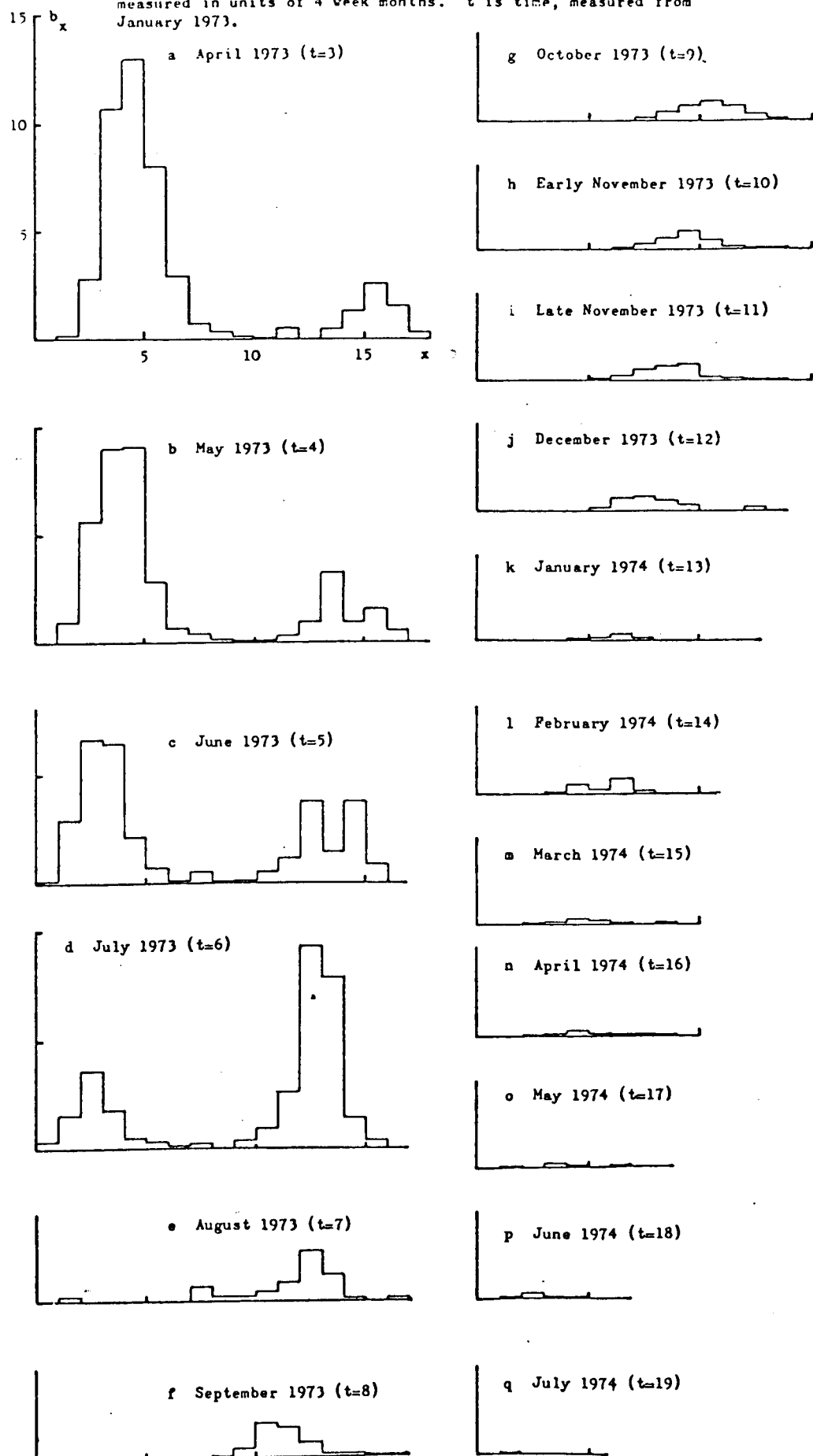have generally been found to be greatest during the growing season

(Harper & White 1974). Mortality still appeared to be loosely related to population density since lowest mortality still occurred when density was lowest. It is conceivable that the first signs of selection were becoming visible, that genotypes with greatest ability to survive at high density were starting to increase in frequency, but analysis of this problem must await more detailed genetic analysis of colonisation.

6.5.4 Reproductive capacity

Inflorescence production expressed as a function of age for the series of monthly cohorts is illustrated in Figure 6.10. The graphs demonstrate a number of clear trends over the course of time. Beginning with the . first cohort recruited in April 1973 (t=3) (Figure 6.10.a), we can see that after a prereproductive period of 1 month, reproduction increased steadily to a maximum of almost 13 inflorescences per plant per month in August 1973. Thereafter it declined to a very low but not zero level in the winter. During the following spring reproduction in those plants still surviving started to increase again, reaching a secondary maximum in June 1974 of about 2.5 inflorescences per plant per month. But by September 1974 there was no more reproduction among the very small numbers still surviving.

Reproduction followed a similar pattern in the cohorts recruited in May, June and July 1973 (Figure 6.10.b,c&d), a period of intense reproductive activity in the first summer being followed by a very low rate in the winter and a second period by those plants still surviving during the next summer. However, there were certain important differences; firstly the period of reproduction in the summer of 1973 moved steadily towards younger individuals, so that maximum reproduction still occurred in September or October. To achieve this some plants had prereproductive periods of less than

FIGURE 6.10 Age-specific reproduction (b_x) of a series of cohorts recruited at monthly intervals (4 week months) during colonisation. Reproduction measured in units of numbers of inflorescences per plant. Age (x) measured in units of 4 week months. t is time, measured from January 1973.

a April 1973 ($t=3$)

b May 1973 ($t=4$)

c June 1973 ($t=5$)

d July 1973 ($t=6$)

e August 1973 ($t=7$)

f September 1973 ($t=8$)

g October 1973 ($t=9$)

h Early November 1973 ($t=10$)

i Late November 1973 ($t=11$)

j December 1973 ($t=12$)

k January 1974 ($t=13$)

l February 1974 ($t=14$)

m March 1974 ($t=15$)

n April 1974 ($t=16$)

o May 1974 ($t=17$)

p June 1974 ($t=18$)

q July 1974 ($t=19$)

one month. Secondly, the total number of inflorescences produced during the first summer declined and by the time of the July 1973 recruits (Figure 6.10.d) the maximum monthly rate of inflorescence production was only about 3.5 per plant. Concurrent with this decline in the first year, there was an increase in the second year among those plants still surviving, the maximum monthly rate of inflorescence production for July 1973 recruits being about 9 per plant. It appears then that neither season nor plant age alone would be sufficient to predict reproductive capacity in this population, as it was a function of an interaction between these 2 factors.

Reproduction by August 1973 recruits (Figure 6.10.e) continued the trends of previous cohorts. There was very little reproduction during the first autumn, none during the winter, most being confined to period during the second summer. However there was an important difference in comparison to previous cohorts; the total number of inflorescences produced was much smaller, the monthly rate barely reaching 2 per plant at any time. The reproductive capacity of plants recruited in September 1973 (Figure 6.10.f) also followed these patterns, almost without reproduction during the first autumn and winter, flowering being confined to a period during the summer of 1974. Like the recruits of August 1973 (Figure 6.10.e), total inflorescence production was much reduced from previous months.

Plants recruited in October 1973 (Figure 6.10.g) did not reproduce at all during the first autumn and winter and began to flower in April 1974 reaching a maximum reproductive rate of 1 inflorescence per plant per month in July 1974. Thus the reduction in total reproductive capacity that started to occur in August 1973 recruits continued further. This pattern of reproduction was maintained in all the cohorts recruited in the winter, (Figure 6.10.

h,i,j,k,l,m), flowering beginning late in the spring, rising to a

maximum in July and August 1974 and declining to zero in the late

autumn. In addition the tendency towards reduced total reproductive

capacity was maintained, the summation of inflorescence production

over all ages in 1974 in for example, January recruits being only

0.64 per plant.

By the time of spring 1974 reproductive capacity of each month's

recruits was very small indeed, the summation of all inflorescences

produced never being greater than 0.5. Like the previous year

prereproductive periods became shorter during early summer as the

reproductive cycle moved towards younger age groups, but unlike the

previous year, no plants initiated reproduction in the first month

after recruitment. The month of greatest flower production was

generally August 1974, the average numbers produced always being less

than 0.3 per plant per month. Recruits after July 1974 (Figure

6.10.q) did not begin reproduction at all during 1974.

It is clear from this series of cohorts that reproductive

capacity per plant declined over the course of colonisation. For

example, the summation of all inflorescence production by April 1974

recruits was 0.012 of the first year's flowering of their 1973

counterparts. Correlating the logarithm of population density at

the time of recruitment with the logarithm of the summation of

inflorescence production over all months (or over the first year, when

it extended for more than one year) (Figure 6.11), we find that the

product-moment correlation coefficient is -0.8350, which assuming

the variables to be normally distributed, is highly significant.

But caution is needed in interpreting this result, because like the

correlation of survival with density, it is possible that other

time-related variables could influence reproduction. This is

FIGURE 6.11 Correlation between the logarithm of the total number of inflorescences per plant (Σb_x) and the logarithm of population density (N), for the first 17 cohorts during colonisation. (Only reproduction in 1973 considered in cohorts recruited from April to July 1973 inclusive.) Density taken as the number of plants/m^2 present at the time of cohort recruitment, irrespective of their age. Population density at t=3 assumed to be 1 plant/m^2. (Product-moment correlation coefficient = −0.8350)
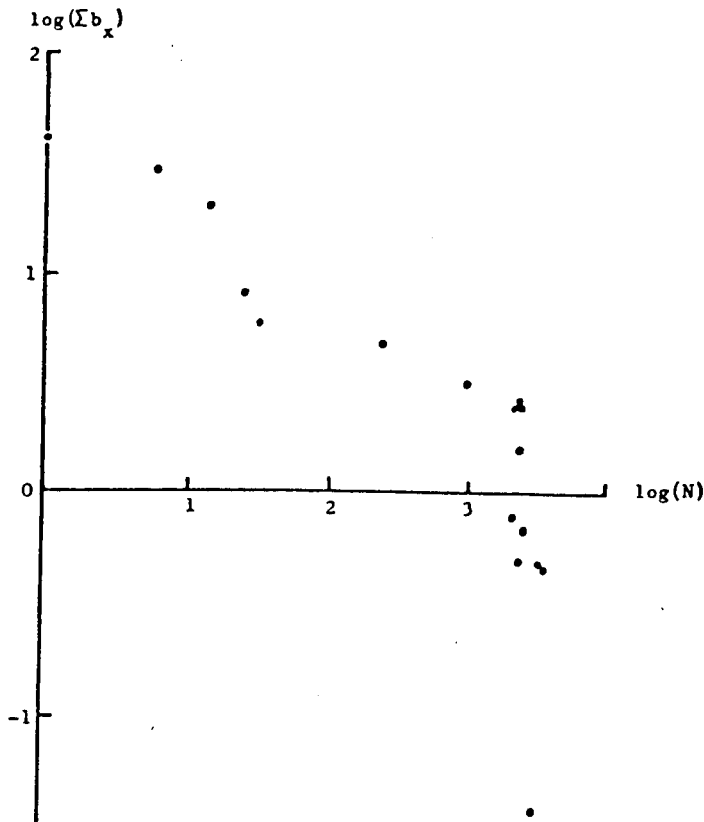
FIGURE 6.12 Age-specific reproduction (b_x) of plants from the 2 quadrats with highest densities and the 2 with lowest densities during autumn 1973. Plants recruited during September, October, early November and late November included, to increase sample size in low density quadrats. (Low density sample size = 11 plants at age 0, high density sample size 449 plants at age 0.) Reproduction measured in units of numbers of inflorescences per plant. Age (x) measured in units of 4 week months.
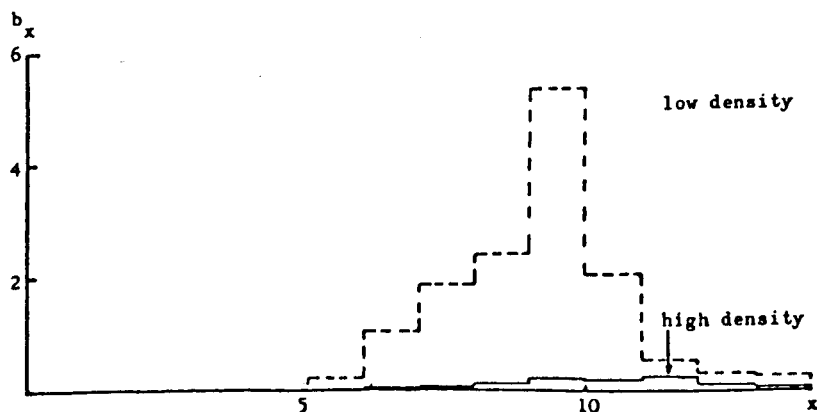
particularly clear for the effect of season since the later in
the spring or summer an individual was recruited, the smaller was
its reproductive capacity that year.

More direct evidence for the effect of population density on
reproductive capacity can be found by comparing the performance of
plants at different densities at the same time. Under these
conditions all other time-related variables, such as season, must be
the same and any differences should be directly related to density.
Figure 6.12 shows the reproductive capacities of plants from the two
highest density and two lowest density quadrats, recruited in the
autumn of 1973 (September, October, early November and late November).
Sample sizes were different, but in spite of this it is clear that
high density was associated with a drastic reduction in numbers of
inflorescences. Thus although inflorescence production was under the
influence of many environmental parameters, population density was
undoubtedly one of the most important.

I have referred to the number of inflorescences per plant as
if it was synonymous with reproductive capacity, whereas the latter
also depends on the number of seeds per inflorescence. The number
of seeds per inflorescence was estimated as 61.93 (SE = 5.55), but
to multiply the number of inflorescences per plant by this figure to
obtain an estimate of reproductive capacity could be misleading.
This is because there is evidence to suggest that number of seeds
per inflorescence was also a function of population density. The
inflorescences sampled came from 3 randomly chosen areas in the
colonising population that were of different densities; mean
number of seeds per inflorescence in each area were: low density
91.36, intermediate 59.13 and high 33.44. Analysis of variance of
seeds per inflorescence between and within densities gives an F
ratio of 8.46 between densities, which with 2 numerator and 41
denominator degrees of freedom is highly significant. Hence estimates

of reproductive capacity based on numbers of inflorescences per plant alone, underestimate the effect of population density. There is another source of bias, as I suspect that number of seeds per inflorescence was a decreasing function of plant age. If this were confirmed it would mean that estimates of reproductive capacity based only on numbers of inflorescences per plant would overestimate the contribution from older plants.

6.5.5 Synthesis

.To complete this survey of colonisation the demographic factors previously considered independently need to be drawn together, to see the way in which they interact to produce the observed patterns. Beginning with the earliest stages of colonisation, it seems that recruitment over the first few months came from a small amount of seed already present when the site was prepared together with some migratory seed. Mortality was low within these first cohorts, the majority of plants surviving to flower in the summer. By August recruitment started to increase rapidly; almost certainly this increase was attributable to germination of seed produced by the cohorts recruited in April, May and June 1973, which were building up to a peak of reproductive activity at this time. This pattern was maintained through September and October, when recruitment became very high indeed.

During the autumn mortality among the earliest recruits started to increase and reproduction to decrease. These 2 demographic changes were probably not coincidentally related, since the probability of tiller survival appeared to be reduced after inflorescence production. Thus the probability of survival of a plant in which most tillers had borne inflorescences was likely to be reduced. In addition the mortality risks of new recruits over the first few months

of life was much greater than in plants recruited during April,

May and June 1973, probably as a result of higher population density.

The other important change during the autumn was a decline in the

rate of monthly recruitment of seedlings. Two possible explanations

for this can be suggested, depending on the dynamics of the seed

population. Either there was only short-term innate dormancy, in

which case the decline was due to exhaustion of the seed population,

or alternatively environmental deterioration could have brought about

enforced and/or induced dormancy.

During the spring recruitment started to increase again; since

flowering did not begin until after this, the burst of germination

must have arisen from environmental improvement bringing seeds out

of enforced and/or induced dormancy. Hence an appreciable proportion

of the seed population must have gone into enforced and/or induced

dormancy during the preceding autumn. Mortality over the first few

months after recruitment fluctuated but generally remained high in

comparison to the same time in the previous year.

As summer approached all cohorts, even the few remaining

survivors of the first cohorts in 1973, increased their reproductive

activities. The total reproductive capacity appeared to depend on

the time when the cohort was recruited, later cohorts producing

fewer flowers. The period of maximum flowering also seemed to depend

on recruitment time, varying from June 1974 in the earliest recruits

of 1973, to August 1974 in individuals recruited in the spring of 1974.

Recruitment declined during the summer while the environment was

less favourable for germination and most seeds probably moved

directly from innate to enforced and/or induced dormancy. But in the

autumn recruitment increased again, when increased environmental

favourability brought more seeds out of enforced and/or induced dormancy.

As well as this there was probably a contribution from seed produced in the late summer germinating immediately after innate dormancy. Like the previous autumn both reproduction and recruitment declined as winter approached.

It is clear that there were two factors of overwhelming importance in the demography of this colonising population. The first of these was season. Recruitment was particularly dependent on season, germination coming in pulses in spring and autumn, leading to a regular periodicity over the course of time. Reproduction was also clearly influenced by season, the onset of flowering being delayed until the spring,and the level of flowering being reduced to a very low level during the winter. But it was nonetheless dependent on plant age, since even under the most favourable seasonal conditions reproduction could only occur after a period of development. Age-specific survival was also a function of season, although to a lesser extent than reproduction. For example a period of heavy mortality occurred at about the same absolute time (t=10,11) for April, May and June 1973 recruits, and therefore in younger age groups among the later recruits.

The other factor of fundamental importance in the colonising population was population density. Obviously recruitment of new individuals was very closely associated with density; as recruitment increased so did population density. But there were more subtle factors, in particular the effect of density on reproductive capacity. It seems that there was a close relationship between population density at the time of recruitment and the reproductive capacity of the recruits; as density increased reproduction decreased. In addition there were signs that survival in the first few months after recruitment was adversely affected by the density of the population at the time of recruitment. Both these factors can be expected to

impose constraints on the rate of population growth limiting the

rapid growth of the earliest stages.

A useful way to establish the effect of season and population

density on the rate of growth of the population, is to calculate the

rate of growth in each month during colonisation. To do this we

need the life-historical data in a form rather different from that

considered earlier. So far demographic parameters of cohorts of

recruits have been considered by following the lives of individuals

('horizontal' life-histories). But here it is more appropriate

to consider the rate of survival and reproduction of individuals of

different ages over a single period of time ('vertical' life histories).

This is equivalent to the extraction of a segment of the life history

of each cohort that corresponds to a particular absolute time period.

(The distinction between these two demographic approaches was

discussed by Deevey (1947).)

To consider the way in which the appropriate life-historical

information can be extracted from 'horizontal' life histories for

'vertical' life histories, it will help to consider an example.

Suppose we need to know the life history of individuals in June 1973

(t=5). This will be made up of plants recruited in June aged 0,

plants recruited in May aged 1 and plants recruited in April aged 2.

Since there were no recruits before April there could be no plants

of age greater than 2. In the time period t=5 to 6, each of these

age groups is subject to mortality and the proportion surviving to

t=6 can be calculated from each of the horizontal life tables as the

proportion alive at t=5 that are still alive at t=6 (Figure 6.7.a,

b, & c). Similarly reproduction may occur in each age class; for

plants aged 0, this is equivalent to reproduction by age class 0

of June 1973 recruits (Figure 6.10.c). For plants aged 1, we need

the reproduction of age class 1 of May 1973 recruits (Figure 6.10.b).

For plants aged 2, we need the reproduction of age class 2 of
April 1973 recruits (Figure 6.10.a). In a similar way it is possible
to construct life histories for all other months during colonisation.

Before population growth rates can be calculated for each month,
it is necessary to define the demographic properties of the seed
population. In doing this we are hampered by incomplete understanding
of their dynamics. In principle it is known that germination was a
function of season, high rates being recorded in spring and autumn,
with lower rates inbetween. But neither the exact rates nor any of
the finer details of gs_x or qs_x were estimated during colonisation.
So instead of making assumptions about the effect of season on gs_x
and qs_x, I have assumed that they were the same as in Chapter 4.2.5.
I have assumed that there was a one month period of ripening
(innate dormancy),after which seeds had a constant mortality and
germination rate irrespective of age, season or population density.
Although this is unrealistic, variation in population growth rate could
then only arise from parameters that had been estimated.

The other factors that need to be taken into account in these
calculations are as follows. Mortality and reproduction are
continuous processes and within a short interval of time such as one
month, the total number of seeds produced will depend on the average
number of individuals alive. If mortality is not negligible the
average number of individuals alive is not the same as the number
alive at the beginning of the interval. So reproduction must be
weighted in some way dependent on mortality. In these calculations,
I have assumed that mortality was linearly distributed within each
time period and that the number of seeds produced can be calculated to
a first approximation by the number of individuals alive at the
midpoint of the time interval. Finally I have ignored the fact that
numbers of seeds per inflorescence was a function of population density

TABLE 6.4 Transition matrices constructed from 'vertical' life histories, used to calculate finite rates of increase in succesive months. Matrices for the first four months only shown; subsequent ones constructed similarly.

April 1973 (t=3)

$$
\begin{bmatrix}
0 & 0 & 0 & 0 \\
1 & .9836 & 0 & 0 \\
0 & .0058 & 0 & 0 \\
0 & 0 & .7857 & 0
\end{bmatrix}
$$

May 1973 (t=4)

$$
\begin{bmatrix}
0 & 0 & 2.92 & 9.81 & 0 \\
1 & .9836 & 0 & 0 & 0 \\
0 & .0058 & 0 & 0 & 0 \\
0 & 0 & .9474 & 0 & 0 \\
0 & 0 & 0 & 1 & 0
\end{bmatrix}
$$

June 1973 (t=5)

$$
\begin{bmatrix}
0 & 0 & 9.62 & 54.47 & 150.1 & 0 \\
1 & .9836 & 0 & 0 & 0 & 0 \\
0 & .0058 & 0 & 0 & 0 & 0 \\
0 & 0 & .9467 & 0 & 0 & 0 \\
0 & 0 & 0 & .9815 & 0 & 0 \\
0 & 0 & 0 & 0 & .9773 & 0
\end{bmatrix}
$$

July 1973 (t=6)

$$
\begin{bmatrix}
0 & 0 & 17.44 & 153.4 & 307.5 & 572.2 & 0 \\
1 & .9836 & 0 & 0 & 0 & 0 & 0 \\
0 & .0058 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & .8182 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & .9718 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 1 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 1 & 0
\end{bmatrix}
$$

and plant age and have used the constant 61.93 throughout,
multiplied by the seed viability at age 0 (0.8713).

Transition matrices calculated from these principles are shown
in Table 6.4; these show only those for the first few months, but
subsequent ones were constructed in a similar way. Finite rates
of increase (λ) for each month were calculated using Leslie's method
(Leslie 1945, 1948) and the results are illustrated in Figure 6.13.
In this figure $\lambda=1$ gives a population which does not increase or
decrease and $\lambda=0.9836$ is the greatest possible rate of decline
(equivalent to the rate of decay of the seed population, when it
is not being replaced by new seed). In the first month, the finite
rate of increase was 0.9836, since no plants had yet started to
reproduce. In the next few months λ increased up to about 1.65 as
reproduction increased; and this was further assisted by high rates
of survival to reproduction. During the winter, as reproduction and
survival of the reproducing age classes declined, λ declined to a
level only just greater than unity. In the spring and early summer
it increased again, but never achieved the level of the previous
summer because there was much less reproduction and prereproductive
survival was much lower. In the autumn λ again declined and by
November was slightly less than unity, due to reduced reproduction
and survival.

To a first approximation, the effect of season on the demographic
properties of the colonising population is represented by periodic
fluctuations in λ in Figure 6.13 and the effect of population density,
by directional change. It is clear therefore that both season and
population density profoundly influence the demographic properties.
However, it is necessary to qualify these conclusions because of the
sometimes unrealistic assumptions that were made in calculating λ .

FIGURE 6.13 Finite rates of increase (λ) during the course of colonisation.
Time (t) measured in units of 4 week months. Values of λ calculated
from 'vertical' life-historical data, as explained in text.
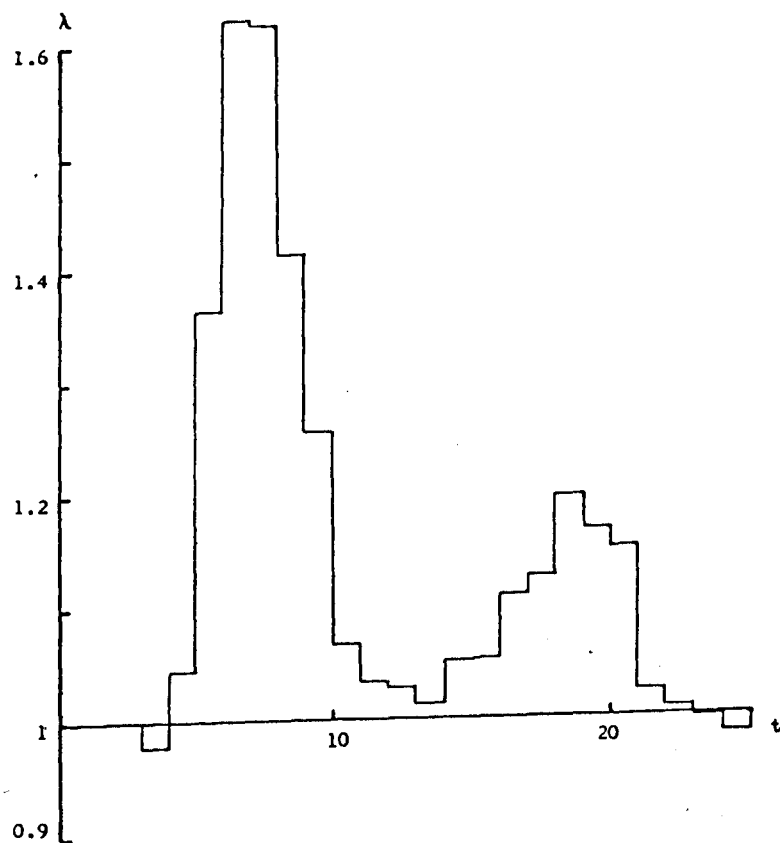
Seasonality in germination can be expected to increase λ in the autumn and spring and to reduce it at other times, particularly in early winter and early summer. The effect of density on number of seeds per inflorescence can be expected to increase the effect of density on λ. And the effect of plant age on numbers of seeds per inflorescence will tend to reduce λ, but to a greater extent when λ is small. It would be misleading to imagine that Figure 6.13 in any way shows the real rate of growth of the population; at best it can only provide a rough comparison of the effects of season and population density.

6.5.6 Discussion

While care was taken in the design and procedures of this experiment, there were certain errors inherent in the observations, some of which were particularly serious because they introduced directional bias into the results. For example, there were occasional losses of the plastic rings marking the plants, which gave a spurious reduction in lifespan and an overestimate of the rate of recruitment. In addition, not all colours of plastic rings were equally visible, so errors in observing rings were not distributed identically over different cohorts. And the errors were probably density dependent, because a ring was more likely to be obscured at high density. Fortunately, the combined effect of small plant size at high density and the removal of all other species from the area of colonisation, kept this source of error to a minimum. Another potential source of error was that the density of recruits each month could only include those seedlings that survived to census time, so unless mortality was negligible recruitment must have been consistently underestimated.

The analysis also has some serious limitations. Although at the outset I mentioned that the results would be estimates of parametric values for the whole population, I have treated them as

though they were the parametric values themselves and have not quoted

any confidence intervals. While in principle it would be possible to

calculate them, the problems involved would be serious (Keyfitz 1968,

p23). Bearing in mind that small migration distances led to

heterogeneity in density, it is likely that confidence intervals

of life-historical estimates would be very large. Nevertheless,

I believe that the values as given are sufficient for this preliminary

analysis.

In passing it might be noted that the size of the confidence

intervals would also be affected by sample size. Sample size varied

considerably from month to month during colonisation, with profound

consequences for the measurements of life histories. Comparing for

example life tables of February 1974 and April 1974 (Figure 6.7.

1 & n), based on sample sizes of 37 and 467 respectively, it is

clear that monthly fluctuations in survival were much greater in the

former. The problem is complicated further because sample size was

a function of age; estimates of life-historical characters made late

in life can be expected to be subject to greater errors than those

made early in life. So for example, monthly reproduction values

of April 1973 recruits (Figure 6.10.a) would have smaller confidence

limits in 1973 than in 1974 when fewer were alive.

Even with all the data here, the colonisation process for this

population is not fully described. The seed population in

particular would require a much more penetrating experimental approach

to establish qs_x and gs_x and the effect of population density and

season on them. Reproductive capacity, particularly the effect of

density on number of seeds per inflorescence, requires further study.

The data that has been collected has so far only been analysed

superficially; the effect of season and population density on survival

and reproduction needs to be studied much more closely. Finally, to

complete the study of colonisation, the experiment would need to be continued for longer.

In spite of all these limitations this experiment still tells us much about the process of colonisation. It demonstrates the rapid rate at which the population can grow and the effectiveness of density constraints in subsequently limiting the rate of growth. It demonstrates the life-historical characters that are most susceptible to population density in bringing about the limitation of population growth. It provides some justification for the parts of the life history assumed to be sensitive to density in Chapter 3, although not for the particular functions used. Unfortunately the life-historical estimates obtained here cannot be immediately applied to the model in Chapter 3, since it was assumed to be in an environment without seasons.

6.6 Genetic change

The final step in the analysis of colonisation is to test for the presence of genetic change. The ideal approach to this problem was outlined in Chapter 3.4; it involved estimation of the life history of each genotype so that its contribution to future generations could be determined. But the ideal could not be achieved in most populations because the number of genotypes present would render the estimates impracticable. Instead I suggested an alternative much less powerful approach (Chapter 3.5), where life histories of samples taken from the population at different stages of colonisation would be compared under standard conditions. This approach to the study of genetic change has been adopted here.

However, there are several arguments that suggest that colonisation did not proceed sufficiently far to warrant such comparisons. Firstly, it is clear from Figure 6.6 that colonisation

was by no means complete by December 1974. Although the period of
rapid growth was over, numbers were still on average increasing
during 1974 and under these conditions density constraints could
not have come into full force. Secondly, under the genetically
simplified conditions of the model in Chapter 3.4, it was not until
after high density had been reached that genotypes favoured at
high density started to increase in relative frequency. The results
from the model of course depend on the parameter values and not too
much weight should be placed on them. Nevertheless, it seems
reasonable to suppose that genotypes favoured at high density in
any system would not start to increase until high density had been
achieved.

For these reasons no test of genetic change during colonisation
has been carried out. Here I consider only the sampling methods
used and discuss the possibilities of genetic change on the basis
of the demographic description of colonisation.

6.6.1 Methods

Samples were collected from the population on several
occasions during colonisation. Only plants within the quadrats were
sampled and those sampled were recorded photographically so that
their lives in situ could later be compared with the lives of their
progeny under standard conditions. The first sample was taken in
June 1973 by removing small tillers from the plants; the choice of
plants depended on whether they were large enough for the removal
of a single tiller to have a negligible effect, only those with
about 30 or more tillers being chosen. Tillers were grown to
flowering in John Innes No. 1 compost in 3 inch plastic pots; seed
was then collected from each plant and stored for later genetic

comparisons. Sampling was repeated in July 1973 because of high mortality among tillers collected the previous month.

The population was sampled again in May 1974, but by this stage of colonisation plants were too small for tiller samples to be taken without disturbance. Instead seed samples were taken, the choice of plants resting on the presence of seed at sampling time. Like the previous samples the seed was stored for later genetic comparison.

A final sample was taken in April 1975. Since demographic work had been terminated, it was possible to sample the population destructively. Complete plants were removed and grown to flowering using the technique for 1973 samples. The number of plants sampled was large (more than 100) and represented many different age groups.

6.6.2 Discussion

Although the definitive experiment in the analysis of genetic change still remains to be carried out, it is possible to draw some tentative conclusions about genetic change during this episode of colonisation from the demographic information. We know that change in the frequency of genotypes depends critically on the presence of genetic variation and the intensity of natural selection. Here these factors can be considered in the light of the demographic results.

The most important sources of genetic variation in this population were probably variation within the gene pool at the time of starting colonisation and variation brought in by migration subsequently. It is reasonable to ignore mutation as a source of significant variation over a time period as short as this. Furthermore the contribution of recombination was probably small, if the degree of selfing was as great as other populations of Poa annua (Ellis 1974).

Genetic change depends on more than just the presence of different genotypes; it depends on their relative frequency. This was shown clearly in Figure 3.11, identical in all respects to Figure 3.8, with the exception that the starting frequencies of two of the genotypes were much lower. In these circumstances it took the low frequency genotypes much longer to spread through the population, even though one of them was more fit at high density. In an analogous way, I suspect that any input of genetic variation from immigrant seed after July 1973 would be at a frequency too low to have a significant effect on this short-term colonisation.

These considerations suggest that the problem of genetic variation is really the problem of whether there were genotypes with different life histories present in the population during the first few months of colonisation and if there were, what their relative frequencies were. It might be argued that the answer to this could be found by comparing life histories of the first recruits, since they were all at low density and under approximately the same environmental conditions. But although there was considerable variation between plants it is not possible to say whether it was genetic or plastic, since it cannot be partitioned between and within families. Hence the answer to this problem must wait for genetic analysis.

The other factor central to the problem of genetic change during colonisation is the intensity of natural selection. To what extent was there a transition from a density-independent selection regime to a density-dependent one? The results of Section 6.5 show that regulatory factors had started to come into force, but probably not fully even by the autumn of 1974, so the transition to a selection regime that was density dependent was probably not complete. Bearing in mind that low migration distances led to heterogeneity in

population density, it is likely that there was still considerable
heterogeneity in selection pressures in the autumn of 1974. Hence
it seems unlikely that selection for genotypes with life histories
favourable at high density would be uniformly occurring.

The other line of evidence for genetic change during colonisation
would come from direct studies of the demographic parameters estimated
in Section 6.5. This should be done with caution since such
parameters contain the effect of density changes as well as any
genetic ones ('population dynamic effect', Chapter 3.5). But it is
reasonable to suppose that over a wide range of densities demographic
parameters of individual genotypes would be non-increasing functions
of population density. Hence if the parameters started to increase
it would suggest that a genotype particularly favourable at high
density was increasing in frequency. It is therefore particularly
interesting that during 1974 the relationship between mortality
over the first two months of life and population density did not
follow the patterns of 1973 (Section 6.5.3). Up to February 1974
these two factors were positively correlated (Figure 6.8), but
subsequently their relationship was much more erratic. However this
evidence is only circumstantial and could only be tested rigorously
by genetic analysis.

While not wishing to pre-empt the results of analysis of
genetic change during colonisation, these considerations make me
suspect that genetic change if it occurred at all was small.

6.7 Conclusion

The intention in undertaking the research outlined in this
chapter was to make an intensive survey of colonisation and to test
for the presence of genetic change. In particular it was an
attempt to estimate the parameters necessary for the model of

colonisation developed in Chapter 3. For several reasons this
research has been only partially successful. Firstly, the model
for the sake of simplicity was developed in a non-seasonal environment,
whereas in reality season exerted a very strong influence on the
pattern of colonisation. It is therefore not possible to relate
the results to the model as it stands; extensive modifications would
first be required, so that life-historical characters could be
functions of season as well as age and population density.

However, the most serious limitation is that the crucial test
of genetic change during colonisation has not been carried out.
On the basis of the results of demographic analysis, I decided that
colonisation could not have proceeded sufficiently far for significant
change in selection pressures. The small distances moved by seed,
leading to heterogeneity in population density and the fact that
population density still seemed to be increasing when demographic
work was terminated, were the most important factors in this
decision. But it means that the final step in this research is still
missing.

Despite these limitations this analysis has still provided
much information about colonisation. We have seen how, over the
space of a few months, population density can increase by over two
orders of magnitude and how effective density-dependent factors can
subsequently be in constraining population growth. We can see how
plant age, population density and season of the year all interact
to mould the life-historical characters of the population into the
form that we see. Closer analysis demonstrates that survival early
in life and reproduction are particularly sensitive to population
density and form the principle regulatory factors. Furthermore we
have seen the profound consequences of small migration distances of
seed on the build up of heterogeneity in population density.

CHAPTER 7

GENERAL DISCUSSION

In this thesis I have attempted to test the hypothesis that specific genetic changes occur in populations of Poa annua during colonisation, due to changes in population density. The hypothesis stems from the presupposition that during colonisation there is a transition from a predominantly density-independent selection regime to one that is predominantly density-dependent. Given that there are genotypes differentially selected under different degrees of density dependence, it can be argued that genetic change should occur.

From a review of the literature of the evolution of life histories, it was possible to predict the kinds of life histories that should be selected in density-independent and dependent regimes (Chapter 2). Broadly, genotypes partitioning resources towards rapid development and high initial seed output should be favoured under predominantly density-independent selection, whereas those partitioning resources towards overcoming competitive stresses should be favoured under predominantly density-dependent selection. In Poa annua some of the most serious competitive stresses are likely to be prereproductive and in these circumstances genotypes with slower development, iteroparity, longer lives and vegetative reproduction should be selected.

In Chapter 3, the theory of genetic change during colonisation was developed in a precise form by the construction of a mathematical model. I suggested that the ideal approach to the problem was to determine the life history of each genotype in the population so that the absolute fitness of each could be estimated. It would then be possible to predict the genotypic composition at all stages during

colonisation and to provide a powerful test of the hypothesis. However, I argued that this would be impracticable in a population of normal genetic complexity and suggested a more pragmatic alternative approach. This involved comparison of samples of unknown genotypic composition, taken at different times during colonisation and grown together under standard conditions, to test for the presence of genetic change.

Genetic change during colonisation would only be expected if certain conditions were fulfilled; these conditions were tested in Chapter 4 on a set of natural populations. The first condition was that there should be genetic variation in life-historical characters. It was shown beyond doubt that such variation existed in the populations analysed. Secondly, it was essential that the genotypes should be of a kind selected differentially under different degrees of density dependence. This condition was also found to be satisfied; opportunist populations in predominantly density-independent environments were different from pasture populations in predominantly density-dependent ones, the differences corresponding closely to those expected from theoretical considerations. The third condition was one of empirical sufficiency, whether the genetic changes were likely to be large enough to be measured. It was tested by comparison of populations at different stages of colonisation, but the results were inconclusive.

With this evidence, the analysis of individual populations was undertaken, to provide a critical test of the hypothesis. Two different approaches were adopted towards this end. Firstly, the test was carried out under conditions designed to maximise the rate of genetic change (Chapter 5). Genetic variation was increased as far as possible by the synthesis of an artificial population from a

large number of natural ones and samples from it were subjected to treatments designed to maintain the extremes of density-independent and dependent selection. Under these conditions small but real genetic changes occurred within 20 months of selection. The changes were as expected from theoretical considerations and were confined to the early stages of life of the plants.

The second test of the hypothesis was the analysis of a natural colonising population (Chapter 6). As part of this analysis a demographic description of colonisation was made, to determine the change in population regulation. The results of the demographic analysis showed that the transition from density-independent to dependent regulation was not completed in the time available for research. In addition it was far from clear how much genetic variation was present in the population, so no test for genetic change was carried out. It must therefore be concluded that the question of genetic change during colonisation in natural populations of Poa annua still remains open.

Apart from the central problem of genetic change during colonisation, there are several other questions raised by the research described in this thesis.

One of the most important questions concerns the genetic basis of life-historical characters. It has been necessary to assume that they were metric characters and the presence of a genetic component within them has been inferred from the presence of variation between families. This is far from satisfactory and before it is possible to develop further our knowledge of their evolution, we will need to know much more about their genetic basis. This can be done most satisfactorily from controlled crosses of different genotypes, which could be difficult to carry out in Poa annua since it is predominantly

inbreeding. However, with appropriate pretreatments it might be possible to prevent anthesis; for example, growing plants at high temperature has been shown to induce male sterility in Poa annua (Hovin 1958a).

The problem of determining the genetic basis of life-historical characters is further confounded by ambiguity about the cytogenetic history of Poa annua. It was originally believed to have arisen from a cross between Poa supina (2n=14) and Poa infirma (2n=14) (Nannfeldt 1937, Tutin 1957), but several diploid populations have been found (2n=14 as opposed to 2n=28) (Hovin 1958b, Ellis et al 1970), one of which always paired to give 7 bivalents at meiosis. This suggests a level of homology in the parent genomes which might be better interpreted in terms of Poa annua being an autotetraploid rather than an allotetraploid. Clearly before the outcome of specific crosses can be understood, it will be necessary to establish unequivocably whether bivalents invariably occur at meiosis.

Analysis of controlled crosses would establish whether the differences in life-historical characters between families were quantitative or whether major genes were involved. Although not wishing to predict the outcome of such experiments, it is interesting to speculate on the possibility of the presence of major genes at least in the control of inflorescence production. One of the most serious problems in testing the theory of evolution by natural selection has been our inability to estimate fitness of genotypes in their natural environments (Lewontin 1974, p236). Differences in fitness between genotypes are believed to be generally small making it difficult to test the theory. Yet here we might be confronted with genes segregating at a single locus with very large differences in fitness, so large in fact, that we could detect them by whether or not the plants were flowering. Naturally such a locus would not be typical

of the majority, but it would nevertheless present an ideal
opportunity for a quantitative test of evolution by natural selection.

Another question raised in this research concerns the breeding
system of Poa annua. For simplicity I have assumed it to be
completely selfing, but this is probably not strictly valid;
Ellis (1974) gave estimates of outcrossing varying from 0 to 15%.
Hence the lack of isolation of the parent plants used in Chapters
4 & 5, could have led to an underestimate of the differences between
families. In addition, we know that even small amounts of outcrossing
can maintain appreciable genetic variability within the genome
(Allard et al 1968). Thus to assume as I did that each family
represents a pure line, so that its life history can be used to
estimate its fitness, could be misleading. As before, to develop our
understanding of the evolution of life histories in Poa annua further,
we will need to learn much more about its breeding system. To do
this it is necessary to find a simple marker locus, as none are at
present known in Poa annua; it is likely that an enzyme locus could
be developed for this purpose.

Turning from the genetic basis of life-historical characters
to their physiological manifestation, it is clear that I have only
considered the partitioning of resources through life insofar as it
influences age-specific reproduction and survival. My approach has
been dictated by expediency; l_x and b_x can be estimated without
destroying the experimental material and provide sufficient information
for the estimation of fitness. However, it would be equally
interesting to study directly the patterns of resource partitioning
through life since l_x and b_x are functions of them. If this were
combined with a genetic analysis, it might be possible to develop
our understanding of the genetic basis of resource allocation. Such
research would entail much more work because measurements could only

be made destructive sampling. Nonetheless, Poa annua would provide good experimental material, since large numbers of even-aged clones of selected genotypes could be established without difficulty.

Another question arising from this research concerns our definition of fitness. It has been convenient to use a deterministic value (the finite rate of increase) estimated from age-specific reproduction and survival of families. However, I suspect that it would be as useful to define fitness in terms of the probability of extinction, since numbers of progeny and length of life are most important insofar as they minimise this probability. There are two ways in which this can be considered statistically, firstly, the probability of leaving no offspring to the next generation and secondly, the probability of ultimate extinction. The problem could be conceived in terms of a probability generating function of the numbers of individuals in the next generation (Feller 1950, p212 et seq). Although this could be done without difficulty in discrete generation models, it would probably be difficult to develop functions that took into account the complexities of life histories with age distributions.

There is a further question arising from the research described in this thesis, which suggests an alternative problem to the one of genetic change during colonisation. It is clear that in spite of the uncertainty surrounding genetic change during colonisation, there are distinct consequences of long term density-independent and dependent selection. An alternative hypothesis could be that specific genetic differences are maintained across boundaries from density-independent population regulation to density-dependent regulation. This hypothesis could be tested by analysis of clines over density-independent/density dependent boundaries, in which migration was in dynamic equilibrium with selection. Such boundaries could be found without difficulty between tracks and pastures or borders and lawns

although care would have to be taken to ensure other environmental variables were at random. However, in such a study the emphasis would be rather different from the present one, since it would not be concerned with genetic change through time. Neither would it be strictly analogous, since gene flow can only occur undirectionally through time from a density-independent environment to a density-dependent one, whereas it would occur in both directions through space.

The ideas in this thesis have been based on evidence from <u>Poa annua</u>. It would be interesting to know if this species is peculiar in its possession of such wide life-historical variation, or if other species have similar characteristics. I suspect that the choice of <u>Poa annua</u> was fortuitous in that it possesses some genotypes able to live and reproduce within a single season and others that need more than one. The transition between an annual and perennial life history must be a major physiological hurdle and genetic variation within a species to encompass it is unusual. Hence a species with both annual and perennial forms must of necessity show a wide range of variation in life-historical characters. Nevertheless, the basic arguments of evolution under different modes of population regulation are completely general and should be applicable to other species, even if in a rather less extreme form.

There is in fact some evidence to suggest that the ideas may at least be applicable to other grass species. There is a well known dilemma among grass breeders that varieties most suitable for grazing (presumably those most vigorous under competitive conditions) are the most expensive to breed as they yield least seed (Humphreys <u>pers comm</u>). A good example of this is S23 <u>Lolium perenne</u>, more suitable for grazing than S24, but later flowering and lower seed yielding and hence more expensive to produce. <u>Festuca rubra</u> S59 is

similar; it is a later flowering variety than Canadian creeping and more expensive to produce. Ideally a grass breeder needs genotypes which partition most of their resources towards reproduction when grown at low density and which redirect it towards 'competitive vigour' at high density, but whether such genotypes exist is an open question. Nevertheless we should be cautious in interpreting life-historical variation in terms of the mode of population regulation, as this is only one of many environmental variables with life-historical consequences. Grazing pressures could have important effects on flowering time in grass species, and more generally factors such as environmental predictability and trophic complexity could be equally important (Wilbur et al 1974).

Another aspect of the research described here that would be interesting if it was more widely applicable is the control of the evolution of life histories by control of population density (Chapter 5). I suspect that this could be usefully applied to natural populations that we harvest, such as fish populations. Merely by harvesting them we are influencing their densities and hence conceivably the evolution of their life histories; it would be interesting to establish the evolutionary consequences of this harvesting. It would be still more interesting to determine the harvesting policies that would select genotypes leading to the greatest numerical productivity in the population. For example, if we knew the range of genetic variation in prereproductive period in a fish population, it would be possible to maintain the minimum age of harvesting slightly greater than the minimum prereproductive period, to select directly for short prereproductive periods, thereby increasing the numerical productivity.

The questions so far raised have been peripheral to the central problem of genetic change during colonisation. In the light of results obtained in the thesis, we can conclude by considering the way in which the problem might be best approached in the future.

In a formal sense this thesis has been concerned with the identification of the parameters necessary to give a dynamically sufficient description of colonisation (using the terminology of Lewontin 1974, p6 et seq). The model developed in Chapter 3 from theoretical arguments, stated that age-specific reproduction and survival as functions of population density and genotype were the necessary parameters. But the results of Chapter 6 suggest that to this the effect of season on age-specific reproduction and survival should be added. In addition it is clear that the spatial distribution of plants is important, adding a new dimension of complexity to the problem. Finally the model would not be complete without inclusion of the mode of inheritance of life-historical characters and the breeding system.

The complexities involved in predicting the outcome of colonisation based on all these parameters would be enormous and probably make the model impracticable. Might it therefore be possible to exclude some of the parameters, to include only those that evidence has shown to be important? The most far reaching simplification would be to reduce the genetic complexity, considering a small set of genotypes. If a completely selfing species was envisaged, the problems of breeding system would be avoided as would many of the problems of inheritance of demographic characters. Under these circumstances it might be possible to predict the genotypic and demographic outcome of colonisation.

Suppose we wished to determine the outcome of colonisation of a population of an apomictic species; Taraxacum officinale might be appropriate, since it is known to consist of genotypically simple populations, with genetic life-historical variation (Gadgil & Solbrig 1972). Initially, it would be necessary to estimate age-specific reproduction and survival of each genotype as a function of population density and season; and in addition the spatial distribution of progeny around their parents. With this information, it would in principle be possible to predict the outcome of colonisation from given starting conditions of numbers of each genotype, their age distributions and their positions in space. For example, given two genotypes that begin the process of colonisation at two fixed positions in space, it would be possible to predict the distribution of their progeny in space one unit of time later. The density of the population could then be used to predict the age-specific reproduction and survival of the genotypes to the next point in time and as before the distribution of individuals through space. By repeating this process the pattern of colonisation could be predicted. Ideally such a model would be stochastic since age-specific reproduction and survival and spatial pattern are all best considered random variables. The model could be tested by setting up controlled colonisation episodes with different starting conditions.

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Appendix 3.1 Derivation of Equation 3.18

Consider an idealised population in which individuals are at exact age x at exact time t (i.e. $_t ns_x$ = no. of seeds aged exactly x at exact time t, $_t n_x$ = no. of adults aged exactly x at exact time t, for x=0,1, 2, ...). Suppose also that gs_x is the proportion of seeds aged exactly x that germinate and that ls_x is the proportion of seeds that survive to exact age x. It is possible to derive an expression for the number of adult individuals aged 0 at time t as follows:

$$_t n_0 = {_t ns_0} \cdot ls_0 \cdot gs_0 + {_{t-1} ns_0} \cdot ls_1 \cdot gs_1 + {_{t-2} ns_0} \cdot ls_2 \cdot gs_2 + \ldots$$

$$= \sum_{x=0}^{u} {_{t-x} ns_0} \cdot ls_x \cdot gs_x \qquad \text{Eq. 3.23}$$

If b_x is the number of seeds produced by an adult at exact age x and l_x is the proportion of adults that survive to exact age x, we can also derive an expression for the number of seeds aged 0 at exact time t:

$$_t ns_0 = {_t n_0} \cdot l_0 \cdot b_0 + {_{t-1} n_0} \cdot l_1 \cdot b_1 + {_{t-2} n_0} \cdot l_2 \cdot b_2 + \ldots$$

$$= \sum_{x=0}^{v} {_{t-x} n_0} \cdot l_x \cdot b_x \qquad \text{Eq.3.24}$$

Substituting Equation 3.24 into Equation 3.23,

$$_t n_0 = ({_t n_0} \cdot l_0 \cdot b_0 + {_{t-1} n_0} \cdot l_1 \cdot b_1 + \ldots)ls_0 \cdot gs_0$$

$$+ ({_{t-1} n_0} \cdot l_0 \cdot b_0 + {_{(t-1)-1} n_0} \cdot l_1 \cdot b_1 + \ldots)ls_1 \cdot gs_1$$

$$+ ({_{t-2} n_0} \cdot l_0 \cdot b_0 + {_{(t-2)-1} n_0} \cdot l_1 \cdot b_1 + \ldots)ls_2 \cdot gs_2$$

$$+ \\ \vdots$$

$$= \sum_{x=0}^{u} (\sum_{i=0}^{v} {_{t-x-i} n_0} \cdot l_i \cdot b_i)ls_x \cdot gs_x \qquad \text{Eq.3.18}$$

It is assumed in these equations that $ls_0 = l_0 = 1$.

Appendix 4.1 Models for analysis of variance

4.1.1 Comparison of families from natural populations grown as

spaced plants

This analysis was designed to partition variation between and within families. Since a random sample of families were chosen, it was a random effect model. The linear model is

$$x_{ij} = \mu + \alpha_i + \varepsilon_{ij}$$

where,

x_{ij} = j'th observation in i'th family, $(j=1,2, \ldots p_i)$,

μ = grand mean of all observations,

α_i = effect of i'th family, $(i=1,2, \ldots o)$,

ε_{ij} = error associated with j'th observation in i'th family.

The analysis of variance is constructed as follows:

Source	df	ms	expected ms
Between families	$o-1$	ms_0	$\sigma^2 + p \cdot \sigma_0^2$
Within families	$\sum_i (p_i-1)$	$ms_{p(o)}$	σ^2
Total	$\sum_i p_i - 1$		

4.1.2 Comparison of populations and families from opportunist and

pasture environments.

This analysis was designed to partition variation between environments, between populations within environments, between families within populations and within families. Environments were fixed but samples were taken at random from all other levels, so a mixed effect model was used. The linear model is:

$$x_{ijkl} = \mu + \alpha_i + \beta_{j(i)} + \gamma_{k(j)(i)} + \varepsilon_{ijkl}$$

where,

x_{ijkl} = l'th observation in k'th family within j'th population within i'th environment, $(l=1,2, \dots p_{ijk})$,

μ = grand mean of all observations,

α_i = effect of i'th environment $(i=1,2, \dots m)$, (here m = 2),

$\beta_{j(i)}$ = effect of j'th population in i'th environment $(j=1,2, \dots n_i)$, (here $n_i = 14$ for all i),

$\gamma_{k(j)(i)}$ = effect of k'th family in j'th population in i'th environment $(k=1,2, \dots o_{ij})$,

ϵ_{ijkl} = error associated with l'th observation in k'th family in j'th population in i'th environment.

The analysis of variance table is constructed as follows:

Source	df	ms	expected ms
Between environments	$m-1$	ms_M	$\sigma^2 + p'' \cdot \sigma^2_{O(N)(M)} + (op)' \cdot \sigma^2_{N(M)} + (nop) \dfrac{\sum_i \alpha_i^2}{m-1}$
Between Pop'ns in environments	$\sum_i (n_i - 1)$	$ms_{N(M)}$	$\sigma^2 + p' \cdot \sigma^2_{O(N)(M)} + (op) \cdot \sigma^2_{N(M)}$
Between families in pop'ns	$\sum_{ij} (o_{ij} - 1)$	$ms_{O(N)(M)}$	$\sigma^2 + p \cdot \sigma^2_{O(N)(M)}$
Within families	$\sum_{ijk} (p_{ijk} - 1)$	$ms_{P(O)(N)(M)}$	σ^2
Total	$\sum_{ijk} p_{ijk} - 1$		

With different numbers of individuals per family and different numbers of families per population, neither, p, p', p'' are equal nor (op), (op)'. Before F ratios can be calculated it is necessary to calculate reconstituted mean squares using Satterthwaite's approximation (Sokal & Rolf 1969). To test the significance of the F ratios, approximate degrees of freedom must also be calculated.

4.1.3 Comparison of opportunist and pasture populations grown at

high density as pure stands

This analysis was designed to partition variation between

environments, between populations within environments and between

replicate pots within populations. Each element of data consisted

of the mean value per pot. The model used was a mixed one, because

environments were fixed, but populations and replicates were chosen

at random. The linear model is as follows:

$$x_{ijk} = \mu + \alpha_i + \beta_{j(i)} + \epsilon_{ijk}$$

where,

x_{ijk} = k'th value in the j'th population in the i'th environment,

(k=1,2, ... o_{ij}), (here o_{ij} = 3 for all i and j),

μ = grand mean of all values,

α_i = effect of the i'th environment, (i=1,2,... m),

(here m = 2),

$\beta_{j(i)}$ = effect of j'th population in i'th environment,

(j=1,2, ... n_i), (here n_i = 2 for all i),

ϵ_{ijk} = error associated with k'th value in j'th population

in i'th environment.

The analysis of variance table is constructed as follows:

Source	df	ms	expected ms
Between environments	m−1	ms_M	$\sigma^2 + o \cdot \sigma^2_{N(M)} + (no) \cdot \dfrac{\sum_i \alpha_i^2}{m-1}$
Between populations	$\sum_i (n_i - 1)$	$ms_{N(M)}$	$\sigma^2 + o \cdot \sigma^2_{N(M)}$
Between pots in populations	$\sum_{ij} (o_{ij} - 1)$	$ms_{O(N)(M)}$	σ^2
Total	$\sum_{ij} o_{ij} - 1$		

4.1.4 Comparison within populations grown in competition with

     other populations

    This analysis was designed to partition variation between 3 treatments, each population being grown as a monoculture and in competition with each of the populations from the other environment. There were 3 replicate pots within each treatment and the data were mean values per pot. A fixed effect model is appropriate and the linear model is:

$$x_{ij} = \mu + \alpha_i + \epsilon_{ij}$$

where,

x_{ij} = j'th value of i'th treatment (j=1,2, ... n_i),

     (here n_i = 3 for all i),

μ = grand mean of all values,

α_i = effect of i'th treatment (i=1,2, ... m), (here m = 3),

ϵ_{ij} = error associated with the j'th value of the i'th

     treatment.

The analysis of variance table is constructed as follows:

Source	df	ms	expected ms
Between treatments	m-1	ms_M	$\sigma^2 + n \cdot \dfrac{\sum_i \alpha_i^2}{m-1}$
Between pots in treatments	$\sum_i (n_i - 1)$	$ms_{N(M)}$	σ^2
Total	$\sum_i n_i - 1$		

4.1.5 Comparison of populations at different stages of colonisation

    This analysis was designed to partition variation between age of population (stage of colonisation), experimental growing density and between populations of the same age. The first 2 factors were fixed and the third random, so a mixed model analysis of variance was used.

Each element of data was the mean of 10 plants per seed tray. The linear model is:

$$x_{ijkl} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \gamma_{k(j)} + (\alpha\gamma)_{ik(j)} + \varepsilon_{ijkl}$$

where,

x_{ijkl} = l'th observation in k'th population within j'th population age group at the i'th density (l=1,2),

μ = grand mean of all values,

α_i = effect of i'th density, (i=1,2),

β_j = effect of j'th population age group, (j=1,2,3),

$(\alpha\beta)_{ij}$ = interaction of i'th density and j'th population age group,

$\gamma_k(j)$ = effect of k'th population in j'th population age group, (k=1,2,3,4),

$(\alpha\gamma)_{ik(j)}$ = interaction of i'th density and k'th population within j'th population age group,

ε_{ijkl} = error associated with l'th value in k'th population within j'th population age group at i'th density.

The analysis of variance table is constructed as follows:

Source	df	ms	expected ms
Density	1	ms_M	$\sigma^2 + 2\sigma^2_{MO(N)} + 24\Sigma\alpha^2$
Population age group	2	ms_N	$\sigma^2 + 4\sigma^2_{O(N)} + 16(\Sigma\beta^2)/2$
Density age group interaction	2	ms_{MN}	$\sigma^2 + 2\sigma^2_{MO(N)} + 8(\Sigma(\alpha\beta)^2)/2$
Populations within age group	9	$ms_{O(N)}$	$\sigma^2 + 4\sigma^2_{O(N)}$
Density population within age group interaction	9	$ms_{MO(N)}$	$\sigma^2 + 2\sigma^2_{MO(N)}$
Error	24	ms_E	σ^2
Total	47		

The F ratio between densities is calculated as $ms_M/ms_{MO(N)}$ with 1 numerator and 9 denominator degrees of freedom. The F ratio between population age groups is calculated as $ms_N/ms_{O(N)}$ with 2 numerator and 9 denominator degrees of freedom.

Appendix 5.1 Models for analysis of variance

5.1.1 Comparison of samples from different selection regimes grown

     at low density

This analysis was designed to partition variation between selection regimes, between plots within regimes, between families within plots and within families. Unselected plants were excluded from the analysis. Selection regimes were fixed, but samples were taken at random at all other levels, so a mixed effect model was used. The linear model is:

$$x_{ijkl} = \mu + \alpha_i + \beta_{j(i)} + \gamma_{k(j)(i)} + \varepsilon_{ijkl}$$

where,

x_{ijkl} = l'th observation in k'th family in j'th plot in i'th

    selection regime $(l=1,2, \ldots p_{ijk})$,

μ = grand mean of all observations,

α_i = effect of i'th selection regime $(i=1,2, \ldots m)$ (here

    $m = 3$),

$\beta_{j(i)}$ = effect of j'th plot in i'th selection regime $(j=1,2,$

    $\ldots n_i)$, (here $n_i = 2$ for all i),

$\gamma_{k(j)(i)}$ = effect of k'th family in j'th plot in i'th selection

    regime $(k=1,2, \ldots o_{ij})$, (here $o_{ij}=15$ for all i and j),

ε_{ijkl} = error associated with l'th observation in k'th family

    in j'th plot in i'th selection regime .

The analysis of variance table is as follows:

Source	df	ms	expected ms
Between regimes	m-1	ms_M	$\sigma^2+p''\cdot\sigma^2_{O(N)(M)}+(op)'\cdot\sigma^2_{N(M)} + (nop)\dfrac{\sum_i \alpha_i^2}{m-1}$
Between plots in regimes	$\sum_i(n_i-1)$	$ms_{N(M)}$	$\sigma^2+p'\cdot\sigma^2_{O(N)(M)}+(op)\cdot\sigma^2_{N(M)}$

Source (contd.)	df	ms	expected ms
Between families in plots	$\sum_i\sum_j(o_{ij}-1)$	$ms_{O(N)(M)}$	$\sigma^2+p\cdot\sigma^2_{O(N)(M)}$
Within families	$\sum_i\sum_j\sum_k(p_{ijk}-1)$	$ms_{P(O)(N)(M)}$	σ^2
Total	$\sum_i\sum_j\sum_k p_{ijk}-1$		

The analysis of variance table given here is in the most general form with different numbers of individuals per family. Under these conditions, before F ratios can be calculated it is necessary to calculate reconsituted mean squares using Satterthwaite's approximation (Sokal & Rolf 1969). To test the significance of the F ratios, approximate degrees of freedom must also be estimated. However, in the data analysed here this makes very little difference because mortality was very small, only one plant having died by age 9 months.

5.1.2 Comparison of samples from different selection regimes grown at high density

This analysis was designed to partition variation between selection regimes, between plots within regimes and between replicate pots within plots. Since selection regimes were fixed but the other levels were random, a mixed model was used. Each element of data was the mean of 8 plants per pot. The linear model is as follows:

$$x_{ijk} = \mu + \alpha_i + \beta_{j(i)} + \varepsilon_{ijk}$$

where,

x_{ijk} = k'th value in j'th plot in i'th selection regime $(k=1,2,\ \ldots\ o_{ij})$, (here k=3 for all i and j),

μ = grand mean of all values,

α_i = effect of i'th selection regime $(i=1,2,\ \ldots\ m)$, (here m=2),

$$\beta_{j(i)} = \text{effect of j'th plot in i'th selection regime}$$

$$(j=1,2, \ldots n_i), \text{ (here } n_i = 2 \text{ for all i),}$$

$$\varepsilon_{ijk} = \text{error associated with k'th value in j'th plot in}$$

i'th selection regime.

The analysis of variance table is as follows:

Source	df	ms	expected ms
Between regimes	$m-1$	ms_M	$\sigma^2 + o \cdot \sigma^2_{N(M)} + (no) \cdot \dfrac{\sum_i \alpha_i^2}{m-1}$
Between plots in regimes	$\sum_i (n_i - 1)$	$ms_{N(M)}$	$\sigma^2 + o \cdot \sigma^2_{N(M)}$
Between pots in plots	$\sum_i \sum_j (o_{ij} - 1)$	$ms_{O(N)(M)}$	σ^2
Total	$\sum_i \sum_j o_{ij} - 1$		

5.1.3 Comparison within samples when grown in competition with samples from the other selection regime.

This analysis was designed to partition variation between three treatments within samples from each plot. The three treatments were competition with plants from the same plot and competition with plants from each of the two plots of the other selection regime. Each element of data was the mean value of 8 plants in each pot. A fixed effect model is appropriate and the linear model is:

$$x_{ij} = \mu + \alpha_i + \varepsilon_{ij}$$

where,

$$x_{ij} = \text{j'th value of i'th treatment } (j=1,2, \ldots n_i),$$

$$(\text{here } n_i = 3 \text{ for all i),}$$

$$\mu = \text{grand mean of all values,}$$

$$\alpha_i = \text{effect of i'th treatment } (i=1,2, \ldots m), \text{ (here } i=3),$$

$$\varepsilon_{ij} = \text{error associated with j'th value of i'th treatment.}$$

The analysis of variance table is as follows:

Source	df	ms	expected ms
Between treatments	$m-1$	ms_M	$\sigma^2 + \dfrac{n\sum_i \alpha_i^2}{m-1}$
Between pots in treatments	$\sum_i(n_i-1)$	$ms_{N(M)}$	σ^2
Total	$\sum_i n_i - 1.$		