

COEXISTENCE OF ECOLOGICALLY  
SIMILAR PLANTS: AN EXTENSION  
OF LOTTERY MODELS TO  
SEROTINOUS FYNBOS SHRUBS WITH  
APPLICATION TO THE SPECIES  
PAIRS Protea repens-Protea  
neriifolia AND Leucadendron  
coniferum-Protea susannae

Botany Honours (1989)

Ecology Project Report by Henri Laurie

Supervisor: Richard Cowling

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.



## Introduction

The coexistence of ecologically equivalent species in communities of sessile organisms poses a problem in terms of classical population biology. The theory states that at competitive equilibrium the number of species cannot exceed the number of resources (May 1974, Levins 1979). However, terrestrial plants for instance use essentially the same resources, and in certain species-rich communities the number of species far outnumber known resources such as light, moisture, and nutrients (Silvertown and Law 1987). One finds co-occurring species with essentially the same growth form, microsite tolerance and life history. The fynbos is rich in examples from ericoids and proteoids, such as the pairs Protea neriifolia-P. repens, and P. susannae-Leucadendron coniferum considered here.

Recently, several so-called lottery models have been proposed to solve this problem (e.g. Chesson and Warner 1981, Shmida and Ellner 1984, Comins and Noble 1985). These authors do not question the classical results regarding competitive equilibrium, but rather propose mechanisms whereby equilibrium is never attained. One interesting result is that the more similar the species, the greater the likelihood of coexistence (Fagerstrom 1988). This is due to the fact that the smaller the difference, the slower is the attainment of equilibrium, and therefore sufficient perturbation may be small and infrequent--in fact for entirely similar species, the randomness inherent in seed dispersal suffices. In the fynbos, this result generally cannot be used, since competitive equivalence of the relevant plants has usually not been established.

In this project, I use the model due to Chesson and Warner (1981), extending it to include systems with partially overlapping and non-overlapping generations such as seeds in the canopy of serotinous fynbos, where there is overlap in the inter-fire period, but no overlap across the fire, when recruitment occurs.

### Chesson and Warner's lottery model

Chesson and Warner's lottery model (Chesson and Warner, 1981) gives formal mathematical expression to the ideas of Sale (1977, 1978 cited in Chesson and Warner, 1981) on the co-existence of fish on coral reefs. The model is based on the following assumptions:

- A1 Recruitment is sufficiently random for probabilistic arguments to apply.
- A2 Recruitment opportunities are separated in time, i.e. they occur in separated episodes.

- A3 The space available to recruits may be partitioned into equivalent finite areas, called homes, one per recruit.

Assumption A1 is common to all lottery models. It allows for mathematical results in probability theory (which is extensive and at times esoteric!) to be applied. For sessile organisms, the simplest way to satisfy this assumption is to show that when space becomes available, it is allocated at random--for instance, to the first candidate that comes along. However, other forms are possible, such as seed orientation or random dispersal in space (Fagerstrom 1988).

The term "lottery" is justified by assumptions (2) and (3), since one may conceive of recruitment as a periodic and random occupation of places. (I like to visualise a giant roulette wheel with space for say 500 plants, and 10 000 balls rolling around on it, each containing a viable seed, attempting to fill the slots. Exactly which 500 will actually give rise to an adult plant is a matter of chance, but on average a species with 60% of the seeds will gain 60% of the slots.)

The first step in developing a model is to assign the probability that a home is occupied by an individual of species  $i$ . Chesson and Warner assume that the lottery is fair, i.e. each individual has an equal chance of getting established. However, they point out that their arguments and results go through even in the case where some species are better at recruitment than others, although they do assume that the ratio of success between individuals of two species ~~two species~~ is constant i.e. the relative advantage is not dependent on density or environment.

The second step in model building is to derive a set of (probabilistic) equations for population growth, from which the main items of interest, the coexistence criteria, are derived. For each species  $i$ , the equation is

$$P_i(t+1) = [1 - \delta_i(t)] P_i(t) + \frac{\beta_i^*(t) P_i(t)}{\sum \beta_j^*(t) P_j(t)}$$

The first term represents survivors. The second term represents recruitment as the product of proportion of homes becoming available and the newborns from species  $i$  as proportion of total candidates, adjusted to include differences in competitive ability. The symbols are:

- $P_i(t)$       proportion of homes occupied by the  $i$ -th species at time  $t$ ;  
 $\delta_i(t)$       death rate of the  $i$ -th species at time  $t$ ;

$B_i^*(t)$  per capita birth rate of the  $i$ -th species at time  $t$ , adjusted to allow for the differences in competitive ability;

and summation is over all species concerned.

Equation (1) is a recursive relation. To obtain results on coexistence, Chesson and Warner investigate solutions to equation (1), i.e. the proportion  $P(t)$  as a function of time. These are not generally explicitly available, but their relevant behaviour can be studied. In particular, whether a species survives or not will depend on its behaviour at small values of  $P$ . This allows considerable simplification, and they derive "invasibility" criteria based on the quantities like

$$E \log\{ 1 + \delta_i(t) [ B_1^*(t)/B_2^*(t) - 1 ] \}$$

for the case of overlapping generations (Chesson and Warner 1981). The symbol  $E$  is the so-called expectation of probability theory. As will be seen below, serotinous fynbos plants do not satisfy all the assumptions involved in using these criteria, so that these criteria cannot be applied to them, and in my adaptation of the model, I use computer simulation to decide on coexistence.

Before describing the adaptation of this model to serotinous Proteaceae, I turn to the species considered in this project.

### The systems of coexisting Proteaceae

(i) Protea neriifolia and Protea repens in Jonkershoek state forest

Protea repens and P. neriifolia commonly occupy canopy space in mature fynbos over a wide range (Rourke 1980). While there may be habitat separation (P. neriifolia preferring greater altitudes and moister sites, Rourke 1980), mixed stands are known, and I use data on two such stands from Jonkershoek State Forest (LeMaitre in prep.). At present there is no evidence of niche separation in the classic resource axes of microhabitat tolerance, life form, phenology, pollination. Vogts (1982) indicates that these species are similar with respect to tolerance of soil factors. While there are slight differences in flowering season, they cannot by themselves account for coexistence, as the overlap is very large.

I used data from LeMaitre (in prep.) to estimate parameters of seed bank dynamics for these plants in mixed stands (see table I). In the stands he reports on, P. repens produces

about 15 viable seeds per inflorescence, and P. neriifolia about 3. However, P. repens seeds are subject to heavy predation, and this results in a higher mortality rate. Degree of serotiny is not equal: after three years P. repens cones open and the seed is lost, which happens only after seven years for P. neriifolia. Number of inflorescences per plant shows variation which could be due to a number of factors, but the data does not allow them to be resolved. To cope with this, I use two models: one assuming equal production of inflorescences, and the other arguing from data on seeds per square meter.

Table I Assumptions about seed bank dynamics

|     | seeds/plant | seeds/infl | seeds/m <sup>2</sup> | seed mortality rate |
|-----|-------------|------------|----------------------|---------------------|
| P n | --          | 3          | 2.5                  | 40%                 |
| P r | --          | 15         | 1.0                  | 72%                 |
| P s | 3 000       | --         | --                   | 20%                 |
| L c | 12 000      | --         | --                   | 40%                 |

(P n = P. neriifolia, P r = P. repens, P s = P. susanna, L c = L. coniferum. Estimates are averages of data from Lemaitre (in prep) and Mustart and Cowling (in prep). Note that L. coniferum is dioecious and the figure is the average for all adult plants, both male and female)

(ii) Protea susanna and Leucadendron coniferum on the Agulhas plain

P. susanna and L. coniferum are endemic to the Agulhas plain (Cowling et al. 1988). They co-occur in canopies with a frequency that amounts to obligate co-occurrence (R Cowling, pers. com.). They are of similar form, grow to much the same size (though according to Rourke (1980) and Williams (1972), L. coniferum attains a larger maximum size), their seeds mature at the same time (P Mustart, pers. com.) and they have a similar wide tolerance of soil factors (Vogts 1982).

I estimated parameters for the seed bank dynamics of these two species (see table I), using data from Mustart and Cowling (in prep.). Both species carry the same amount of seed per adult plant when a new crop matures, but P. susanna seeds survive longer, the effective mortality rate being about 20% as opposed to L. coniferum 40%.

### A lottery model for serotinous Proteaceae

Coexistence in Chesson and Warner's lottery model is due to overlap among generations (Chesson and Warner 1981, 1983). For plants, this would usually be overlap of adult generations, though seed generations could also be used (Ellner 1984). However, we are considering post-fire recruitment, and there is no overlap of seeds before and after the fire. Hence, in its original form, their model cannot be applied to serotinous Proteaceae.

I propose the following adaptation: at every fire, one allocates a number of adults for each species in proportion to the number of seeds in the canopy. In between fires, one calculates the number of seeds in the canopy as a function of time. It is necessary to do this with a time scale significantly shorter than a year, to allow for the effects of seed mortality and fire season.

In effect, this is a two-stage model: in between fires, one has the overlapping generations of seeds, but no recruitment, and after a fire one has recruitment but no overlap of seed or adult generations with pre-fire generations. Results from current lottery model theory (Ellner 1984, Fagerstrom 1988) do not apply to such a two stage model, since at recruitment there is no overlap. As yet a general mathematical analysis is not available. However, it is fairly easy to investigate particular instances of the model by means of computer simulations. Since the arguments are probabilistic, such simulations do not result in proof, but by running very many trials the uncertainty can be reduced to very little. I provide a specimen program in the appendix, with some graphic displays of simulations.

In the cases I investigated, it is necessary to dispense with stochasticity altogether, because here all the data are from one season, and thus the all-important parameter of variance in time is not available. Therefore I used deterministic models. The question of the role of variation is considered in the discussion.

For the Jonkershoek system, I modelled seed numbers as a function of time in two ways: first is a Leslie matrix model with three age classes in P. repens and seven age classes in P. neriifolia. It calculates new seeds per season per plant (inflorescence number times number of viable seeds per inflorescence) by using some reasonable function imitating inflorescence production as a function of age, and a constant number of seeds per inflorescence. In effect, this assumes no variation in inflorescence production other than with age. The data seem to indicate that there is such variation, so I used a second model based on seeds per square meter for each species. In this case it is notable

that P. neriifolia had more seeds per square meter in the stand where it had the minority as well as in the stand where it had the majority of stems--albeit to a lesser extent.

For the Agulhas system, the model is based on viable seed set per plant, with different mortality rates as shown in Table I.

### Results

In summary, the model's results are: in the Jonkershoek system, P. repens seeds never decline below P. neriifolia seeds if inflorescence production is equivalent, while P. neriifolia seeds never declines below P. repens seeds if we extrapolate from seed/m<sup>2</sup> data. In the Agulhas system, L. coniferum seeds are always above P. susannae

(i) Assuming equal production of inflorescences: While the seed bank of P. repens shows very large annual oscillations, as compared to P. neriifolia, it never declines below it (see fig 1). This conclusion is fairly robust under changes in seed bank parameters. For instance, I investigated decreasing the mortality of P. neriifolia seeds, and found that reducing it to 30% does not affect the conclusion.

(ii) Taking as a basis data on seeds per square metre (see Table I). The estimate is based on data from two separate sites; in both cases the proportion of P. neriifolia to P. repens was higher in the seeds than in the adults. The conclusion, without needing to resort to calculation, is that on recruitment P. neriifolia will increase its percentage cover at the expense of P. repens.

(iii) L. coniferum vs P. susannae seed production for an equal number of plants over a number of years is plotted in figure 2, assuming seed output and exponential decline as in Table I. The result is that the proportion of L. coniferum seeds in the seed bank exceeds its proportion in the adult, though due to its lesser mortality P. susannae does gain a bit as the year goes on.

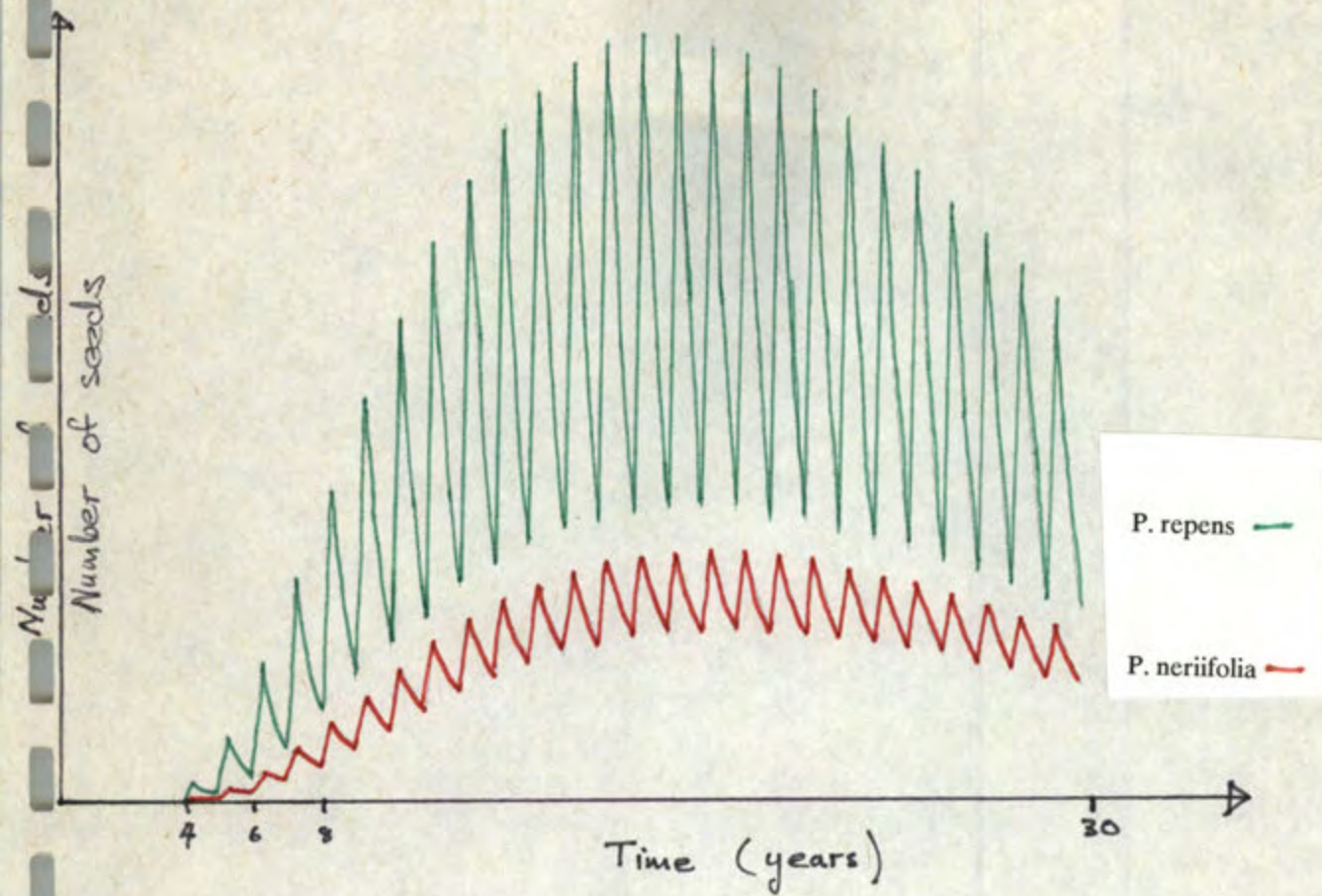


Figure 1. Jonkershoek system: number of seeds as a function of time calculated by means of the program in the appendix using the parameters in Table I.

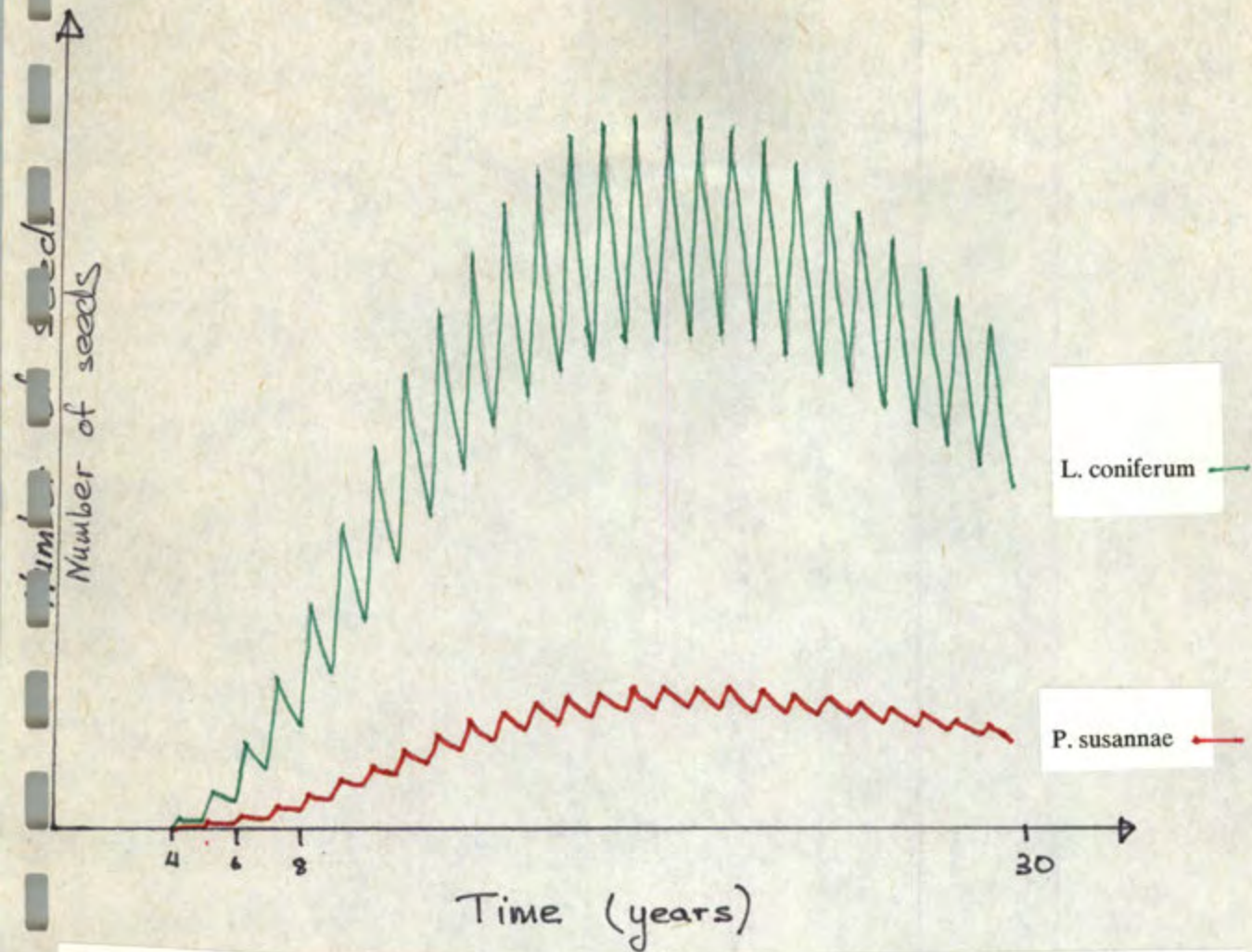


Figure 2. Agulhas system: number of seeds as a function of time calculated by means of the program in the appendix using the parameters in Table I.

## Discussion

The models above are deterministic, and do not allow for coexistence. No matter which of the models one chooses, the one species out-recruits the other one, and should eventually drive it out of the system. To enable coexistence, one must postulate some sort of variability.

In the case of Jonkershoek, the results above give strong evidence that from considering seeds per inflorescence only, P. repens should drive out P. neriifolia. Here the data, although taken at one point in time, does refer back to previous seasons, though not conclusively so since one cannot quantify loss. Since variation over the years is unknown, it is conceivable that variation in seeds per inflorescence or seed mortality may sometimes allow the number of P. repens seeds to decline below P. neriifolia seeds, but the variation has to be very large for P. neriifolia to benefit significantly, and the less frequent such variation, the larger it has to be.

If one accepts this argument, it means that for mixed stands to persist, there must be independent variation in the production of inflorescences. In Jonkershoek, it seems that P. neriifolia will produce more inflorescences per plant than P. repens, and in this way ensure more viable seeds per plant and an increase in percentage cover with each recruitment episode. This would account for its success on the basis of seeds per square metre. However, there is some variation between the two sites, suggesting there may also be variation from year to year. One obvious test of this hypothesis is by surveys of new inflorescences per plant covering several sites and several years. Perhaps one could find similar information in the records of the wild-flower industry.

Another possibility that may allow P. repens to persist is that predation may vary in time. At present, seed predation and consequent mortality is very high, but stands of repens with low predation are known (R Cowling, pers. com.). Variation in predation intensity would follow large fluctuations in the predator population (for example due to disease or predation from a higher predator). However, these would need to have a period longer than roughly two years, or be rare, otherwise one would expect to have noticed them here. Variation may also occur if predator numbers established at different levels after each fire, for instance being low in response to a low density of P. repens. If such predation were sufficiently low, P. repens would effectively be more serotinous, and this would offset a lower rate of production of inflorescences. Such an hypothesis could be tested by obtaining data on predation rate from many different sites--not necessarily mixed, not necessarily with P. neriifolia--to survey the possibility of

variation, and by longitudinal studies covering the inter-fire period as well as changes across fires.

There may be significant variation in time of recruitment success, similar to the suggestion made below for the Agulhas system. This could be tested by experiments investigating germination and seedling survival, of which there seem to have been very few.

On the other hand, one may finally conclude that mixed stands of P. repens and P. neriifolia are ephemera due to a fire that covers the areas of dominance of both, with wind dispersal subsequently spreading the seed across the whole burnt area. In that case, one would expect current stands to reflect the pattern of the burn that gave rise to them. In particular, the number of the two species should reflect the relative sizes and maturity of the contributing pure stands. Moreover, burning a mixed stand should result in a clear recruitment tendency favouring one species above the other, the winning species being the one who dominates in that environment.

Turning to the Agulhas system, the results above present a conundrum. They indicate that P. susannae should rapidly be driven out by L. coniferum. However, what is observed is that, at present at least, P. susannae is the more common of the two. In fact, in seeds per hectare P. susannae comes to nearly half of the value for L. coniferum, in spite of being carrying only a quarter as much per plant (Mustart and Cowling, in prep.). As indicated above, the higher rate of seed mortality in L. coniferum is not enough to offset its dominance at the level of seed per plant.

The central prediction from the lottery model is that adults occupy space in the canopy in proportion to their species' representation in the seed bank at the time of fire. This is easily tested by having an experimental burn, with a pre-fire seed census and a post-fire seedling census. If seedling establishment fails to follow the predictions of the lottery model, there must be some mechanism interfering with random allocation of establishment success. Two possible mechanisms are differences in germination--though experiments by Mustart suggest that if anything what differences there are favour L. coniferum (pers. com.)--and differences in dispersal, which could be due to different aerodynamic characteristics of the seeds. I favour the second possibility, and it should be possible to conduct experiments without burning the veld, by using wind-tunnels and beaches with appropriate obstacles and air flow. One would expect P. susannae seeds to be deposited more uniformly in general, perhaps by requiring smaller obstacles or frequent secondary dispersal (though by itself this does not ensure uniform distribution--it needs to apply only to "extra" seeds in an oversupplied area), and to stay in the

burnt area more successfully by travelling shorter distances before final deposition.

If seedling numbers do match the predictions of the lottery model, one would expect eventually to have a canopy largely composed of L. coniferum. Regular censuses would be needed to test this prediction, and if in fact P. susannae recruited into the canopy with more success than L. coniferum, one would have the remarkable state of affairs where a smaller shrub out-competed a larger one.

Finally, if L. coniferum does occupy space in the mature canopy as predicted by the lottery model, one would have to explain coexistence on the basis of some variation on seed production. The possibilities are numerous, ranging from responses to drought to differences in rate of viable seed production at different ages to density-dependent predation.

### Conclusion

The lottery model of Chesson and Warner does not apply directly to the fynbos, because the assumption of overlapping generations is violated. Thus their mathematical results cannot illuminate coexistence in this species-rich biome. I extend their underlying ideas to apply to serotinous canopy shrubs by means of a two stage model which combines overlapping seed generations between fires with recruitment based on lottery allocation of seeds to homes after a fire. To apply this fully, one needs data on the temporal variation in seed production, but such data are not available. Applying the model deterministically allows one to suggest how variation would enable coexistence. For P. repens vs P. neriifolia, I suggest that coexistence is due either to variation in number of inflorescences per plant, or in variations of predation in P. repens. For P. susannae vs L. coniferum, I suggest that coexistence is due either to superior recruitment of P. susannae seedlings into the canopy, or to differences in seed production, or to differences in their pattern of seed dispersal. Some tests for these suggestions are mooted.

Bibliography

- Abele LG and Walters K (1979) The stability-time hypothesis: reevaluation of the data  
Am Nat 114:559-568
- Abrams PA, Roughgarden J, Giller P and den Boer PJ (1986) The competitive exclusion principle: other views and a reply  
TREE 1:131-133
- Abugov R (1982) Species diversity and phasing of disturbance  
Ecol 63:289-293
- Bond WJ (1985) Canopy-stored seed reserves (serotiny) in Cape Proteaceae  
S Afr J Bot 51: 181-186
- Bond JW, Vlok J and Viviers M (1984) Variation in seedling recruitment of Cape Proteaceae after fire  
J Ecol 72:209-221
- Chesson P (1982) The stabilizing effect of a random environment  
J Math Biol 15:1-36
- Chesson PL (1986) Environmental variation and the coexistence of species pp240-256
- Chesson PL and Case TJ (1986) Overview: non-equilibrium community theories: Chance, variability, history and coexistence pp229-239
- Chesson, P and Warner RR (1981) Environmental variability promotes coexistence in lottery competitive systems  
Am Nat 117: 923-943

- Comins HN and Noble IR (1985) Dispersal, variability, and transient niches: species coexistence in a uniformly variable environment  
Am Nat 126:706-723
- Cowling RM (1987) Fire and its role in coexistence and speciation in Gondwanan shrublands  
S Afr J Sc 83:106-112
- Cowling RM Campbell BM Mustart P McDonald DJ Jarman ML and Moll EJ (1988) Vegetation classification in a floristically complex area: the Agulhas plain  
S Afr J Bot 54:290-300
- Cowling RM and Gxaba T (<sup>in prep.</sup>~~unpub~~) Effects of a fynbos overstorey shrub on understorey community structure: implications for the maintenance of community-wide species richness
- Ellner S (1984) Asymptotic behaviour of some stochastic difference equation population models  
J Math Biol 19:169-200
- Fagerstrom T (1988) Lotteries in communities of sessile organisms  
TREE 3:303-306
- Gaedeke A and Sommer U (1986) The influence of the frequency of periodic disturbance on the maintenance of phytoplankton diversity  
Oecologia 71:25-28
- Goldberg DE and Werner PA (1983) Equivalence of competitors in plant communities: a null hypothesis and a field experimental approach  
Amer J Bot 70:1098-1104
- Grubb PJ (1977) The maintenance<sup>of</sup> of species-richness in plant communities: the importance of the regeneration niche  
Biol Rev 52:107-145

- Grubb PJ (1986) Problems posed by sparse and patchily distributed species in species-rich plant communities  
in: Community Ecology, Case and Diamond (eds)  
(Harper and Row) pp 207-225
- Hanski I (1983) Coexistence of competitors in patchy environment  
Ecol 64:493-500
- Lamont BB, Collins BG and Cowling RM (1985) Reproductive biology of the Proteaceae in Australia and South Africa  
Proc Ecol Soc Aust 14:213-224
- LeMaitre DC (in prep.) Influence of age, size and stand density on canopy-stored seed banks of two co-occurring fynbos shrubs (Protea repens and Protea neriifolia, Proteaceae) in South Africa
- Levins R (1979) Coexistence in a variable environment  
Am Nat 114:765-783
- Malanson GP (1984) Intensity as a third factor of disturbance regime and its effect on species diversity  
Oikos 43:411-413
- Mustart P and Cowling RM (in prep.) Reproductive strategies of two related species pairs (Protea susannae-Leucadendron coniferum; P. obtusifolia-L. meridianum) co-occurring on different soil types on the Agulhas Plain, South Africa
- Rourke JP (1980) The Proteas of southern Africa  
(Purnell)
- Shmida A and Ellner S (1984) Coexistence of plant species with similar niches  
Vegetatio 58:29-55
- Silvertown J and Law R (1987) Do plants need niches? Some recent developments in plant community ecology  
TREE 2:24-26

- Van Wilgen BW (1982) Some effects of post-fire age on the above-ground plant biomass of the fynbos (macchia) vegetation of South Africa  
J Ecol 70:217-225
- Van Wilgen BW and Viviers M (1985) The effect of season of fire on serotinous Proteaceae in the western Cape and the implications for fynbos management  
SA For J 113:49-53
- Vogts M (1982) South Africa's Proteaceae. Know then and grow them  
(Struik)
- Williams IJM (1972) A revision of the genus Leucadendron (Proteaceae)  
(Bolus Herbarium)

Appendix: The computer implementation of the model

The listing is annotated, and the structure of the program need not be analysed here. Note that the program only goes so far as to simulate a single time series of fires, and for stochastic information, and to investigate stochastic events a shell running this program repeatedly and analysing the results statistically needs to be used.

The program is user-friendly in that the user is prompted to enter the inflorescence and fire frequency parameters, and the results are graphically displayed. However, changing the probability density function of the fires can only be done by changing the code.

Attached are some sample results obtained from values near the data for the P. repens-P. neriifolia system. These are illustrative only, since the values were chosen arbitrarily.

PROTEA COEXISTENCE

through variation in seed numbers at time of fire

This is a program to compare the rate of seedbank development over several fire cycles of two very similar proteas. The seedbank dynamics are a simple approximation of guesswork about inflorescence per plant. The seeds per inflorescence and number of adult plants are constants.

RANDOMIZE

```

DIM Seeds1( 0:300 )      !Simulation period 300 years maximum
DIM Seeds2( 0:300 )
DIM Plants1( 0:20 )      !20 fires maximum
DIM Plants2( 0:20 )
DIM Nersd( 7 )           !7 generations of neriifolia seeds
DIM Reprd( 3 )           !3 ditto repens

CALL Choices              !Parameters
CALL Testrun              !Generate the results
CALL Output                !Plot the results

```

SUB Choices

```

INPUT PROMPT "Protea 1 seeds/inflorescence, decay rate?": Sdno1, M1
INPUT PROMPT "Protea 2 seeds/inflorescence, decay rate?": Sdno2, M2
INPUT PROMPT "Average total number of plants?": K
LET K = 500
LET Plts1 = K/2           !Spp start w equal number of plants
LET Plts2 = K/2
INPUT PROMPT "Average fire interval?": AveTau
INPUT PROMPT "How many fires?": Nsims

```

END SUB

SUB Testrun

```

FOR Fires = 0 TO Nsims - 1
  MAT Nersd = ZER          !No old seeds around after germination
  MAT Reprd = ZER
  LET Plants1( Fires ) = Plts1      !Record current number of plants/species
  LET Plants2( Fires ) = Plts2
  CALL MakeTau              !Randomises fire interval
  CALL Seedbank              !Calculate no seeds from each post-fire
  CALL MakeK                 !Randomises carrying capacity; inactive
  CALL Drawlots              !Allocate number of plants for each spec
NEXT Fires
END SUB

```

SUB MakeTau

LET Tau = AveTau + .6 + 10\*(Rnd-.5)

LET IntTau = INT( Tau )

LET Season = Tau - IntTau

PRINT "Fire interval"; IntTau; "years", "burnt at "; 12\*season; "months"

END SUB

SUB MakeK

END SUB

SUB Seedbank

FOR J = 4 TO IntTau !Flowering starts at year 4

CALL Inf1( Flwrs, J )

LET Sdb1 = 0 !Clear the count

LET Sdb2 = 0

FOR I = 7 TO 2 STEP -1 !Age the seeds & let them die

LET Nersd( I ) = Nersd( I - 1 ) \* EXP( -M1 )

NEXT I

LET Nersd( 1 ) = Flwrs \* Sdno1 !Get newly set seeds

FOR I = 1 TO 7 !Count up seeds

LET Sdb1 = Sdb1 + Nersd( I )

NEXT I

FOR I = 3 TO 2 STEP -1 !Age seeds &c, as for Nersd above

LET Reprd( I ) = Reprd( I - 1 ) \* EXP( -M2 )

NEXT I

LET Reprd( 1 ) = Flwrs \* Sdno2

FOR I = 1 TO 3

LET Sdb2 = Sdb2 + Reprd( I )

NEXT I

LET Sdb1 = Sdb1 \* Plts1

LET Sdb2 = Sdb2 \* Plts2

LET Seeds1( Years + J ) = Sdb1 !Record seeds from this year

LET Seeds2( Years + J ) = Sdb2

NEXT J

LET Years = Years + IntTau

END SUB

SUB Drawlots

LET Sdb1 = Sdb1 \* EXP( -M1\*Season ) !Season is time from seed set to fi

LET Sdb2 = Sdb2 \* EXP( -M2\*Season )

LET Totseed = Sdb1 + Sdb2

LET Plts1 = K \* Sdb1 / Totseed

LET Plts2 = K \* Sdb2 / Totseed

END SUB

SUB OUTPUT

FOR I = 1 TO Years

LET Test = MAX( Seeds1( I ), Seeds2( I ) )

LET YMax = MAX( YMax, Test )

NEXT I

SET WINDOW 0, Years + 3, 0, 1.2 \* YMax

FOR I = 1 TO Years

FOR J = 0 TO 3

PLOT I + J/4, Seeds1( I ) \* EXP( -M1 \* J/4 ) ;

NEXT J

NEXT I

PLOT

FOR I = 1 TO Years

FOR J = 0 TO 3

PLOT I + J/4, Seeds2( I ) \* EXP( -M2 \* J/4 ) ;

NEXT J

NEXT I

END SUB

END

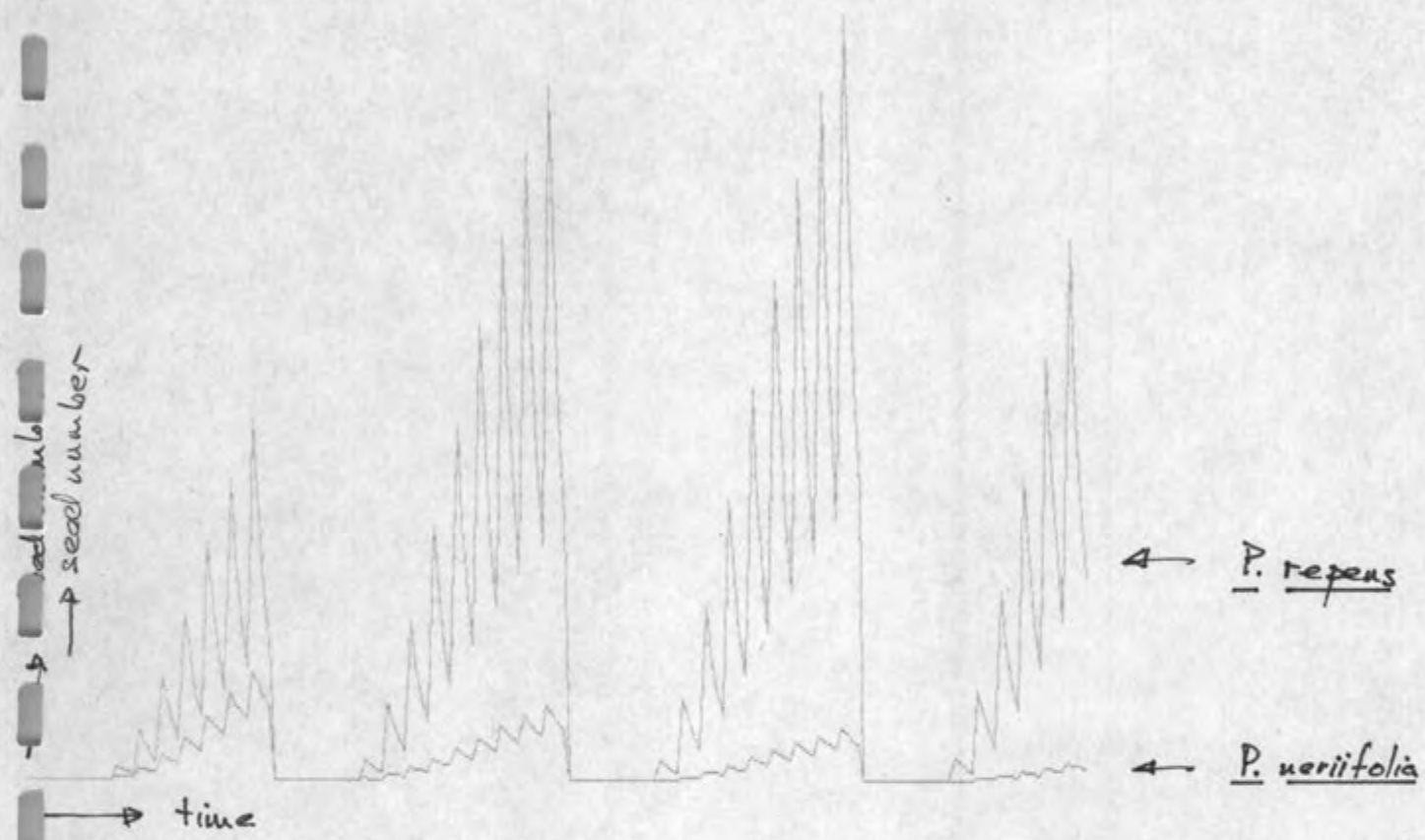
SUB Infl( Flwrs, I )

READ A, B

LET Flwrs = A \* ( I-4 )<sup>2</sup> \* EXP( B \* I )

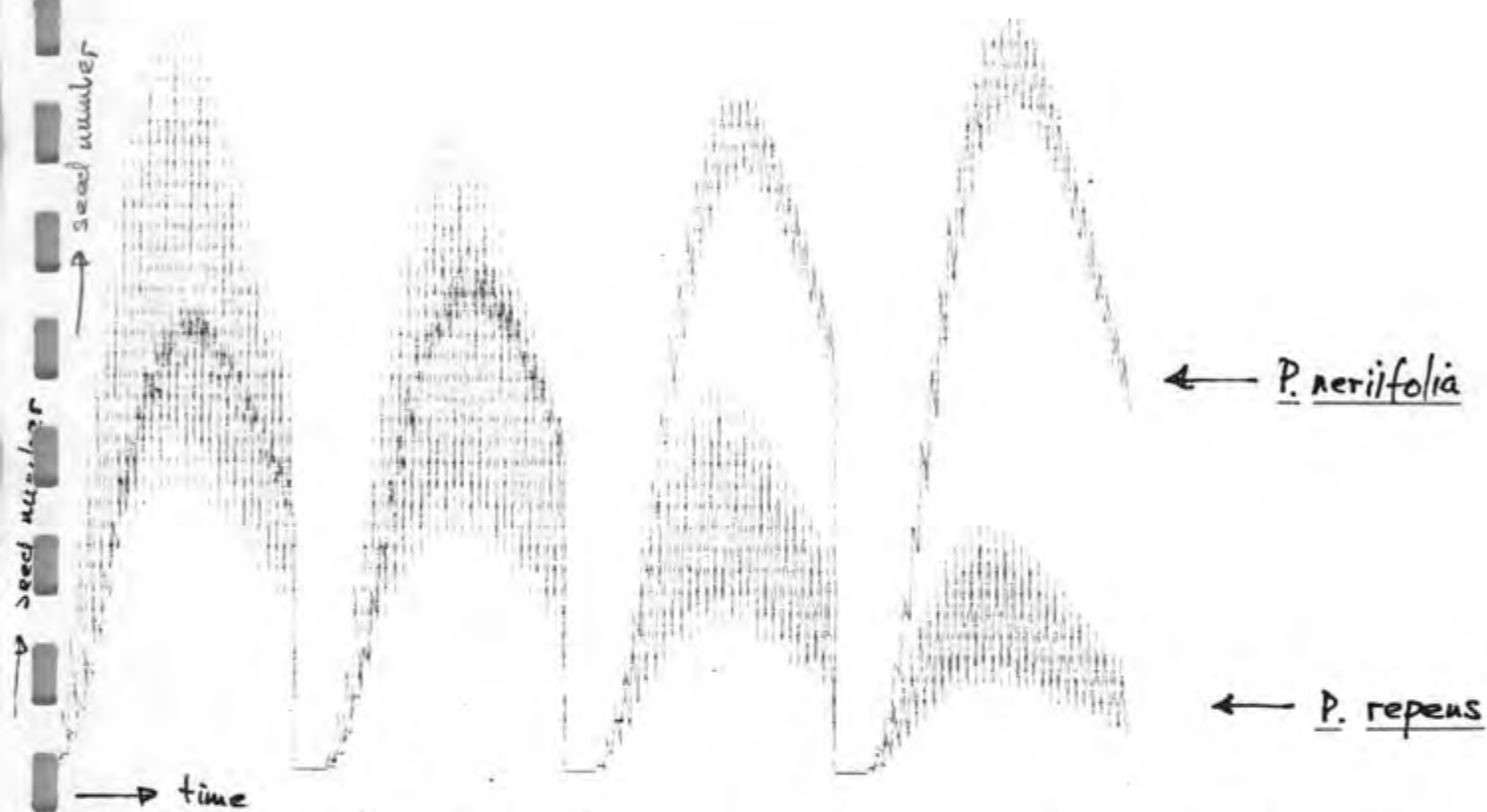
DATA 6, -.14

END SUB



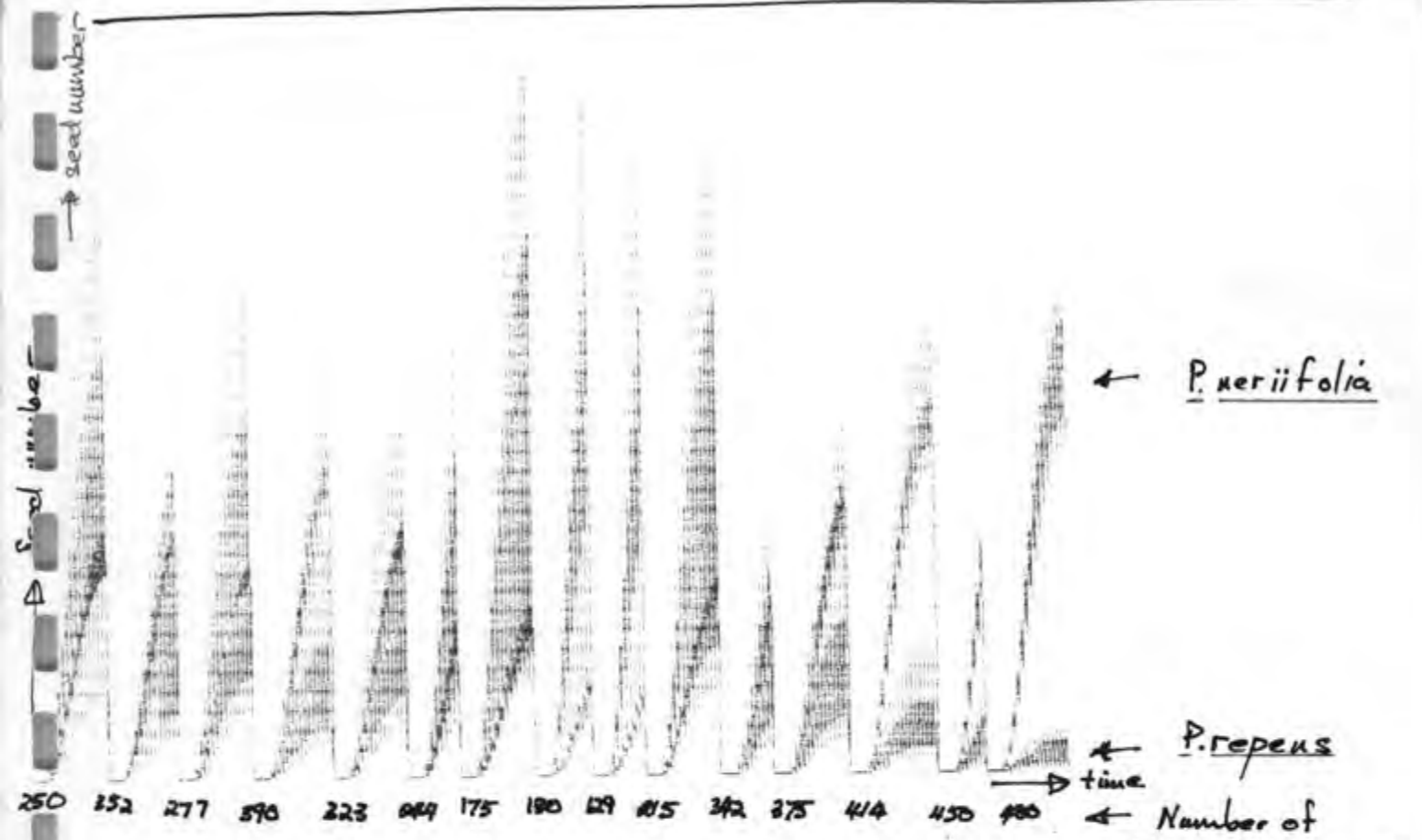
↳ Fires: random interfire interval of between 10.6 and 20.6 years

↳ Mortality; seeds/inf : 40%, 3 P. verifolia  
 72%, 15 P. repens



→ time  
 4 Fires; fire interval random between 25.6 and 35.6 years

seed Mortality; seeds/in fl :  
 18%, 3 P. neriifolia  
 72%, 15 P. repens



15 Fires covering 236,  
inter fire interval random between 25.6 + 35.6 years

seed Mortality, seeds/inf | ~~3, 40%~~ 40%, 3 P. veriiifolia  
93%, 15 P. repens