



The dynamics of coexistence in annual plants

Gebreselassie Asefa

Thesis submitted for the degree of Doctor of Philosophy of Imperial College London

2011

Department of Biology, Imperial College London

Silwood Park

Ascot, Berkshire

Abstract

This thesis is about coexistence mechanisms in a guild of seven species of annual plants that inhabit dry, open, compacted ground in Silwood Park, Berkshire.

Annual plants were chosen for the study because of the importance of obtaining whole-generation estimates of the vital rates, and because short-lived plants help/hold out the prospect of being able to assess the importance of year-to-year variation in the rates of recruitment, growth, survival and fecundity.

The field work was carried out at Pound Hill for the seed bank experiment, at Walled Garden for the seed dispersal experiment and at Ashurst for the main experiment in Silwood Park, Berkshire. The location was chosen because the area was already fenced and beds were laid out for a previous pilot study experiment in 1996.

The intention was to have a range of contrasting ecologies within our guild of annual plants. All species were capable of germination in autumn followed by over-winter survival as rosettes, and then rapid growth and early seed set in spring. Some species were immediately precluded from consideration as a result of their thuggish behaviour in the pilot studies.

*The final choice consisted of a grass (*Aira praecox*), a legume (*Ornithopus perpusillus*), three contrasting herbs (*Myosotis discolor* (Boraginaceae), *Cerastium glomeratum* (Caryophyllaceae) and *Veronica arvensis* (Scrophulariaceae)), and two tiny crucifers (*Erophila verna* and *Arabidopsis thaliana*). All were locally frequent on gravel paths and other compacted open habitats within Silwood Park.*

The thesis describes 7 separate replicated experiments, each carried out over 5 years: monocultures of each of the seven species; saturation sowing; two-species mixtures (21 of them) and multispecies mixtures.

I show clear pattern of year effects in both inter and intra-specific density dependence. The time series experiments are backed up by quantification of seed dispersal and seed bank dynamics.

Declaration

This work was carried out under a National Environment Research Council grant to M.J. Crawley: Pattern and process: experimental tests of theoretical models of competition in spatially structured communities of annual plants.
NER/A/S/2001/00493

Mick Crawley wrote the grant application and designed the layout of the experiments.

Gebreselassie Asefa carried out all of the field work, plot maintenance, data collection, and data management over 5 years.

Gebreselassie Asefa and Mick Crawley collaborated on data analysis and drafting the text.

It is intended that the chapters will be published in due course as joint-authored works by Asefa, G. and Crawley, M.J.

Signed: G Asefa

M J Crawley

Contents

Chapter 1	16
------------------------	-----------

The Dynamics of Coexistence in Annual Plants

1.1 Overview.....	16
1.2 The species.....	18
1.3 Theoretical background.....	19
1.4 Chapter outlines.....	22

Chapter 2.....	26
-----------------------	-----------

Density dependence in monocultures of seven coexisting annual plants

2.1 Introduction.....	26
2.2 Materials and Methods.....	29
2.2.1 The site.....	29
2.2.2 Raised beds.....	29
2.2.3 The species.....	32
2.2.4 Seed collection.....	33
2.2.5 Spatial layout of the sowing densities within each monoculture.....	34
2.2.6 Seed sowing.....	34
2.2.7 Monitoring.....	35
2.2.7 Statistical analysis.....	37
2.3 Results.....	38
2.3.1 Recruitment.....	38
2.3.2 Survival.....	39
2.3.3 Fecundity.....	39
2.3.4 Density dependence.....	41
2.3.4.1 Density dependence in recruitment.....	41
2.3.4.2 Adult survival from seedling recruitment.....	43
2.3.4.3 Density dependence in fecundity.....	44
2.3.4.4 Density dependence in net rate of population increase, λ	47
2.3.4.5 Year effects on density-dependence in λ assessed by piecewise regression....	50
2.3.4.6 Adult size classes	54
2. 4 Discussion.....	55

Chapter 3.....	60
-----------------------	-----------

Seed bank dynamics

3.1 Introduction.....	60
3.2 Theory.....	61
3.3 Materials and methods.....	65

3.3.1 Site	65
3.3.2 Seed sowing.....	65
3.3.3 Seedling appearance.....	66
3.3.4 The Ashurst Seed Bank Experiment.....	67
3.3.5 Layout of the sectors.....	67
3.3.6 Statistical modeling.....	68
3.4 Results.....	69
3.4.1 Emergence from the seed bank.....	70
3.4.2 Time course of seedling emergence at Pound Hill.....	70
3.4.3 Time course of seedling appearance at Ashurst.....	76
3.4.4 Seed size and longevity in the seed bank.....	78
3.5 Discussions.....	78

Chapter 4.....81

Dispersal kernels

4.1 Introduction.....	81
4.2 Methods.....	88
4.2.1 Site.....	89
4.2.2 Parent plants.....	89
4.2.3 Recruitment.....	91
4.2.4 Statistical modeling.....	92
4.3 Results.....	92
4.3.1 Recruitment.....	92
4.3.2 Dispersal kernels.....	92
4.3.3 Plot to plot dispersal at Ashurst.....	101
4.4 Discussion	102

Chapter 5.....106

Testing the Pacala-Rees model of Competitive Exclusion through saturation sowing

5.1 Introduction.....	106
5.2 Materials and Methods.....	109
5.2.1 The plots and seed sowing.....	109
5.2.2 Sowing densities.....	109
5.2.3 Estimating recruitment.....	110
5.2.4 Statistical modeling.....	111
5.3 Results.....	112
5.3.1 Biomass.....	112
5.3.2 Recruitment.....	113
5.3.3 Survival from seedling to adult.....	114
5.3.4 Year effects	116
5.3.5 Size classes distributions.....	119
5.3.6 Lambda.....	121

5.3.7 Identity effects.....	122
5.3.7.1 Recruitment: dominant identity from saturation sowing.....	122
5.4 Discussion.....	123

Chapter 6.....125

Two-species interaction: the dynamics of time series of 21 species pairs with and without seed redistribution

6.1 Introduction.....	126
6.2 Materials and Methods.....	130
6.2.1 Site and the plots.....	130
6.2.2 Seed sowing.....	130
6.2.3 Estimating recruitment.....	131
6.2.4 Seed redistribution.....	132
6.2.5 Harvesting.....	132
6.2.6 Statistical analysis.....	133
6.3 Results.....	134
6.3.1 Trends.....	134
6.3.2 Behaviours of pairs of species.....	138
6.3.3 Population stability	147
6.3.4 Identity effects on biomass.....	147
6.3.5 No-shows and Local extinctions.....	150
6.4 Discussion	151

Chapter 7.....153

Inter-specific competition in fine-grained mixtures

7.1 Introduction.....	153
7.2 Materials and Methods.....	155
7.2.1 The study plots.....	155
7.2.2 Seed sowing.....	155
7.2.3 Redistribution.....	155
7.2.4 Estimating recruitment.....	156
7.2.5 The final harvest at the end of the 5 th year.....	156
7.2.6 Statistical modeling.....	157
7.3 Results.....	157
7.3.1 Dominance rank by species.....	158
7.3.2 Time series.....	158
7.3.3 Trends in abundance	161
7.3.4 No shows and extinction.....	161
7.3.5 Treatment effects.....	162
7.3.6 Year effects	164

7.4 Discussion.....	165
---------------------	-----

Chapter 8.....167

Inter-specific competition in coarse-grained mixtures

8.1 Introduction.....	167
8.2 Methods.....	168
8.2.1 Seed sowing.....	168
8.2.2 Estimating recruitment.....	169
8.2.3 The final harvest (biomass).....	169
8.2.4 Statistical modeling.....	169
8.3 Results.....	171
8.3.1 Big pattern.....	171
8.3.1.1 Trends in recruitments	172
8.3.1.2 Biomass	172
8.3.2 No-shows.....	173
8.3.3 Year effects.....	173
8.3.4 Dispersal in coarse-grained mixture and convergence to fine-grained.....	174
8.3.4.1 Dispersal in coarse-grained mixture.....	174
8.3.4.2 Convergence to fine-grained mixture.....	175
8.3.4.3 Mixed-effects model.....	177
8.3.4.4 Coefficient of variation (CV) in cgm.....	177
8.3.5 Stability in recruitment.....	181
8.4 Discussion.....	181

Chapter 9.....184

Overall discussion.....184

9.1 Seed size versus mean log fecundity per plant.....	186
9.2 Seed size versus log mean biomass.....	187
9.3 The ideal next experiment.....	199
9.4 Conclusions.....	202

References.....210

List of figures

Fig 1.1 Lotka Volterra competition model.....	21
Fig 2.1 Theory of plant monocultures.....	28
Fig 2.2 Lay-out of the 250 plots at Ashurst experimental site in 10 columns.....	31
Fig 2.3 Showing (a) shape and size of one of the experimental plots (1m x 1m); a 75cm x 75cm frame overlaid in the centre forming 9 squares (25cm x 25cm).....	32
Fig 2.4 Inverse correlation between rank seedling recruitment and rank mean fecundity per adult for the 7 species at intermediate sowing density.....	40
Fig 2.5 Year effects on density dependence in recruitment	41
Fig 2.6 Year effects on density dependence in adult survival to adulthood.....	43
Fig 2.7 Fecundity and plant size in seven species	44
Fig 2.8 Linear regression of density dependence in log lambda.....	47
Fig 2.9 Year effects on the nature of density dependence in log (lambda).....	50
Fig 2.10 Species differences in the relationship between log(lambda) and log(sowing density)	53
Fig 2.11 Size structure for <i>A. praecox</i> for 2006	54
Fig 3.1 Seedling recruitment curves.	63
Fig 3.2 Contrasting seed banks.....	64
Fig 3.3 A 75cm x 75cm frame with nine sectors ranging from 1 to 9	68
Fig 3.4 Emergence from the seed bank by <i>Erophila verna</i> at Pound Hill.....	71
Fig 3.5 Time series of emergence of 7 species at Pound Hill.....	72
Fig 3.6 Decline in log (seedling appearance) with time for <i>Aira praecox</i>	73
Fig 3.7 Emergence from the seed bank by <i>Erophila verna</i> at Ashurst.....	76
Fig 3.8 Time series of emergence of 7 species at Ashurst.....	77
Fig 3.9 Seed size plotted against longevity in seed bank.....	78

Fig 4.1 The importance of model choice.....	86
Fig 4.2 Dispersal kernels compared for one (dotted line) and two (solid line) classes of seeds.....	87
Fig 4.3 Seed rain data, expressed as transect data (left) and probability density (right)...	93
Fig 4.4 Dispersal kernels for 7 species.....	94
Fig 4.5 Year effects on dispersal kernels as exemplified by the case of <i>Aira praecox</i>	95
Fig 4.6 Year effects on dispersal kernels as exemplified by the case of <i>Cerastium glomeratum</i>	96
Fig 4.7 Compass directions as exemplified by <i>Aira praecox</i>	97
Fig 5.1 Size distribution of adult plants of sown species.....	119
Fig 5.2 Year effects (2003 - 2007 from top to bottom) and sowing density effects as exemplified by <i>Veronica arvensis</i>	120
Fig 5.3 Mean log lambda (seed out/seed in) plotted against mean log sowing density.	121
Fig 6.1 Equilibrium population densities (two species)	127
Fig 6.2 Linear trend in mean recruitment abundant over time for <i>Veronica arvensis</i> ...	137
Fig 6.3 Recruitment time series of control replicates for Apva pair	138 - 139
Fig 6.4 Recruitment time series in control replicates for Atcg pair.....	140 - 141
Fig 6.5 Log biomass of <i>Aira</i> when it was paired with the other 6 species.....	149
Fig 6.6 Log biomass of <i>Erophila</i> when it was paired with the other 6 species.....	150
Fig 7.1 Time series in log recruitment for each of the 4 redistributed replicates aggregated across all sectors for each of the 7 species.....	159
Fig 7.2 Time series in log recruitment for each of the 4 redistributed replicates aggregated across all sectors for each of the 7 species.....	160
Fig 7.3 Recruitment of the 7 species across 5 years.....	165
Fig 8.1 Recruitment time series from all sectors combined in each of the 7 cgm plots for all species.....	171

Fig 8.2 Spatial coefficient of variation (CV) in seedling recruitment for 3 species.....	178
Fig 8.3 Spatial coefficient of variation plotted against years in each of the 3 levels.....	179
Fig 8.4 Mean recruitment per plot of the 7 species plotted against years for coarse and fine-grained mixture.....	180
Fig 9.1 Mean log seed number per plant plotted against log seed size.....	186
Fig 9.2 Log (mean biomass) plotted against log (seed size).....	187
Fig 9.3 Box plots showing log biomass for Aira in comparisons with the other 6 sp.....	194
Fig 9.4 Biomass in 2007 across all the experiments (log scale).....	198

List of tables

Table 1.1 Some traits of the 7 species (data from Ecoflora).....	19
Table 2.1 Total weights of seeds collected in summer 2002 by species.....	33
Table 2.2 Sowing densities for each of the 9 sectors for monoculture.....	35
Table 2.3 Dates of seed sowing and plant harvest for the 7 species over five years.....	35
Table 2.4 Mean recruitment for seven annual plant species over 5 years.....	38
Table 2.5 Mean survival from seedling to adult (as a proportion) for seven annual plant species over 5 years.....	39
Table 2.6 Mean seed productions per adult of the seven annual plant species for 5 years from an intermediate seed sowing.....	40
Table 2.7 Year effects on density dependence of log fecundity from sown density.....	45
Table 2.8 Year effects on density dependence of log fecundity from log biomass.....	46
Table 2.9 Year effects in log lambda shown from intermediate log sown density.....	48
Table 2.10 Year effects in log lambda for <i>Aira praecox</i> shown from log sown density.....	49
Table 2.11 Maximum and minimum values of lambda 7 species across 5 years.....	49
Table 2.12 Mixed effects model in lambda in monocultures.....	51
Table 3.1 Seed sowing rates, sowing dates and dates of the first seedling count for each of the seven species at Pound Hill seed bank experiment.....	66
Table 3.2 Seed bank of the seven species, showing dates when appearing seedling were counted and removed from the plots after seeds were sown in 2002.....	67
Table 3.3 Total recruitments from seeds sown in 2002 at Pound Hill summed over 4 plots and years.....	69
Table 3.4 Total recruitments from seeds sown in 2004 at Ashurst summed over 5 quadrats for 6 species, 6 quadrats for 1 species, each quadrat sown with 600 seeds.....	70
Table 3.5 Effects and their standard errors for a generalized additive model fitting non-parametric smoothers to the trends shown in Fig 3.4.....	74
Table 3.6 Total seedling counts (summed over 4 replicate plots) for 7 species.....	74
Table 4.1 Transplanting dates in each of the four years when the seedlings were transplanted from the green house to the Walled Garden).....	90
Table 4.2 Linear mixed effects model for dispersal distance	98
Table 4.3 Estimated seed crop compared with seedling appearances for all species aggregated.....	99

Table 4.4 Summary statistics on dispersal distances (cm) for each species and year.....	100
Table 4.5 Total number of weeds for the 7species over the course of the experiment....	101
Table 4.6 Maximum dispersal distances (cm) are compared for the two methods of recruitment sampling.....	101
Table 5.1 Sowing dates used in the experiment. Moderate (a) and saturation (b) sowing densities for each of the seven species.....	109
Table 5.2 Recruitment count dates (2 per year) for saturation plots from 2002 to 2007...	110
Table 5.3 Seed sowing and harvesting dates for saturation sowing plots.....	111
Table 5.4 Linear mixed effects mode for biomass.....	112
Table 5.5 Seedling recruitment in the saturation experiments.....	113
Table 5.6 Survival modelled as a proportion with binomial errors.....	114
Table 5.7 Biomass for species and years at each of three sowing treatments.....	115
Table 5.8 Year effects in the saturation experiments, summed for recruitment (a), survival (b) and biomass(c).....	118
Table 5.9 The effect of saturation sowing on log lambda for each species.....	122
Table 6.1 Recruitment count dates for all species in each of the five years.....	131
Table 6.2 Harvest dates for each of the twenty one pairs are summarized	133
Table 6.3 Effects of seed redistribution on mean log abundance.....	134
Table 6.4 Effects of competitor identity and seed redistribution on mean log (seedling count +1).....	135 - 13
Table 6.5 Effects of seed redistribution on population stability as measured by the standard deviation of log (seedling count +1).....	136
Table 6.6 Year effects on mean seedling counts.....	136
Table 6.7 Trends in the times series for species in pairs.....	137
Table 6.8 Identity effects on mean biomass from 2007.....	147
Table 6.9 Log biomass of the 6 species when paired with <i>Aira praecox</i>	148
Table 6.10 Log biomass of the 6 species when paired with <i>Erophila</i>	149
Table 6.11 Non-appearances and local extinction. Species scored zero counts for recruitments out of a total of eight counts over the course of 5 years.....	151
Table 6.12 Non-appearance of <i>Ornithopus</i> when paired with 6 other species.....	151

Table 7.1 Recruitment sampling dates for the multi-species experiment in all 5 years for all 7 species.....	156
Table 7.2 Species ranked based on their dominance in recruitment, adult survival and biomass.....	158
Table 7.3 Trends in mean log seedling abundance over 5 years.....	161
Table 7.4 The frequency of “no show” counts of seedlings and adults.....	161
Table 7.5 Effects of seed redistribution on population stability in 7-species fine-grained mixtures.....	162
Table 7.6 Effects of seed redistribution on mean log abundance in 7-species fine-grained mixtures.....	162
Table 7.7 Mixed effects model	163
Table 7.8 Effect size is the largest mean divided by the smallest mean.....	164
Table 8.1 Seedling recruitment sampling dates for the cgm from 2003 to 2007.....	169
Table 8.2 Trends in recruitment.....	172
Table 8.3 Biomass of <i>Ornithopus perpusillus</i>	172
Table 8.4 Number of zero recruits from 7 plots each with 7 sectors with 7 seedlings counts for each species (343 sectors).....	173
Table 8.5 Year effects on mean recruitment for all species in each of the years.....	174
Table 8.6 Dispersal of the 7 species away from where they were originally sown.....	174
Table 8.7 Species ranked by their mean recruitment adults and biomass in the fifth year..	175
Table 8.8 Log seedling recruitment counts in each of the three levels for all species and years.....	175
Table 8.9 Comparison of mean biomass and the effect size between cgm and fgm.....	176
Table 8.10 Mean biomass (mg) comparisons of cgm replicates between sectors.....	176
Table 8.11 Population stability between fgm and cgm.....	181
Table 9.1 Mean biomass (mg) comparison between four different experiments.....	195
Table 9.2 Mean biomass (mg) comparison of 1 year (2007) between 4 experiments.....	196
Table 9.3 Number of species (out of 7) showing best and worst seedling recruitment.....	196
Table 9.4 Spatial & temporal heterogeneity in recruitment from 4 different experiment...	197

Acknowledgements

This research project was funded by an NERC grant initially for five years which was extended by one year. I thank *Mick Crawley* for allowing me to do the project in the first place, and for allowing me to register for my part time PhD studies as part of the project. I also thank him for his relentless and unrivalled supervision, advice and help at every step of the way, especially in problem solving, plant identification, statistical computing and also for offering me the privilege of attending various courses relevant to the project and to my studies.

I am indebted to *Peter Wilkinson* for all his services in providing all the field tools that I needed for the project; putting up and securing fences around the plots, mowing weeds in the paths of the experimental plots, transporting soil to the experimental plots, purchasing essential tools for the project, and also in numerous other ways. *Chris*, who sadly passed away a while back, and *Matt* helped me in laying out weed control plastic sheeting (Mipex), transporting ballast to the experimental sites and filling up the experimental plots. The following people contributed to the daily activities of the project such as soil mixing, plot preparations, weeding, counting plants, harvesting and weighing dry matter: *Tariq, Panos, Muhammad, Ali, Mohsen, Asim, Jo, Laura, Erin, Alla, Javad, Steve, Dan, Nikos, Ahnie, Roshan, Marcus, Evangelia, Andre, Nieves, Gwen, Asyraf, Tom, Ian and Bish*.

Help was always on hand from *Dave, Luca and Owen* with statistical modelling. I would like to thank the administrative and support staff at Silwood particularly *Christine Short, Diana Anderson, Barbara Sanger, Karen Drew and Ros Jones* for making my life here at Silwood a lot easier and for all their help.

A few of my friends kindly read earlier drafts with useful comments and also in other ways relevant to my writing up. *Tim, Jorge, Maria and John*. Thanks also to members of the Ascot Shotokai College for their encouragement and help for the smooth running of my studies.

And finally, I am thankful to my family for their unreserved support throughout my studies.

Units

All counts, biomass data and analysis came from a **quadrat/sector** of area **25cm x 25cm (625 cm²)**, unless stated.

cm = centimeters

mg = milligrams (for seed weight and dry matter (biomass))

m = metre

mm = millimetre

λ = lambda (seed out/seed in)

count = relates to seedling and adult counts

Abbreviations

sp = species

Ap = *Aira praecox*

At = *Arabidopsis thaliana*

Cg = *Cerastium glomeratum*

Ev = *Erophila verna*

Md = *Myosotis discolor*

OP = *Ornithopus perpusillus*

Va = *Veronica arvensis*

Cgm = Coarse-grained mixtures

Fgm = Fine-grained mixtures

Fgmc = Fine-grained mixtures control

Fgmt = Fine-grained mixtures treated

Monoc = Monocultures

fig = figure

wt = weight (in mg relating to seed weight or plant biomass)

CV (coefficient of variation) = sd/mean

% = percentage

treat = Treatment

p = p value (at 5% unless specified)

t = Student t-test

α = Alpha

n = Number of observations (sample size)

df = Degree of freedom

lm = Linear model

lmer = Linear mixed effects model

(t) = treated (seed redistribution)

(c) = Control

Chapter 1

The Dynamics of Coexistence in Annual Plants

1.1 Overview

This thesis is about coexistence mechanisms in a guild of seven species of annual plants that inhabit dry, open, compacted ground in Silwood Park, Berkshire. Annual plants were chosen for the study because of the importance of obtaining whole-generation estimates of the vital rates, and because short-lived plants hold out the prospect of being able to assess the importance of year-to-year variation in the rates of recruitment, growth, survival, and fecundity. The field work was carried out at three locations within Silwood Park, Berkshire: Pound Hill for the seed bank experiment, Walled Garden for the seed dispersal experiment, and Ashurst for the main experiment.

The key finding of this body of work is that competitive exclusion is the exception rather than the rule. Of course, it could be argued that we have not studied the system for long enough to make firm conclusions. We counter this by pointing out that rather few field studies have followed five entire consecutive generations for such a large number of competing species.

The monoculture experiments showed a rather high degree of uniformity in their general outcomes. We note that density dependence was observed in all of the vital rates we studied: we expected to observe density dependence in fecundity and mortality, but we were intrigued to observe density dependence in seedling recruitment for so many species in so many years (suggestive of either allelopathic suppression of germination or strong post-dispersal pre-emergence seedling mortality). Overall, there were clear species-specific patterns in density dependence in net population multiplication rate (λ) and in the relative magnitude of year effects on the vital rates.

The seed bank studies indicated that seeds of all seven species were capable of survival for more than one year. Equally, however, none of the species produced any seedlings more than 5 years after the seeds were sown. We conclude that the seed bank is a potentially important factor in coexistence for all these species, but that more work needs to be done to determine whether very long-lived seed banks can form (e.g. by sowing larger numbers of seeds and repeating the experiment in many different kinds of years).

The dispersal kernels for the seven species were highly consistent across the four years, allowing us to rank the dispersal abilities of the seven species. All of the species showed increased seedling densities with distance along transects from the parent plant over the first 2 to 4 cm (a feature exhibited by none of the common parametric functional forms used in dispersal studies). This is probably a result of the

skeleton of the parent plant inhibiting recruitment in its immediate vicinity. We also determined the dispersal ability of the species over larger distances (plot-to-plot, rather than within-plot) using data collected during the quantitative weeding of the 250 plots at Ashurst. Intriguingly, the dispersal kernels measured at small, within-plot scales were poor predictors of long-range dispersal.

Saturation sowing investigated identity effects, priority effect and year effects in the outcome of inter-specific competition. We found no compelling evidence in support of Pacala and Rees (1998) hypothesis: all seven species were capable of passing the invasion criterion even in the presence of high densities of seeds of a putative superior competitor. It turns out that, for these seven species at least, there is no obviously identifiable “superior competitor”. Equally, there was little evidence for micro-site pre-emption effects based on the order of seed sowing.

The 21 two-species pairs allowed us to test the importance of seed dispersal in coexistence. Theoretical models showed the potential importance of limited seed dispersal kernels in promoting coexistence by increasing the rate of intra-specific competition and reducing the rate of inter-specific competition (in accordance with the Lotka Volterra criteria). We tested this by gathering all the seeds before dispersal on half of the plots, then sowing the seeds of both species in a random spatial pattern. If the theory was correct, then redistributing the seeds should increase the rate of competitive exclusion. We found no evidence to support this prediction but intriguingly, we found several cases where redistribution increased the adult population size of both plant species, suggesting that intra-specific competition was relatively important for *both* species in the control plots.

The fine-grained mixture plots showed no compelling evidence of competitive exclusion within 5 years for any of the seven species. We did not observe any tendency for any of the species to form within-plot spatial clustering. There are interesting similarities and differences in the years effects for different species between the saturation sowing and fine-grained mixtures; both experiments examine interspecific competition but the saturation experiments are begun afresh each year, whereas the fine-grained mixtures are time series experiments with the potential for carry-over effects from year to year (i.e. effects of history are confounded with year effects).

The coarse-grained mixtures quickly converged to the fine-grained case. Within three years, most of the plots sown as 7 separate monocultures were indistinguishable from the plots sown as fine-grained mixtures. There was little evidence of reduced rates of competitive exclusion in the coarse-grained mixtures where the experimental design ensured that intraspecific competition was more important than interspecific competition.

Overall, the experiments provide evidence for multiple potential mechanisms for coexistence, and showed few cases of competitive exclusion. Temporal heterogeneity

(year effects) showed strong evidence for different species doing best in different kinds of years. Spatial heterogeneity in substrate was minimized by the design of the experiment, but there was little evidence of spatial segregation developing in those treatments that ran as 5-year time series. Experimental seed redistribution did not increase the rate of competitive exclusion, but was associated with increases in population size for several species in various years, indicating that intraspecific competition was relatively important in both 2-species and seven-species experiments, and highlighting the prevalence of at least one component of the Lotka Volterra coexistence criterion.

If we were to do a similar study again, we would repeat the seed bank sowing in every year. We would also focus more intently on long-distance seed dispersal, since the detailed small-scale dispersal kernels (within-plot) were relatively poor predictors of longer-range dispersal (between plots). The seed redistribution work was interesting but exceptionally demanding in terms of time commitment; it is not obvious that the rewards justify the effort. If we did repeat this kind of study, it would be important to redistribute one species but not the other in a factorial combination (we redistributed both species or neither species in the current study).

The combination of multi-year seed banks, year effects in the density-dependence of recruitment, survival and fecundity, restricted seed dispersal around parent plants, (which increases the importance of intraspecific competition) and the ability for long-distance (between-plot) dispersal, provides ample reason to predict that competitive exclusion within this guild of competing annual plants would not be likely to be observed under field conditions in Silwood Park in the short to medium term.

1.2 The Species

The intention was to have a range of contrasting ecologies within our guild of annual plants. All species were capable of germination in autumn followed by over-winter survival as rosettes, and then rapid growth and early seed set in spring. Some species were immediately precluded from consideration as a result of their thuggish behavior in pilot studies. Most notable amongst these exceptionally vigorous annuals were *Cardamine hirsuta*, *Geranium molle*, *Myosotis arvensis*, *Lamium perpureum* and *Poa annua*, any one of which was capable of carpeting an entire study area within just a few weeks.

The final choice consisted of a grass *Aira praecox*), a legume (*Ornithopus perpusillus*), three contrasting herbs (*Myosotis discolor* (Boraginaceae), *Cerastium glomeratum* (Caryophyllaceae) and *Veronica arvensis* (Scrophulariaceae)), and two tiny crucifers (*Erophila verna* and *Arabidopsis thaliana*). The traits of the species are summarized in Table 1.1. All were locally frequent on gravel paths and other

compacted open habitats within Silwood Park (Crawley 2005a) so that collection of sufficient seed to initiate the experiments was not likely to be a major problem.

A huge amount was known about the physiology and genetics of *Arabidopsis thaliana* (Tonsor et al. 2005), but rather less about its ecology and demography. Very little was known about the ecology of the other six species (e.g. none had a Biological Flora account written about them).

Table 1.1 Some traits of the 7 species (data from Ecoflora). Numbers in brackets are original data from this thesis. *Arabidopsis* and *Erophila* are the smallest in seed size while *Ornithopus* is the largest.

Species	<i>Aira praecox</i>	<i>Arabidopsis thaliana</i>	<i>Cerastium glomeratum</i>	<i>Erophila verna</i>	<i>Myosotis discolor</i>	<i>Ornithopus perpusillus</i>	<i>Veronica arvensis</i>
Family	Poaceae	Brassicaceae	Caryophyllaceae	Brassicaceae	Boraginaceae	Fabaceae	Scrophulariaceae
Growth form	Annual	Annual	Annual	Annual	Annual	An/biennial	Annual
Functional Group	Grass	Herb	Herb	Herb	Herb	Legume	Herb
Plant height cm	19	26	25	16	25	17	21
Seed size mm	1.6	0.5	0.6	0.7	1.3	1.8	1.1
Seed weight mg	0.19	0.023	0.033	0.023	0.20	0.5	0.10
Seed number per fruit	2	10-100 (48)	10-100 (42)	(41)	(4)	5 (6)	10-100 (16)

1.3 Theoretical Background

The competitive exclusion principle asserts that in a spatially uniform environment that is temporally invariant then, given long enough for transient dynamics to damp away, one species will exclude all of the others (Elton 1927, Gause 1934, Hardin 1960).

The identity of the winner is predicted to be the species with the lowest value for R^* for the most limiting resource (i.e. the species that exhibits the ability to increase when rare at the lowest rate of resource supply as described by Tilman (1982, 1988)).

It is interesting that the theory was fully developed long before the semantics of the word models was sorted out (Hardin 1960). There is experimental support for the competitive exclusion principle from field (Harlan 1938), laboratory (Titman 1976), and chemostat experiments (Passarge et al. 2006).

Perhaps the most enduring of all the models in theoretical ecology predicts a wider range of behaviours that is predicted by the competitive exclusion principles; this is the celebrated Lotka Volterra competition model (Lotka 1925, Volterra 1926):

$$\frac{1}{N} \frac{dN_i}{dt} = r_i (1 - \alpha_{ii} N_i - \sum_j \alpha_{ij} N_j)$$

where N_i is the number of species i , r_i is the initial low-density per capita growth rate of species i (assumed to be greater than zero, to ensure that all species pass the invasion criteria and hence exhibit the ability to increase when rare) and α_{ij} is the per capita effect of species j on species i .

The explanatory variables are the population densities of the S-1 competing species N_j . The instantaneous rate of population change of species i is assumed to be a declining linear function of the impacts of each of the competing species $\alpha_{ij} N_j$ and a declining linear function of its own density $\alpha_{ii} N_i$. When rare, the species are all capable of population growth ($r_i > 0$) for all i). This model predicts competitive exclusion under a wide range of circumstances, some deterministic, others dependent on initial conditions (i.e. alternate stable 1-species states). There is an important case, however, in which this extremely simple model predicts stable coexistence (i.e. failure of competitive exclusion): this is the case where intra specific competition is more important than interspecific competition for all the coexisting species. For instance, in the two-species case

$$\alpha_{11} > \alpha_{21}$$

and

$$\alpha_{22} > \alpha_{12}$$

This result is shown graphically in Figure 1.1.

Since the 1920's a huge amount of theoretical work has been done on coexistence (Chesson and Warner 1981, Chesson 1985, Chesson 1994, Pacala and Tilman 1994, Chesson 2000a, 2003) but it is striking that all of these subsequent investigations boil down to this same simple set of inequalities in one guise or another. In short, they require every species to benefit from "rare species advantage". Another way of thinking about this is to look for mechanisms creating *abundant* species *disadvantage* (e.g. density-dependent depression of the vital rates).

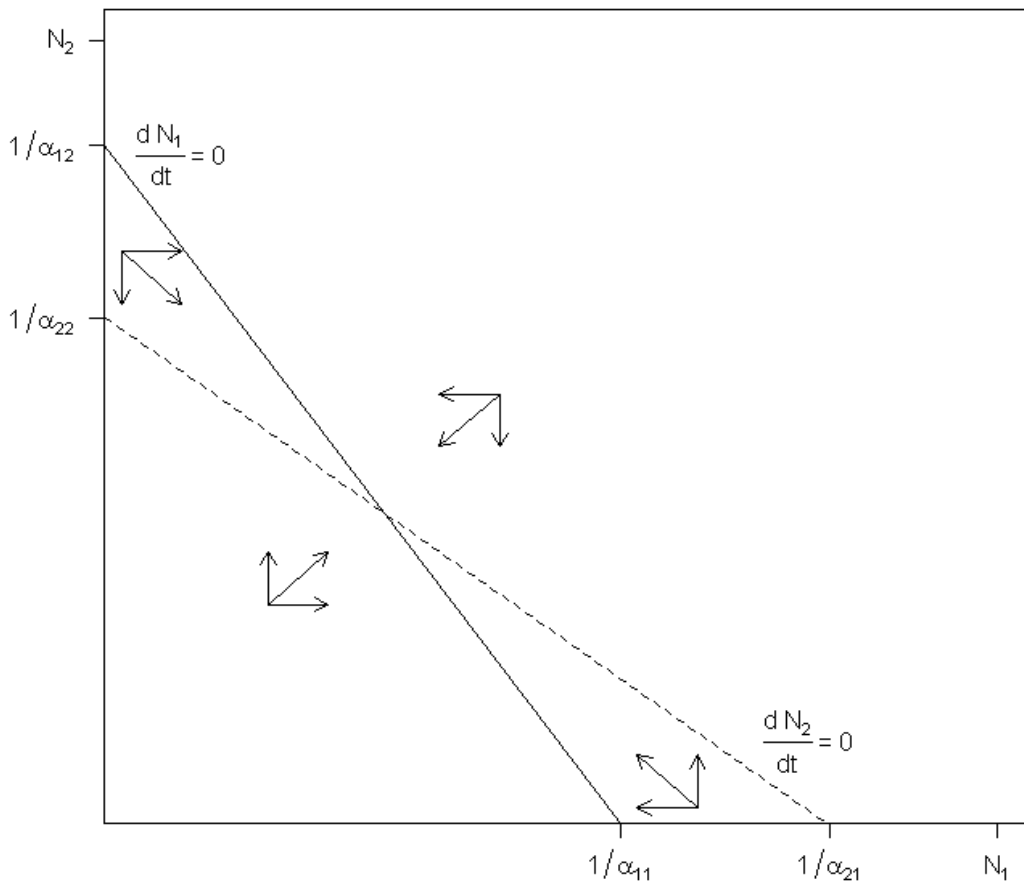


Fig 1.1 Lotka Volterra competition model, for the coexistence case, showing the zero-growth isoclines of two species (dashed line N_2 on the y axis and solid line N_1 on the x axis). The isoclines show the densities of species 1 and 2 at which $dN/dt=0$ for a given species. Species increase in abundance *below* their isoclines and decline in abundance *above* their isoclines. Where the isoclines cross, the two- species equilibrium point is stable because all of the resultant motions in the phase plane (the arrows at 45 degrees to the vertical) point towards the equilibrium. Each species effectively inhibits itself more than it inhibits the other species. For details, see text.

We now know that there are four unique classes of mechanisms that can produce the necessary rare species advantage (Pacala and Crawley 1992, Pacala and Tilman 1994, Bolker and Pacala 1999, Chesson 2000a):

1. Spatial heterogeneity with resource partitioning
2. Colonization competition trade-off
3. Selective herbivory acting in a frequency dependent manner; e.g. spatial density dependence in regeneration niche (the so-called Janzen-Connell effect).

4. Temporal variability in recruitment combined with a storage effect and sub additivity.

A central aim of the thesis is to quantify as many of these process as possible over 5 complete generations.

1.4 Chapter outlines

The body of the thesis comprises 8 chapters, which address the questions listed below. We prefer to state our aims in terms of questions rather than as hypotheses for purely stylistic reasons. We know that everything we measure will vary, and we are interested in quantifying effect sizes and their standard errors, rather than in rejecting hypotheses that there is no significant variation.

Chapter 2 Monocultures

How does seedling recruitment vary with seed density across species and years?

How does seedling survival vary with seedling density across species and years?

How do mature plant size and biomass vary with plant density across species and years?

How does fecundity vary with mature plant size across species and years?

How does total seed production vary with biomass across species and years?

How does lambda (λ = net multiplication rate, calculated as seed output/seed input) vary with seed input across species and years?

What plant traits are associated with density-dependence and year-dependence in lambda?

The answers to these questions are used to help predict about the behaviors of two-species and multi-species competition in chapters 5 – 8.

Chapter 3 Seed banks

Persistence of viable seed for more than one year represents a potentially important coexistence mechanism by buffering the risk of total crop failure within one or more growing seasons.

What is the time course of seedling appearance across years and with season within years?

How do these patterns differ with species?

Is there any immigration to unsown blank plots that might be mis-interpreted as recruitment from seed bank?

Chapter 4 Dispersal

The object is to quantify the dispersal kernel for each species. The different kernels illustrate the probability of seed recruiting at different distances from the parent plant, and this distance-dependence in seed rain and germination may vary with compass direction (e.g. in wind dispersed species) as well as with year-dependent weather conditions (most importantly in temperature and moisture).

How do dispersal kernels differ across years and species across four (presumably different) years?

Is there a parametric model that best describes these dispersal kernels across species and years?

How does appearance of seedlings relate to estimated seed crop with species and years?

Are there any special adaptations for seed dispersal in our species (e.g. tumbleweeds)?

In multi-year population studies, does immigration of seed from adjacent plots contribute to coexistence (e.g. a rescue effect?)

Chapter 5 Saturation sowing

We set out to test the prediction of Pacala and Rees (1998) that competitive exclusion should occur if seeds of the superior competitor are sown at such high densities that all recruitment micro-sites are likely to contain at least one seed of the superior competitor. We therefore sowed each species in each year at extremely high densities, in competition with the other 6 species sown at moderate densities.

Which of the 7 species could be said to be the ‘superior competitor’?

What is the relative performance across years of species sown at saturation densities, and does this provide evidence for over-compensating density dependence?

Is there a difference in demographic performance between first sowing and last sowing for the species sown at saturation density?

Does the performance of a species that is sown at low density depend upon the identity of the species sown at saturation density, and does this vary with years?

Do any species suffer competitive exclusion within a growing season in any of the years or in any of the replicates within years?

How does the distribution of plant sizes at maturity vary with sowing density across species and years?

Chapter 6 Two-species time series

At the centre of this work is a 5-year study of the population dynamics of all 21 pair-wise combinations of all 7 species in replicate plots.

Is there a characteristic pattern of density trajectories across years (e.g. a trend towards competitive exclusion of one of the two species)?

How similar are the time series for the same species across replicates?

How often is local extinction observed?

Are there consistent identity effects in terms of dominance rank (e.g. if $A > B$ and $B > C$ then $A > C$)?

How does experimental redistribution of seed affect the outcome compared with control replicates, where seed is naturally dispersed (presumably in clumps around adult plants)?

Are the years of peak abundance in paired combinations in time series predicted by the monoculture and/or saturation data for the same years?

Chapter 7 Seven-species time-series sown as fine-grained mixtures

All seven species were sown in fine-grained mixtures in replicated plots and divided into 7 spatial subdivisions.

Is there a characteristic pattern of density trajectories across years (e.g. a trend towards competitive exclusion of one or more species)?

How similar are the seven parallel time series across spatial replicates?

How often is local extinction observed?

Are there consistent identity effects in terms of dominance rank (e.g. if $A > B$ and $B > C$ then $A > C$)?

Are the peak years of species abundance by the behavior of predicted by the monoculture and/or saturation data for the same years?

How does experimental seed redistribution affect the outcome?

Chapter 8 Seven-species time-series sown as coarse-grained mixtures

All seven species were sown initially as monocultures in of the seven subdivisions in each of 7 replicate plots. We refer to this as a coarse-grained mixture. Over subsequent years, the species were allowed to colonize the different subdivisions within each plot.

How long does the system remember its spatial history (i.e. which species were sown where)?

Do the coarse-grained plots converge towards the fine-grained case?

If so, how long does this convergence take?

Did species persist longer in the coarse-grained than in the fine-grained case, as predicted by the Lotka-Volterra criterion?

Chapter 9 Overall discussions

This chapter extracts the key findings from each of the seven experimental chapters (2-8), paying particular attention to species and year effects. We discuss the evidence for competitive exclusion in each of the experiments.

Finally we re-assess the four mechanisms of coexistence for these 7 species in Silwood Park.

Chapter 2

Density dependence in monocultures of seven coexisting annual plant species

Abstract

We grew seven annual plants species in replicated monocultures at 9 sowing densities and repeated the experiment in 5 years with contrasting growing conditions. As expected, all seven species showed strong density dependence in both survival and fecundity. More surprisingly, several species showed density dependence in seedling recruitment, indicative of either density dependent germination or density dependent pre-emergence mortality. All species showed significant year effects in one or more components of their density dependent behaviour. All species passed the invasion criterion >1 at low densities and some even at our highest sowing densities. A minority of species showed a consistent threshold sowing density, below which λ was density independent. Most species had reasonably consistent overall patterns of density dependence in λ , and these were well described by a linear relationship between $\log(\lambda)$ and $\log(\text{sowing density})$ with slopes varying between -0.5 and -0.8 across species. We hypothesize that average biomass in monoculture could be a useful surrogate for interspecific competitive ability.

2.1 Introduction

Agricultural monocultures were the basis of the law of constant yield, which indicated that above a relatively low threshold seed density, the final yield of the monoculture was independent of seed density (Fig 2.1a). This is due to reciprocal relationship between population density and individual plant size in the monoculture at maturity (i.e. independent of whether or not that final population size involved self thinning density dependent mortality in its genesis) (Fig 2.1b).

The study of plant monocultures has contributed substantially to the development of theory in plant ecology. The first insight, sometimes known as Suckachev's rule (in Harper 1977), was that population density is inversely related to productivity.

Infertile soils tend to support high population densities of individually small plants, while on productive soils, the dominant plants are capable of growing sufficiently large that they kill their suppressed neighbours, thereby reducing adult population density (Fig 2.1b). This, in turn, led to Yoda's rule (Yoda 1963) which formalized the time-course of density dependent mortality in monocultures (so-called "self-thinning"). This proposed $-3/2$ relationship between log individual dry mass and log population density (Fig 2.1c). These days it is realized that the axes in Yoda's Rule were the wrong way round. Rather than plants being smaller at high densities as in Fig 2.1b, increased biomass causes increased mortality, with the extra deaths concentrated in the smallest size classes. A better representation of the mechanism of self thinning would be to have log population density as the response variable and log biomass as the explanatory variable (Fig 2.1d).

The hypothesis is that increase in biomass can only be accommodated through death of the smaller suppressed individuals. Growth causes mortality, rather than higher density causing individuals to be smaller.

In recent years there has been renewed interest in monocultures in the context of biodiversity manipulation experiments (Tilman 1994, Crawley et al. 1999, Marquard et al. 2009). Monocultures of each species are grown in order to parameterize models of plant community performance, and to distinguish over-yielding from sampling effects or complementarity (Loreau 2001).

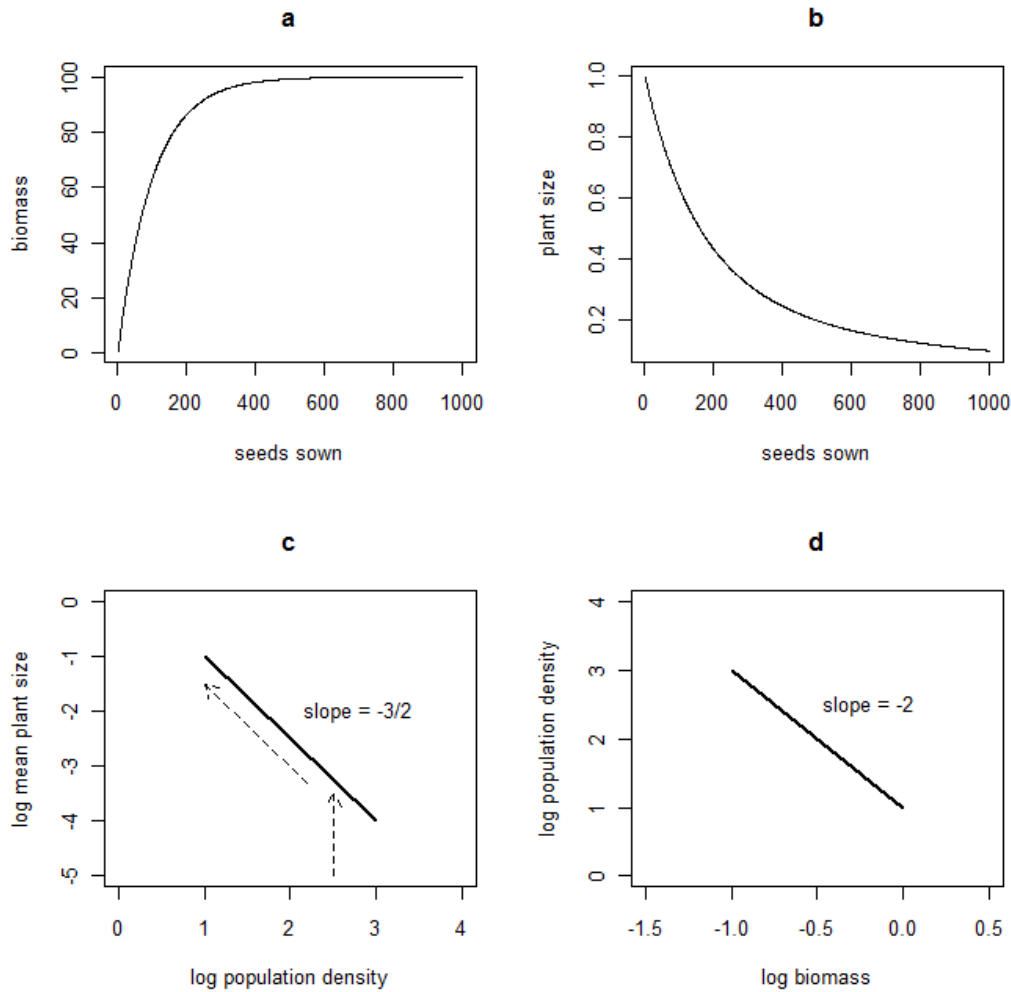


Fig 2.1 Theory of plant monocultures. (a) The Law of Constant Yield. Total biomass increases with the number of seeds sown, up to the point at which intraspecific plant competition begins to reduce mean adult plant size (about 100 seeds per unit area in this figure). Eventually, total biomass becomes independent of initial seed density, as a result of the assumed extreme size plasticity of the individual plants (above about 600 seeds per unit area in this figure). (b) Size plasticity of individuals. Above the competition threshold, doubling plant density is assumed to halve individual plant size. Fecundity is typically assumed to be a linear function of plant size (as measured by dry mass). (c) Yoda's Rule (The Self-Thinning or $-3/2$ Law). At the start of the season, plants are small and population density is high (say 2.5 on this log scale). At first, the plants increase in size without any change in population density (the vertical part of the dotted arrow). Once the arrow hits the self thinning line (the bold line with a slope of $-3/2$), population density starts to decline as a result of density dependent mortality. The population then follows the self thinning line in a trajectory from bottom right to upper left. (d) The modern view of Yoda's Rule has log biomass as the explanatory variable and population density as the response. The hypothesis is that increases in biomass can only be accommodated through death of the smaller suppressed individuals. Growth causes mortality, rather than higher density causing individuals to be smaller (compare with (b), above). The slope of the function is -2 .

In this chapter we investigate the extent to which the demography of species in monoculture varies with population density and how “year effects” can alter the expression of this density dependence. We concentrated on three vital rates: 1) seedling recruitment. 2) seedling-to-adult survival. 3) fecundity (seed production per adult plant) in a size-structured population). We make no attempt to estimate germination rate in the field. In due course, we shall use the parameters estimated from monoculture to attempt to predict the outcome of interspecific competition in two-species and multi-species settings, and hence to discover which plants traits are most influential in determining the outcome of interspecific interactions within our guild of annual plants.

2.2 Materials and Methods

2.2.1 Site

The field work was carried out at Ashurst in Silwood Park, Berkshire (Grid Reference SU 938 694) in an enclosure measuring 60m x 25m. The location was chosen because the area was already fenced to exclude deer and rabbits, and a weed-free gravel base had been created for a previous pilot study in 1996. The soil surface was covered with Mipex plastic sheeting (a weed suppressant fabric) purchased from Horticultural Equipment and Supplies, Monro (South), Chichester, West Sussex, UK to stop weed growth. The herbivore enclosure was 1.4 meter high fence with a flat top of wire mesh 45cm in width, designed to prevent animals from climbing or jumping over the fence.

2.2.2 Raised beds

In 2002 we built 250 raised beds, each measuring 1.5m by 1.5m, laid out in ten columns of twenty five plots, with the area between the plots covered in gravel for ease of maintenance (Fig 2.2). Each plot was built from the timber of two creosote-treated second-hand railway sleepers (2.6 m in length) cut in half. The four half-sleepers were arranged to enclose a square on top of the Mipex (plastic sheeting) to make a raised bed, measuring 1.0m x 1.0m interior dimension, as illustrated in Figure 2.3. The plots were separated from one another by a gravel-filled gap of 50cm

between their row neighbour and their column neighbour. The base of the interior of the raised bed was filled with 20mm ballast to within 3cm of the rim of the sleepers, then smoothed using a spirit level.

Using a mechanical cement mixer, we created a sterile artificial soil to fill the top 1cm of each of the raised beds. Irish moss peat, horticultural grit and sharp sand were tumbled together for 30 minutes to create a 1/3, 1/3, 1/3 mixture by volume. No fertilizers were added to the mix. Ten liters of this mixture was spread on the surface of each bed to give an even coverage of 10mm depth on top of the ballast. Finally, the surface was smoothed using a spirit level.

An engraved plastic label (12cm x 7cm) was nailed to railway sleeper on the eastern edge of each of the 250 plots, showing plot number, treatment (monoculture in this case), and the identity of the sown specie (Fig 2.3). The labels were manufactured from an Excel spreadsheet we provided to www.tcelabels.co.uk/Plant_Labels.

The 250 raised beds were allocated to treatments at random in 2002, and each plot received the same treatment over the 5-years of the study. For the monocultures, there were 7 species each replicated 4 times, taking up 28 of the raised beds. The experiment was divided into four blocks for the purpose of statistical modeling; there were 60 plots in the two blocks and 65 plots in the other two blocks (Fig 2.2). The plots supporting monocultures were dug up and rebuilt using fresh soil mixture each year to ensure no carry-over of seed, no resource depletion and no allelopathic or natural-enemy build-up.



Fig 2.2 Lay-out of the 250 plots at Ashurst experimental site in 10 columns (left to right, lettered A – K excluding I) by 25 rows (numbered 1 to 25 bottom to top). Block A bottom left quarter, Block B top left, Block C lower right, and Block D upper right.

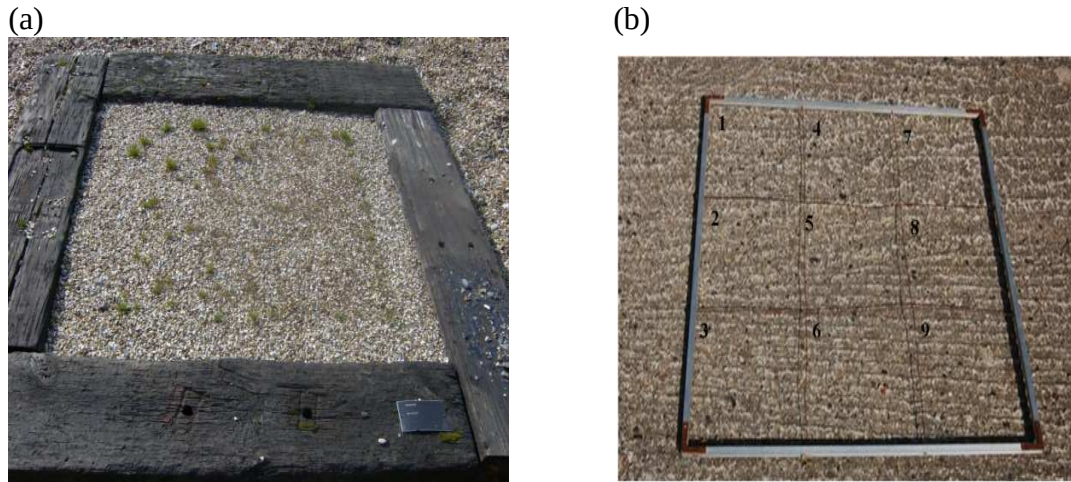


Fig 2.3 (a) The shape and size of one of the experimental plots (internal dimensions 1m x 1m); (b) a 75cm x 75cm frame overlaid in the centre forming 9 square quadrats, each 25cm x 25cm (625cm²). The quadrats were numbered 1 – 9, column-wise, starting at the top left. One population density treatment was sown in each quadrat.

2.2.3 The species

The intention was to have species that represented a range of contrasting ecologies within our guild of annual plants. All species were capable of germination in autumn followed by over-winter survival as rosettes, and then rapid growth and early seed set in spring.

Our pilot experiments identified some species that could be immediately precluded from consideration as a result of their thuggish behaviour. Most notable amongst these exceptionally vigorous annuals were *Cardamine hirsuta* (Brassicaceae), *Geranium molle* (Geraniaceae), *Myosotis arvensis* (Boraginaceae), *Lamium perpureum* (Lamiaceae) and *Poa annua* (Poaceae), any one of which was capable of carpeting an entire plot within just a few weeks.

The final choice consisted of a grass (*Aira praecox*), a legume (*Ornithopus perpusillus*), three contrasting herbs (*Myosotis discolor* (Boraginaceae), *Cerastium glomeratum* (Caryophyllaceae) and *Veronica arvensis* (Scrophulariaceae), and two tiny crucifers *Erophila verna* and *Arabidopsis thaliana* (Brassicaceae). All were locally frequent on gravel paths and other compacted open habitats within Silwood

Park (Crawley 2005a, Crawley 2005b, Crawley et al. 2005) so that collection of sufficient seed to initiate the experiments was not likely to be problem.

A huge amount was known about the physiology and genetics of *Arabidopsis thaliana* (Tonsor et al. 2005) but rather less about its ecology and demography. Very little was known about the ecology of the other six species (e.g. none had a Biological Flora account written about them).

2.2.4 Seed collection

Prior to the start of the experiment, we determined the number of seeds per fruit for each of the 7 species using thirty fruits of different sizes collected at random for each of the species. To create the monocultures, seeds of the seven species were collected in the spring and summer of 2002 (March – August) from various locations in Silwood park and surrounding areas. The seeds were separated from their pods in brass sieves, using four different mesh sizes, ranging from the largest (1.4 mm diameter) to the smallest (180 micrometer). Table 2.1 summarizes the amount of seed collected in 2002.

Table 2.1 Total weights of seeds collected in summer 2002 by species, showing the total mass of seed collected, and the estimated numbers of seeds based on the 100-seed-weight (mg) of each species. The average number of seeds per fruit (based on dissection of 30 fruits for each species) is shown in the final column.

Species	Total seed weight (mg)	Weight of 100 seeds in (mg)	Estimated total seed number	Mean number of seeds per fruit
<i>A. praeox</i>	13,553.27	19	71,333	14
<i>A. thaliana</i>	33,436.20	2.28	1,466,500	48
<i>C. glomeratum</i>	6,620.00	3.3	200,606	41.5
<i>E. verna</i>	2,995.45	2.33	128,560	42
<i>M. discolor</i>	6,380.00	20	31,900	3.64
<i>O. perpusillus</i>	310	50	310	5.6
<i>V. arvensis</i>	18,430.00	10	184,300	16

For each species, 100 individual seeds were carefully counted out. The mean weight of 100 seeds in milligrams was estimated from 10 batches, providing a mean seed mass (mg) and standard error (s.e.) as follows: *Aira* 14.0, s.e. =0.4; *Arabidopsis* 2.28,

s.e. =0.05; *Cerastium* 3.3, s.e=0.03; *Erophila* 2.33, s.e=0.03; *Myosotis* 20.0, s.e.=0.24; *Ornithopus* 50.0, s.e=0.66; *Veronica* 10.0, s.e=0.3. There was no significant difference in the weight of 100 seeds in any of the ten batches.

2.2.5 Spatial layout of the sowing densities within each monoculture

We decided to have 9 sowing densities in a 3 x 3 grid within each raised bed, ranging from ultra-low to ultra-high density (as assessed from pilot studies). Rather than randomize the location of the 9 quadrats (25cm x 25cm) within each raised bed, we organized the densities in a regular pattern from lowest in the top left hand quadrat to highest in the bottom right quadrat (see Fig 2.3). The idea was to minimize the risk of sowing the wrong seed density in a given quadrat, and to make subsequent data collection easier and less error-prone. The 9 densities were selected to represent a roughly logarithmic scale between the highest and lowest densities: these sowing densities are shown in Table 2.2.

2.2.6 Seed sowing

Seeds collected seeds from various sites were combined and thoroughly mixed. Seeds of each species were weighed into appropriate batches to match the nine sowing densities (see Table 2.2).

Seed was gently sprinkled from pre-prepared paper packets onto the soil surface for the appropriate 25cm x 25cm quadrat. The first half of the seed was sown column-wise, then the second half of the seed was sown row-wise to ensure even coverage. Sowing dates for the five years are shown in Table 2.3. After sowing, the surface of the entire interior of the raised bed was covered by with fine gravel mulch to a depth of 1cm to protect the seeds and the soil surface from rain-splash and to reduce the surface area to be weeded.

Table 2.2 Sowing densities for each of the 9 sectors for monoculture experiment 2003-2006. Sowing densities in the first year (2002) were half of the values shown here. dc = density class.

dc	<i>A. praecox</i>	<i>A. thaliana</i>	<i>C.glomeratum</i>	<i>E. verna</i>	<i>M. discolor</i>	<i>O. perpusillus</i>	<i>V. arvensis</i>
1	7	60	60	60	7	7	60
2	15	150	150	150	15	15	150
3	30	300	300	300	30	30	300
4	60	600	600	600	60	60	600
5	250	1200	1200	1200	250	125	1200
6	500	2500	2500	2500	500	250	2500
7	1000	5000	5000	5000	1000	500	5000
8	2000	10000	10000	10000	2000	1000	10000
9	4000	20000	20000	20000	4000	2000	20000

Table 2.3 Dates of seed sowing and plant harvest for the seven species over five years in monocultures.

year	Activity	<i>Aira</i>	<i>Arabidopsis</i>	<i>Cerastium</i>	<i>Erophila</i>	<i>Myosotis</i>	<i>Ornithopus</i>	<i>Veronica</i>
2002/2003	Sown	19/09/2002	12/09/2002	17/09/2002	12/09/2002	18/09/2002	19/09/2002	20/09/2002
	harvested	26/06/2003	22/05/2003	03/06/2003	30/04/2003	18/06/2003	03/09/2003	25/06/2003
2003/2004	Sown	28/08/2003	16/07/2003	07/08/2003	15/07/2003	13/08/2003	09/09/2003	14/08/2003
	harvested	18/06/2004	11/05/2004	28/05/2004	10/05/2004	03/06/2004	29/07/2004	21/06/2004
2004/2005	Sown	23/07/2004	12/07/2004	13/07/2004	09/07/2004	14/07/2004	02/08/2004	26/07/2004
	harvested	15/06/2005	23/05/2005	03/06/2005	06/05/2005	09/06/2005	15/07/2005	14/06/2005
2005/2006	Sown	28/07/2005	11/07/2005	14/07/2005	08/07/2005	18/07/2005	02/08/2005	19/07/2005
	harvested	06/06/2006	19/05/2006	23/05/2006	09/05/2006	23/05/2006	06/06/006	05/06/2006
2006/2007	Sown	14/07/2006	07/07/2006	10/07/2006	04/07/2006	11/07/2006	26/07/2004	13/07/2006
	harvested	07/06/2007	25/04/2007	30/04/2007	12/04/2007	09/05/2007	07/07/2007	27/05/2007

2.2.7 Monitoring

Seedling appearances were monitored weekly after sowing. In the first years, seedlings emerged for six species between 29/11/2002 and 06/12/2002. The remaining species (*Ornithopus perpusillus*) emerged in late January 2003 (22/01/2003). We did not attempt to estimate germinate rate in the field, because we wanted monitoring to be minimally intrusive, and we did not try to estimate pre-emergence mortality (for more detail, see Chapter 3 on the Seed Bank).

Seedling densities were estimated using 30 randomly-located 1cm square mini-quadrats drawn on a clear acetate sheet and laid over the 25cm quadrat. Numbers were multiplied by 20.83 to estimate total seedling numbers per quadrat (625cm^2).

Apart from the first year (when there was a single bout of recruitment in the spring of 2003), at least two recruitment estimates were made for all species in subsequent years. One count was made in autumn for the early recruits (late summer to fall), following seed sowing in the summer, and then a second count was made for the late recruits (late winter to early spring) in the following spring.

Although all the species are facultative winter annuals, survival from autumn recruitment was very low in most years because of seedling mortality resulting from frost heave and exposure of heaved roots to low temperatures. In years when autumn and winter temperatures were mild, for example in 2004, some adult plants were present at the spring seedling count. There was no evidence that seed produced by these adults contributed to spring seedling counts.

At maturity (dates in Table 2.3) all of the plants within each 25cm quadrat were uprooted, bagged and returned to the laboratory. Here, they were sorted into 7 size classes, counted then dried at 80°C and weighed to determine total biomass per quadrat and the size distribution (both by numbers and by mass) was summarized for the seven classes. The number of fruits in each size class was counted, and this was used to estimate total seed production per quadrat (using the fecundities data in Table 2.1). The mean dry weight in each size class ($\bar{y}_i$) was used along with the number of individual plants (n_i), to estimate approximate plant size variance for the quadrat as a whole, using the overall mean plant size y ($\bar{y}$).

Variance in plant dry weight is approximated by:

$$s^2 \approx \frac{\sum n_i (\bar{y}_i - u)^2}{\sum (n_i - 1)}$$

where there are n_i plants in each size class i , overall mean plant size is u , and the size class means are $\bar{y}_i$. The alternative of weighing all the tiny plants individually was not practicable.

The net per-generation multiplication rate, λ , was obtained by dividing the total number of seeds produced per quadrat by the total number of seeds sown per quadrat.

2.2.8 Statistical analysis

Density dependence was assessed by regression of the logarithm of the response variable (seedling recruitment, adult density, seed production, and net multiplication rate) against the logarithm of the relevant population density (seed sown, seedlings recruited, adult density). A significant reduction in the slope of this log-log regression below 1.0 indicates density dependence (Dennis and Taper 1994) and shows that the proportion recruiting or surviving declines as density rises.

Year effects and species effects (as two categorical explanatory variables with 4 and 6 degrees of freedom respectively) were assessed in an analysis of covariance with log population density as a continuous covariate. For log λ and log biomass we used linear models, while for recruitment and survival we used logistic regression in generalized mixed models with quasibinomial errors to allow for overdispersion (Crawley 2007). The pseudoreplication represented by the 9 quadrats nested within each plot was dealt with by fitting plot as a random effect within each of the 4 blocks in lmer (R core development team 2011), as follows.

$$y \sim \text{density} * \text{species} * \text{year} + (1|\text{block}) + (1|\text{plot})$$

In addition to straightforward regression, we used piece-wise regression to test for the existence of a threshold density, below which there was no evidence for density dependence in that particular response variable. The nine sowing densities were split into 6 groups (2 lowest densities & 7 higher densities, 3 & 6, 4 & 5, 5 & 4, 6 & 3, 7 & 2) and linear regressions were fitted separately to the 4 replicates of each section of the relationship (four parameters estimated in all; two slopes and two intercepts). The piecewise model with the lowest residual deviance was then used to choose the optimal split (this was often 3 & 6). Finally, the existence of a threshold was assessed by comparing the best piecewise regression model (with its 4 parameters) with the overall linear regression (with its two parameters), using anova. The more complex piecewise model was retained only if it was significantly better than the simple linear regression. See Crawley (2005) for details of the procedure. Values of $\lambda > 1$ indicate

an increasing population, values of $0 < \lambda < 1$ indicate a declining population. Negative values of λ are not permitted.

One of the ironies of population dynamics is that in a perfectly regulated population, it would be impossible to detect the density-dependence that was responsible stability, because there will be too little variation in population density to use regression to estimate the values of the demographic parameters (Hassell 1975, Turchin and Taylor 1992). This is one of the principal justifications for the experimental manipulative approach to density dependence adopted in this study (Murdoch 1994).

2.3 Results

2.3.1 Recruitment

The proportion of seeds appearing as seedling recruits varied from species to species and from year to year. Mean proportional recruitment was highest for *M. discolor* with almost 50% of sown seed producing seedlings, and lowest for *A. thaliana* with just 8% of seeds producing seedlings averaged across years and densities (Table 2.4). There were significant year effects on mean recruitment for all species, with *Cerastium glomeratum* showing the largest year effects (more than 10-fold) and *Erophila verna* the smallest (less than 2-fold).

Table 2.4 Mean recruitment in monocultures (seedlings observed as a proportion of seeds sown) for seven annual plant species over 5 years. The species are ranked by mean proportional recruitment at intermediate sowing density (quadrat 5 out of 9). Year effects are illustrated by the column headed “fold”, which shows maximum recruitment divided by the minimum recruitment. Standard error of the proportion (s.e.) was calculated from 20 data points (4 replicates x 5 years).

Species	2003	2004	2005	2006	2007	Mean	Rank	fold	s.e.
<i>M. discolor</i>	0.604	0.207	0.667	0.479	0.521	0.496	1	>3	0.1
<i>O. perpusillus</i>	0.088	0.354	0.500	0.500	0.750	0.438	2	>8	0.2
<i>A. praecox</i>	0.187	0.646	0.161	0.229	0.563	0.357	3	>4	0.12
<i>V. arvensis</i>	0.503	0.165	0.455	0.130	0.200	0.291	4	>3	0.05
<i>C. glomeratum</i>	0.343	0.041	0.135	0.204	0.464	0.237	5	>10	0.07
<i>E. verna</i>	0.187	0.145	0.161	0.169	0.078	0.148	6	<2	0.06
<i>A. thaliana</i>	0.056	0.050	0.025	0.069	0.195	0.079	7	>7	0.11

2.3.2 Survival

Survival from seedlings to adult is shown for the five years in Table 2.5. Average survival to adulthood was highest for *Aira praecox* (almost 75%) and lowest for *Veronica arvensis* (less than 12%).

Table 2.5 Mean survival from seedling to adult (as a proportion) for seven annual plant species over 5 years. The species are ranked by mean proportional survival at intermediate sowing density (quadrat 5 out of 9). The top row shows the year in which the plants were harvested (the year after seeds were sown), followed by mean proportion germination (averaged over years) and the rank of the means (1-7). Fold indicates the ratio of largest to smallest mean survival across each year. S.e is the standard error of the mean.

Species	2003	2004	2005	2006	2007	Mean	s.e.	Rank	Fold
<i>A. praecox</i>	0.828	0.621	0.926	0.881	0.402	0.732	0.4	1	2
<i>E. verna</i>	0.605	0.409	0.594	0.464	0.781	0.57	0.15	2	1.5
<i>A. thaliana</i>	0.814	0.354	0.819	0.3	0.086	0.475	0.28	3	9
<i>O. perpusillus</i>	0.568	0.373	0.443	0.192	0.149	0.345	0.34	4	3
<i>M. discolor</i>	0.111	0.398	0.275	0.188	0.25	0.244	0.19	5	3
<i>C. glomeratum</i>	0.114	0.726	0.039	0.046	0.054	0.196	0.21	6	13
<i>V. arvensis</i>	0.057	0.221	0.116	0.045	0.155	0.119	0.21	7	4

There were significant year effects in mean survival for all species, with *Cerastium glomeratum* showing the largest year effects (more than 13-fold) and *Erophila verna* the smallest (less than 2-fold). *Aira praecox* has the highest survival rate (1) as opposed to *Ornithopus perpusillus* (7).

2.3.3 Fecundity

Mean fecundity (seeds produced per surviving plant) was highest for *Arabidopsis thaliana* (more than 450 seeds per plant) and lowest for *Myosotis discolor* (fewer than 55 seeds). There were strong year effects on fecundity that acted mainly through changes in the size structure at maturity, leading to at least two-fold variation from year to year in fecundity for each species (2.6).

Table 2.6 Mean seed production per adult of the seven annual plant species for 5 years from an intermediate seed sowing (quadrat 5 of 9). The species are ranked by mean seed production. The column headed “fold” shows the maximum seeds produced divided by the minimum seeds produced over 5 years. Standard error was calculated from 20 data points (4 replicates x 5 years). Fold indicates the ratio of largest to smallest mean seed production across each year. S.e is the standard error of the mean.

Species	2003	2004	2005	2006	2007	Mean	s.e.	Rank	fold
<i>A. thaliana</i>	561	732	590	315	217	483	169	1	<4
<i>C. glomeratum</i>	452	280	185	558	164	328	275	2	<3
<i>E. verna</i>	127	239	112	152	103	147	44	3	<2.5
<i>V. arvensis</i>	207	90	191	82	62	126	42	4	<4
<i>O. perpusillus</i>	92	112	45	44	61	71	54	5	<3
<i>A. praecox</i>	73	49	35	53	88	60	19	6	<3
<i>M. discolor</i>	88	64	48	34	29	53	24	7	<3

Across species, there was a correlation of -0.9 ($t = -5.5943$, $df = 5$, $p=0.0025$) between seedling recruitment and fecundity per surviving adult (Fig 2.4). Seedling recruitments and fecundity per surviving adult were first log-transformed.

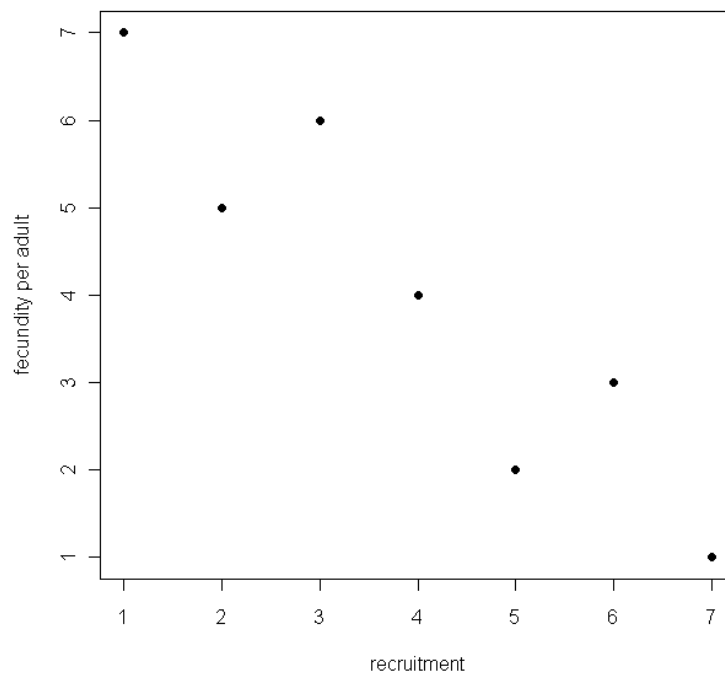


Fig 2.4 Inverse correlation between rank seedling recruitment and rank mean fecundity per adult for the 7 species at intermediate sowing density. $t = -5.59$, $df = 5$, $p = 0.0025$). Higher rates of recruitment correlated with lower fecundity rates per plant for all 7 species.

2.3.4 Density dependence

2.3.4.1 Density dependence in recruitment

Density dependence was detected in recruitment, survival, fecundity, lambda and plant population size. In the figures that follow, density dependence is indicated by the flatness of the regression lines (slope significantly less than 1.0), representing relative constancy in the number of plants surviving or recruiting, roughly independent of the number of seeds sown.

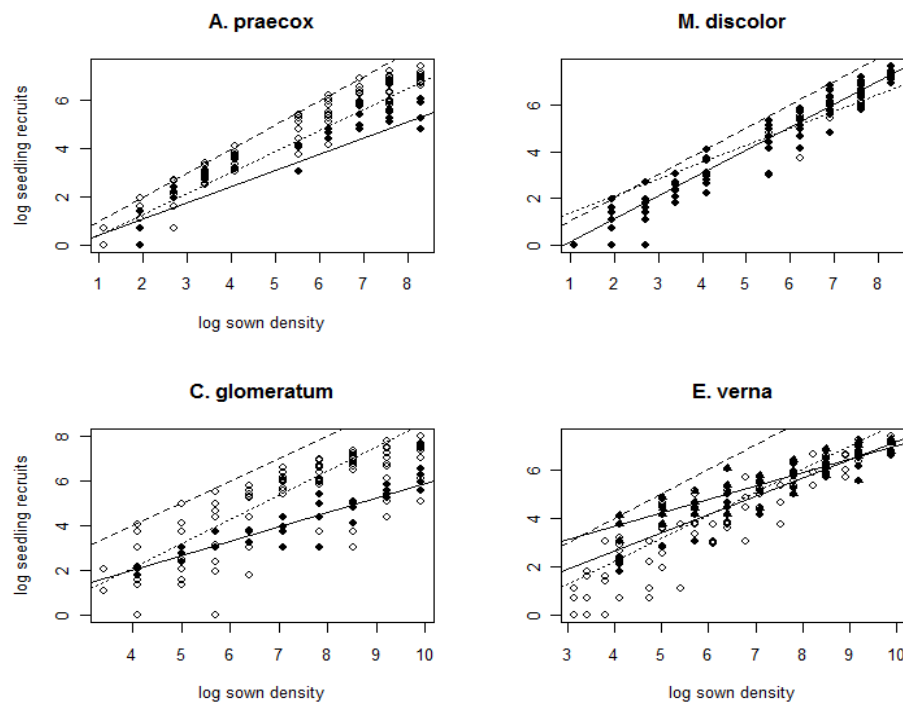


Fig 2.5 Year effects on density dependence in recruitment for *Aira praecox*, *Myosotis discolor*, *Cerastium glomeratum* and *Erophila verna*. The remaining three species (not shown here) exhibited intermediate patterns. The strength of density dependence is measured by the degree to which the slope of the log-log plot is lower than 1.0. The upper (dashed) line has a slope of 1 to indicate that all of the sown seed produced seedlings. Year effects in density dependence are indicated by the contrast between the solid lines (mean slope across year (or years) where density dependence was most pronounced; i.e. the regression line is shallowest) and the dotted lines (mean slope across years (or year) where density dependence was least pronounced; i.e. steepest). In *Aira praecox*, more intense density dependence was in years when mean recruitment was lowest (solid line below dotted line), whereas in *Erophila verna*, density dependence was most severe in years of highest mean recruitment (solid line below dotted line). See text for details. Each data point comes from 625cm².

Recruitment was density independent not significantly < 1 for *Aira praecox* in 2006 and 2007 but density dependent in all other years (Fig 2.5). The most extreme density dependence was in 2004 (intercept=0.24, slope=0.67, $p=0.014$). In contrast, recruitment was density independent for *Myosotis discolor* in all years. Recruitment was density independent for *Cerastium glomeratum* in all but one year density dependent in 2004 (intercept=0.57, slope=0.65, $p=0.26$). Recruitment was density independent for *Erophila verna* in 2003, 2004 and 2007 but density dependent in 2005 and extremely density dependent in 2006 (intercept=1.44, slope=0.55, $p=0.00028$). In all 4 species, the density dependence and extreme density dependence in recruitment is shown in solid circles and unbroken regression line. The dashed line shows maximum possible survival (adult density = seedling density). The dotted line shows the regression line for all years combined. D.f = 9 and 170 for all species.

2.3.4.2 Adult survival from seedling recruitment

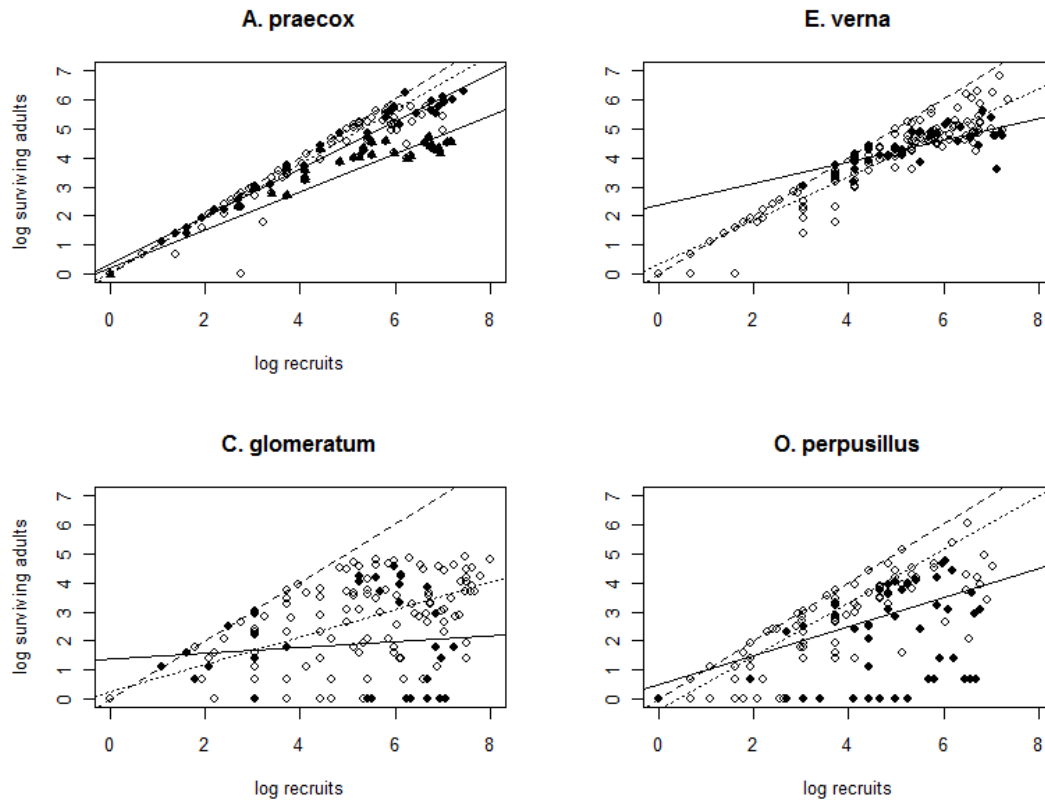


Fig 2.6 Year effects on density dependent survival to adulthood in *A. praecox*, *C. glomeratum*, *E. verna* and *O. perpusillus*. Survival was density independent (slope not significantly different from 1.0) for *A. praecox* in 2005 but density dependent in all other years. The most extreme density dependence was in 2004 and 2006 data as combined solid squares and unbroken regression line, intercept=0.2, slope=0.82, $p=0.012$), also in 2007 (solid triangles and unbroken regression line, intercept=0.23, slope=0.66, $p=0.0000488$) which was significantly shallower than in 2004 and 2006. Adult survival was density dependent in all years for *E. verna* with the largest density effect in 2006 (intercept=2.35, slope=0.37, $p=0.0000027$). Adult survival was density independent in 2004 but density dependent in all other years for *C. glomeratum* with extreme dependence in 2003 (intercept=1.4, slope=0.1, $p=0.0017$). Adult survival was density independent for *O. perpusillus* in 2004 and 2005 but density dependent in all other years with extreme dependence in 2006 (intercept=0.12, slope=0.36, $p=0.00044$). In all 4 species, the density dependence and extreme density dependence in adult survival is shown in solid circles, solid triangles and unbroken regression line. The dashed line shows maximum possible survival ($b=1$, seedling density = adult density). The dotted line shows the regression line, and the elevation of differences between the dotted and dashed lines indicate of the mean effect sizes. Each data point comes from 625cm².

2.3.4.3 Density dependence in fecundity

This study supports a mass of previous work indicating that log (seed production) in annual plants is well described by a linear function of log shoot biomass, (Fig 2.7). However, the relationship between fecundity and final biomass is significantly non-linear in many species (cf Harper 1977 and his modular plant argument).

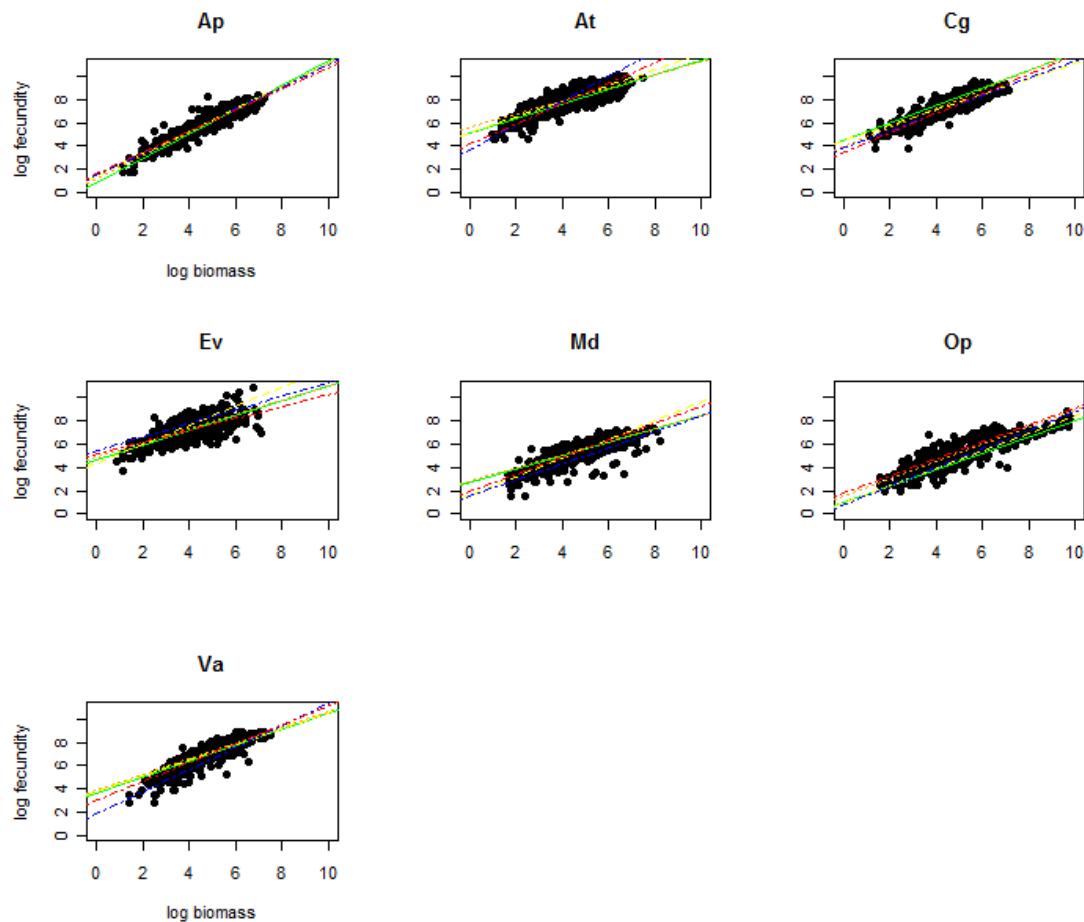


Fig 2.7 Fecundity and plant size in seven species (Ap = *Aira praecox*, At = *Arabidopsis thaliana*, Cg = *Cerastium glomeratum*, Ev = *Erophila verna*, Md = *Myosotis discolor*, Op = *Ornithopus perpusillus*, Va = *Veronica arvensis*) shown on a log-log scale. The points are for individual quadrats (9 densities from 625cm² in each of 4 replicates per year). The lines are linear regressions for each of 5 years (2003 = green; 2004 = yellow; 2005 = orange; 2006 = blue; 2007 = red). Details of the intercepts and slopes are in Table 2.8 (a) and 2.8 (b).

In these plots, the slope = 1 would indicate modular construction and constant proportional investment. The slopes for *Erophila verna* (0.58) were shallower than any of the other 6 species ($p < 0.01$), showing that seed production per unit biomass

was strongly density dependent for this species (i.e. allocation of biomass to reproduction at higher sowing densities was lower than in the other 6 species). In contrast, *Aira praecox* had a slope of 0.96 showing a small (but still statistically significant) effect of density on fecundity per unit biomass.

Table 2.7 Year effects on density dependence of fecundity. (a) Intercepts (int) of the plot of log fecundity against log sown density with their standard errors (se). (b) Slopes (sl) of the plot of log fecundity against log sown density with their standard errors (se).

(a)

years	2003		2004		2005		2006		2007	
species	int	se	int	se	int	se	int	se	int	se
<i>ap</i>	5.51	0.27	6.18	0.15	5.76	0.22	7.28	0.22	7.72	0.36
<i>at</i>	8.25	0.31	6.31	0.39	7.63	0.34	5.47	0.77	6	1.17
<i>cg</i>	9.44	0.63	7.91	0.51	3.17	0.75	6.01	0.66	4.86	1.06
<i>ev</i>	6.16	0.47	6.5	0.35	7.58	0.33	8.98	0.26	8.13	0.25
<i>md</i>	4.72	0.96	5.62	0.26	6.52	0.36	7.21	0.37	6.51	0.33
<i>op</i>	10.32	4.37	4.11	0.61	6.15	0.56	6.09	1.38	5.81	1.04
<i>va</i>	8.96	0.5	7.71	0.37	9.76	0.41	4.74	0.73	7.86	0.33

(b)

years	2003		2004		2005		2006		2007	
species	slope	se	slope	se	slope	se	slope	se	slope	se
<i>ap</i>	0.5	0.05	0.35	0.07	0.39	0.07	0.16	0.07	0.08	0.07
<i>at</i>	0.27	0.08	0.51	0.12	0.28	0.12	0.4	0.12	0.2	0.13
<i>cg</i>	0.02	0.1	0.22	0.13	0.61	0.15	0.23	0.14	0.4	0.14
<i>ev</i>	0.4	0.05	0.38	0.05	0.24	0.05	0.07	0.05	0.15	0.05
<i>md</i>	0.34	0.12	0.32	0.13	0.08	0.13	0.12	0.13	-0.02	0.13
<i>op</i>	-0.48	0.76	0.41	0.77	0.13	0.77	0.02	0.77	-0.85	0.78
<i>va</i>	-0.07	0.07	0.12	0.09	-0.1	0.09	0.17	0.09	-0.01	0.09

There were significant years effects in fecundity from sown density, as shown by the intercepts and slopes with their standard errors, for each of the 7 species, as measured by the parameters of a regression of log seed production against log number of seeds sown (Table 2.7).

Table 2.8 Year effects on density dependence of fecundity. (a) Intercepts (int) of the plot of log fecundity against log biomass with their standard errors (se). (b) Slopes (slope) of the plot of log fecundity against log biomass with their standard errors (se).

(a)

year	2003		2004		2005		2006		2007	
sp	int	s.e	int	s.e	int	s.e	Int	s.e	int	s.e
<i>Ap</i>	0.85	0.12	1.4	0.18	1.24	0.17	1.3	0.17	1.62	0.16
<i>At</i>	5.07	0.25	5.2	0.27	5.7	0.28	3.71	0.29	4.06	0.28
<i>Cg</i>	4.5	0.24	4.4	0.29	3.91	0.31	3.87	0.28	3.45	0.28
<i>Ev</i>	4.62	0.18	4.28	0.28	4.93	0.27	5.45	0.29	5.12	0.24
<i>Md</i>	2.75	0.26	1.56	0.03	2.86	0.03	2.59	0.03	1.92	0.03
<i>Op</i>	1.03	0.32	0.93	0.35	1.6	0.37	0.77	0.39	1.86	0.37
<i>Va</i>	3.59	0.18	3.67	0.26	3.91	0.25	1.83	0.27	2.98	0.26

(b)

year	2003		2004		2005		2006		2007	
sp	slope	s.e	Slope	s.e	slope	s.e	slope	s.e	slope	s.e
<i>Ap</i>	1.05	0.02	0.98	0.03	0.97	0.03	0.95	0.03	0.9	0.03
<i>At</i>	0.63	0.05	0.67	0.05	0.7	0.06	1.1	0.06	0.89	0.06
<i>Cg</i>	0.75	0.05	0.67	0.06	0.81	0.07	0.75	0.06	0.84	0.06
<i>Ev</i>	0.64	0.05	0.83	0.07	0.61	0.06	0.58	0.07	0.51	0.06
<i>Md</i>	0.57	0.05	0.8	0.06	0.57	0.06	0.69	0.06	0.7	0.06
<i>Op</i>	0.7	0.05	0.75	0.05	0.73	0.06	0.83	0.06	0.72	0.06
<i>Va</i>	0.69	0.04	0.68	0.05	0.68	0.05	0.43	0.07	0.57	0.06

There were significant year effects in fecundity from biomass, as shown by the intercepts and slopes with their standard errors, for each of the 7 species, as measured by the parameters of a regression of log seed production against log biomass (Table 2.8). There was highly significant density dependence in lambda in all seven species, Fig 2.8. Across species, mean lambda varied significantly with years.

2.3.4.4 Density dependence in net rate of population increase, λ

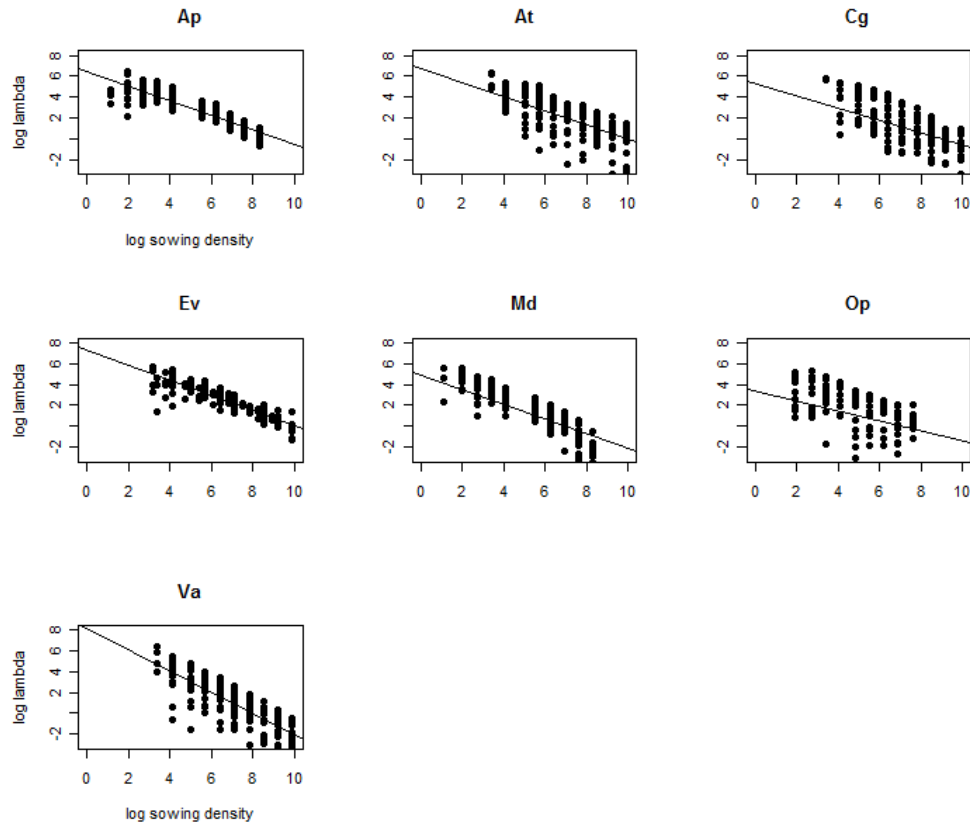


Fig 2.8 Linear regression of density dependence in log λ (seed out/seed in) across nine sowing densities for 7 species aggregated across all 5 years. Ap = *Aira praecox*, At = *Arabidopsis thaliana*, Cg = *Cerastium glomeratum*, Ev = *Erophila verna*, Md = *Myosotis discolor*, Op = *Ornithopus perpusillus*, Va = *Veronica arvensis*. $df = 1$ and 178, p -value: $< 2.2e-16$ for all species. There is a clear indication of a threshold at low densities in *Aira*, but only more subtle effects in *Erophila*, *Myosotis* and *Ornithopus* (see text). Each data point comes from 625cm².

We hypothesized that, there might be a threshold seed density below which competition would be negligible, and λ would be density independent. However, there was no evidence of such a threshold for most species in most years, with λ decreasing monotonically from the lowest sowing densities (Fig 2.9). In contrast, *Aira praecox* showed density-independence in λ across the three lowest seed-sowing densities (Fig 2.9). Three other species (*Erophila*, *Myosotis* and *Ornithopus*) showed a threshold seed density as shown by the piece-wise regression.

Table 2.9 Year effects in log lambda shown from intermediate log sown density (a) the intercepts (int) and their standard errors (s.e.) and (b) the slopes and their standard errors for each of the 5 years. Species (Sp): Ap = *Aira praecox*, At = *Arabidopsis thaliana*, Cg = *Cerastium glomeratum*, Ev = *Erophila verna*, Md = *Myosotis discolor*, Op = *Ornithopus perpusillus*, Va = *Veronica arvensis*.

(a)

years	2003		2004		2005		2006		2007	
sp	int	se	int	se	int	se	int	se	int	se
ap	3.67	0.35	3.18	0.39	2.93	0.39	3.26	0.39	3.31	0.39
at	3.4	0.29	2.6	0.31	2.33	0.31	1.64	0.33	1.55	0.42
cg	4.03	0.31	3.84	0.33	2.12	0.42	1.68	0.38	1.48	0.4
ev	2.14	0.3	2.42	0.34	2.09	0.34	1.89	0.35	2.06	0.35
md	1.47	0.43	2.6	0.42	2.69	0.44	2.7	0.44	2.57	0.45
op	0.83	0.6	1.62	0.56	2.1	0.56	1.73	0.56	1.7	0.56
va	2.39	0.38	1	0.47	1.41	0.47	-1.8	0.47	0.2	0.47

(b)

sp	2003		2004		2005		2006		2007	
sp	slope	se	slope	se	slope	se	slope	se	slope	se
ap	-0.5	0.06	-0.65	0.03	-0.62	0.04	-0.85	0.04	-0.55	0.04
at	-0.74	0.05	-0.5	0.05	-0.72	0.05	-0.6	0.11	-0.63	0.05
cg	-0.98	0.1	-0.77	0.07	-0.39	0.1	-0.76	0.09	-0.49	0.07
ev	-0.61	0.07	-0.62	0.06	-0.76	0.05	-0.93	0.04	-0.71	0.06
md	-0.66	0.16	-0.68	0.05	-0.92	0.06	-1.12	0.07	-0.80	0.07
op	-1.48	0.71	0.49	0.12	-0.87	0.11	-0.97	0.26	-0.79	0.3
va	-1.07	0.08	-0.88	0.05	-1.11	0.06	-0.83	0.1	-0.95	0.07

On log-log axes, the response of lambda to seed density was well approximated by a linear function (Fig 2.8). There were significant year effects and spatial effects (across the four blocks within Ashurst) on the slopes and intercepts of these linear regressions of log(lambda) on log(density) (see Table 2.9). The threshold seed density for the invasion criterion ($\lambda = 1$) occurred at sowing density 7 or higher for all species, though, again this varied somewhat from year to year, due to intense competition. At the range of sowing densities we employed, not all species showed $\lambda < 1$ but where this did occur, it was at sowing density 8 or 9 for all species.

There were strong year effects on lambda, both in terms of the presence of a density threshold and in the maximum lambda value observed at low densities. There were relatively small year effects on the slope of the log-log plot of lambda against sowing density, indicating that this is a rather species specific parameter. There were also

spatial effects on log lambda from sown densities as shown by intercepts and slopes, see Table 2.10

Table 2.10 Year effects in log lambda for *Aira praecox* shown from log sown density (a) the intercepts (int) and their standard errors (s.e.) and (b) the slopes and their standard errors for each of the 4 replicates. Abbreviations: int = intercept, se = standard error. df = 7 and 28.

(a)

replicates	replicate 1		replicate 2		replicate 3		replicate 4	
year	int	se	int	se	int	se	int	se
2003	6.09	0.43	4.9	0.61	4.79	0.61	6.2	0.61
2004	6.65	0.24	6.07	0.33	6.11	0.33	5.88	0.33
2005	6.2	0.38	6.04	0.54	5.02	0.54	5.8	0.54
2006	7.46	0.3	7.19	0.43	6.77	0.43	6.34	0.43
2007	8.71	0.65	7.14	0.56	7.11	0.56	5.9	0.56

(b)

replicates	replicate 1		replicate 2		replicate 3		replicate 4	
year	slope	se	slope	se	slope	se	slope	se
2003	-0.49	0.09	-0.46	0.13	-0.46	0.13	-0.5	0.13
2004	-0.66	0.04	-0.64	0.06	-0.66	0.06	-0.63	0.06
2005	-0.71	0.07	-0.65	0.1	-0.58	0.1	-0.55	0.1
2006	-0.78	0.05	-0.9	0.07	-0.83	0.7	-0.87	0.07
2007	-1.05	0.17	-0.97	0.17	-1	0.17	-0.66	0.17

Table 2.11 Maximum and minimum values of lambda 7 species across 5 years. Species were ranked based on their minimum log lambda (λ) from slowest (*Ornithopus perpusillus*; rank = 1) to fastest increasing (*Aira praecox*; rank = 7) Abbreviations: fec = fecundity, sowden = sowing density, λ = lambda (seed output/seed input), sp = species, rep=replication, Ap = *A. praecox*, At = *A. thaliana*, Cg = *C. glomeratum*, Ev = *E. verna*, Md = *M. discolor*, Op = *O. perpusillus*, Va = *O. perpusillus*.

species	λ at N=1	Fec	max log λ	fec	year	rep	year	rank by max log λ	min log λ	sowden	year	rep	rank by min log λ
Ap	4.69	109	6.53	685	2006	1	2005	1	-0.64	9	2005	2	7
At	6.34	567	6.34	567	2002	1	2004	2	-3.39	8	2006	1	5
Cg	5.82	337	5.82	337	2002	3	2005	4	-3.41	9	2006	3	4
Ev	5.75	314	5.75	314	2003	3	2006	5	-1.36	9	2005	3	6
Md	5.5	245	5.63	279	2005	3	2006	6	-3.45	9	2005	4	3
Op	2	1	5.3	200	2005	2	2006	7	-5.19	9	2006	3	1
Va	6.39	596	6.39	596	2002	3	2002	3	-4.24	8	2005	2	2

2.3.4.5 Year effects on density-dependence in lambda assessed by piecewise regression

Piecewise regression of log lambda against log sowing density fit separately for all species and year, are shown in Fig 2.9. There are significant thresholds for several species in some years.

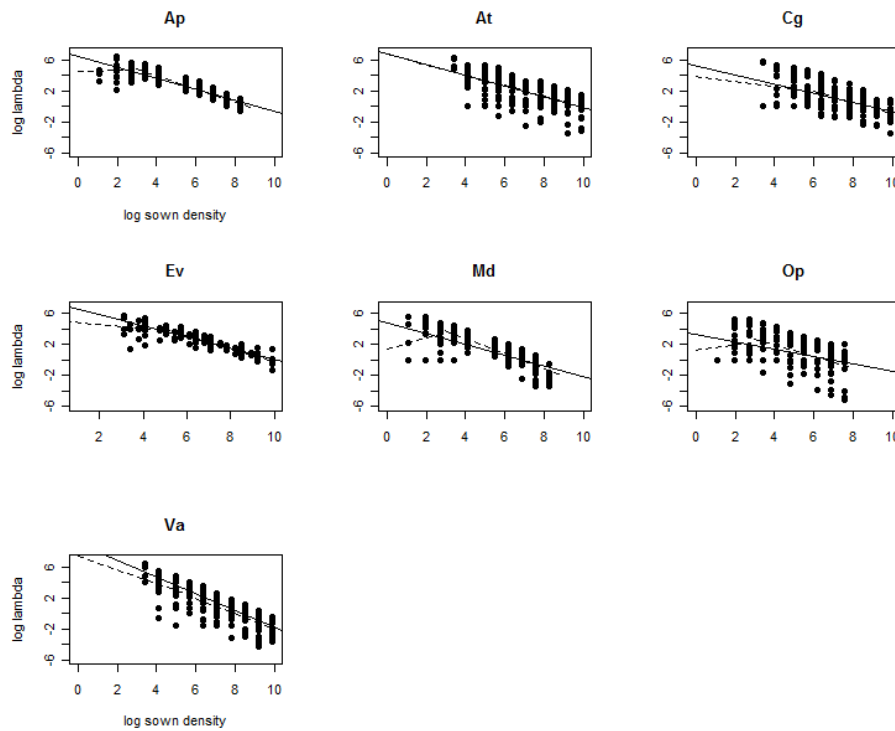


Fig 2.9 Year effects on the nature of density dependence in log (lambda) for all seven species shown in a piece-wise regression in log lambda against log sown density for the 7 species. Comparisons of two models showed, there was a significant threshold in log lambda for *A. praecox* ($I = 4.55298$, $S = 0.029$, $I = 7.36333$, $S = -0.844$, $p = 1.271e-09$), *E. verna* ($I = 5.1$, $S = -0.25$, $I = 8.05$, $S = 0.83$, $p = 4.776e-05$), *M. discolor* ($I = 1.41$, $S = 0.7$, $I = 6.78$, $S = 0.99$, $p = 2.813e-09$) and *O. perpusillus* ($I = 0.31$, $S = 0.76$, $I = 4.53$, $S = -0.68$, $p = 0.0098$) at lower to intermediate sowing density (3rd, 5th, 3rd and 3rd log sowing density respectively) as shown by the first (segment) dotted shallower regression line on the left-hand side ($I = 4.55298$, $S = 0.029$) before declining linearly in subsequent sown densities as shown by the second (segment) steeper dotted regression line on the right-hand side ($I = 7.36333$, $S = -0.844$). The other 4 species did not show a significant threshold at lower or intermediate sowing densities. The solid single regression line shows the overall regression line, where lambda decreases linearly as sowing density increases. Some species showed a significant threshold at lower or intermediate sowing densities at least in one of the 5 years. Abbreviations: I = Intercept, S = slope, p = p-value. $DF = 9$ and 170 , p -value: $< 2.2e-16$. Each data point comes from 625cm^2 .

Table 2.12 Mixed effects model in log lambda. Formula :

$\log(\lambda) \sim \log(\text{sowden}) * \text{sp} * \text{yr} + (1 | \text{plot})$. Most species showed rather little variation in slope or intercept of the relationship between log (lambda) and log (sowing density) across most years. Four species, however, did show significant differences in slope or intercept (or both) in one or more years, as shown in the following mixed effects model. Here, $\log(\lambda) = \log(\text{seed output} / \text{seed sown})$ is modelled as a function of species and year, with plot as a random effect explaining about half of the variance unexplained by the fixed effects (year, species and sowing density). For *Aira praecox* (the Intercept species) the slope was significantly lower and the intercept significantly higher in 2006 than in the other 4 years. Of the other 6 species in 2002 (the first year), *Cerastium glomeratum* and *Veronica arvensis* had significantly higher intercepts than *Aira praecox* and *Veronica arvensis* had a significantly steeper negative slope than *Aira praecox*. Across the 5 years, *Aira praecox* had a significantly higher intercept in 2006 than in 2002. The year-by-species interaction effect on slope was significant for *Cerastium glomeratum* in three years (2004, 2005 and 2006 when the relationship was significantly shallower than in 2002), and for both *Arabidopsis thaliana* and *Veronica arvensis* in two years (2005 and 2006 when the relationship was significantly shallower than in 2002). The other 4 species showed non-significant year effects on the slope. For intercepts, the year-by-species interaction effect was greatest in *Cerastium glomeratum* (lowest in 2006 and never significantly higher than in 2002), and substantial in *Arabidopsis thaliana* and *Veronica arvensis* (both were lowest in 2005 and never significantly higher than in 2002). The model is based on data from 1059 quadrats gathered from 28 plots over 5 years (see text for details).

Linear mixed model fit by REML

Formula: $\log(\lambda) \sim \log(\text{sowden}) * \text{sp} * \text{yr} + (1 | \text{plot})$

AIC	BIC	logLik	deviance	REMLdev
2648	3005	-1252	2337	2504

Random effects:

Groups	Name	Variance	Std.Dev.
plot	(Intercept)	0.49562	0.7040
	Residual	0.51811	0.7198

Number of obs: 1059, groups: plot, 28

Fixed effects:

	Estimate	Std. Error	t value
(Intercept)	6.758378	0.675172	10.010
log(sowden)	-0.710795	0.099073	-7.174
spAt	1.487590	0.871785	1.706
spCg	2.616875	0.917435	2.852
spEv	-0.598215	0.871785	-0.686
spMd	-1.100894	1.011961	-1.088
spOp	-0.101206	2.099056	-0.048
spVa	2.196164	0.871785	2.519
yr2003	-0.487120	0.769647	-0.633
yr2004	-0.123210	0.769647	-0.160
yr2005	1.080044	0.769647	1.403
yr2006	2.269194	0.769647	2.948
log(sowden):spAt	-0.024728	0.117962	-0.210
log(sowden):spCg	-0.246866	0.126810	-1.947
log(sowden):spEv	0.105966	0.117962	0.898
log(sowden):spMd	-0.089771	0.148996	-0.603
log(sowden):spOp	-0.318457	0.331368	-0.961
log(sowden):spVa	-0.361247	0.117962	-3.062
log(sowden):yr2003	0.050137	0.128543	0.390
log(sowden):yr2004	-0.035873	0.128543	-0.279

log(sowden):yr2005	-0.217177	0.128543	-1.690
log(sowden):yr2006	-0.405047	0.128543	-3.151
spAt:yr2003	-1.449867	0.999402	-1.451
spCg:yr2003	-0.982287	1.039462	-0.945
spEv:yr2003	0.826977	0.969050	0.853
spMd:yr2003	0.522639	1.169896	0.447
spOp:yr2003	-0.959028	2.173334	-0.441
spVa:yr2003	-0.757166	0.999402	-0.758
spAt:yr2004	-0.495278	0.999402	-0.496
spCg:yr2004	-6.365949	1.141579	-5.576
spEv:yr2004	1.544180	0.999402	1.545
spMd:yr2004	2.256845	1.138886	1.982
spOp:yr2004	-0.316993	2.173334	-0.146
spVa:yr2004	0.923487	0.999402	0.924
spAt:yr2005	-3.857160	0.999402	-3.859
spCg:yr2005	-4.561660	1.072308	-4.254
spEv:yr2005	1.735596	0.999402	1.737
spMd:yr2005	1.174103	1.138886	1.031
spOp:yr2005	-3.066807	2.201211	-1.393
spVa:yr2005	-5.206515	1.021404	-5.097
spAt:yr2006	-4.711697	1.043101	-4.517
spCg:yr2006	-7.269735	1.095649	-6.635
spEv:yr2006	-0.303059	0.999402	-0.303
spMd:yr2006	-0.757058	1.138886	-0.665
spOp:yr2006	-2.190076	2.183149	-1.003
spVa:yr2006	-3.369016	0.999402	-3.371
log(sowden):spAt:yr2003	0.185832	0.157619	1.179
log(sowden):spCg:yr2003	0.134903	0.164346	0.821
log(sowden):spEv:yr2003	-0.063420	0.157293	-0.403
log(sowden):spMd:yr2003	0.052193	0.196782	0.265
log(sowden):spOp:yr2003	0.312158	0.354882	0.880
log(sowden):spVa:yr2003	0.143687	0.157619	0.912
log(sowden):spAt:yr2004	0.047900	0.157619	0.304
log(sowden):spCg:yr2004	0.640143	0.173307	3.694
log(sowden):spEv:yr2004	-0.116574	0.157619	-0.740
log(sowden):spMd:yr2004	-0.271758	0.188721	-1.440
log(sowden):spOp:yr2004	0.189712	0.354882	0.535
log(sowden):spVa:yr2004	0.001985	0.157619	0.013
log(sowden):spAt:yr2005	0.356529	0.157619	2.262
log(sowden):spCg:yr2005	0.429277	0.167405	2.564
log(sowden):spEv:yr2005	-0.103312	0.157619	-0.655
log(sowden):spMd:yr2005	-0.205229	0.188721	-1.087
log(sowden):spOp:yr2005	0.439733	0.359939	1.222
log(sowden):spVa:yr2005	0.447291	0.159526	2.804
log(sowden):spAt:yr2006	0.364243	0.161488	2.256
log(sowden):spCg:yr2006	0.812711	0.169193	4.803
log(sowden):spEv:yr2006	0.165002	0.157619	1.047
log(sowden):spMd:yr2006	0.084754	0.188721	0.449
log(sowden):spOp:yr2006	0.288316	0.356259	0.809
log(sowden):spVa:yr2006	0.466231	0.157619	2.958

Taking the data for all species above a threshold density ($\log(\text{sowing density}) > 3$) produces the mixed effects model in Table 2.12, based on 1059 quadrats for 7 species over 5 years on 28 plots (4 replicates per species, with the same treatment on a plot over each of the 5 years). The random effect for plot is substantial (0.496 compared

with a residual variance of 0.518). Log lambda is observed to decline more or less linearly with increasing log sowing density but there are significant species and year effects on slope and intercept (Fig 2.8, 2.9 and Table 2.12). The existence of threshold densities, below which there was no negative effect of increasing density on lambda are explained in Table 2.12.

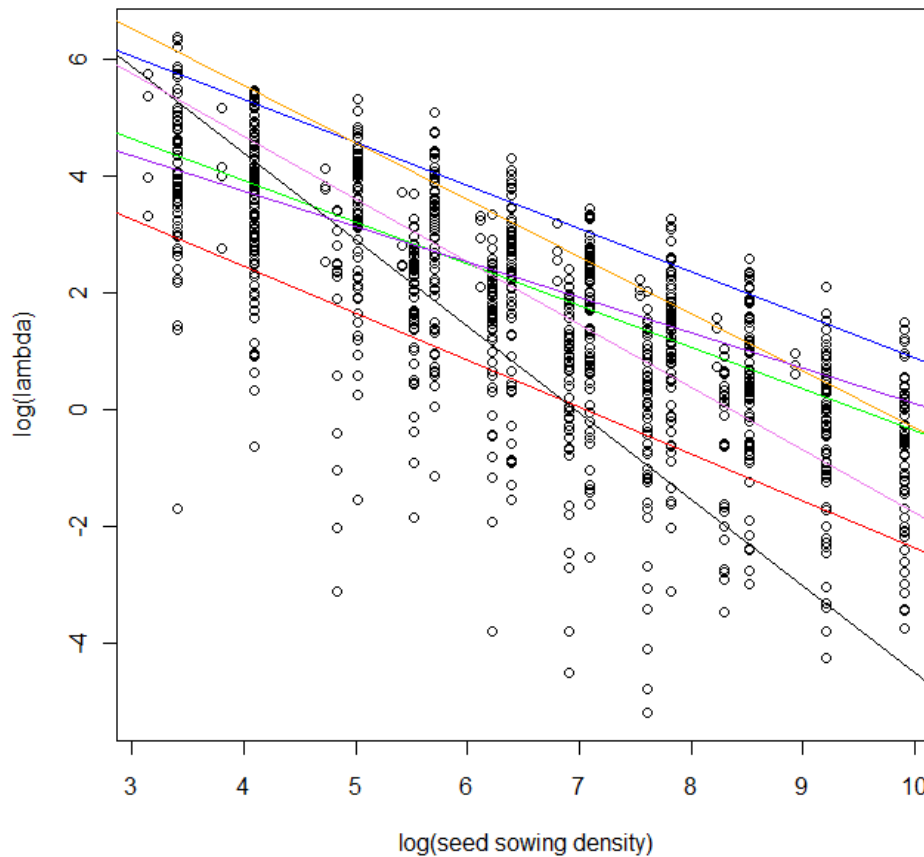


Fig 2.10 Species differences in the relationship between log (lambda) and log (sowing density) in 2002, shown by the 7 solid regression lines. There are significant differences across species in both intercept and slope in this, the first year of the experiment. The scatter plot shows the data for all 5 years to give an impression of the size of the year effects relative to the species effects. *Aira* (green), *Arabidopsis* (blue), *Cerastium* (orange), *Erophila* (purple), *Myosotis* (red), *Ornithopus* (black) and *Violet* (violet). At intermediate sowing densities, the species fall into 3 significantly different groups in 2002: high mean log(lambda) (*Arabidopsis thaliana*, *Cerastium glomeratum*), intermediate log(lambda) (*Aira praecox*, *Erophila verna*, *Veronica arvensis*) and low log(lambda) (*Myosotis discolor*, *Ornithopus perpusillus*). Four of the species passed the invasion criterion on average ($\lambda > 1$) even at the highest densities (*Aira praecox*, *Arabidopsis thaliana*, *Cerastium glomeratum*, *Erophila verna*), while three species failed ($\lambda < 1$) at very high seed sowing densities (*Myosotis discolor*, *Ornithopus perpusillus*, *Veronica arvensis*). Data from 625cm².

2.3.4.6 Adult size classes

The size distribution of adult plants exhibited a clear pattern of density dependence (Fig 2.11).

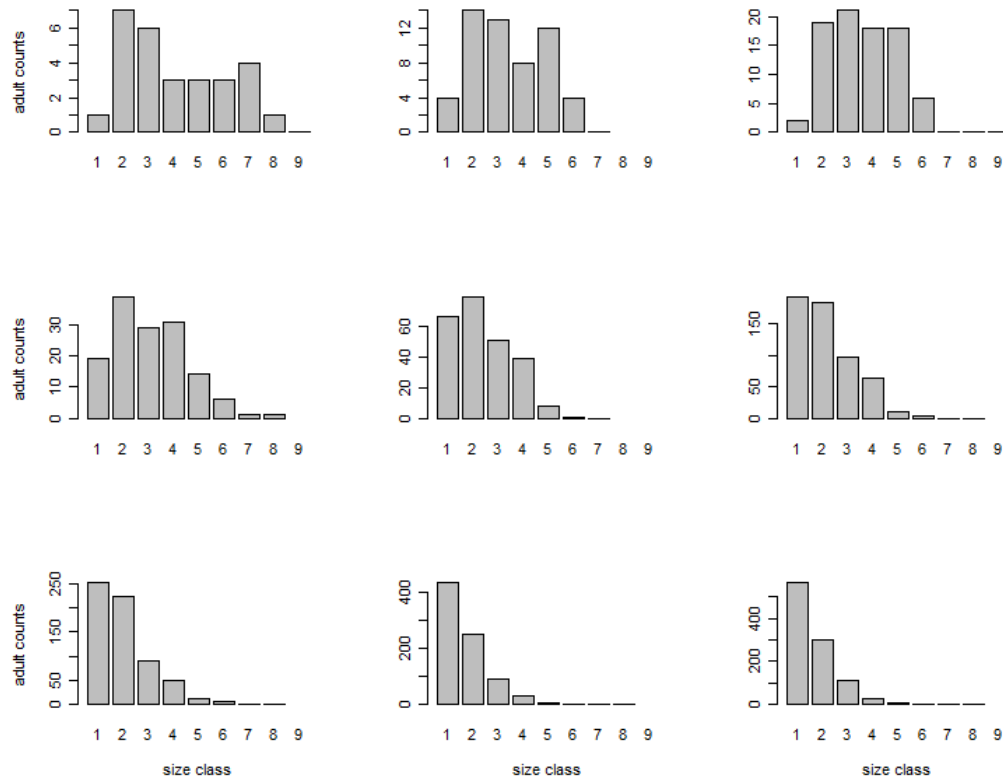


Fig 2.11 Size structure (total adult counts) for *A. praecox* for 2006 in each of the 9 sowing densities (top left = lowest densities; bottom right = highest densities). Other species were less clear but all conform broadly to the decrease shown in total adult counts in each size class with increasing density. Each data point comes from 625cm².

The classic size hierarchy, with many small plants and few large plants, leading to an L-shaped histogram, was observed at the highest sowing densities for all seven species. However, the sowing density at which this L-shaped size structure first appeared varied from species to species. For *Aira praecox* the L-shaped distribution (Fig 2.11) did not appear until sowing density eight; prior to that the histogram showed that the second-smallest size class (sowing densities 1, 2, 4 and 5) or the third-smallest size class (sowing density 3) was the most frequent. The other 6 species also showed a similar pattern although the appearance and magnitude of the L-shaped histogram varied slightly for each species.

2.4 Discussion

All three demographic parameters (recruitment, survival and fecundity) proved to be strongly density dependent in at least some species for all years. Per generation net multiplication rate (λ), which synthesizes these parameters ($\lambda = (\text{proportion recruiting} \times \text{proportion surviving} \times \text{fecundity per survivor})$, with $\lambda > 1$ describing an increasing population) and $\log(\lambda)$ was linearly related to $\log$ sowing density with significant year effects on both slope and intercept. We had hypothesized that at the lowest sowing densities mature plants would be sufficiently well-spaced that they did not interfere with one another (density independent population growth), which would manifest itself as a horizontal relationship between $\log(\lambda)$ and $\log$ sowing density. This was observed, but only for 4 of the seven species and then in only 3 out of 5 years. Either the root systems of the individual plants spread much further at low densities than we anticipated or uncontrolled heterogeneity in substrate created recruitment hot-spots in which plants did compete, despite the overall low density.

Most species showed a significant threshold at lower or intermediate sowing densities in at least one of the 5 years. In some years recruitment was low due to pre-emergence seedling mortality as a result of competition, allelopathy, diseases, microsite-limitation, etc..... Allelopathy is bound to increase at higher plant densities, which is one of the possible reasons for pre-emergence seed/seedling mortality in monocultures. However, it is difficult to distinguish between chemical interference (allelopathy) and competition (Harper 1977a, Weidenhamer 1996).

Density dependent recruitment was first described by (Palmblad 1969) and has been documented subsequently in several experimental systems (Eriksson and Ehrlén 1992, Coomes et al. 2002a, Goodwin et al. 2006). We did not attempt to measure germination in the field, so our measure of recruitment confounds failure to germinate with pre-emergence seedling mortality. Although several plausible mechanisms for density dependent germination are described in the literature (germination suppression chemicals produced by the first to germinate; heterogeneity in propensity to germinate across clutches of seed from the same fruit; allelopathy; microsite-limitation; etc.), we have no evidence of such processes for any of our seven species. We know that the species differ in their propensity for delayed germination

(quiescence plus dormancy; see Chapter 3) so it is quite likely that some of the species germinated progressively smaller fractions of their seeds in autumn or year one and spring of year two as sowing density increased, but we have no direct measure of this. Density dependent mortality, immediately post-germination but pre-emergence, is perhaps the most likely of the two especially in these relatively small-seeded species and in our ultra nutrient-poor experimentally created substrate. The 2mm gravel mulch with which the plots were covered might have crushed to death the tiny seedlings, and this could well have operated in a density-dependent manner.

Density dependent mortality is one of the most widely studied aspects of plant population ecology (Suckachev in Harper 2006, (Yoda 1963, Harper 1977a, Hector et al. 2007). The first studies concentrated on the impact of soil fertility on adult plant population density, making the point that population densities tend to be greatest where the soil conditions are the poorest, and drawing attention to the fact that plants are most likely to kill other plants when they are growing rapidly under conditions of plentiful nutrient and water supply. It is most often competition for light that separates the winners in this contest from the losers (Harper 1977). Much of the work on density dependent mortality concentrated on what came to be known as “self-thinning”. In the context of annual plants, this represented a period of exponential growth when all the plants grew free from competition, then a period when the largest plants began to suppress the smallest individuals, then a final phase during which the total biomass of the community could only increase if suppressed individuals died, allowing the large, surviving plants to grow even larger. In this last phase, the log of the number of surviving plants declined linearly with a slope of -2 as the log of the mean size of the surviving plants increased. Note that as originally formulated, the self thinning rule had the axes confused (with density on the x axis), which gave the misleading impression that increased numbers of plants caused the individual plants to be smaller (as in the Law of Constant Yield; (Weiner and Freckleton 2010)) rather than increasing total biomass causing the smaller plants to die, and hence density (on the y axis) to decline.

We did not attempt to measure the temporal course of self thinning within our cohorts of maturing plants, relying instead on just two density estimates: the number of seedlings and the number of adult plants at fruiting. Nevertheless, our data show very strong patterns of density dependent mortality for all species and for all years.

Species-effects, sowing-density effects and year-effects were all significant. It was very rare to observe 100% mortality, even at the highest sowing densities, indicating that these small plants typically exhibited contest rather than scramble competition (Begon et al. 1996).

The modular construction of vascular plant shoots systems (a leaf subtending a bud that may or may not go on to produce a further leaf and bud or to terminate the line by replacing the vegetative meristem with a (lethal) floral meristem). Fecundity in plants is so plainly related to plant size that it is commonplace to assume a linear relationship between plant shoot size (e.g. shoot dry weight) and total seed production (fecundity) as suggested by Harper (1977). Our data give little support to this simple model for plant fecundity: as mean plant size decreases with increasing plant density, so total seed production per plant declines non-linearly with total shoot dry mass (a pattern that applies equally well across all seven species and all five years, although there are species-specific and year-specific effects on mean seed production).

Seed predation by birds and/or small mammals may have had an important effect on our estimates of fecundity per unit biomass, especially for species like *Erophila verna*, by reducing the apparent number of seeds. The same was true for *Veronica arvensis*, which suffered smut incidence in one year.

Synthesizing the three demographic components (recruitment, survival and fecundity) allows us to calculate a per-generation estimate of net population performance for every combination of species, year and sowing density. We have chosen lambda as the simplest synthetic measure available: this is the average number of seeds produced per seed sown. This was the first published metric for plant demography (The Parable of the Sower: Mark 4... some increased sixty-fold) and is just as useful today as then.

For our seven species, the mean value of lambda was broadly correlated with seed size, as expected (Table 2.11). On log-log scales, lambda decreased more or less linearly with increasing sowing density for all seven species in all five years (with little or no evidence for an hypothesized competition threshold at low densities). Year effects were relatively large in most species. None of the species, however, exhibited extreme or greatly over-compensating density dependence in lambda, and while most species had $\lambda < 1$ at the very highest sowing densities in most years, there were

very few cases where no seed at all was ripened (and even here, of course, we would need to factor in the long-term stabilizing effect of living but non-germinated seed, on the long-term geometric mean value of λ ; see, Seed Bank in Chapter 3).

These simple experiments show that density-dependent effects and year effects are intricately bound up together. For instance, you could argue that seed density was itself a year effect. Alternatively, you might argue that my year effects are, in fact, responses to density differences. Semantics aside, it is clear that a full understanding of plant population dynamics requires that detailed attention is paid to both the main effects of years (weather, disturbance regime, etc) and population density, and to their interaction because we have shown substantial variation in the responses of recruitment, survival and fecundity to the same experimentally controlled population densities, across years of different kinds. The year effects are large, but seldom as great as our experimentally-created range of density effects.

Individual plants are expected to be all relatively small at higher sowing densities due density dependent competition. However, individuals in the largest size classes were found even at the highest densities. There were only a few individuals that showed such characteristics in some years.

Given that shoot biomass was very low in a few cases at low sowing densities, and individual plants were widely spaced, it is most likely that competition was principally below ground. Consistent with this, casual observation did indicate that these small plants had remarkably extensive root systems. We did not attempt to map the root systems in this study. The net multiplication rate at low density was highest for *Veronica arvensis* (6.39) and lowest for *Ornithopus perpusillus* (2). Note that lowest species comfortably passes the invasion criterion ($\lambda = 1$) even in the ultra-low-nutrient environment provided by our experimental raised beds. As expected, λ was smallest in the species with the largest seeds (Levin et al. 2003, Falster et al. 2008, Chisholm and Muller-Landau 2011).

If the field plots are internally heterogeneous, with a few outstandingly good micro sites (e.g. small pockets of well-above-average resource availability), then at low levels of seed input, these rare ultra-good sites might not receive seeds, so no plants grow outstandingly large. On the other hand, at very high seed densities, all the

micro-sites are likely to be occupied, so the ultra-good sites will produce big plants, despite the high density because of asymmetric competition (to the winners go the spoils).

The classic size hierarchy, with many small plants and few large plants leading to an L-shaped histogram, was observed at the highest sowing densities for all seven species. However, the sowing density at which this L-shaped size structure first appeared varied from species to species. Log fecundity increased linearly as biomass increased for all species although the degree of linearity varied from species to species with *Erophila* showing a shallower slope compared with the other 6 species.

Chapter 3

Seed bank dynamics

Abstract

All seven species showed the ability to recruit from seed that had survived in the soil seed bank for at least 12 months. However, all of the species appear to have exhausted their soil seed banks within 4 years of the cohort entering the soil. It is possible that unusual dormancy-breaking conditions might produce further bouts of recruitment, and we have no guarantee that any remaining seeds are dead rather than quiescent or dormant. The seed bank clearly has great potential to enhance coexistence in this system by buffering against total failure of cohorts recruiting in one or more years.

3.1 Introduction

The existence of a bank of viable seeds in the soil provides a potentially important mechanism of coexistence (Cohen 1968). Complete failure of one or more cohorts need not necessarily lead to extinction (Baskin and Baskin 1998). Species that respond to different germination cues might be to coexist more readily than species responding to the same germination cues (Venable and Brown 1988).

The study of seed banks has a long history in agriculture (e.g. the Broadbalk Experiment at Rothamsted, which was begun in 1852) and has been recognized as a potentially important mechanism of coexistence, especially for annual plant species, for many years (Palmblad 1969, Linhart 1976, Inouye 1980, Baskin and Baskin 1987, Baskin 1989, Baskin and Baskin 1989, Baskin and Baskin 2004). The fundamental idea is a straightforward extension of risk-spreading: if all of the seeds germinate at one time, then they may all perish before setting seed and local extinction could result. A more sophisticated strategy might involve seeds that were capable of sensing the local environment, and germinating only when conditions for seedling establishment were ideal, e.g. using the red-to-far-red ratio as a gap-detection mechanism (Pons 1989, Corkidi et al. 1991, Pearson et al. 2002).

Experimental studies of seed banks quickly drew attention to a number of complicating issues, especially to do with differences in usage of the term ‘seed dormancy’. The important point is that not all seeds in the soil are dormant. Many (sometimes most or even all) of the non-germinated seeds in soil will germinate as soon as they are provided with the appropriate conditions of light, moisture, temperature, oxygen, etc. (Baskin 1989, Thompson 2010). These seeds are best referred to as quiescent .

A seed which is alive as assessed by a test such as trizolium or tetrazolium (Yaklich and Kulik 1979, Vanwaes and Debergh 1986, Don et al. 1990) but which will not germinate when provided with the appropriate conditions is said to be dormant. Dormancy can be ‘broken’ in a number ways. One of the classic mechanisms of breaking dormancy is a chilling requirement. This ensures that seeds that ripened in summer will not germinate until after the winter, so their seedlings are not exposed to potentially lethal frosts. Thus, a “spring annual” with frost sensitive seedlings would be expected to remain dormant, and would not germinate in warm, moist soil in autumn, but would delay germination until the same temperatures and soil moistures occurred in spring, once their dormancy had been broken by winter frosts. Some species show dormancy breaking mechanisms of exquisite complexity, e.g. the South African fynbos species that require treatment with specific kinds of smoke that indicate that a recent fire has created conditions suitable for seedling recruitment, free from competition from adult plants (Brown 1997).

3.2 Theory

The theory of seed bank dynamics is relatively straightforward. A uniform cohort of seeds with no dormancy will germinate synchronously given that all of the seeds are exposed to the temperature, light and soil moisture required for germination. If some of the seeds are in different microhabitats (e.g. buried in soil, and hence not exposed to light), then they might not germinate, and their numbers would decline exponentially over time as a result of seed mortality (predation, rotting, etc). Eventually, the surviving seeds might be brought within a suitable microhabitat (e.g. by soil disturbance through cultivation, or as a result of soil movement by earthworms

or moles) and these seeds would then germinate. Thus, even with no dormancy, seed germination could occur over a protracted period.

The simplest seed bank model would have a single class of seeds (i.e. all seeds alike in all their attributes): the essential parameters are the death rate of the seeds in soil, and their germination rate (both measured as fractions of surviving seeds per unit time). Let the germination rate = 20% and the death rate = 10%. If we start with 100,000 seeds at time 0 then the number of seeds appearing each time period is as shown in Fig 3.1a. Note that on a log scale, the number of seedlings appearing declines linearly with time (Fig 3.1b): this is a pure exponential decay process.

Now suppose that there were *two* classes of seed in a cohort: both suffer the same death rate in the soil (say 10% per time period), but one has only half the germination rate of the other (say 10% of surviving seeds per time period compared with 20%). The time course of seedling appearance looks superficially similar (compared with (cf) Fig 3.1a) but, when we plot the log of the number of seedlings appearing per time period, the relationship is curved figure (3.1d).

The curvature is not large, but it is highly significant when assessed by fitting a quadratic term for time ($p < 0.00001$): the simulated two-class data are shown as a solid line in Fig 3.1d, and a linear regression as a dotted line. In field data, however, it would require a substantial effect of the two classes for this to be detectable as a significant curvature in the time series of seedling appearance, against the inevitable background variance derived from spatial and temporal heterogeneity.

The size of the seed bank at any point in time is a balance between input of fresh seed by resident adult plants and immigration of seed (possibly of various ages and states of dormancy) from elsewhere, against losses through export and germination. Fig 3.2 shows a simple model system for a cohort of seeds with two dormancy states. The greater the dormancy the larger the seed bank, but the greater the delay in production of the next generation of seeds. This means that the fitness consequence of different dormancy strategies are potentially complex (Cohen 1968). Of course, seeds that germinate early and survive to adulthood may have considerably higher fitness than seeds that exhibit delayed germination. The optimal seed strategy for a parent might

be for a mix of germination strategies amongst its offspring, some germinating early and some entering long-term dormancy. This figure is based on two classes of dormancy behaviour, but in practice we would never know how many classes there were, nor their different rates of loss of dormancy.

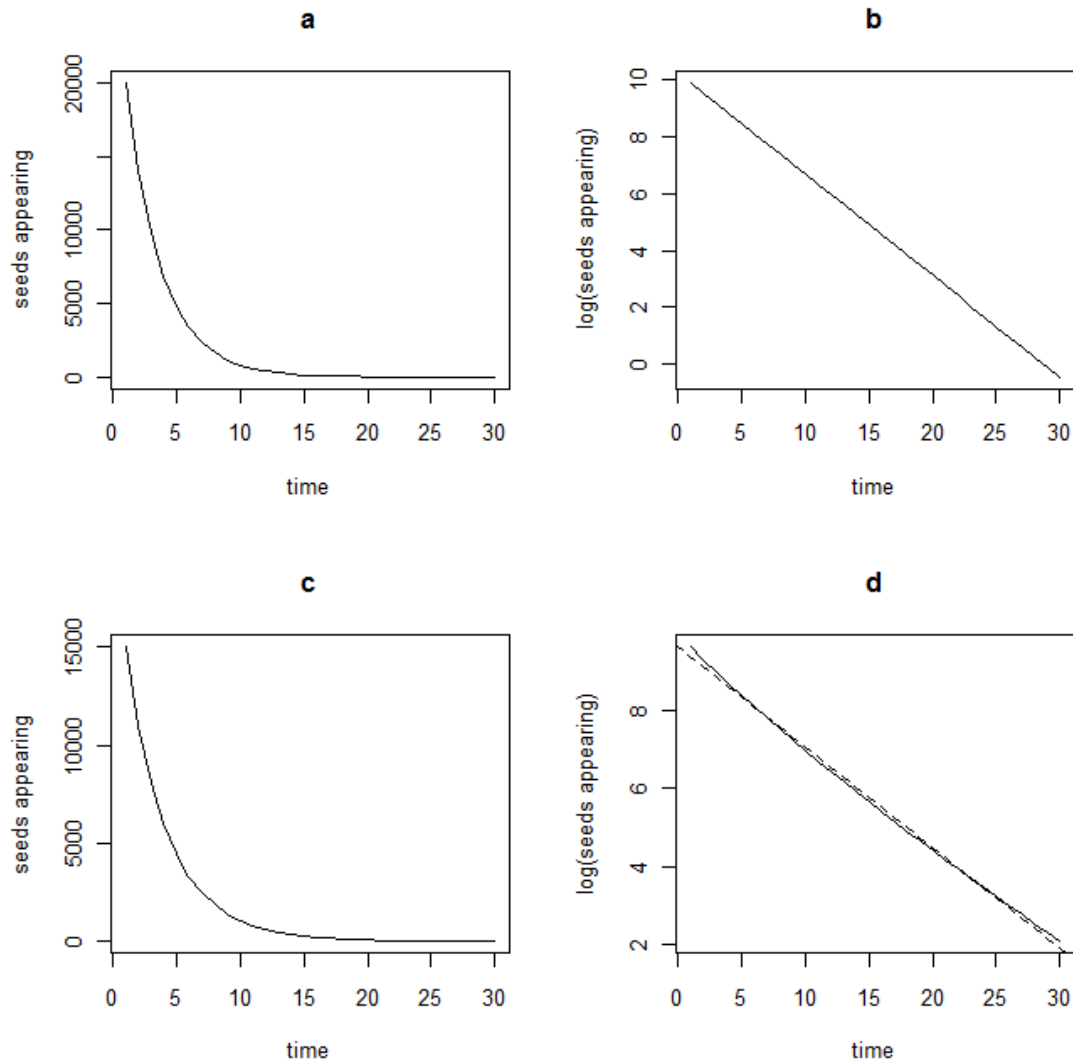


Fig 3.1 Seedling recruitment curves. (a) seeds appearing as a function of time for a pure exponential decay process; (b) the same as a log scale; (c) seeds appearing as function of time with two classes of seeds (see text); (d) the same on a log scale.

Seed dormancy has been considered, almost without exception, as a bet-hedging strategy in a temporally varying environment (Cohen, 1968). However, seed dormancy can improve the reproductive success of the mother plant when competition between sibling seedlings and adult plants is intense even if the environment is temporally invariable (Nilsson et al. 1994).

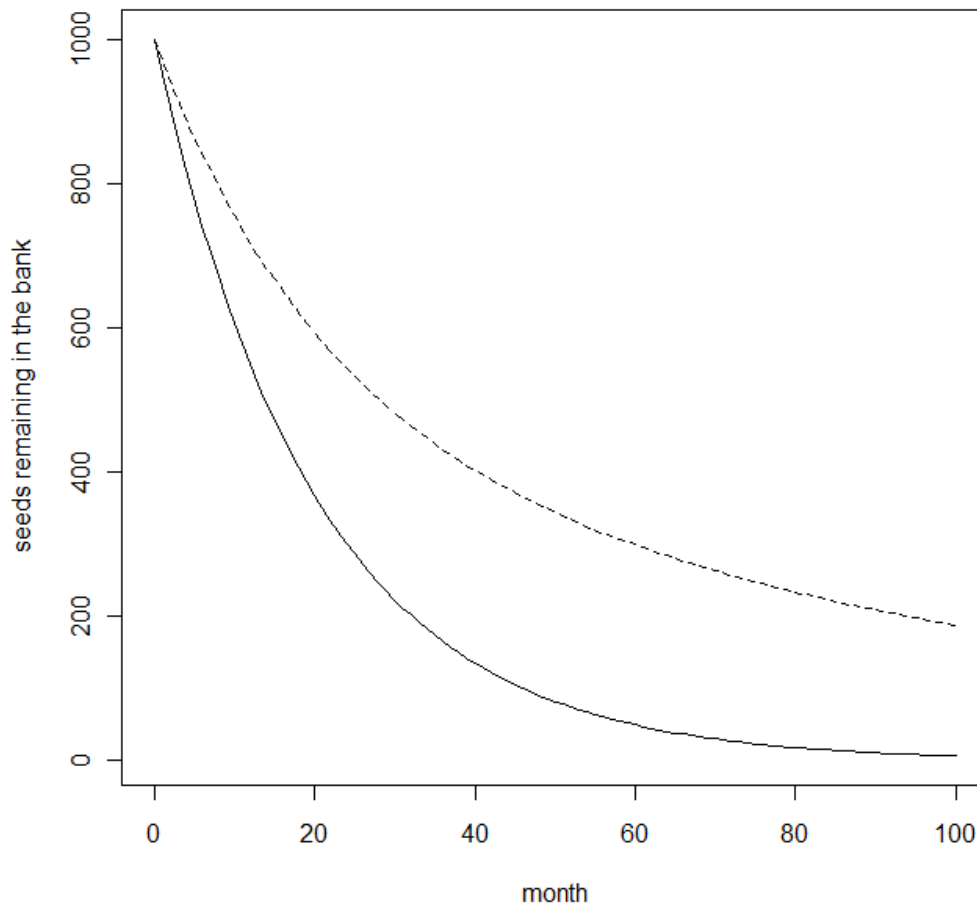


Fig 3.2 Contrasting seed banks: the solid line shows the decay of a seed bank with a constant fraction of germination per month with numbers, declining exponentially over time; the dotted line shows a seed bank comprising two classes of seed, half of the initial seeds had a germination rate the same as the solid curve and half had a higher rate of dormancy. The risk-spreading advantage of the higher dormancy class is illustrated by the “fatter tail” of the dotted line.

In field situations, of course, it is impossible to know how many classes of dormancy are represented by the seeds present within the seed bank (Roberts 1986, Rees and Long 1992). Likewise, in practice, we typically know little or nothing about the precise disturbance regime necessary to expose the germinable but quiescent fraction of seeds to germination conditions. Thus, there is no quantitative theory predicting the duration of viability in a given cohort of seeds.

In addition, real soils do not contain single cohorts of seeds. Instead, the soil seed bank is made up of seeds produced in (possibly many) different years. There is no way of knowing how many cohorts of seeds are present in any body of soil, nor how abundant each cohort is, nor the rate at which dormancy is being broken in different cohorts. For six of our seven species, there is only rather sparse information, but a great deal is known about germination and dormancy in *Arabidopsis thaliana* (Bewley 1982, Debeaujon et al. 2000, Donohue et al. 2007).

3.3 Materials and methods

3.3.1 Site

The work was carried out at Pound Hill in Silwood Park Berkshire UK (Grid Reference SU 938 694), with the area chosen because of its relative isolation from populations of the study species (Table 1) in order to minimize the rate at which seeds would be expected to immigrate to the plots. A herbivore-proof site (deer and rabbit enclosure) with a fence height of 1.8m was set up in 2002. In total, thirty six plots were set out in four blocks in a 4 x 9 grid, inside a 27m x 27m fence; 28 plots were sown (four replicates for each of 7 species) and 8 plots were left blank, four to estimate the rate of seed immigration and four to estimate the amount of seed imported with the ballast that had been used to construct the base of the raised beds.

3.3.2 Seed sowing

Seeds for each species were weighed into appropriate batches (Table 3.1) and were sown on 12/09/2002 by sprinkling the seeds evenly over a 25cm x 25cm sector located in the centre of the raised bed. One species was sown in each raised bed, with the identity of the sown species randomized independently for each of the four blocks. The key design feature of this experiment was to remove any of the 7 experimental species before they had a chance to flower, thus ensuring that all the seedlings had come from the seed bank of the initial sown cohorts and not from subsequent reproduction.

Table 3.1 Seed sowing rates, sowing dates and dates of the first seedling count for each of the seven species at Pound Hill seed bank experiment.

Species	sowing density per 25 cm x 25 cm	sowing date	first seedling count dates
<i>Aira praecox</i>	2,000	19/09/2002	02/06/2003
<i>Arabidopsis thaliana</i>	10,000	12/09/2002	12/05/2003
<i>Cerastium glomeratum</i>	10,000	17/09/2002	21/05/2003
<i>Erophila verna</i>	10,000	12/09/2002	10/03/2003
<i>Myosotis discolor</i>	2,000	18/09/2002	21/05/2003
<i>Ornithopus perpusillus</i>	1,000	19/09/2002	05/09/2003
<i>Veronica arvensis</i>	10,000	17/09/2002	02/06/2003

3.3.3 *Seedling appearance*

The first seedlings were noted on 12/12/2002. Counting and removal of the emerged seedlings was carried out over the following years (2003 - 2007). The last survey was on 15/04/2007. All emerged (above ground) plants were counted and then uprooted with minimum disturbance to the soil surface. Plants were removed as soon as they were identifiable, and well before they were able to flower. Seedlings that germinated and might have died below ground were not counted.

Table 3.2 Seed bank of the seven species, showing dates when plants were counted and removed from the plots. Seeds were sown in September 2002.

<i>A. praecox</i>	<i>A. thaliana</i>	<i>C. glomeratum</i>	<i>E. verna</i>	<i>M. discolor</i>	<i>O. perpusillus</i>	<i>V. arvensis</i>
02/06/2003	12/05/2003	21/05/2003	10/03/2003	21/05/2003	05/09/2003	02/06/2003
23/10/2003	18/12/2003	18/12/2003	18/12/2003	18/12/2003	18/12/2003	18/12/2003
18/05/2004	11/04/2004	04/05/2004	20/03/2004	04/05/2004	29/06/2004	18/05/2004
10/12/2004	10/12/2004	10/12/2004	10/12/2004	10/12/2004	10/12/2004	10/12/2004
06/05/2005	05/04/2005	05/04/2005	05/04/2005	05/04/2005	30/06/2005	05/04/2005
28/09/2005	28/09/2005	28/09/2005	28/09/2005	28/09/2005	28/09/2005	28/09/2005
06/04/2006	06/04/2006	06/04/2006	06/04/2006	06/04/2006	06/04/2006	06/04/2006
05/05/2006	05/05/2006	05/05/2006	05/05/2006	05/05/2006	05/05/2006	05/05/2006
26/05/2006	26/05/2006	26/05/2006	26/05/2006	26/05/2006	26/05/2006	26/05/2006
08/09/2006	08/09/2006	08/09/2006	08/09/2006	08/09/2006	08/09/2006	08/09/2006
29/09/2006	29/09/2006	29/09/2006	29/09/2006	29/09/2006	29/09/2006	29/09/2006
23/10/2006	23/10/2006	23/10/2006	23/10/2006	23/10/2006	NA	23/10/2006
NA	01/11/2006	01/11/2006	01/11/2006	NA	NA	01/11/2006
NA	14/12/2006	14/12/2006	14/12/2006	NA	NA	14/12/2006
NA	15/02/2007	15/02/2007	15/02/2007	NA	NA	15/02/2007
NA	15/04/2007	NA	15/04/2007	NA	NA	15/04/2007
NA	06/06/2007	NA	06/06/2007	NA	NA	06/06/2007

3.3.4 The Ashurst Seed Bank Experiment

The 2002 seed bank experiment at Pound Hill was repeated at Ashurst (Grid Reference 41/938 694) in fall 2004. This design confounds year effects with spatial effects. There was no attempt to assess year effects at either site for want of space to accommodate the extra plots.

3.3.5 Layout of the sectors

Seed of each of the seven species was collected in the summer of 2004 and were sown in the only available four plots in a randomly located 3 x 3 sectors, each measuring 25cm x 25cm of 75cm x 75cm total size within 1m x 1m plot identical to that of the monoculture experiment, on 03/11/2004 at the rate of 600 seeds per sector.

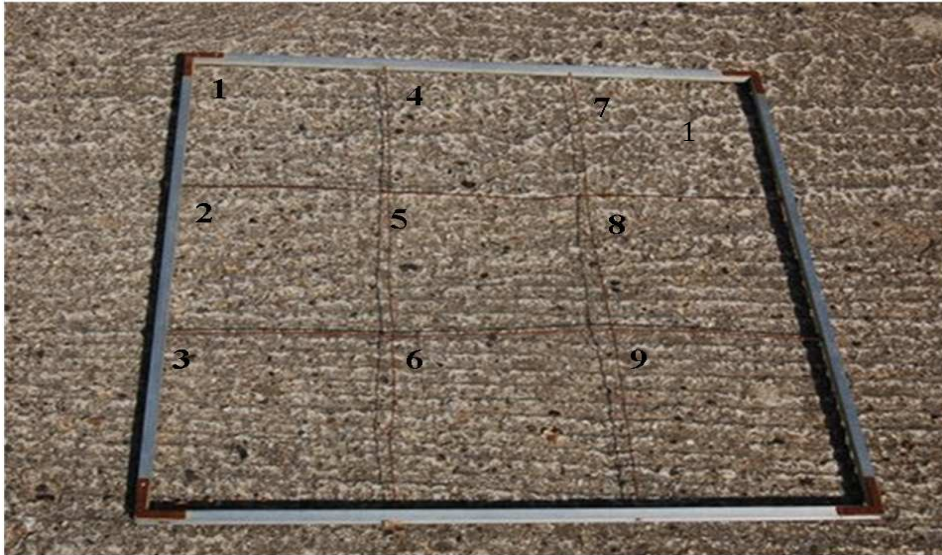


Fig 3.3 A 75cm x 75cm frame with nine sectors (each 25 cm x 25 cm) ranging from 1 to 9 was placed in the centre of the 1m x 1m plot for seed sowing and locating of recruits before they were counted and removed.

Instead of sowing one species per plot (as at Pound Hill) we sowed 9 quadrats per plot (as for the monocultures described in chapter 2) using four spare plots left over from the main experiment. Thus, there were $4 \times 9 = 36$ quadrats in all, allowing 5 replicates for six of the species, 6 replicates for one species (chosen at random to be *Veronica arvensis*).

Seeds were sown on 03 November 2004. Emerging seedlings were counted and removed for the next two years until 31/03/2007 which marked the end of the experiment.

3.3.6 Statistical modeling

Because of the time course of seedling emergence turned out to be idiosyncratic with species and spatial replicate, we used generalized additive models (Wood 2006) rather than parametric models (like the exponential) to interpret species differences. The models were fitted in R (R Core Development Team 2011) using `gam` in the `mgcv` package. The non-parametric smoothers with time were fit by species with a parametric main effect for each species.

```
Model<-gam(counts~s(days), by = sp) + sp, data=data)
```

Analysis of devians (one-way anova) with poisson error was performed for seedling counts over time for each species. Proportion test was also carried out to assess the fraction of recruitment from sown density for each species. Comparisons were made between seed size and longevity for each species with a simple linear regression, to look for trends.

3.4 Results

Total recruitment over 5 years from the Pound Hill sowing of 2002 was low for all species (maximum 22% for *Ornithopus perpusillus*), and exceptionally low for 5 others (*Myosotis discolor*, *Erophila verna*, *Arabidopsis thaliana*, *Veronica arvensis* and *Cerastium glomeratum* which were all less than 10% ; Table 3.3). Total recruitment was much higher from the Ashurst sowing of 2004 (Table 3.4). Across species, the rank of total recruitment was reasonably consistent for some species (e.g. *Aira* was first at Ashurst, second at Pound Hill), but highly inconsistent for others (e.g. *Ornithopus* was first at Pound Hill but sixth at Ashurst). Unfortunately, we have no way of knowing whether these were year effects or site effects, because we have no replication of sowing year at either site.

Table 3.3 Total recruitments from seeds sown in 2002 at Pound Hill summed over 4 plots and years. Recruitment was highest for *Op* but lowest for *Cg*. Sowing density was summed over 4 quadrats.

Species	Sown density	Recruitment	% Recruitment
<i>Ornithopus perpusillus</i>	4000	876	21.9
<i>Aira praecox</i>	8000	1481	18.5
<i>Myosotis discolor</i>	8000	707	8.8
<i>Erophila verna</i>	40000	2435	6.1
<i>Arabidopsis thaliana</i>	40000	2049	5.1
<i>Veronica arvensis</i>	40000	2031	5.1
<i>Cerastium glomeratum</i>	40000	1262	3.2

Table 3.4 Total recruitments from seeds sown in 2004 at Ashurst summed over 5 quadrats for 6 species, 6 quadrats for 1 species, each quadrat sown with 600 seeds. Recruitment was highest for *Ap* but lowest for *At*. Each quadrat is 625cm² and sowing density was summed over 5 or 6 quadrats.

Species	Sown density	Recruitment	% Recruitment
<i>Aira praecox</i>	3000	2490	83
<i>Myosotis discolor</i>	3000	2100	70
<i>Veronica arvensis</i>	3600	1980	55
<i>Cerastium glomeratum</i>	3000	1392	46.4
<i>Erophila verna</i>	3000	1383	46.1
<i>Ornithopus perpusillus</i>	3000	1050	35
<i>Arabidopsis thaliana</i>	3000	480	16

3.4.1 Emergence from the seed bank

If we quantify the seed bank by the number of days after sowing when the last seedling was observed, then the species were ranked as follows: at Pound Hill, *Erophila verna* (1565 days) > *Arabidopsis thaliana* (1560 days) > *Veronica arvensis* (1550 days) > *Aira praecox* (1189 days) > *Myosotis discolor* (1179 days) > *Ornithopus perpusillus* (1152 days) > *Cerastium glomeratum* (929 days). At Ashurst, over a shorter period of time, the ranking was *Erophila verna* (1082 days) > *Veronica arvensis* (1080 days) > *Arabidopsis thaliana* (830 days) > *Cerastium glomeratum* (607 days) > *Myosotis discolor* (600 days) > *Aira praecox* (555 days) > *Ornithopus perpusillus* (463 days) .

Comparing the two experiments, *Erophila verna* showed the longest-lived seed bank in both cases and *Ornithopus perpusillus* was in the bottom two in both cases. *Arabidopsis thaliana* and *Veronica arvensis* occupied either second or third position in both trials, but the other four species were variable in their ranks (between four and seven).

3.4.2 Time course of seedling emergence at Pound Hill

Spatial and temporal heterogeneity in seedling emergence from the bank is illustrated by the behaviour of *Erophila verna* at Pound Hill (Fig 3.4).

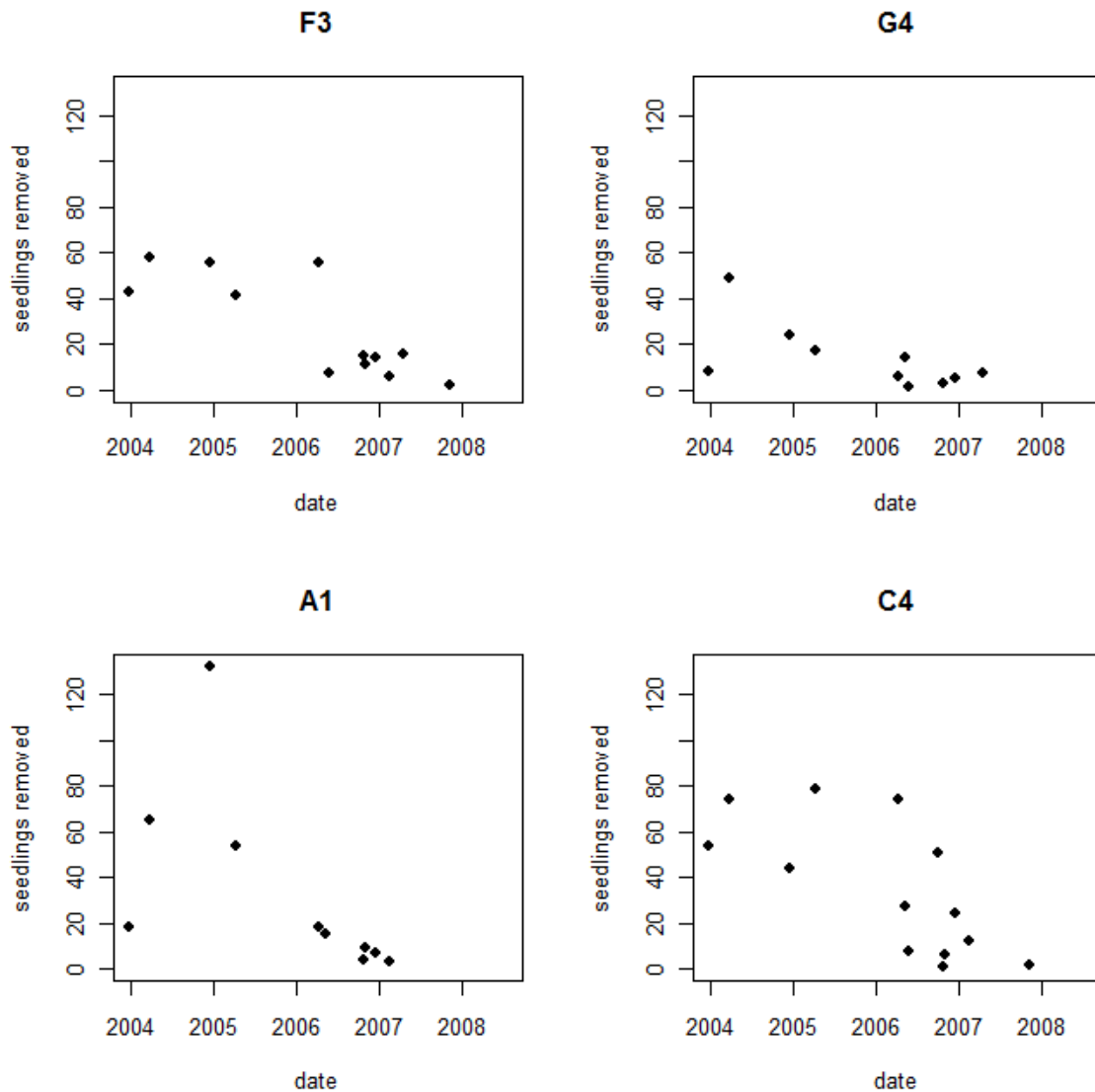


Fig 3.4 Emergence from the seed bank by *Erophila verna* at Pound Hill, showing numbers of seedlings removed on each sampling occasion against date of sampling in four replicate plots (F3, G4, A1 and C4). In none of the four replicates does the time series look anything like the exponential decay predicted by simple theoretical models like Fig 3.1. Plots F3 and C4 showed relatively constant emergence over the period 2003- 2006 (c. 60 seedlings per sample, while emergence rises at first then falls on Plots G4 and A1, but peak emergence was more than twice as high on Plot A1 than on G4. In the face of this heterogeneity, model choice for the statistical part of the exercise was impossibly difficult. No simple parametric form would adequately describe the different outcomes for replicates or species. Each data point comes from count dates (date) in an area of 625cm².

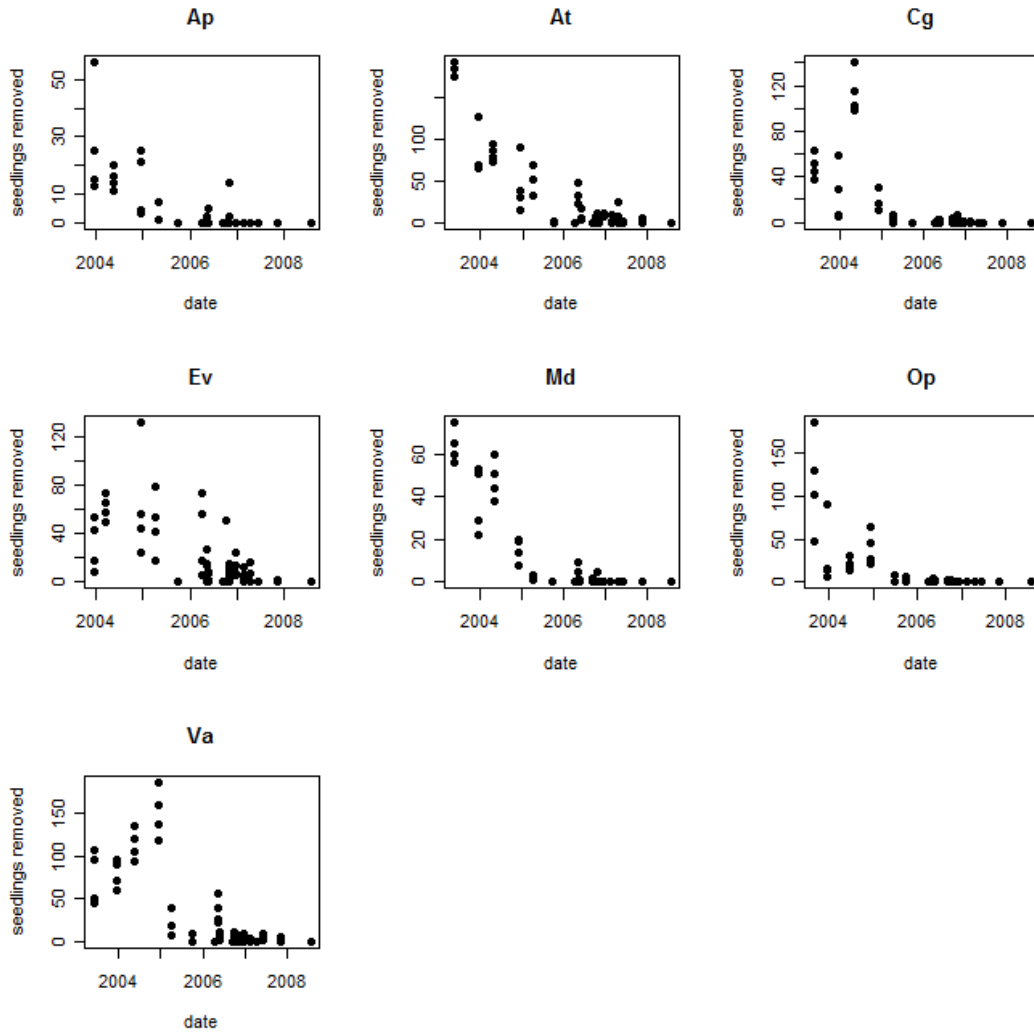


Fig 3.5 Time series of emergence of 7 species at Pound Hill aggregated across 4 replicate plots. Four of the species approximated a monotonic decline over time (Ap, At, Md and Op) but Va showed a protracted period of increasing seedling appearance (up to 2005) and Cg and Ev showed shorter periods of increase. None of the species showed any seedling appearance in 2008. Abbreviations: Ap = *Aira praecox*, At = *Arabidopsis thaliana*, Cg = *Cerastium glomeratum*, Ev = *Erophila verna*, Md = *Myosotis discolor*, Op = *Ornithopus perpusillus*, Va = *Veronica arvensis*. Each data point comes from count dates (date) in an area of 625cm².

As an example of a species showing approximately exponential decline, Fig 3.6 shows the time series for seedling appearance of *Aira praecox* at Pound Hill. The four replicates fall into two groups that are significantly different from one another in decay rate ($p = 0.05$). Within the two groups, there is too little data to compare a one-class exponential model with a two-class exponential (as illustrated in Fig 3.2).

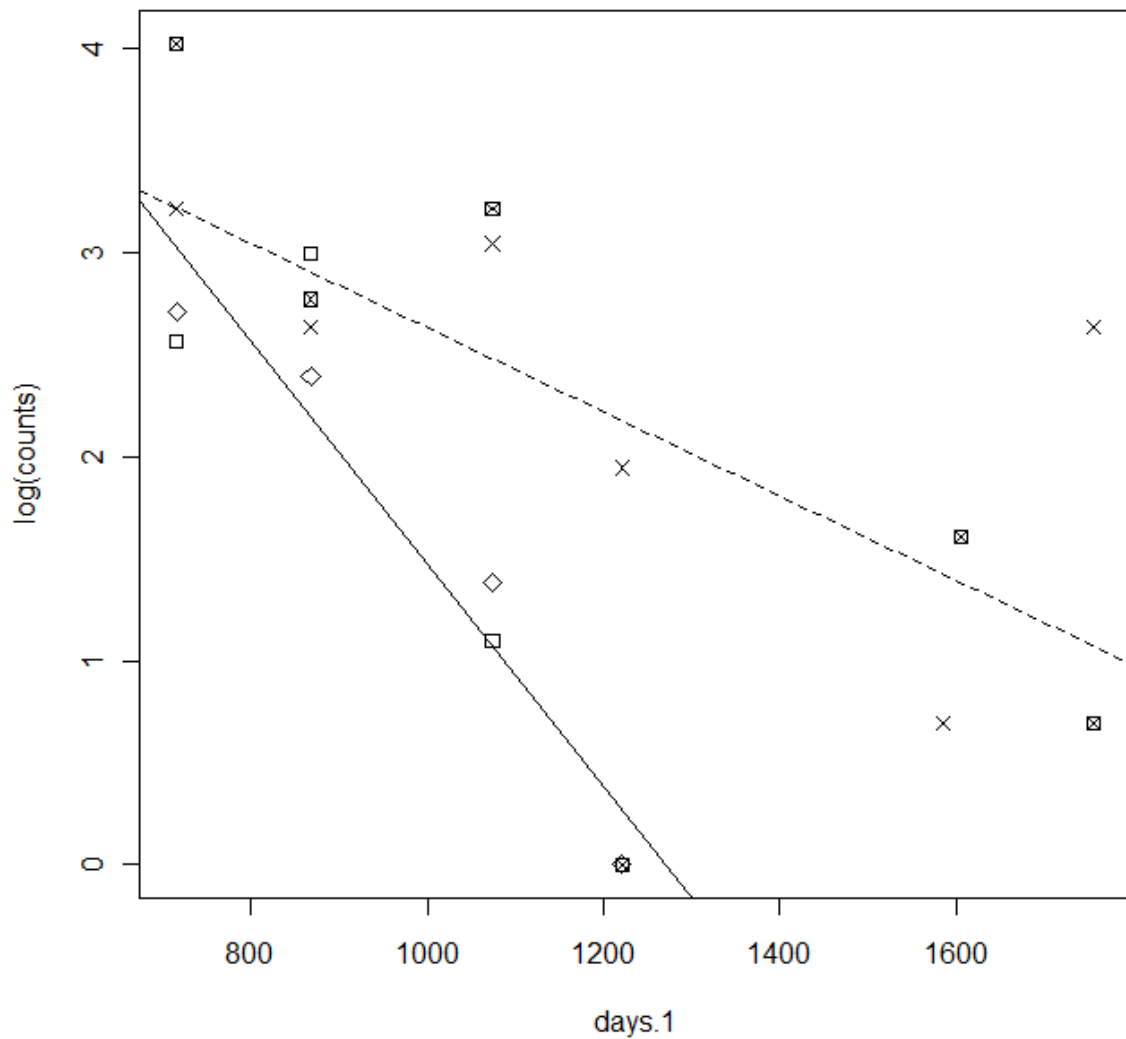


Fig 3.6 Decline in log (seedling appearance) with time for 4 replicate plots (625cm²/replicate) sown with *Aira praecox*. The two plots A3 and F2 (open square and diamond) have a significantly ($p = 0.05$) steeper decay rate solid line; slope = -0.005472) than the two plots D4 and H3 (cross and filled square; dashed line = -0.002065). The spatial heterogeneity across 4 replicate plots would have caused the data set as a whole to appear to consist of two classes of dormancy if the data had been lumped together, with significant curvature in the plot of log(counts) against time (quadratic term has $p = 0.02$). This draws attention to the fact that spatial heterogeneity can be misinterpreted as temporal heterogeneity when data are aggregated inappropriately. Data points (days) show days when recruitments were recorded.

Table 3.5 Effects and their standard errors for a generalized additive model fitting non-parametric smoothers to the trends shown in Fig 3.5. The form is
`model <- gam(counts~s(days.1, by =sp)+sp,data=data)`
 fitting 7 trends and 7 intercepts, one for each species. The Intercept is sp = AP (*Aira praecox*). The other species are AT = *Arabidopsis thaliana*, CG = *Cerastium glomeratum*, EV = *Erophila verna*, MD = *Myosotis discolor*, OP = *Ornithopus perpusillus*, VA = *Veronica arvensis*. Compared with *Aira*, *Ornithopus* showed a significant decline in recruitment from the seed bank following seed sowing but *Myosotis* showed no significant difference. The other 4 species showed a significant increase in the seed bank over time.

Parametric coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	111.359	9.258	12.029	< 2e-16	***
spAT	373.445	13.096	28.517	< 2e-16	***
spCG	370.475	13.099	28.282	< 2e-16	***
spEV	308.003	13.099	23.513	< 2e-16	***
spMD	-9.903	13.099	-0.756	0.449981	
spOP	-46.620	13.117	-3.554	0.000413	***
spVA	388.009	13.101	29.617	< 2e-16	***

Approximate significance of smooth terms:

	edf	Ref.df	F	p-value	
s(days.1):spAP	8.434	8.904	249.37	<2e-16	***
s(days.1):spAT	8.992	9.000	6133.77	<2e-16	***
s(days.1):spCG	8.993	9.000	6146.47	<2e-16	***
s(days.1):spEV	8.996	9.000	6113.97	<2e-16	***
s(days.1):spMD	8.810	8.988	244.66	<2e-16	***
s(days.1):spOP	6.520	7.521	71.96	<2e-16	***
s(days.1):spVA	8.992	9.000	6136.46	<2e-16	***

R-sq.(adj) = 0.997 Deviance explained = 99.8%
 GCV score = 7707.9 Scale est. = 6836.5 n = 608

Table 3.6 Total seedling counts (summed over 4 replicate plots) for 7 species over years 2002 – 2008. The statistics were carried out as the proportions to account for different sowing densities. Significance was assessed using GLM with Poisson errors, comparing the counts across species one year at a time in a simple one-way analysis of deviance.

(a)

species	2002	2003	2004	2005	2006	2007	2008
<i>Aira</i>	8000	1334	114	10	23	0	0
<i>Arabidopsis</i>	40000	1090	501	185	222	56	0
<i>Cerastium</i>	40000	298	923	15	25	1	0
<i>Erophila</i>	40000	1322	502	191	376	48	0
<i>Myosotis</i>	8000	411	254	9	33	0	0
<i>Ornithopus</i>	4000	591	240	23	22	0	0
<i>Veronica</i>	40000	612	1053	95	244	27	0

(b) As above but showing proportions (total seedlings for each year/seed sown).

species	Seed sown	2003	2004	2005	2006	2007	2008
<i>Aira</i>	8000	0.1668	0.0143	0.0013	0.0029	0.0000	0.0000
<i>Arabidopsis</i>	40000	0.0273	0.0125	0.0046	0.0056	0.0014	0.0000
<i>Cerastium</i>	40000	0.0075	0.0231	0.0004	0.0006	0.0000	0.0000
<i>Erophila</i>	40000	0.0331	0.0126	0.0048	0.0094	0.0012	0.0000
<i>Myosotis</i>	8000	0.0514	0.0318	0.0011	0.0041	0.0000	0.0000
<i>Ornithopus</i>	4000	0.1478	0.0600	0.0058	0.0055	0.0000	0.0000
<i>Veronica</i>	40000	0.0153	0.0263	0.0024	0.0061	0.0007	0.0000

There was no recruitment of any species observed in 2008 (Table 3.6). In 2007 At and Ev still showed significant recruitment (56 and 48 seedlings respectively), while Va produced significantly fewer seedlings (27 with $p < 0.001$). In 2006 all species produced some seedlings; Ev had significantly more than any other species ($p < 0.01$), At and Va were not significantly different from one another (222 and 244 respectively), and the other species were very similar (Ap = 23 seedlings, Cg = 25, Md = 33 and Op = 22), but significantly fewer than At or Va ($p < 0.001$). In 2005 the pattern was complicated by the fact that recruitment in Va was still increasing (Fig 3.5).

3.4.3 Time course of seedling appearance at Ashurst

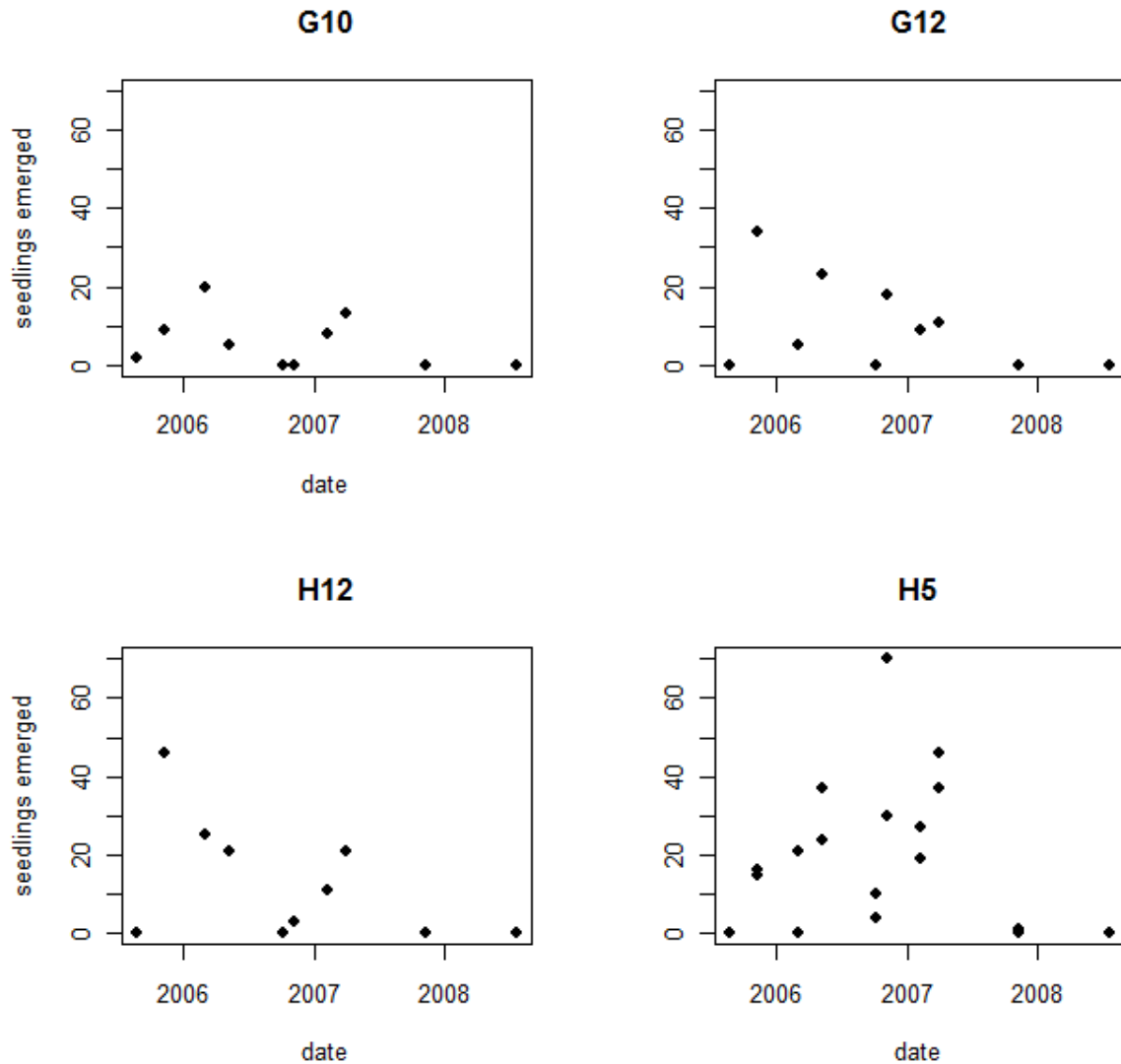


Fig 3.7 Emergence from the seed bank by *Erophila verna* at Ashurst, showing numbers of seedlings removed on each sampling occasion against date of sampling in four replicate plots (G10, G12, H12 and H5). In none of the four replicates does the time series look anything like the exponential decay predicted by simple theoretical models like Fig 3.1. Plots H12 and G12 showed relatively constant emergence over the period 2006- 2008 (c. 35 - 45 seedlings per sample) while emergence rises at first then falls on Plots H5, but peak emergence was more than twice as high on Plot H5 than on G12. In the face of this heterogeneity, model choice for the statistical part of the exercise was impossibly difficult. No simple parametric form would adequately describe the different outcomes for replicates or species. Each data point relates to count dates (x-axis, date) which comes from 625cm².

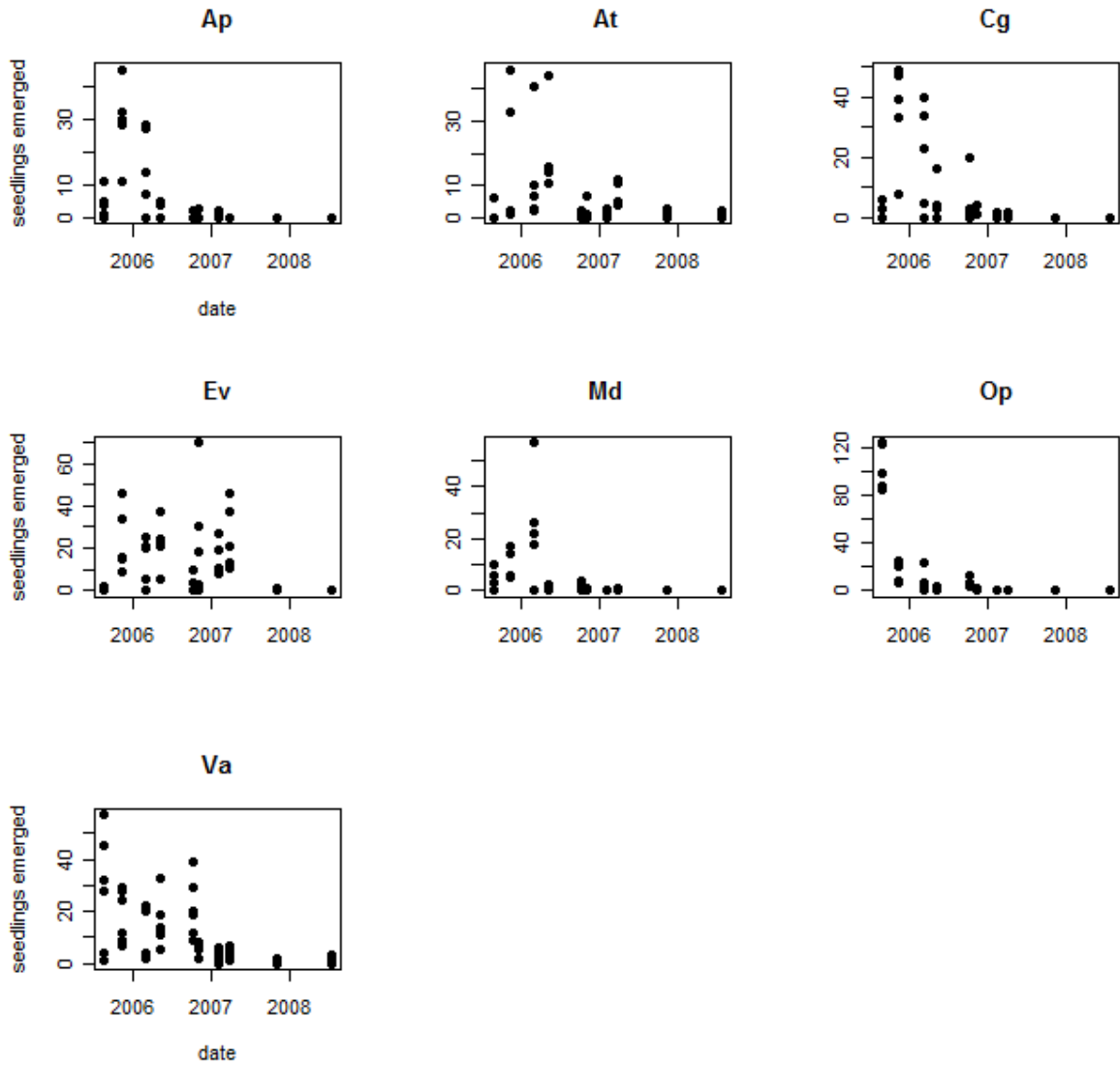


Fig 3.8 Time series of emergence of 7 species at Ashurst aggregated across 5 replicate plots for the 6 species and across 6 replicates for 1 species (*Veronica arvensis*). Two of the species approximated a monotonic decline over time (Ap and Op) but At, Ev, Cg, Md and Va showed a protracted period of increasing seedling appearance (before 2007). Most of the species showed no seedling appearance in 2008, except Ap and Va. Abbreviations as in Fig 3.5. Each data point relates to count dates (x-axis, date) which comes from 625cm².

3.4.4 Seed size and longevity in the seed bank

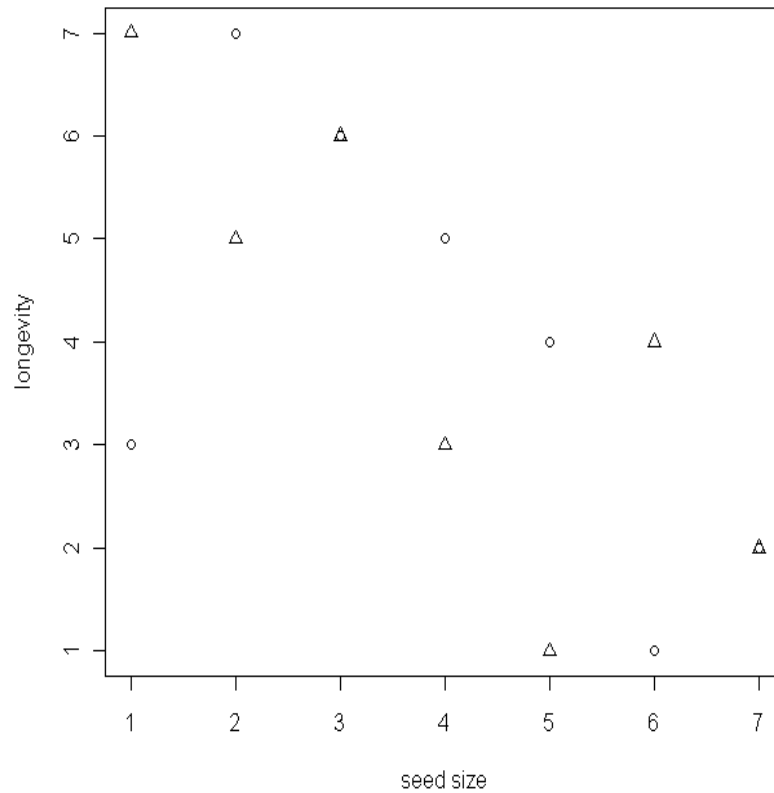


Fig 3.9 Seed size (log wt in mg) plotted against longevity (log days) in seed bank. The 7 species are ranked in their seed size (seed weight in mg) from the smallest (1) to the biggest (7). The species are also ranked by their seed bank from the shortest time in seed bank (1) to the longest (7) for the two seed bank sites. Open circles are for Pound Hill seed bank, open triangles are for Ashurst seed bank. Seed size is inversely correlated to longevity in the seed bank for both sites. Kendall's match correlation showed: Pound Hill seed bank: slope = -0.61, $p = 0.148$. Ashurst seed bank: slope = -0.79, $p = 0.036$.

Seed bank results from the two sites indicate large-seeded species have much shorter seed bank than small-seeded species (Fig 3.9). Seed bank (temporal heterogeneity) is one of the coexistence mechanisms in annual plant communities.

3.5 Discussion

All seven species exhibited some degree of protracted seedling appearance. However, recruitment from seeds more than one year old was relatively low for all seven species at both sites. The match between simple theory and field experiments was very poor.

Heterogeneity between replicates was significant in many of the species. Across species, the duration of the seed bank was inversely correlated with seed size (Fig 3.9).

If we measure the seed bank in terms of the number of days after sowing when the last seedling was observed, then the species were ranked as follows: *Erophila verna* (1565 days) > *Arabidopsis thaliana* (1560 days) > *Veronica arvensis* (1550 days) > *Aira praecox* (1189 days) > *Myosotis discolor* (1179 days) > *Ornithopus perpusillus* (1152 days) > *Cerastium glomeratum* (929 days). The maximum effect size was 1.7 fold.

At Ashurst, over a shorter period of time, the ranking was *Erophila verna* (1082 days) > *Veronica arvensis* (1080 days) > *Arabidopsis thaliana* (830 days) > *Cerastium glomeratum* (607 days) > *Myosotis discolor* (600 days) > *Aira praecox* (555 days) > *Ornithopus perpusillus* (463 days). The maximum effect size was 2.3 fold.

The shorter longevity of seeds in the seed bank at Ashurst could be due to the fact that Pound Hill is relatively cooler and drier compared with Ashurst. The other reason could be due to differences in the number of sown seeds. There were 2-3 as much seeds per quadrat at Pound Hill as there were at Ashurst, and as a result, it is likely for a higher density dependent below ground mortality.

Comparing the two experiments, *Erophila verna* showed the longest-lived seed bank in both cases and *Ornithopus perpusillus* was in the bottom two in both cases. *Arabidopsis thaliana* and *Veronica arvensis* occupied either second or third position in both trials, but the other four species were variable in their ranks (between four and seven).

There was no immigration of the 7 species recorded in any of the unsown replicates at Pound Hill. In fact, the commonest weeds were mainly *Senecio*, *Cirsium*, *Betula*, *Agrostis* and *Rubus*. There was immigration of seeds at Ashurst, as described in Chapter 4. This was not ideal, as we should not over-interpret the Ashurst seed bank results.

In summary, an exponential or double exponential model was reasonable for a minority of species (Ap and Op) and these were the species with the most short-lived seed banks. One species (Va) showed a significant increase in seedling appearance across time up to 2005, and this increase was consistent across four replicates (see Fig 3.5) The species with the most long-lived seed banks (the small-seeded crucifers Ev and At) showed a pattern of roughly constant recruitment across the first 4 years (rather than exponentially declining recruitment).

With hindsight it would have been preferable to build more plots and to initiate the seed bank experiment from scratch in each of our years. Similarly, now that we know that seed dispersal distances for our 7 species are reasonably short, it would have been useful to have seed bank experiments inside the Ashurst Exclosure, so that year effects were not confounded with location events in making inferences about the importance of recruitment from the seed bank in population dynamics and species coexistence. As it is, we have just one year-of-initiation at Pound Hill (2003) and one year-of-initiation at Ashurst (2005), so the generality of our findings is limited. Nevertheless, it is clear that we can rank the species in terms of their propensity to form persistent seed banks as follows.

In both sites, the majority of seeds of all species germinated at once and did not enter a long-term seed bank. We know that there was no local input of seeds to the bank, because we uprooted all seedlings before they had a chance to set seed or to inhibit germination of other seeds. There was no immigration to any of the blank (unsown) plots at Pound Hill. Of the seed that was viable but did not germinate at once (the quiescent and dormant fractions, comprising what we define as the seed bank) more than half germinated in their second year.

Although the seed banks were not large, it is clear that all seven species were capable of forming a seed bank that could last at least one year, and hence the population could survive complete failure of both the autumn and spring cohorts in the same calendar year. No doubt, this represents a substantial potential stabilizing mechanism in their population dynamics under field conditions. Although the effects are small, their consequences may be profound.

Chapter 4

Dispersal kernels

Abstract

*We measured dispersal kernels using seedling recruitment rather than seed traps. We discuss the pros and cons of these contrasting approaches to the problem. Species showed rather consistent dispersal kernels across replicates within years, but some species showed strong year effects on the attributes of their seed shadows. Because of the way we monitored seed rain we cannot discriminate between factors affecting germination, survival and seed dormancy rates and factors influencing seed dispersal directly (wind speed, turbulence, gustiness, animal numbers and activity levels, and so forth). Longer distance dispersal was assessed by counting the numbers of seedlings weeded from the 250 plots at Ashurst. Plot-to-plot dispersal (of order 2m in distance, rather than the <1m within plot dispersal kernels) was not correlated with attributes of the small-scale dispersal kernels, except that the lowest rates of plot-to-plot movement were by *Ornithopus perpusillus* which also showed the lowest mean and maximum dispersal distances in the within-plot kernel studies. This draws attention to the perennial problem of understanding the “tails of the distribution” and predicting rare cases of long-distance dispersal. The weeding data provide strong evidence that longer-range dispersal (of order of metres) could be important in promoting coexistence by providing a “rescue effect” for reversing episodes of local extinction caused by small-scale competitive exclusion.*

4.1 Introduction

Dispersal is an important part of the story of this thesis, because non-random spatial mixing is a potentially important mechanism for coexistence (see Chapter 1). If there is a superior competitor, and that species was also the superior disperser, then coexistence would be impossible, because the inferior competitor would always find itself confronted by neighbours of the superior competitor. Limited dispersal by the superior competitor is a necessary but not sufficient condition for coexistence through spatial separation (Pacala and Tilman 1994, Chesson 2000a). This process conforms to the Lotka-Volterra coexistence criterion (intraspecific competition must be more important than interspecific competition) because limited dispersal can produce spatial clumps of seedlings around parents, and within these clumps, competition is mainly with individuals of the same species (Law et al. 2003, Murrell et al. 2004).

Dispersal in space is often described by what is traditionally called a dispersal kernel. In theoretical models this describes the probability density of seed fall with distance from a parent plant located at distance = 0 (e.g. the positive half of a normal distribution).

The theory underpinning the relationship between dispersal and coexistence is straightforward. In the simplest case, there is complete random mixing of the species. The inferior competitor finds itself everywhere in close proximity to the superior competitor, so competitive exclusion occurs rapidly. Under these circumstances, there is no prospect of rare species advantage for the inferior competitor, so it is unable to invade a monoculture of the superior competitor and its exclusion is therefore ensured. If, however, the superior competitor exhibits a clumped spatial distribution (say as a result of limited seed dispersal) then this could create a spatial refuge from competition and the inferior competitor might be able to persist. This mechanism of coexistence is often referred to as a colonization competition trade-off (Armstrong 1976, Shmida and Ellner 1984, Crawley and May 1987, Tilman 1994). If there is a perfect negative correlation between dispersal ability and competitive ability, then there is no limit, in principle, to the number of species that could coexist in an otherwise spatially homogenous and temporally invariant environment (Hastings, 1980). In such a case, it should be straightforward to bring about competitive exclusion simply by sowing the seeds of the superior competitor at random over the entire area, thereby removing the refuge from competition previously enjoyed by the inferior competitor. The Lotka-Volterra coexistence criterion is realized in the case of a colonization competition trade-off because both the superior and inferior competitors occur in spatially explicit clumps, with the result that both species suffer more from intra- than from inter-specific competition.

When the superior competitor exhibits limited seed dispersal, its offspring are clustered around the female parent in a spatial arrangement known as the 'dispersal kernel'. This is characterized by several features. In the parametric case, a probability density function (pdf) is specified (e.g. the Normal distribution) and its parameters (in this case the standard deviation) are estimated from spatially explicit data in one dimension (for instance, along a transect from one edge of the kernel to the opposite edge, passing through the location of the parent where recruitment is typically

assumed to be greatest. In the non-parametric case, the kernel is specified entirely by the data. From a map, or from transects away from the parent, we estimate the location of the offspring as a set of distances from the parent: e.g. minimum and maximum distances, median distance and the 25th and 75th percentiles of distance moved). A non-parametric smoother can be used to sketch the shape of the dispersal kernel through (or over) the data. The horizontal projection of the dispersal kernel onto a map centered on the parent plant is called the seed shadow.

Dispersal beyond the kernel is typically referred to as “long distance dispersal”. Needless to say, this is very difficult to estimate with precision, but could be of the greatest importance in terms of the ecology and evolution of the dispersing species. The theoretical analysis of long-distance has attracted considerable attention, and is generally modeled by selecting probability density functions that have “fat tails” (Nathan 2006). That is to say, the total probability of dispersing more than 3 standard deviations is much greater than with a Normal pdf for instance (Okubo 1989). An alternative is to fit an empirical regression of the log (seed number) against log (distance) and use the slope as a measure of dispersal rate (for a given intercept, the shallower the slope, the greater the mean long-distance dispersal distance (Kot 1996, Skarpaas and Shea 2007) .

There is a small literature on the optimal behaviour of parents in relation to dispersal distance. For instance, the consensus is that if a fraction of the seeds are to be dispersed in a dormant state, then these should be the locally dispersed seeds, while the long distance seeds should germinate at once if they encounter suitable conditions (Cohen 1968). The hypothesis is that this behaviour minimizes competition between sibling seedlings as well as providing future potential recruits for what is evidently a suitable micro-site (in that the parent plant was able to set seed here).

We estimate the attributes of the dispersal kernel by monitoring seedling recruitment from experimentally planted parent plants. This is in contrast to studies that estimate seed dispersal by observing the movement of individual seeds directly (Clark et al. 1999, Cain et al. 2000, Clark et al. 2001, Bullock et al. 2006, Skarpaas et al. 2006), or by using seed traps to estimate seed rain at different distances from a known seed

source (Bullock and Clarke 2000), or within a grid of multiple potential seed parents (Clark et al. 1999, Clark et al. 2001).

We argue that the advantage of using seedling recruitment is that the entire kernel is directly observable; its shape, size and internal density variation can be measured with reasonable precision. The disadvantage is that extra sources of uncertainty are introduced, over and above the movement of the seeds themselves. Thus, we do not know the germination rate, so we cannot be sure that the germination rate is constant with distance from the parent plant (e.g. germination is known to vary with the local density of seeds, as described for our monoculture studies in Chapter 2, and in other systems; (Palmbad 1968)). Likewise, we do not know the death rate of seeds between dispersal and seedling appearance. Again, this might be density dependent, and if this were to be the case, we could not be sure that the spatial pattern of seedlings mirrors exactly the spatial pattern of seed fall (as we would like to be able to assume). However, we feel that on balance the costs of monitoring seedlings (uncertainties associated with spatial variability in germination rates, and the possibility of density dependent failures of seedling appearance) are considerably outweighed by the benefits (being able to map the entire kernel, and to observe any variations in kernel shape directly with, for instance, wind direction, any variations in kernel shape directly). Studies based on seed traps typically sample only a tiny fraction of the area over which the seeds of a single parent are dispersed (often only a few square meters of trap for several hundreds of square meters of seed shadow), and are usually arranged in spatial grids or on regularly-spaced transects that may not be ideal for estimating the parameters of the chosen parametric distribution.

Historically, two parametric kernels have been used more frequently than any others, both in theoretical models and the description of field data on seed dispersal: the exponential and the inverse power law.

The exponential is attractive because the underlying mechanism is so straightforward and intuitively appealing: if half of the dispersing seeds fall in the first meter, then half of the remainder falls in the next meter, and so on, then the number of seeds on the ground declines exponentially with distance:

$$y = a \exp(-bx)$$

where the response variable y is seed rain (number of seeds per unit area), and the explanatory variable x is distance from the parent. This is a 2-parameter model with parameter a being the seed rain at distance 0, and parameter b as the decay rate with distance (specifically, the slope of the decline in $\log_e$ seed rain with distance).

The power law was often preferred for the analysis of real dispersal data because it had the potential to describe a situation where that the proportion of still-dispersing seed that was deposited at a given distance was not constant:

$$y = ax^{-b}$$

where the two variables y and x are the same as before, but the two parameters (a and b) have quite different meanings: a is the seed rain at distance $x = 1$ (the power law model is not defined at $x = 0$) and b is the slope of a plot of $\log(\text{seed rain})$ against $\log(\text{distance})$. The two models are compared in Fig 4.1.

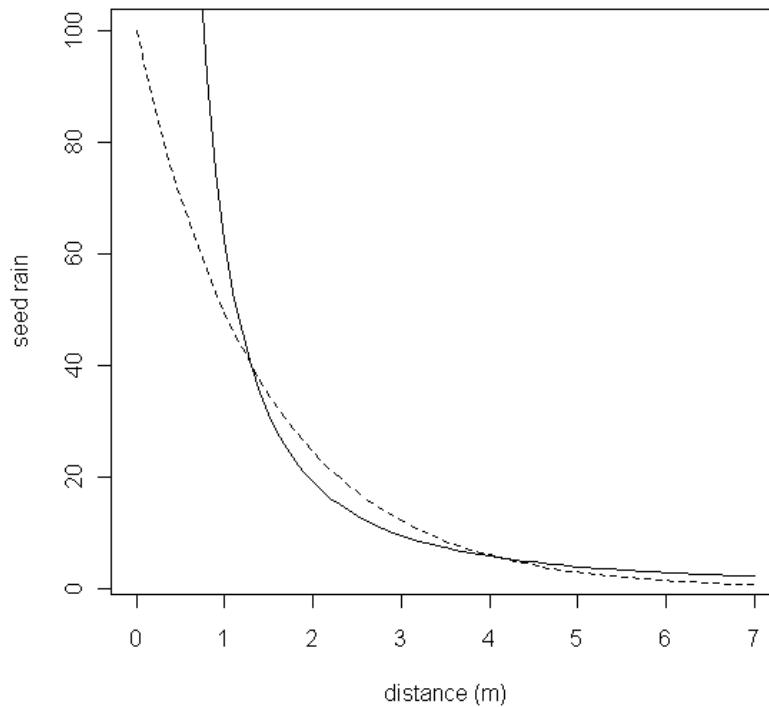


Fig 4.1 The importance of model choice. Exponential (dashed line) and Power Law (solid line) models fitted by least-squares regression to the same hypothetical data on seed rain with distance. The important point to note is that the power law creates a dispersal kernel that has “fatter tails” than the exponential, and this means that the power law will always predict greater long-distance dispersal than the exponential from the same data. In this example, the inverse power law has parameters $a = 62.7$ and $b = 1.71$ (solid line) while the exponential (dotted lined) has parameters $a = 100$ and $b = -0.7$. Note that below 1m distance the two models are wildly different in their predictions, but they are roughly comparable over the range of the distances from 1m to 6m.

If seeds were not identical to one another (e.g. some were heavier than others, some had more effective parachutes, some were dispersed from higher up the plant, or some were dislodged only by stronger winds), then some form of mixed model might be more appropriate. Suppose that there were just two classes of seed produced: we might call them “fallers” and “fliers”. The fallers were heavy, and evolved to optimize the use of the space where the clearly successful parent had grown. The fliers were lighter and had more effective parachutes.

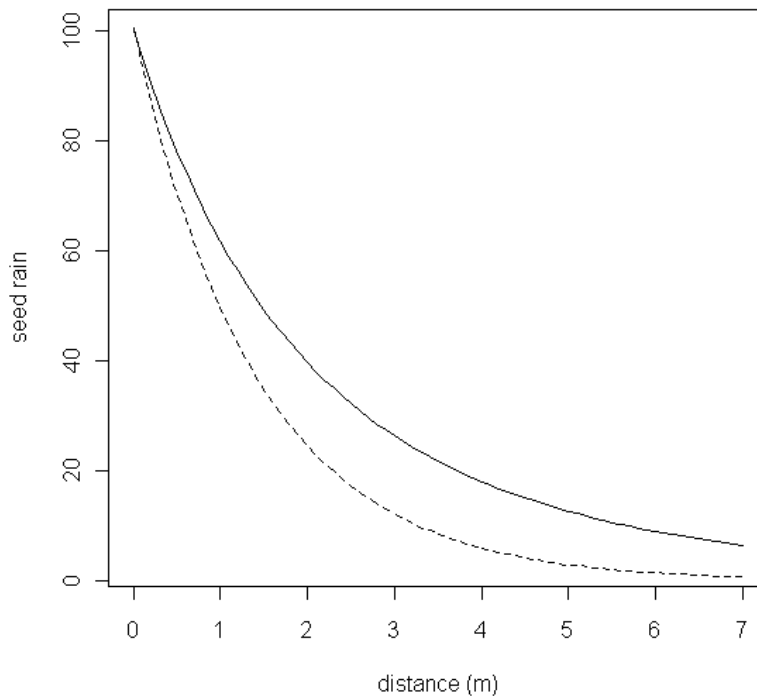


Fig 4.2 Dispersal kernels compared for one (dotted line) and two (solid line) classes of seeds. Note the much “fatter tail” of the two-class distribution, illustrating that a greater fraction of the seeds display long-distance dispersal. The dotted line illustrates an exponential kernel where all of the seeds are “fallers” ($b = 0.7$). In the double exponential (solid line) half of the initial seeds were “fallers” ($b = 0.7$) and half were “fliers” ($d = 0.3$). In reality, of course, one would probably not know the initial proportions of the two kinds of seed, nor indeed the number of classes of disperser (here assumed to be 2). As always, model choice would be crucial in determining the values of the parameters and their mechanistic interpretation and in predicting the number of seeds that would undergo long-distance dispersal (requiring extrapolation beyond the range of the greatest measured distance).

Then a double exponential might better describe the rain of all seeds (Fig 4.2), requiring the estimation of four parameters (two for each of the classes of seed): a decay rate (high for the fallers (b) and lower for the fliers (d)) and an initial composition (a plus c):

$$y = a \exp(-bx) + c \exp(-dx)$$

The two contrasting ways of estimating the shape and size of the dispersal kernel are *seed traps* and seedling emergence. The advantage of seed traps is that:

- Seed rain is controlled directly

The disadvantages of seed traps are:

- The traps cover a tiny fraction of the area over which the seed rain is falling
- Sticky traps are a pain to work with; extracting and identifying the seeds from the glue, ensuring that the glue remains sticky while in the field, etc.
- Seed-feeding animals can remove seeds from traps
- It is not necessarily obvious which parent was the source of trapped seed
- One has to assume that the seeds would not have dispersed any further had they not been caught in the trap (i.e. secondary dispersal is prevented by the act of trapping).

The disadvantages of using seedling appearance are:

- Pre-emergence seed mortality is unknown
- Dormancy and quiescence are unknown
- There may be density dependence in seedling emergence
- Hence, numbers underestimate seed rain by an unknown amount.

To compensate for these disadvantages,

- Seed dispersal is not influenced by interception in traps
- Secondary seed dispersal can occur unhindered
- Complete census of seedlings is possible (total ground coverage)
- No assumption is made about maximum dispersal distance (e.g. the location of the furthest trap).

4.2 Methods

There were two parts to this study of seed dispersal: (1) detailed within-plot seedling shadows were calculated from replicate plots in 4 different years in the Walled Garden; and (2) plot-to-plot dispersal of seeds in the main Ashurst experiment was estimated from weeding data.

4.2.1 Site

The aim of the study is to quantify the shape of the dispersal kernel from experimentally planted isolated individuals of each species under field conditions. In order to minimize seed immigration, the work was carried out in the Walled Garden (Grid Ref: SU 940690), in an isolated part of Silwood Park. This site is in a different area from that used for the seed bank work and is separated from the main experimental plots at Ashurst by 120 m.

Inside the Walled Garden, a herbivore-proof site (deer and rabbit enclosure) with fence post height of two metres was set up in the summer of 2002. The soil was surface covered with Mipex plastic sheeting (weed suppressant fabric) to stop weed growth. Ten plots were laid in two columns of five inside a 7m x 16m fence, and the area between the beds was covered in gravel for ease of maintenance. Construction of the plots is described in Chapter 2.

At a larger spatial scale, plot lot-to-plot dispersal was studied at Ashurst plots which are described in Chapters 2 and 6. Individuals of our 7 study species were regularly hand-weeded from plots where they had not been sown. All seedlings were identified to species and counted. This gives us data on recruitment for each of our study species on a substantial fraction of the total of 250 raised beds at Ashurst over a period of 5 years.

4.2.2 Parent plants

During the winter of 2002 to 2003, seeds of each species were sown in square plastic pots (7cm x 8cm) filled with multi-purpose compost (purchased from Home Base, Bracknell) to within 2 cm of the rim. Pots were kept in the greenhouse (18 degree centigrade and 70% relative humidity) on an open tray to aid drainage. Pots were regularly watered and seedling appearances were monitored daily.

Individual healthy seedlings were transferred to larger circular plastic pots (6.5cm (base) x 9.5cm (height) x 10cm (top)) filled with multi-purpose compost to within 1cm of the rim. Seedlings were allowed to grow until they began to produce flowers.

Pot-grown individuals of each species were removed with their soil intact from the pot and planted individually (Table 4.1), just prior to seed ripening, in the centre of each of the seven sectors in each plot.

Demographic data (seedling height, number of branches, numbers of fruits, estimated fecundity and orientation of the seedling) were collected for each species after two – three weeks following transplanting prior to seed setting. Seeds were left to disperse naturally. For *Cerastium* species there was secondary dispersal by wind (tumble weeds) once branches had fallen on to the ground from the parent plant. The location and attributes of seedling recruits were measured the following season/year.

The total numbers of recruits for each species were compared with estimated fecundity (number of fruits x mean number of seeds per fruit calibrated) to assess percentage recruitment. A 1cm mulch of fine gravel (3-6mm) was spread on the beds to within 1cm of the rim of the sleepers to protect the soil surface from rain-splash (as in monoculture plots) before the pot-grown individuals were transplanted.

Table 4.1 Transplanting dates in each of the four years when the seedlings were moved from the greenhouse to the Walled Garden.

species	2003	2004	2005	2006
<i>Aira praecox</i>	05/05/2003	15/05/2004	20/05/2005	29/05/2006
<i>Arabidopsis thaliana</i>	05/05/2003	15/05/2004	11/05/2005	09/05/2006
<i>Cerastium glomeratum</i>	05/05/2003	15/05/2004	11/05/2005	09/05/2006
<i>Erophila verna</i>	05/05/2003	15/05/2004	11/05/2005	09/05/2006
<i>Myosotis discolor</i>	05/05/2003	15/05/2004	11/05/2005	09/05/2006
<i>Ornithopus perpusillus</i>	29/05/2003	06/06/2004	15/06/2005	25/06/2006
<i>Veronica arvensis</i>	05/05/2003	15/05/2004	11/05/2005	09/05/2006

4.2.3 Recruitment

Plots were monitored on a regular basis and any weeds removed (see chapter 2). The recruits were never allowed to grow large enough to flower, to ensure that there was no recruitment from in situ seed production.

To estimate recruitment, depending on the nature of seedling establishment for each species, three different methods were chosen over the course of the experiment (4 years). As in monocultures, there were at least two periods of seedling recruitment, one in the autumn following transplanting in the summer, and a second the following spring. Almost all the autumn recruits died in the winter due to cold temperatures in most years. In years when autumn recruits survived following recruitment, they were removed before flowering stage.

Four transects running north, south, east and west from each seed parent were set up. The transects were 2 cm wide and divided into a column of 2 cm squares, within which the number of seedlings were counted. For the purposes of estimating the parametric attributes of the dispersal kernel, all of the seedlings within one of these mini-quadrats were assumed to be at a distance of 1, 3, 5, ... or $(2 \times n) - 1$ cm from the parent plant.

When seedling densities were very low, the transect detected too few plants to form a good image of the kernel. Instead, an A4 film (1-4) was placed on top of each sector with the location of each parent plant marked on the paper. Orienteering compass (HI-GEAR, scale 1:50000) was used to show the position and direction of the recruits. At the peak seedling emergence, all recruits were traced using a permanent marker pen. In the event that there were appearances of recruits for more than one species in the same sector, different color marker pens were used to locate them. Back in the lab, digitized the locations of the parent plant and each of the seedlings using a flat-bed digitizer, to produce vectors of x and y coordinates. Finally, we used Pythagoras theorem to convert these locations into distances of each seedling from the parent plant.

4.2.4 Statistical modeling

We used a linear mixed effects model to investigate species effects, with year and plot fitted as random effects. We used lmer in package lme4 (Bates 2011) to fit the model.

$$Y \sim \text{spp} + (1|\text{year}) + (1|\text{plot})$$

to estimate a fixed effect for species (spp, 7 levels) and plot (10 levels).

The weeding data (counts) were analyzed using a glm with Poisson errors, fitting the number of neighboring plots (out of 8) on which the species in question was allowed to set seed. We hypothesized that the number weeded would increase with the number of neighboring plots producing and dispersing seeds. The five-number summary was made for each species. Kendals rank correlation test was done to compare the two methods of recruitments sampling.

4.3 Results

4.3.1 Recruitment

The overall percentage recruitment from estimated seed production by the parent plant averaged across ten replicates and four years was as follows: *A. praecox* 116.5% > *M. discolor* 73.5% > *O. perpusillus* 55.5% > *C. glomeratum* 52.4% > *Veronica arvensis* 40.7% > *E. verna* 21% > *A. thaliana* 5. *Aira* continued to produce tillers after transplanting, so total recruitment was higher than the estimated fecundity. *Cerastium* and *Myosotis* also showed an increased recruitment >100% recruitment in at least one out of four years due to extended flowering (See Table 4.4).

4.3.2 Dispersal kernels

Transect data can be converted into probability density data by multiplying the seed rain per unit area at a given distance (the vector of transect data) by a multiplier, which is the total ground area at each distance from the parent (the annulus) divided by the area of each quadrat on the transect. Fig 4.3 shows two plots of the same data: the transect data are negative exponential, showing monotonic decline in seed rain with distance, whereas the dispersal distances for the total seed production of the

parent (probability density) show a peak at 5m. In this chapter, the data are presented in transect form.

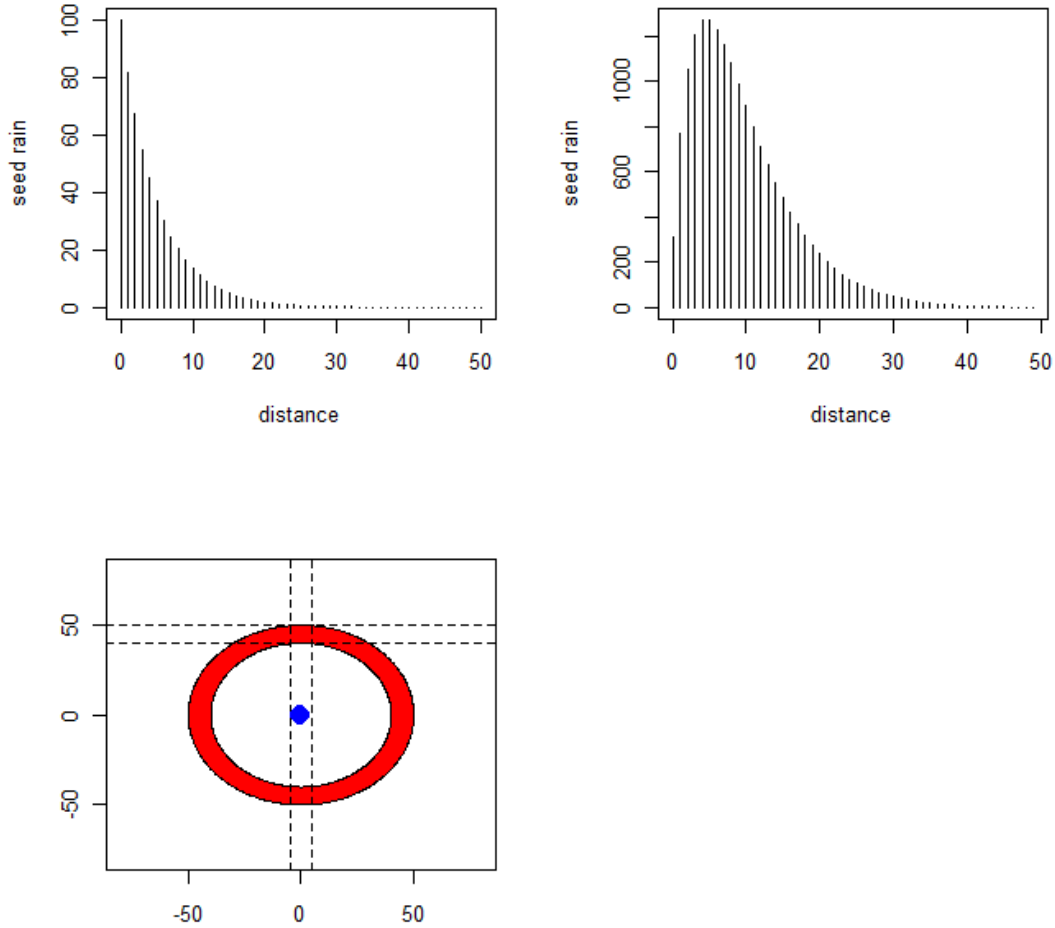


Fig 4.3 Seed rain data, expressed as transect data (left) and probability density (right). In this example, the quadrats are 1x1m and the transect distances are in metres from the parent (at $d = 0$). The area to 1m is $\pi \times 1^2 = \pi$ and the annulus area between distances i and $i+1$ is $\pi r_i^2 - \pi r_{i+1}^2$. The model assumes that seeds are dispersed in all compass directions from the parent with equal probability. A map of the annulus is shown in the bottom left panel, with the width of the annulus exaggerated for the purpose of illustration. The parent plant (blue circle) is located at coordinates (0,0). The area of the zone between two distances (the “annulus”) is shown in red. A single quadrat at this distance from the parent is shown by the intersection of the dotted lines. The “multiplier” is the area of the annulus divided by the area of the quadrat.

The average dispersal kernel is shown for each species in Fig 4.3 as a transect away from the parent (at $x = 0$) this is mean of 4 compass directions and 4 years. Dispersal

was greatest in *Cerastium glomeratum* and least in *Ornithopus perpusillus*. Note that for all species maximum recruitment was not at the origin (location of the parent plant) but at 3 to 5 cm.

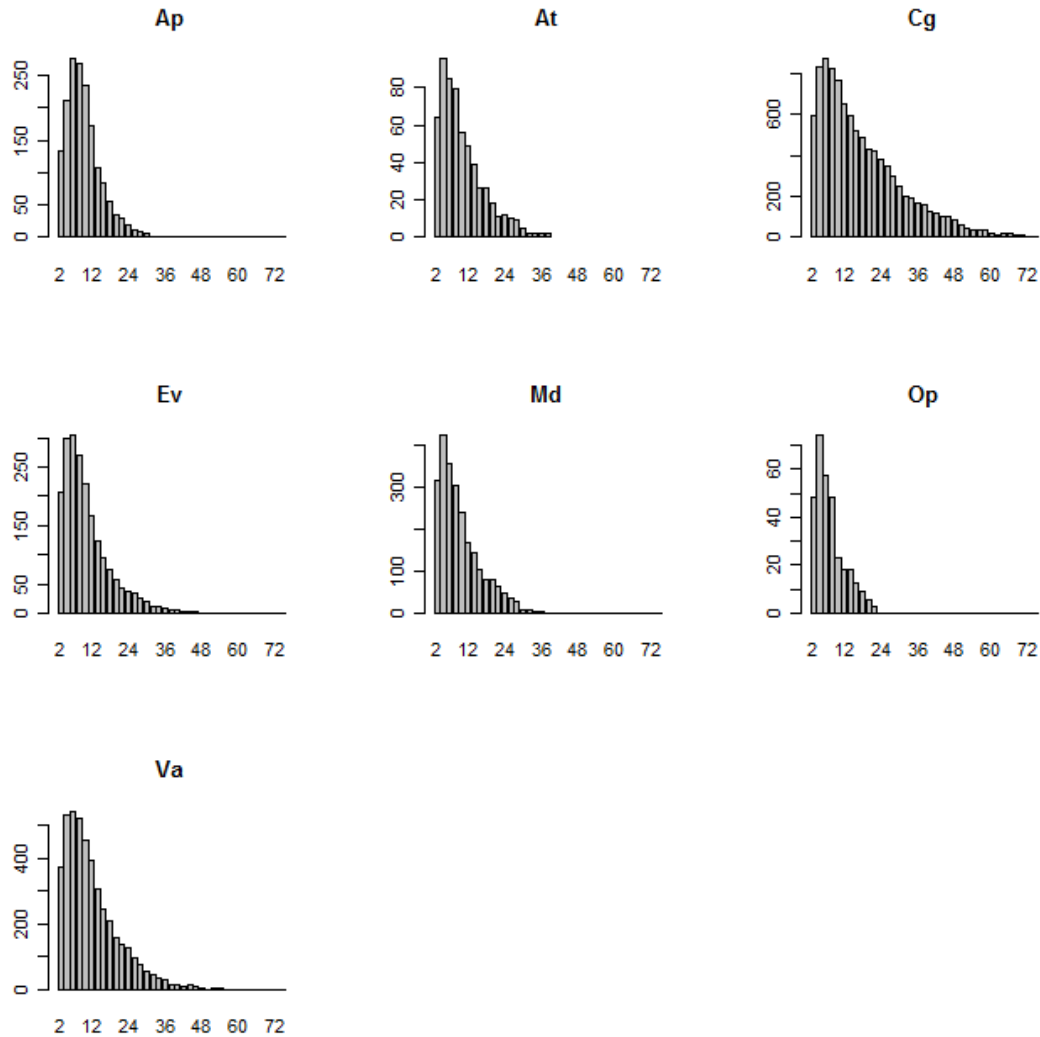


Fig 4.4 Dispersal kernels for 7 species aggregated across years, compass directions and replicates. *Cerastium glomeratum* showed consistently the highest mean and maximum dispersal distances and *Ornithopus perpusillus* consistently the lowest. Note that all kernels had a maximum some distance (x-axis) away from the parent plant (maximum 3cm in At, Md and Op, 5cm in the other 4 species). Note also the different scales on the y axis, reflecting the differing fecundities and recruitment rates of the species.

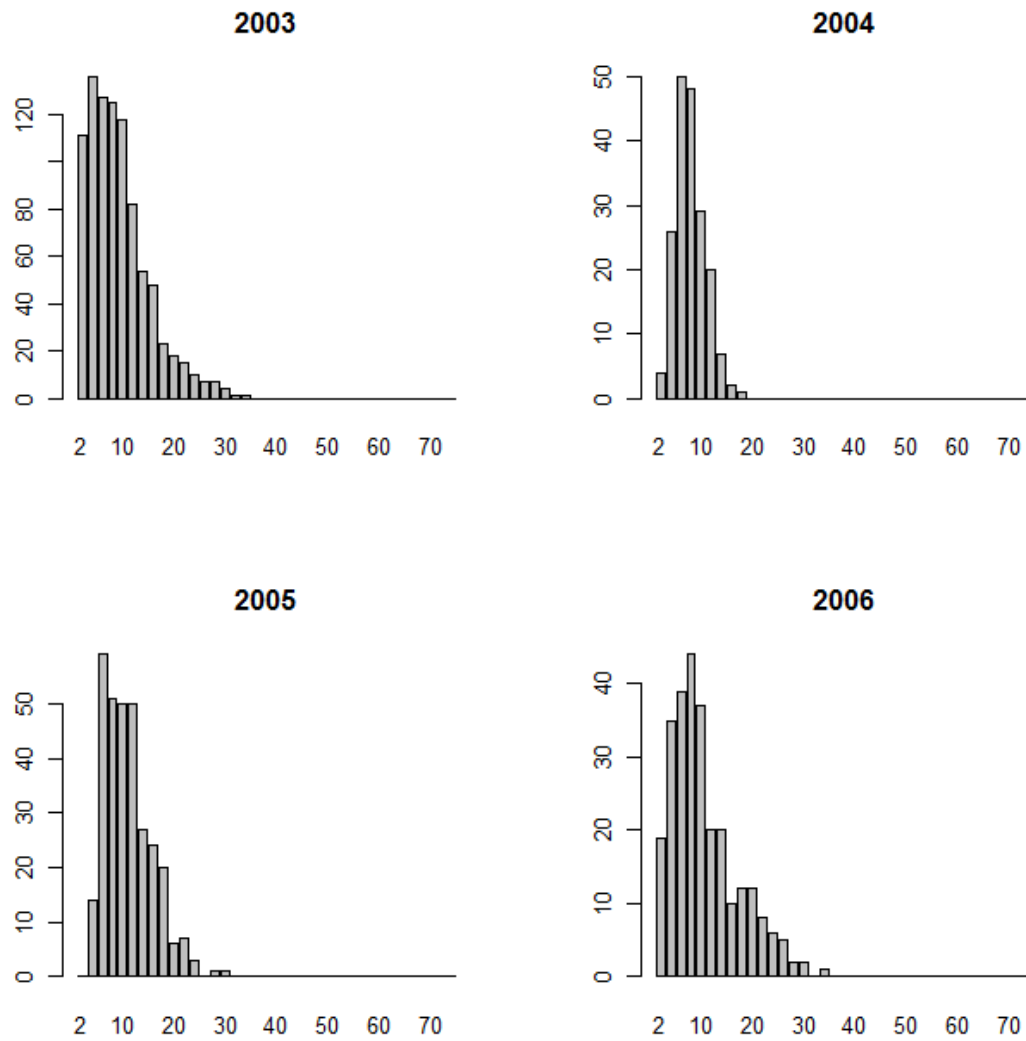


Fig 4.5 Year effects on dispersal kernels as exemplified by the case of *Aira praecox*. The modal distance (x-axis) varied from 3cm in 2003 and 2005 to 7cm in 2006. The 5-number summary statistics for each year are given in Table 4.4. Note also the different scales on the y axis, reflecting the differing fecundities and recruitment rates of the species.

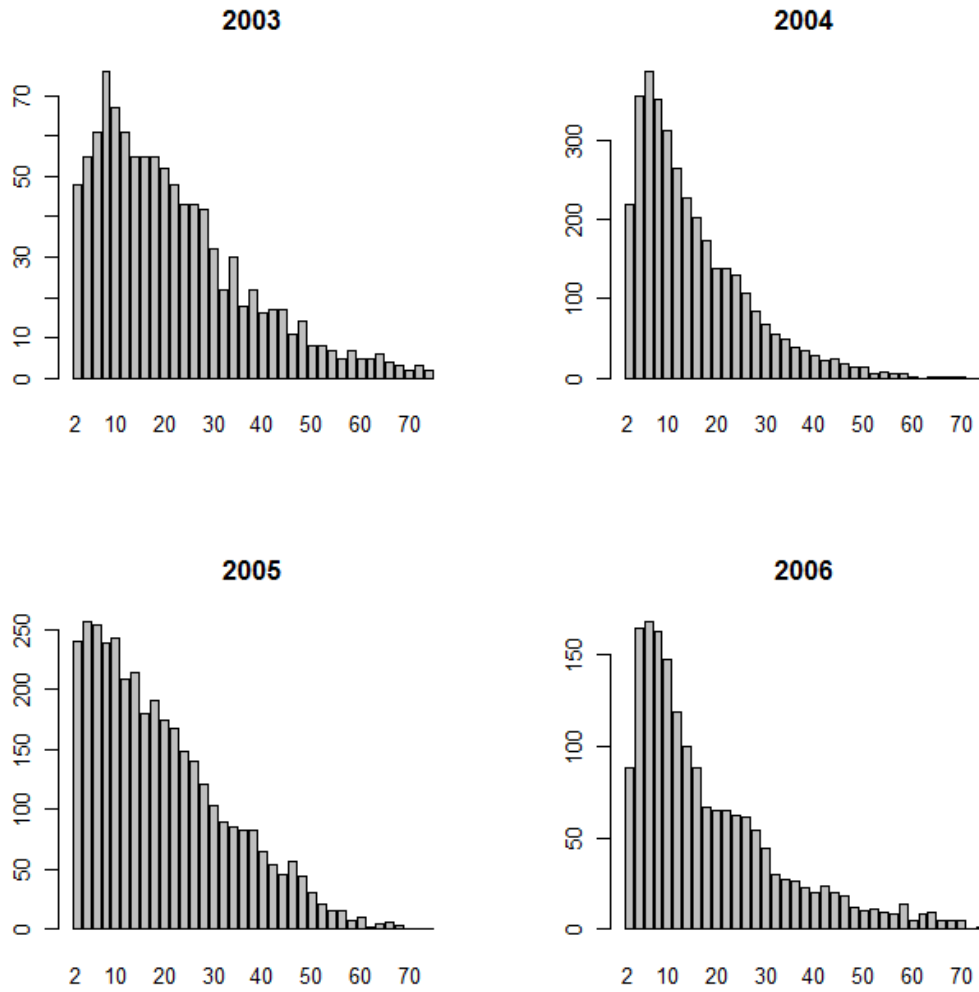


Fig 4.6 Year effects on dispersal kernels as exemplified by the case of *Cerastium glomeratum*. The modal distance (x-axis) varied from 3cm in 2005 to 7cm in 2003. The 5-number summary statistics for each year are given in Table 4.4. Note also the different scales on the y axis, reflecting the differing fecundities and recruitment rates of the species.

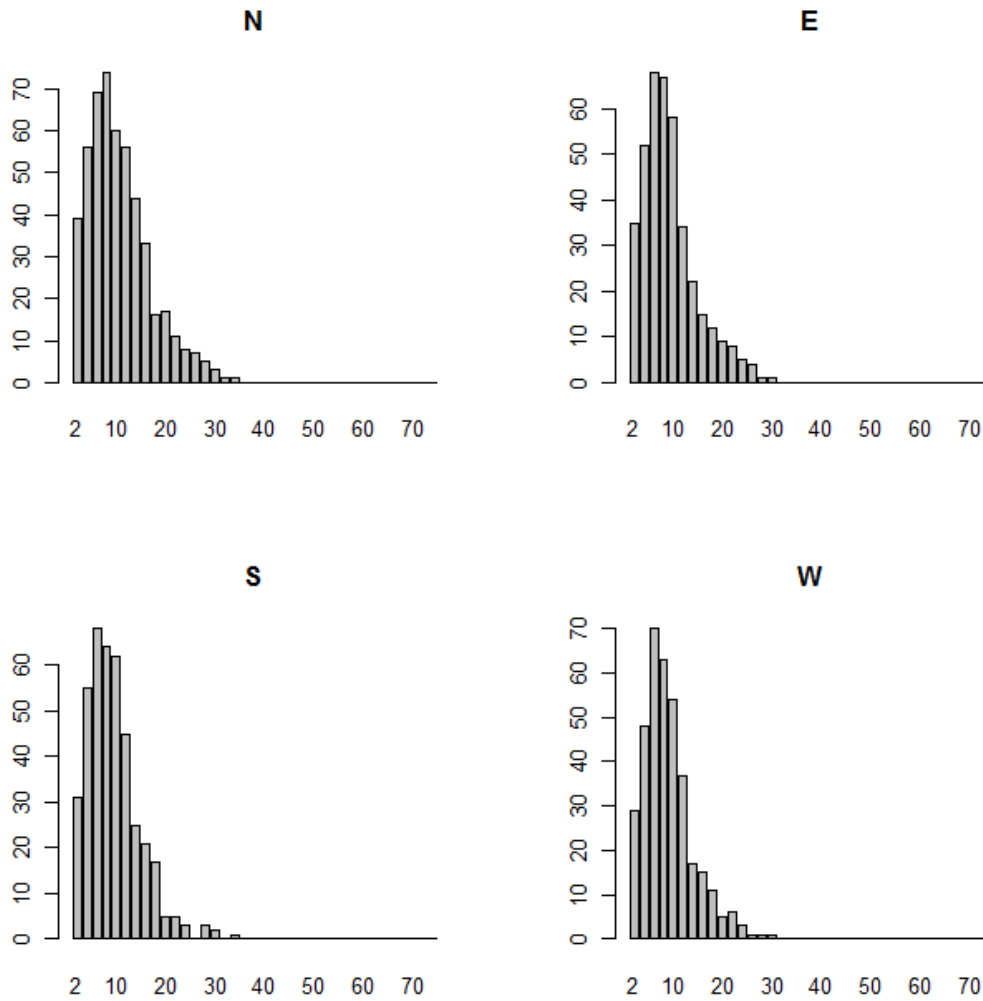


Fig 4.7 Compass directions of seed dispersal as exemplified by *Aira praecox*. Counts (y axis) aggregated across plots and years. N=north, E=east, S=south, W=west. There was no significant compass effect for any species in any year. X – axis is dispersal kernel distances.

Cerastium glomeratum showed consistently the highest seed dispersal distances (mean = 17.9 cm, se = 0.29), then *Veronica arvensis* (mean = 12.2 cm, se = 0.33). A group of 4 species (*Erophila verna*, *Arabidopsis thaliana*, *Myosotis discolor* and *Aira praecox*) had similar mean dispersal distances (10.7, 10.2, 9.6 and 9.6 respectively), but *Ornithopus perpusillus* showed significantly lower mean dispersal than any of the other species (mean = 7.5 cm, se = 0.66, $p < 0.001$).

Table 4.2 Linear mixed effects model for dispersal distance (y , cm) with species (spp) as a fixed effect and plot (pl) and year (yr) as independent random effects, with 10 and 4 levels respectively. Dispersal distances were measured for 21,293 individuals. Of the random effects, plots accounted for roughly twice as much variation in dispersal distance than did years. For the species, *Cerastium glomeratum* had significantly higher mean dispersal than *Veronica arvensis* ($t = 27.02$, $p < 0.001$), which in turn had significantly higher mean dispersal ($t = 6.19$, $p < 0.001$) than a group of 4 species that were not significantly different from one another (Ap, At, Ev, Md). *Ornithopus perpusillus* showed significantly lower mean dispersal than any of the other species ($t = 5.46$, $p < 0.001$).
Linear mixed model fit by REML

Formula: $y \sim spp + (1 | yr) + (1 | pl)$

AIC	BIC	logLik	deviance	REMLdev
161010	161090	-80495	160989	160990

Random effects:

Groups	Name	Variance	Std.Dev.
pl	(Intercept)	2.0135	1.4190
yr	(Intercept)	1.0880	1.0431
	Residual	112.2559	10.5951

Number of obs: 21293, groups: pl, 10; yr, 4

Fixed effects:

	Estimate	Std. Error	t value
(Intercept)	9.8842	0.7395	13.367
sppAt	-0.1495	0.5144	-0.291
sppCg	8.0103	0.2964	27.023
sppEv	0.3343	0.3562	0.939
sppMd	0.6516	0.3485	1.870
sppOp	-3.6124	0.6617	-5.460
sppVa	2.0160	0.3257	6.190

Table 4.3 Estimated seed crop compared with seedling appearances for all species aggregated over 5 years. Estimated fecundity and recruitment wss summed over 10 replicates.

year	species	estimated fecundity	estimated recruitment
2003	<i>Aira praecox</i>	3140	5681
2004	<i>Aira praecox</i>	4700	2460.65
2005	<i>Aira praecox</i>	1422.77	1010.81
2006	<i>Aira praecox</i>	362	2064.81
2003	<i>Arabidopsis thaliana</i>	9360	3801.33
2004	<i>Arabidopsis thaliana</i>	59712	4202
2005	<i>Arabidopsis thaliana</i>	30048	667
2006	<i>Arabidopsis thaliana</i>	93888	856
2003	<i>Cerastium glomeratum</i>	57372	17389
2004	<i>Cerastium glomeratum</i>	126672	51979
2005	<i>Cerastium glomeratum</i>	27384	38418
2006	<i>Cerastium glomeratum</i>	39228	23566
2003	<i>Erophila verna</i>	9198	9185
2004	<i>Erophila verna</i>	29736	6312
2005	<i>Erophila verna</i>	14154	3443
2006	<i>Erophila verna</i>	48972	3729
2003	<i>Myosotis discolor</i>	4696	3729
2004	<i>Myosotis discolor</i>	5980	708
2005	<i>Myosotis discolor</i>	6476	8601
2006	<i>Myosotis discolor</i>	5424	3546
2003	<i>Ornithopus perpusillus</i>	972	189.35
2004	<i>Ornithopus perpusillus</i>	3396	1414.79
2005	<i>Ornithopus perpusillus</i>	4386	3845
2006	<i>Ornithopus perpusillus</i>	4386	1839
2003	<i>Veronica arvensis</i>	5536	1811.13
2004	<i>Veronica arvensis</i>	35792	14446.61
2005	<i>Veronica arvensis</i>	33344	9094.91
2006	<i>Veronica arvensis</i>	20320	13285.8

Table 4.4 Summary statistics on dispersal distances (cm) for each species and year from 10 replicates. 25% of seedlings were observed within the 1st quartile and 75% of seedling within a 3rd quartile of the parent plant. These data are converted by the area of the annulus (see Fig 4.3).

species	years	1st quartile	median	3rd quartile	maximum
<i>Aira</i>	2004	7	11	17	33
	2005	7	11	15	29
	2006	5	7	11	17
	2007	9	13	19	33
<i>Arabidopsis</i>	2004	9	13	21	37
	2005	3	7	11	17
	2006	9	13	19	27
	2007	1.26	1.83	2.65	5.99
<i>Cerastium</i>	2004	19	29	43	73
	2005	17	27	39	71
	2006	13	21	31	69
	2007	15	27	41	73
<i>Erophila</i>	2004	9	17	25	63
	2005	7	11	17	49
	2006	4.34	7.36	10.61	20.71
	2007	1.48	2.23	3.32	11.51
<i>Myosotis</i>	2004	7	11	19	35
	2005	9	15	21	35
	2006	9	13	21	39
	2007	7	13	19	47
<i>Ornithopus</i>	2004	4.5	7.32	11.85	23.43
	2005	7	11	15	21
	2006	4.05	7.77	11.46	23.95
	2007	1.19	1.71	2.43	4.68
<i>Veronica</i>	2004	5	9	13	29
	2005	11	17	23	47
	2006	11	17	25	53
	2007	9	17	25	47

4.3.3 Plot to plot dispersal at Ashurst

The total number of weeds of our sown seven species removed from all plots at Ashurst over 5 years are shown in Table 4.5.

Table 4.5 Total number of weeds for the 7 species over the course of the experiment from all plots.

species	total weeds
<i>Aira praecox</i>	4289
<i>Arabidopsis thaliana</i>	1380
<i>Cerastium glomeratum</i>	1730
<i>Erophila verna</i>	3042
<i>Myosotis discolor</i>	397
<i>Ornithopus perpusillus</i>	35
<i>Veronica arvensis</i>	206

Weed numbers were modeled as a function of the number of neighbouring plots that had seed setting neighbours. None of the 6 species showed a significant effect.

Table 4.6 Maximum dispersal distances (cm) are compared for the two methods of recruitment sampling. Kendall's rank correlation: there is no similarity in the two measures of dispersal ($p = 0.773$, $\tau = 0.143$).

Species	transect	mapping	difference	rank by furthest	Rank by weeds
<i>Aira praecox</i>	33	26	7	6	1
<i>Arabidopsis thaliana</i>	37	24	13	5	4
<i>Cerastium glomeratum</i>	73	17	56	1	3
<i>Erophila verna</i>	63	21	42	2	2
<i>Myosotis discolor</i>	47	24	23	4	5
<i>Ornithopus perpusillus</i>	21	24	-3	7	7
<i>Veronica arvensis</i>	53	27	26	3	6

4.4 Discussion

There was substantial variation in the seed dispersal kernels of the seven species, as reflected in significant differences in mean distance, maximum distance and the location of the percentiles. Some of the species had remarkably similar kernels across replicates within years and from one year to another (e.g. *Aira praecox*). Others showed massive differences from year to year (e.g. *Arabidopsis thaliana*, *Erophila verna* and *Ornithopus perpusillus*). From the data at hand, it is not possible to conclude whether these differences were due to differences in the conditions influencing seed dispersal (wind, rain, animal activity) or in the numbers of seeds produced by the experimental plants (despite our best efforts to ensure similarity of plant size and fruit number), or in the pre-recruitment fates of the seeds (dormancy differences, granivore activity, seed mortality, germination rate, pre-emergence seedling mortality).

In all years, seed dispersal was greatest for *Cerastium glomeratum*, with parents producing extremely flat-topped (platykurtotic) dispersal kernels with very high values for median (data) and 3rd quartile dispersal (data). The maximum distance for *Cerastium glomeratum* was often impossible to measure because seeds had clearly dispersed beyond the edge of the experimental plots. At the other extreme, the grass *Aira praecox* showed consistently tight and well-defined dispersal kernels (median = 11; 3rd quartile = 15). Even maximum dispersal distance, which is famously difficult to quantify (“the seed that gets on a train”), was well behaved for *Aira praecox* (data in Table 4.4).

Previous pilot trials with direct seed traps (e.g. sticky traps) indicated that any benefits of direct estimation of the seed rain were outweighed by massive heterogeneity between replicates and by the difficulties of ensuring uniform rates of seed capture across time in the sticky traps. We decided, therefore, to forgo attempts to estimate seed input directly, instead relying on seedling appearance as a surrogate for seed rain.

It is possible there were differences in the size and shape of the parent plants of each of the 7 species transplanted from the greenhouse each year. However, an effort was made to keep such differences to a minimum, both between years and within years.

Some species in some years continued to grow and to produce more fruits following the initial fecundity estimation, perhaps due to favourable weather. Seed dispersal distances may vary from year to year with differences in plant height or fecundity. There was no evidence that seedlings of one species affected the shape of the dispersal kernel of another species, despite the fact that the seven species were grown in the same 1m² plots.

In rare cases, a few parent plants were replaced by new ones, either due to herbivore damage (mainly birds) or below ground factors (diseases, etc). This was likely to cause differences in the time of seed setting and possibly on subsequent seedling recruitment.

Secondary dispersal (e.g. tumble weeds) was common in most years for *C. glomeratum* and to a lesser extent for *A. thaliana*. This could be one of the reasons that *C. glomeratum* exhibited the greatest dispersal.

There is a potentially important carry-over effect, that Bergelson (1991) referred to as “skeletons in the micro-sites”. This is the notion that the dead body of the parent plant takes up space directly that might otherwise be occupied by offspring. Also by dint of its still tenacious anchorage, the skeleton can blow hither and thither in the wind, and this can act as a powerful agent of disturbance, preventing seedling establishment within a radius of the parental rootstock. Thus, while most of the parametric models for dispersal kernels are monotonic declining from an origin marked by the centre of the root of the parent, all seven of our species in all years show significantly depressed seedling recruitment immediately surrounding the parent. As a result of this, recruitment peaks on transects at a distance of 3-5 cm, even though it is possible that primary seed rain peaked directly beneath the centre of the parent plant canopy.

Because of our protocol of using living plants as seed sources (to increase the realism of the source of seed release) we inevitably introduce an extra level of variation that contributes part of the year effect (e.g. different fecundities of similar sized individuals from one year to the next, different temporal patterns of seed release across time in different years, the possibility of continued growth and flowering,

following transplantation of the parent plants in some years (particularly in the case of *Aira praecox*), and so on.

In terms of their overall population dynamics, our dispersal data suggest that local seed limitation is likely to be greatest for *Aira praecox* and least for *Cerastium glomeratum*. The latter species is clearly capable of substantial dispersal to distances greater than our between-plot separation in the multi-year population studies (Chapters 6 and 7 & 8). In terms of coexistence mechanisms, increased levels of intraspecific competition imposed by seed aggregation are likely to be ranked, from most to least important, across species as follows:

Aira>*Erophila*>*Cerastium*>*Veronica*>*Arabidopsis*>*Myosotis*>*Ornithopus*

This, in turn, would be likely to be consequential for coexistence to the extent that interspecific competitive ability (“dominance”) would be ranked in the same order (see Chapter 1). The dispersal data also predict the order of effect sizes in response to experimental seed redistribution: we should expect the greatest response in *Aira praecox* because we would be putting seeds into places where they would otherwise not get, and least in *Cerastium glomeratum* because its seeds would get these places with or without experimental redistribution (see Chapter 6).

In terms of abundance from weeded plots at Ashurst, the 7 species were ranked as follows (Table 4.5):

Aira>*Erophila*>*Cerastium*>*Arabidopsis*>*Myosotis*>*Veronica*>*Ornithopus*

It is intriguing that the correlation between small-scale kernel-based estimates of dispersal distances (e.g. mean distance or maximum observed distance) and longer-range (plot-to-plot) dispersal was so poor (Kendall’s tau = 0.143, n = 7, p = 0.77). This draws attention to the perennial problem with small scale experimental studies of seed dispersal; it is always likely that the rare long-distance dispersal events are going to be most important in practice under field conditions, but impossibly difficult to parameterize accurately with reasonable levels of cost and effort. The tails of the distribution are always poorly quantified (Okubo 1989, Kot 1996, Bullock and Clarke 2000, Cain et al. 2000, Clark et al. 2001, Bullock et al. 2006). The fact that larger-scale dispersal was so poorly predicted by attributes of the kernels suggests strongly that variation in seed number might be more important than variation in dispersal rate in determining the year effects in real field situations. Certainly the species that had

the greatest plot-to-plot dispersal, as measured by the weeding data from Ashurst, were not the most fecund species (e.g. *Aira praecox*), so it is obvious that factors other than mean short-distance dispersal distance and total seed production are important in determining the observed rate of immigration. Plant stature (especially height) is likely to be important, and this may well interact with the abiotic factors influencing primary and secondary seed dispersal behaviour (wind speed, gustiness, turbulence, and so on).

The picture is clearest for *Ornithopus perpusillus*: this had the shortest mean dispersal distance from the kernels and the lowest mean fecundity. It would be predicted to have the lowest rates of plot-to-plot dispersal, and this was indeed what we observed from the weeding data (only 35 plants established on plots where they were not sown; compare this with 4,289 plants of *Aira praecox*, and 206 for *Veronica arvensis*, the next poorest plot-to-plot disperser (Table 4.5).

The other species show no clear patterns, either with fecundity or small scale dispersal kernel behavior. This draws attention once again to the enormous uncertainties in trying to predict dispersal over spatial scales larger than those over which the measurements were made.

It is a moot point whether the effort expended in developing precise and well-parameterized small scale dispersal kernels is of any practical value for the purposes of prediction. We are reminded of the problems posed by “the bee that got on a train” when trying to predict pollen-flow distances from transgenic crops.

Chapter 5

Testing the Pacala-Rees model of Competitive Exclusion through saturation sowing

Abstract

We test the hypothesis of Pacala and Rees that competitive exclusion is likely to be observed in multi-species mixtures when seed of the superior competitor is sown at saturating densities. The model makes several assumptions: the existence of a limited number of microsites in which seedling recruitment can occur; and contest competition for the occupation of these microsites. The contest could take an extreme form (presence of one seed per microsite guarantees occupancy by a seedling of the superior competitor) or a more relaxed form (occupation is a lottery whose outcome is stochastic, with probability proportional to the fraction of seeds occupying the microsite that belong to a given species). We found little evidence for competitive exclusion in a single year. In several years and with several species sown at high densities, most of the species produced surviving adult plants despite the intensity of interspecific competition. There was no strong evidence of a pervasive effect of the order in which the seeds were sown for different species. There appear to be sufficient niche differences in the timing of germination and growth, and in plasticity of adult size, that coexistence of these 7 species under field conditions is not surprising. Other coexistence mechanisms (like heterogeneities in space and temporal differences between years) are likely only to make coexistence more likely.

5.1 Introduction

Simple lottery models of interspecific competition usually make one of two assumptions about the outcome of the struggle to obtain possession of a microsite when the site is occupied by seeds of more than one species. The “strong assumption” is that the superior competitor will take possession of the microsite whenever it has one or more seeds in the microsite. This leads rapidly to competitive exclusion in population dynamics models of interspecific competition. The “weak

assumption” is that the probability of ownership of the microsite in the next adult generation is a simple lottery, with the probability of occupancy equal to the fraction of all seeds in a microsite that belong to a given species. This means that the superior competitor does not always win the contest for a particular microsite. However, because the superior competitor will typically be more abundant, it will tend to produce the largest number of seeds, so that in the absence of a strong colonization-competition trade-off, it will tend to win an increasing proportion of microsites with the passage of time. This, too, will lead to competitive exclusion, but exclusion takes longer, and this buys time during which the inferior competitor might experience one of its rare good years (Chesson 2000a).

The Competition-Colonization Model was formulated most clearly by Hastings and Tilman (1980, 1994). There are two fundamental ideas. First, species can be ordered in terms of competitive ability into a perfect linear competitive hierarchy, so that if species A outcompetes species B, and species B outcompetes species C, then species A is bound to outcompete species C. Second, there is a trade-off between competitive ability and colonization ability. The simplest biological mechanism for this would be if the competitive species put most of its resources into leaves, whereas the less competitive species put most of its resources into seeds (but there are numerous other trade-offs that would produce the same outcome). The Competition-Colonization Model is based on the assumption that there is a perfect inverse correlation between competitive ability and colonizing ability. Analysis of the model indicates that with this admittedly very strong assumption, there is no limit to the number of species that can coexist (Hastings, 1980). The superior competitor is always rare because of its very low colonizing ability (low seed production and/or poor seed dispersal), and this leaves plenty of space for the inferior competitors to persist in equilibrium (Crawley and May 1987).

The model of Pacala and Rees (1998) produces testable hypotheses about the outcome of seed-to-seed competition for microsites during seedling recruitment. Specifically, if seed of the superior competitor is sown in excess, then all microsites will contain multiple seeds of the superior competitor and competitive exclusion will soon be observed. They do not specify exactly what “soon” means, but the sense of the model is clear enough.

We tested this hypothesis using what we call a “saturation sowing” approach. The argument is simply that if we sow a sufficiently high density of seeds of the superior competitor, then every microsite will contain at least one seed of the superior competitor, and if the strong assumption is correct, then we shall observe immediate competitive exclusion. Repeating the experiment over different years allows the possibility of discovering effective competitive exclusion by different species in their “kind of year”.

If the physical location of the seed within the microsite is important in determining the outcome of the contest for the microsite, then the order in which the seeds are sown might influence the outcome. If the best place for a seed to be is in contact with the soil (i.e. at the bottom of the stack of seeds) then there will be an advantage to being sown first, whereas if there is an advantage to being close to the surface (and hence close to the light) then there will be an advantage to being sown last.

Species may exhibit density-dependent germination (Palmbiad 1969), with enforced dormancy of an increasing fraction of the seeds as seed density increases. This behaviour creates a refuge from mass mortality and is likely to be highly stabilizing to long term population dynamics.

Because the sowing densities for this kind of experiment are so high (of order of thousands of seeds per metre square per year), the possibility exists of observing interesting post-seedling-recruitment density dependent behaviour, including over-compensating density dependent seedling mortality, for instance.

The experiment also addresses the fundamental question as to whether the concept of “the superior competitor” is useful in real environments that are both spatially and temporally heterogeneous. After all, every species that persists in a natural habitat must pass the invasion criterion: it must exhibit the ability to increase when rare. This means that, at least when it is scarce, it is a “good enough competitor” under at least one combination of environmental conditions. We ask whether there is a correlation between seed size, growth (biomass) and reproductive performance (λ), which we might be able to use *a priori* to rank our species in terms of

competitive ability. Equally, we could find that competitive exclusion is not the norm under experimental conditions in the field, and that there is no need for a concept like “the superior competitor” beyond the confines of simple theoretical models.

5.2 Materials and Methods

5.2.1 The plots and seed sowing

For the construction of the beds, the soil mixture, seed collection, method of seed sowing, mulch and weeding are all described in Chapter 2.

5.2.2 Sowing densities

Seeds were sown in a single 25 cm x 25 cm quadrat in the center of a raised bed. There were two sowing densities for each species in the saturation experiment. The first was a moderate sowing density identical to the medium sowing density for monoculture plots, (sector five of nine, see chapter 2, 2.2) in the first year. The second density was a saturation sowing which was at least 60 times the moderate sowing density (Table 5.1). We used 14 raised beds for this experiment: each of the seven species was sown at saturation density either first or last. The other six species were sown at moderate densities in a sequence that was independently randomized for each plot. There was no replication due to the limited number of plots available (250 plots) for all experiments.

Table 5.1 Sowing dates used in the experiment. Moderate (a) and saturation (b) sowing densities for each of the seven species. Each plot represents an area of 625cm².

	(a)	(a)	(b)	(b)
species	seeds/plot	Seed wt (mg)	Seeds /plot	Seed wt (mg)
<i>A. praecox</i>	250	38	30,000	4,500
<i>A. thaliana</i>	600	14	50,000	1,140
<i>C. glomeratum</i>	600	20	50,000	1,650
<i>E. verna</i>	600	14	50,000	1,165
<i>M. discolor</i>	250	50	15,000	3,000
<i>O. perpusillus</i>	125	125	15,000	15,000
<i>V. arvensis</i>	600	60	50,000	5,000

5.2.3 Estimating recruitment

Seedlings were counted on the dates shown in Table 5.2 and the plots were harvested on the dates shown in Table 5.3. For seedling counts, an A4 acetate sheet divided into 1cm x 1cm mini-quadrats was placed over the study area in the center 25cm x 25cm of the plot. Within each of the thirty randomly selected mini-quadrats, the numbers of recruits of the seven species were counted. The protocol was the same as in monocultures, except that there were typically several species per quadrat to count. Although the species are ostensibly winter annuals, survival from autumn and winter recruitment was very low due to seedling mortality resulting from frost heave and low temperatures. In years when autumn and winter temperatures were mild, as for example in 2004, some adults from certain plots survived and produced seeds the following spring/summer. In most cases, seed production was from plants originating from spring recruitment. In the event when there were no recruits to be sampled within any of the thirty mini-quadrats (due to very low recruitment at low sowing densities) all recruits were counted.

In some years, in some plots, the legume (*O. perpusillus*) formed a mat-like-structure, making it difficult to sample seedling recruitment for the other 6 species. When this was the case, the legume was rolled back with minimum disturbance to enable recording of the seedlings underneath.

Table 5.2 Recruitment count dates (2 per year) for saturation plots from 2002 to 2007.

year	count	<i>A. praecox</i>	<i>A. thaliana</i>	<i>C. glomeratum</i>	<i>E. verna</i>	<i>M. discolor</i>	<i>O. perpusillus</i>	<i>V. arvensis</i>
2002/2003	fall	NA	NA	NA	NA	NA	NA	NA
	spring	20/02/2003	17/02/2003	17/02/2003	17/02/2003	20/02/2003	20/02/2003	20/02/2003
2003/2004	fall	13/10/2003	30/10/2003	30/10/2003	30/10/2003	30/10/2003	13/10/2003	30/10/2003
	spring	05/03/2004	05/03/2004	05/03/2004	05/03/2004	10/03/2004	05/03/2004	10/03/2004
2004/2005	fall	09/09/2004	15/09/2004	15/09/2004	09/09/2004	09/09/2004	09/09/2004	15/09/2004
	spring	16/11/2004	16/11/2004	16/11/2004	16/11/2004	16/11/2004	16/11/2004	16/11/2004
2005/2006	fall	26/09/2005	26/09/2005	26/09/2005	26/09/2005	26/09/2005	26/09/2005	26/09/2005
	spring	10/04/2006	05/03/2006	05/03/2006	05/03/2006	05/03/2006	10/04/2006	05/03/2006
2006/2007	fall	16/08/2006	04/09/2006	04/09/2006	04/09/2006	04/09/2006	30/08/2006	04/09/2006
	spring	06/03/2007	NA	05/03/2007	NA	NA	NA	NA

Table 5.3 Seed sowing and harvesting dates for saturation sowing plots from 2002 – 2007.

year	activity	<i>Aira</i>	<i>Arabidopsis</i>	<i>Cerastium</i>	<i>Erophila</i>	<i>Myosotis</i>	<i>Ornithopus</i>	<i>Veronica</i>
2002/2003	sown	16/10/2002	16/10/2002	16/10/2002	16/10/2002	16/10/2002	16/10/2002	16/10/2002
	harvested	18/06/2003	16/06/2003	16/06/2003	28/04/2003	16/06/2003	15/07/2004	21/06/2003
2003/2004	sown	16/09/2003	16/09/2003	16/09/2003	16/09/2003	16/09/2003	16/09/2003	16/09/2003
	harvested	29/06/2004	18/06/2004	18/06/2004	18/06/2004	29/06/2004	23/07/2004	29/06/2004
2004/2005	sown	03/08/2004	03/08/2004	03/08/2004	03/08/2004	03/08/2004	03/08/2004	03/08/2004
	harvested	13/06/2005	06/06/2005	06/06/2005	06/06/2005	09/06/2005	27/06/2005	13/06/2005
2005/2006	sown	16/08/2005	16/08/2005	16/08/2005	16/08/2005	16/08/2005	16/08/2005	16/08/2005
	harvested	25/05/2006	18/05/2006	18/05/2006	09/05/2006	18/05/2006	06/06/2006	25/05/2006
2006/2007	sown	21/07/2006	21/07/2006	21/07/2006	21/07/2006	21/07/2006	21/07/2006	21/07/2006
	harvested	18/06/2007	05/05/2007	08/05/2007	20/04/2007	05/05/2007	13/07/2007	05/05/2007

5.2.4. Statistical modelling

There were two classes of modeling. We analyzed the five principal response variables (recruitment, survival, fecundity, lambda and biomass) for each of 14 plots over 5 years. The model has two fixed effects: the sowing density treatment (a three-level factor; saturation sown first, saturation sown last and moderate sowing density) and species identity (a seven-level factor). These are fitted in a linear mixed effects model with year and plot as random effects. The model looks like this

```
lmer(y ~ treatment * species + (1|year) + (1|plot))
```

with normal errors for biomass and lambda and Poisson errors for the count data (recruits and survivors). We also fit, but do not report here, analyses with binomial errors where we used proportion recruiting and proportion surviving as two-variable response variables; the results were the same as with the count data.

Identity effects (the performance of a species when sown at moderate densities as a function of the specific identity of the species that was sown at saturation density) were analyzed using a generalized linear model (glm) with data from one species as the response variable (recruitment, survival, fecundity, lambda or biomass) and the identity of the species sown at saturation density as a six-level factor. Lambda of the 7 species was compared across the two sowing densities by performing a linear model (lm).

5.3 Results

5.3.1 Biomass

The biomass results are presented in full in Table 5.4. This shows data from each of the five years, broken down by species and by sowing treatment. The saturation densities (levels 1 and 3) are unreplicated raw data, while the medium sowing density data (level = 2) are the average biomass calculated across six different competitor identities and two different sowing orders (i.e. the mean of 12 numbers in each year). The most striking feature of the data is the species-by-year interaction effects: *Ornithopus* is most often the dominant species in terms of final biomass, but *Myosotis* and *Aira* have years of dominance. The other interesting insight is that for most species, order of saturation sowing is unimportant, but there are some years when the order of sowing has dramatic effects for one or two species. For instance, *Arabidopsis* in 2004 and 2006 had more than 10 times the biomass when sown last than first, but in 2007 it failed completely (zero biomass) when sown last at saturation density. These are profound year effects.

Overall, mean biomass was ranked as follows: *Ornithopus* (2019.9 mg) > *Myosotis* (911.2) > *Veronica* (855.9), > *Aira* (661.6), > *Cerastium* (383.7) > *Erophila* (108.0) > *Arabidopsis* (87.8). The effects of sowing density and order are shown in Table 5.5. The influence of *Ornithopus* swamps the analysis by inflating the variance for the other species, even following log transformation of the biomass.

Table 5.4 Linear mixed effects mode for biomass as a function of species (sp) and sowing treatment (levels) with years and plot as random effects. The two random effects are roughly equal in their effects on biomass variation (roughly 10% of the variance explained). The significant effects are confined to *Ornithopus*: compared to sowing first at saturation densities it had significantly lower biomass when sown at moderate densities ($t = 3.205$) and significantly higher biomass when sown last rather than first at saturation densities ($t = 2.284$).

Fixed effects:

	Estimate	Std. Error	t value
(Intercept)	1536.2	1250.8	1.228
levels2	-992.7	1290.7	-0.769
levels3	-332.0	1753.7	-0.189
spAt	-1417.2	1753.7	-0.808
spCg	-651.8	1753.7	-0.372
spEv	-1150.0	1753.7	-0.656
spMd	703.0	1753.7	0.401
spOp	5967.6	1753.7	3.403
spVa	-947.0	1753.7	-0.540
levels2:spAt	930.7	1825.3	0.510
levels3:spAt	639.0	2480.2	0.258
levels2:spCg	458.1	1825.3	0.251
levels3:spCg	-262.0	2480.2	-0.106
levels2:spEv	674.3	1825.3	0.369
levels3:spEv	258.2	2480.2	0.104
levels2:spMd	-414.9	1825.3	-0.227
levels3:spMd	-1368.7	2480.2	-0.552
levels2:spOp	-5849.6	1825.3	-3.205
levels3:spOp	5665.5	2480.2	2.284
levels2:spVa	1238.0	1825.3	0.678
levels3:spVa	1123.2	2480.2	0.453

5.3.2 Recruitment

Table 5.5 Seedling recruitment in the saturation experiments. The random effect for years was more than 4 times as important than that for spatial variation between plots. Not surprisingly, seedling densities were significantly higher following saturation sowing (levels 1 and 3) than from sowing at intermediate densities (levels = 2). Only *Ornithopus* showed a significant interaction with levels, being significantly less abundant at intermediate sowing rate ($t = 2.19$, $p < 0.05$).

Linear mixed model fit by REML

Formula: $y \sim \text{factor}(\text{levels}) * \text{sp} + (1 \mid \text{factor}(\text{year})) + (1 \mid \text{plot})$

Data: data

AIC	BIC	logLik	deviance	REMLdev
1961	2061	-956.3	1926	1913

Random effects:

Groups	Name	Variance	Std.Dev.
plot	(Intercept)	0.12490	0.35342
factor(year)	(Intercept)	0.53919	0.73429
Residual		2.95450	1.71886

Number of obs: 490, groups: plot, 14; factor(year), 5

Fixed effects:

	Estimate	Std. Error	t value
(Intercept)	7.26421	0.87127	8.337
factor(levels)2	-2.78429	0.83684	-3.327
factor(levels)3	0.30138	1.13663	0.265
spAT	-1.85656	1.13701	-1.633
spCG	-1.93288	1.13701	-1.700
spEV	-2.35299	1.13701	-2.069
spMD	-0.69507	1.13701	-0.611
spOP	0.34824	1.13701	0.306
spVA	-1.72335	1.13701	-1.516
factor(levels)2:spAT	-1.86685	1.18806	-1.571
factor(levels)3:spAT	-0.97063	1.60744	-0.604
factor(levels)2:spCG	0.52948	1.18806	0.446
factor(levels)3:spCG	0.15702	1.60744	0.098
factor(levels)2:spEV	-0.67101	1.18806	-0.565
factor(levels)3:spEV	-1.42027	1.60744	-0.884
factor(levels)2:spMD	0.23382	1.18806	0.197
factor(levels)3:spMD	-0.02893	1.60744	-0.018
factor(levels)2:spOP	-2.60142	1.18806	-2.190
factor(levels)3:spOP	-0.28244	1.60744	-0.176
factor(levels)2:spVA	0.58587	1.18806	0.493
factor(levels)3:spVA	0.45356	1.60744	0.282

5.3.3 Survival from seedling to adult

Survival responses are shown in Table 5.6.

Table 5.6 Survival modelled as a proportion with binomial errors. The two random effects had quite different impacts with spatial effects (plots) much smaller than temporal (years). Survival was significantly lower in the two crucifers and significantly higher in *Ornithopus* and *Aira* (the intercept). There were some curious interaction effects: for instance, Veronica survived significantly better at moderate sowing densities and at saturation densities when sown last than when sown first at saturation density.

Generalized linear mixed model fit by the Laplace approximation

Formula: $y \sim \text{levels} * \text{sp} + (1 | \text{years}) + (1 | \text{plot})$

Data: data

AIC	BIC	logLik	deviance
10745	10841	-5349	10699

Random effects:

Groups	Name	Variance	Std.Dev.
plot	(Intercept)	0.032371	0.17992
years	(Intercept)	0.154219	0.39271

Number of obs: 490, groups: plot, 14; years, 5

Fixed effects:

	Estimate	Std. Error	z	value	Pr(> z)
(Intercept)	-5.13584	0.18852	-27.24	< 2e-16	***
levels2	3.71969	0.05539	67.16	< 2e-16	***
levels3	-0.22527	0.07017	-3.21	0.00133	**
spAt	-2.72303	0.12055	-22.59	< 2e-16	***
spCg	-0.60519	0.07414	-8.16	3.26e-16	***
spEv	-0.85517	0.07795	-10.97	< 2e-16	***
spMd	-0.95755	0.09782	-9.79	< 2e-16	***
spOp	1.12605	0.06730	16.73	< 2e-16	***
spVa	-1.93396	0.09555	-20.24	< 2e-16	***
levels2:spAt	-1.14539	0.14358	-7.98	1.50e-15	***
levels3:spAt	1.28685	0.14917	8.63	< 2e-16	***
levels2:spCg	-1.34259	0.08604	-15.60	< 2e-16	***
levels3:spCg	-0.89175	0.11678	-7.64	2.23e-14	***
levels2:spEv	-1.44789	0.09129	-15.86	< 2e-16	***
levels3:spEv	-0.95816	0.11445	-8.37	< 2e-16	***
levels2:spMd	0.05471	0.10705	0.51	0.60933	
levels3:spMd	0.13483	0.14072	0.96	0.33802	
levels2:spOp	-2.38718	0.08774	-27.21	< 2e-16	***
levels3:spOp	0.19513	0.09650	2.02	0.04316	*
levels2:spVa	0.46541	0.10387	4.48	7.44e-06	***
levels3:spVa	0.80041	0.12920	6.19	5.83e-10	***

The order of sowing had subtle effects for some of the species (Table 5.4).

Table 5.7 Biomass for species and years at each of three sowing treatments. First = saturation density sown first (n=1); medium = moderate density sown in a random sequence with a different species sown at saturation density (n=12); Last = saturation density sown last (n=1).

2003

sp	1	2	3
Ap	3323.0	351.50000	2571
At	379.0	56.17083	428
Cg	55.0	156.41667	43
Ev	818.0	128.33333	254
Md	147.0	373.16667	359
Op	31613.4	1622.08333	58050
Va	363.0	931.50000	1965

2004

	1	2	3
Ap	645	314.33333	196
At	91	68.91667	1266
Cg	2303	615.66667	749
Ev	47	12.08333	33
Md	5475	608.25000	348
Op	2032	272.58333	1921
Va	29	557.08333	2801

2005

	1	2	3
Ap	552	163.16667	657
At	92	5.50000	154
Cg	0	151.16667	26
Ev	457	40.66667	461
Md	3290	1028.16667	240
Op	983	40.83333	1576
Va	135	606.50000	1171

2006

	1	2	3
Ap	65	684.66667	745
At	22	108.45833	282
Cg	844	291.08333	434
Ev	395	110.62500	318
Md	468	466.16667	422
Op	2828	75.16667	2631
Va	1560	896.66667	671

2007

	1	2	3
Ap	3095.80	1203.56667	1852.00
At	10.94	45.94500	0.00
Cg	1219.60	534.43333	199.80
Ev	213.80	47.13333	496.20
Md	1816.00	1682.07417	1323.66
Op	62.50	1296.60833	8.50
Va	858.60	1180.30000	294.00

5.3.4 Year effects

The biomass of *Myosotis discolor* was remarkably unresponsive to seed sowing in some years (2003, 2006, 2007) but there were substantial effects of sowing order in other years (2004 for instance, showed 15.7 fold higher in first vs. last saturation sowing and 2005 had 13.7 fold higher in first vs. last). No other species showed such consistent or large effects of sowing order. *Veronica arvensis* showed very few significant biomass effects, but the response to order of sowing was highly variable (e.g. saturation last was peak in 2003, 2004 and 2005, but lowest in 2006 and 2007 ($t = 2.05$, $p < 0.05$)).

Arabidopsis thaliana showed extremely high variation in biomass with sowing order and with years. In 2007, for instance, there was very low biomass from the saturation sowing (first or last) compared with moderate seed density (over-compensating density dependence); in all the other years, biomass from the saturation sowing was significantly higher than from moderate seed density. Moderate sowing densities produced very low biomass in 2005.

Perhaps the most complicated responses were shown by the grass *Aira praecox*. Biomass was particularly high in 2003 and 2007, and particularly low when sown first at saturation density in 2006. The most variable responses to sowing order were shown by *Cerastium glomeratum* in 2003 and 2005 there was overcompensating density dependence, with lower biomass in both first and last saturation sowing, but in 2004 and 2007 there was much higher biomass from first than from last saturation sowing. Across all 3 sowing densities, 2005 was a very low year for biomass in *Cerastium glomeratum*.

There were year effects in the 3 different treatments. When *Myosotis* was sown first at high density, mean seedling recruitment was over 2000 in 4 of the 5 years. In 2003 there was no recruitment for this species at all when sown first but there was also a very low recruitment in the same year when sown last. There was little difference for *Aira* when sown first or last at high density. *Arabidopsis* showed higher seedling recruitment when sown last. *Cerastium* has slightly higher recruitment when sown last unlike *Erophila* when recruitment was higher when sown first. There was no

recruitment in 2003 for both treatments for this species (CG). *Erophila* failed to recruit in 2004 when sown last. *Ornithopus* has more abundant in recruitment when sown first, although there was no recruitment in 2004 when sown last despite 2000 mean seedling recruitments when sown first, as was *Veronica* except there was no recruitment in 2004 when sown first compared with 605 mean seedlings when sown last. Five or six species have highest recruitment in 2007 for both treatments compared to the other 4 years.

For the intermediate sowing, again there was a year effect for all species in recruitment. *Aira* showed consistently mean seedling recruitment over 80 for 4 years and over 50 for one year; it has the highest recruitment followed by *Myosotis*. There was no recruitment for *Arabidopsis* in 2003 and 2004. The highest mean recruitment (28) was in 2006. Highest mean recruitment (144) for *Cerastium* was in 2004 and 2006 and the lowest was in 2003 and 2007. There was no recruitment for *Erophila* in 2004. The highest recruitment (63) was in 2006. *Myosotis* discolor showed mean recruitment over 57 over the 5 year period with the highest (178) in 2005. The best year for *Ornithopus* was in 2007 and the worst in 2003. It showed the lowest recruitment average after *Arabidopsis*. *Veronica* was more abundant in 2004 (186) and least abundant in 2007 (14).

According to field notes (from visual observation), there were no obvious differences between sowing first or last for the saturated species. There were year differences in recruitment and final adult count for most species in each of the 3 levels of sowing.

Table 5.8 Year effects in the saturation experiments, summed for recruitment (a), survival (b) and biomass (c). Comparisons of recruitments between years for all species across the 5 years and effect size between years. Effect size in recruitment was highest for *Erophila*, however, effects sizes in adult survival and also in Biomass were highest for *Ornithopus*.

(a) Recruitment

Species	2003	2004	2005	2006	2007	effect size	effect size rank
<i>Ap</i>	192.071	551.928	281.285	448.21	410.785	2.9	6
<i>At</i>	23.785	28.285	10.571	80.428	105.714	10	4
<i>Cg</i>	26.857	259.142	105.785	260.5	366.071	13.6	2
<i>Ev</i>	77.357	3	196.571	104.285	9	65.5	1
<i>Md</i>	52.357	484.785	565.642	437.428	425.57	10.8	3
<i>Op</i>	145.857	349.785	235.785	212.857	409.071	2.8	7
<i>Va</i>	150.357	202.5	96.785	340.857	425.714	4.4	5

(b) Survival

species	2003	2004	2005	2006	2007	Effect size	effect rank
<i>Ap</i>	103.5	108	62.142	57.357	35.571	3.1	6
<i>At</i>	7.714	16.5	3.071	10.142	2.785	5.9	4
<i>Cg</i>	9.5	99.714	16.857	29.5	13.357	10.5	2
<i>Ev</i>	38.642	5.5	25.571	28.642	27.071	7	3
<i>Md</i>	16.571	37.785	28.857	35.5	8.5	4.4	5
<i>Op</i>	93	49.785	12.857	78.357	4.785	19	1
<i>Va</i>	31.785	29.357	33.571	55.857	37.285	1.8	7

(c) Biomass

Species	2003	2004	2005	2006	2007	effect size	effect ranks
<i>Ap</i>	722.286	329.5	226.214	644.714	1385.04	6	4
<i>At</i>	105.789	156	22.285	114.679	40.162	7	3
<i>Cg</i>	141.071	745.714	131.429	340.786	559.471	5.7	5
<i>Ev</i>	186.571	16.071	100.429	145.75	91.1143	11.7	2
<i>Md</i>	356	937.286	1133.43	463.143	1666.04	4.7	6
<i>Op</i>	7794.89	516	217.786	454.357	1116.45	35.8	1
<i>Va</i>	964.714	679.643	613.143	927.929	1094.01	1.8	7

5.3.5 Size classes distributions

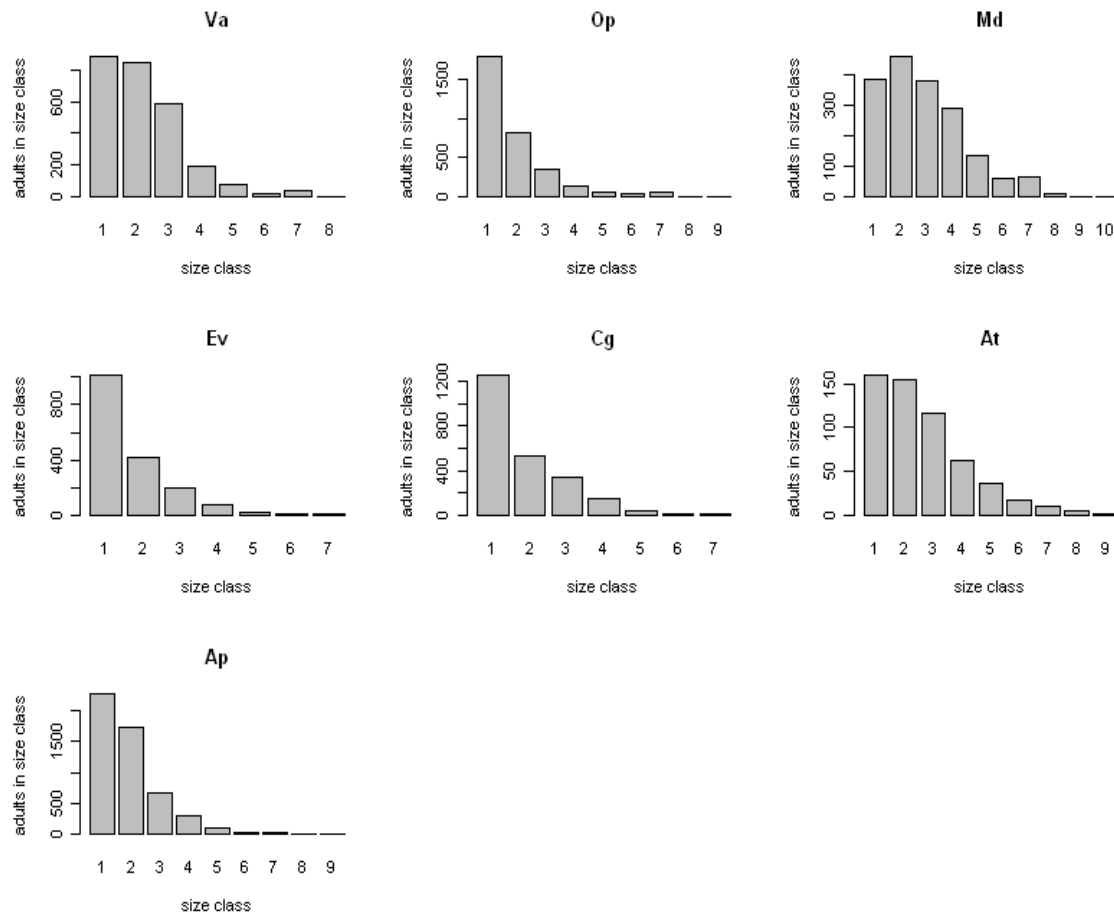


Fig 5.1 Size distribution of adult plants of sown species. *Ap* = *Aira praecox*, *At* = *Arabidopsis thaliana*, *Cg* = *Cerastium glomeratum*, *Ev* = *Erophila verna*, *Md* = *Myosotis discolor*, *Op* = *Ornithopus discolor*, *Va* = *Veronica arvensis*. Data combined over all sowing rates and five years to illustrate average species effects. Quadrat size (for data) = 625cm².

The distribution of size plants across size classes are shown for the combined dates (all sowing rates and times) in Fig 5.1. The range of the size classes categories are 1-10. All species showed the typical L-shaped size distribution (as in monocultures) with fewer individuals at higher size classes.

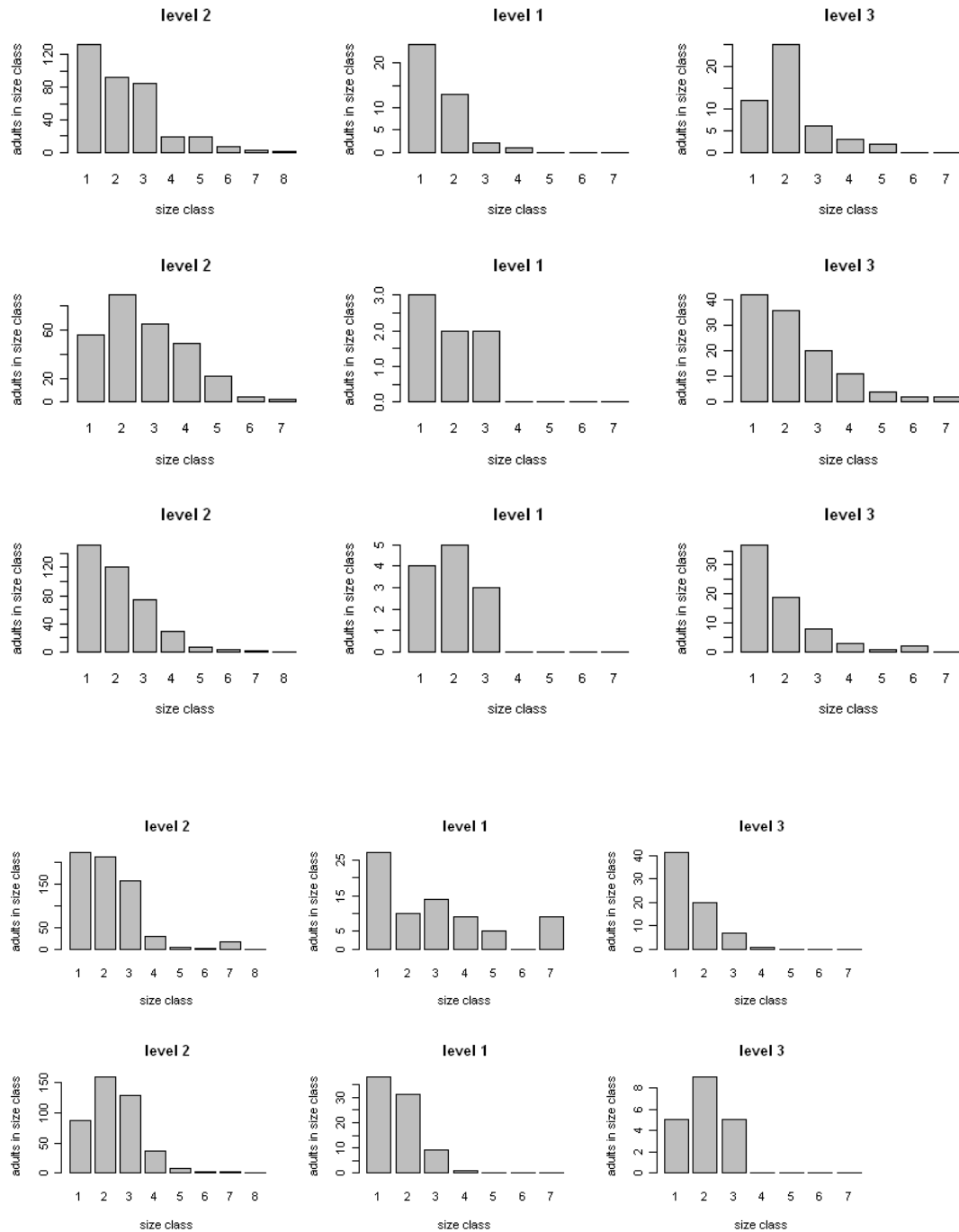


Fig 5.2 Year effects (2003 - 2007 from top to bottom) and sowing density effects as exemplified by *Veronica arvensis*. The range of the size classes categories are 1-8. There is a clear year effect on the three levels of seed sowing. Quadrat size (for data) = 625cm².

5.3.6 *Lambda*

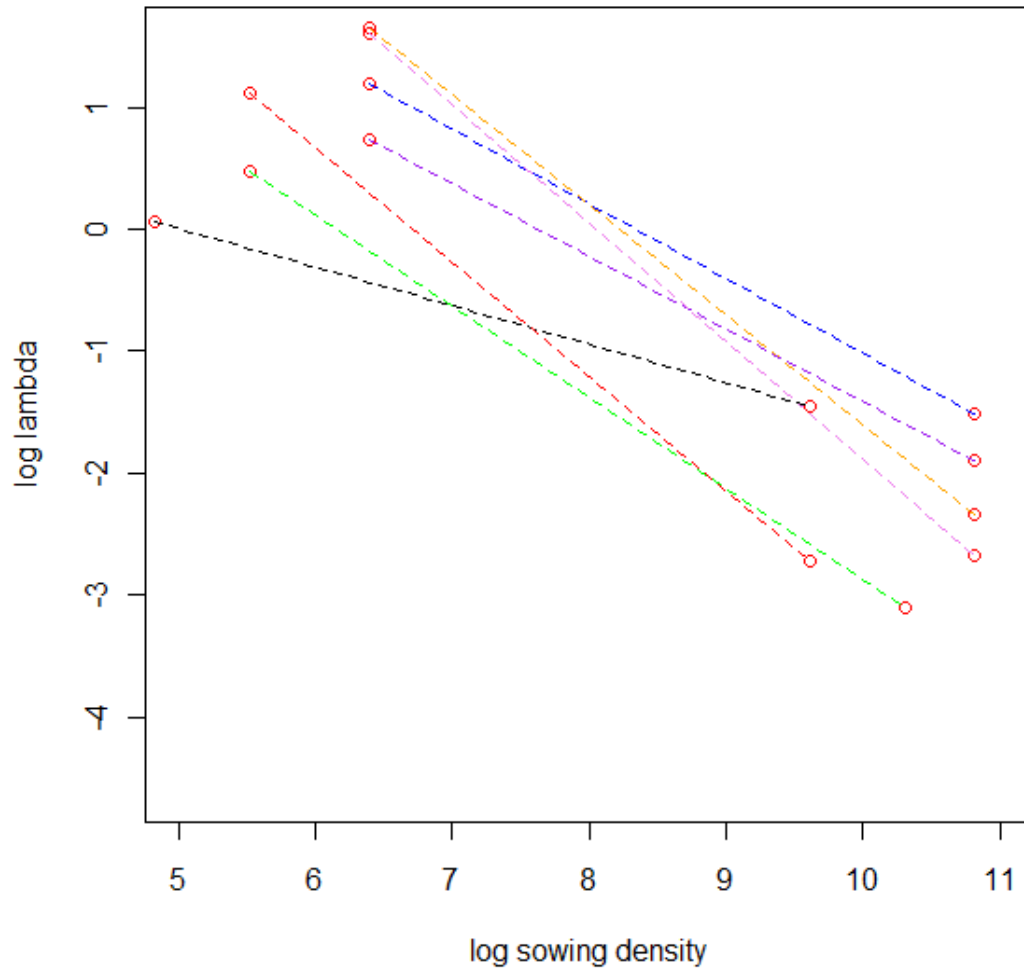


Fig 5.3 Mean log lambda (seed out/seed in) plotted against mean log sowing density (intermediate or saturation sowing) for each of the seven species for all 5 years on saturation plots. Log sowing densities values on the left hand side are for intermediate sowing density while those on the right hand side are for saturation sowing. *Ornithopus* has a significantly shallower slope than *Arabidopsis* and *Erophila*, which in turn, have a shallower slope than *Aira*, *Cerastium*, *Myosotis* and *Veronica*. Line colors: Green = *Aira*, Blue = *Arabidopsis*, Orange = *Cerastium*, purple = *Erophila*, Red = *Myosotis*, Black = *Ornithopus*, Violet = *Veronica*. Quadrat size from which lambda was calculated is = 625cm^2 .

Table 5.9 The effect of saturation sowing on log lambda for each species. *Ornithopus* has a significantly shallower slope than *Arabidopsis* and *Erophila*, which in turn, have a shallower slope than *Aira*, *Cerastium*, *Myosotis* and *Veronica*.

*lm(formula = lnlambda ~ sp * lnsowden)*

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	4.61210	0.54265	8.499	3.43e-16	***
spAT	0.47718	0.90793	0.526	0.599472	
spCG	2.80038	0.87292	3.208	0.001439	**
spEV	-0.06602	0.85699	-0.077	0.938635	
spMD	1.67056	0.82889	2.015	0.044501	*
spOP	-3.04011	0.81800	-3.717	0.000230	***
spVA	3.20699	0.85269	3.761	0.000193	***
lnsowden	-0.74806	0.08443	-8.861	< 2e-16	***
spAT: lnsowden	0.13824	0.12972	1.066	0.287195	
spCG: lnsowden	-0.15283	0.12765	-1.197	0.231888	
spEV: lnsowden	0.15302	0.12467	1.227	0.220371	
spMD: lnsowden	-0.18874	0.13028	-1.449	0.148172	
spOP: lnsowden	0.43417	0.13307	3.263	0.001194	**
spVA: lnsowden	-0.22229	0.12442	-1.787	0.074721	.

5.3.7 Identity effects

5.3.7.1 Recruitment: dominant identity from saturation sowing

Recruitment of *Aira* was significantly lower when *Cerastium* or *Myosotis* were sown at saturation densities (86.65) than when any of the other 4 species was sown at saturation densities (124.78, $p = 0.0183$). Recruitment of *Cerastium* was significantly higher when the *Erophila* (162.9) was sown at saturation densities than when any of the other 5 species was sown at saturation densities (58.12, $p = 0.000463$). In comparing *Cerastium* with *Erophila*, the recruitment of *Cerastium* was significant ($p < 0.0365$).

There was significantly higher recruitment of *Erophila* (33.4) when *Aira*, *Cerastium* or *Ornithopus* were sown at saturation densities than when they were *Arabidopsis*, *Myosotis* or *Veronica* (mean = 11.17, $p = 0.0267$). However, there was identity effect of saturation sowing on *Arabidopsis* and *Ornithopus*.

The only other significant effects of saturation sowing involved *Myosotis* and *Veronica*. Mean *Myosotis* density was significantly lower (60.9) when *Veronica* was sown at saturation density ($p = 0.0169$; contrast *Veronica* against the other 6 species (mean = 133.5, $p = 0.0206$). Mean *Veronica* density was lowest (60.6) when *Myosotis*

was sown at saturation density but highest when *Aira* was sown at saturation density (160.8, $p = 0.0437$). The posteriori contrast grouping of *Aira* and *Erophila* against the other species gave $p = 0.00725$ indicating that for *Veronica*, density was high when either *Aira* or *Erophila* were sown at saturation densities, and low when *Arabidopsis*, *Cerastium*, *Myosotis* or *Ornithopus* were sown at saturation densities. *Aira* and *Veronica* always had at least one surviving adult on every plot in every year, but *Cerastium* failed in 2 cases, *Erophila* in 3 cases, *Myosotis* in 4 cases, and *Ornithopus* in 9 cases, and *Arabidopsis* in 19 cases (out of a total of 70 plots: 14 treatments and 5 years).

5.4 Discussion

The experiment was inspired by the prediction of Pacala and Rees that competitive exclusion should follow rapidly (or be observed in a high proportion of cases) when seed of the superior competitor was sown in excess. The hypothesis is that recruitment is microsite limited, and that competition for a finite number of microsites occurs as a contest (or at least as a weighted lottery) within each microsite. Thus, in the extreme form of the model, if at least one seed of the superior competitor is found in every microsite, then each microsite will produce a plant of the superior competitor and competitive exclusion of all but one of the species will occur after the first year. In the less extreme version of the model, the weighted lottery predicts the same outcome (exclusion of all but one species) but over an unspecified but extended period, during which chance alone allows persistence of one or more inferior competitors in each microsite.

Our task, therefore, was to attempt to predict the identity of the superior competitor, then to convince ourselves that this species remains the superior competitor over the span of years that we waited for competitive exclusion to be observed. Our results represent as comprehensive a refutation of the hypothesis as an ecological field experiment is ever likely to provide. In no case (in any replicate or in any year) did one species prevent the recruitment and eventual seed set of all other species. In the majority of cases, all seven species produced individuals that survived to reproductive maturity independent of the identity of the species that was sown at saturation densities. There were significant identity effects on the performance of some species,

but they were quantitative rather than qualitative (i.e. they did not usually result in competitive exclusion, merely in reduced population-level seed production).

Year effects were pronounced in this experiment, suggesting that concepts like “the superior competitor” may be too broad to be useful. For our system of seven coexisting species it may be preferable to ask under which combinations of spatial and temporal conditions does each species do best. In the face of spatial and temporal heterogeneity of the scale we have documented in these experiments, it may be naïve to assume that competitive exclusion would ever be expected to be observed in such short-term experiments, especially if it were combined with stabilizing processes such as local dispersal and possession of a seed bank.

In short, there is no evidence from this study to support the extreme model of contest competition within microsites (i.e. one seed of the superior competitor guarantees site occupancy) and rather little to support the weighted-average lottery model. All species get some individuals to adulthood and produce a seed crop even in the face of extreme interspecific competition from five other species sown at normal densities and one species sown at saturation densities. There is a ranking of suppressive effects caused by the species sown at saturating densities, but it seldom matters whether these seeds were sown first or last (see Table 5.5).

There was no support for the hypothesis that the presence of seed of a superior competitor in a microsite prevents recruitment of inferior competitors. All species showed recruitment on almost all plots, typically at rates that were independent of the identity of the species that was sown at peak densities (but see below for details of those identity effects that were significant). *Aira* and *Veronica* always had at least one surviving adult on every plot in every year, but *Cerastium* failed in 2 cases, *Erophila* in 3 cases, *Myosotis* in 4 cases, and *Ornithopus* in 9 cases, and *Arabidopsis* in 19 cases (out of a total of 70 plots: 14 treatments and 5 years).

Chapter 6

Two-species interaction: the dynamics of time series of 21 species pairs with and without seed redistribution

Abstract

*We studied replicated sets of all 21 pair-wise combinations of seven annual plant species over 5 generations. In half the plots we collected the seeds before ripening and redistributed the same number of seeds at random over the whole of the 25cm x 25cm study plot. The other plots were controls in which seeds were allowed to disperse naturally. We tested the hypothesis that seed redistribution would increase the rate of competitive exclusion, by exposing the inferior competitor to the superior competitor over the entire area (i.e. by removing local spatial refuge from interspecific competition resulting from limited seed dispersal by a putative superior competitor). If this were to occur, then the abundance of the superior competitor should increase after redistribution (because it was previously dispersal-limited) and the abundance of the inferior competitor should decrease after redistribution (because of greater negative impacts of interspecific competitive). In fact, in cases where effects of seed redistribution were observed, it was most often observed that one species (or both) increased in abundance, and the other species was unaffected. As to population stability (measured by the standard deviation of the log of seedling population density) we did not record substantial numbers of local extinctions within 5 years, and only one species showed significant effects of the identity of the competing species on the probability of a zero count (*Arabidopsis* was significantly more likely to be absent on any sampling occasion when growing with the other crucifer *Erophila verna*). This interaction would repay further detailed field work, to discover the mechanism(s) behind this effect (e.g. allelopathy or shared natural enemies).*

6.1 Introduction

The principal aim of this chapter is to investigate the extent to which the dynamics of two species competitive interactions can be understood from the study of species separately in monoculture. We have seen from Chapter 2 that monocultures of the seven species grown in replicated monocultures at 9 densities over 5 years give reasonably consistent estimates of population increase (λ), and that density dependence is observed to varying degrees across the different species in seedling recruitment, seedling mortality, plant size and fecundity. The question is how these vital rates, determined entirely by intra-specific interactions, are altered under the influence of interspecific competition.

In pair-wise competition, simple models predict that a superior competitor will competitively exclude an inferior competitor (Chapter 1), but these models typically make no attempt to predict how long it will take for competitive exclusion to occur. We hypothesize that if competitive exclusion was not observed within 5 years, then it might be predicted to occur subsequently if one species exhibited significant increasing trend in abundance over time while the other showed a significant declining trend in abundance.

Alternatively, two species may coexist and exhibit no tendency towards competitive exclusion. This will occur when both species benefit from “rare species advantage”, meaning that each species could invade a monoculture of the other species with both species persisting thereafter (Chapter 2, (Chesson 2000a)).

Neither the coexistence criterion derived from Lotka Volterra models of interspecific competition (namely that intraspecific competition must be more important than interspecific competition for both species; see Chapter 2), nor the R^* theory (Tilman, 1982) make testable predictions about the way that monoculture behaviour ought to create rare species advantage and hence promote coexistence. Indeed, the monocultures do not even predict the identity of the winning and losing species, unless the dynamics of the resource for which they are competing is modeled explicitly. The present work is based on the assumption that both competing species pass the invasion criterion, and therefore that both species could increase when rare,

when growing on their own. This sets both species off on a trajectory of exponential population growth, but it makes no prediction about the population density (or the biomass) at which the species would come to equilibrium. That depends on the context-specific details of the density dependence exhibited by both species (see Fig 6.1).

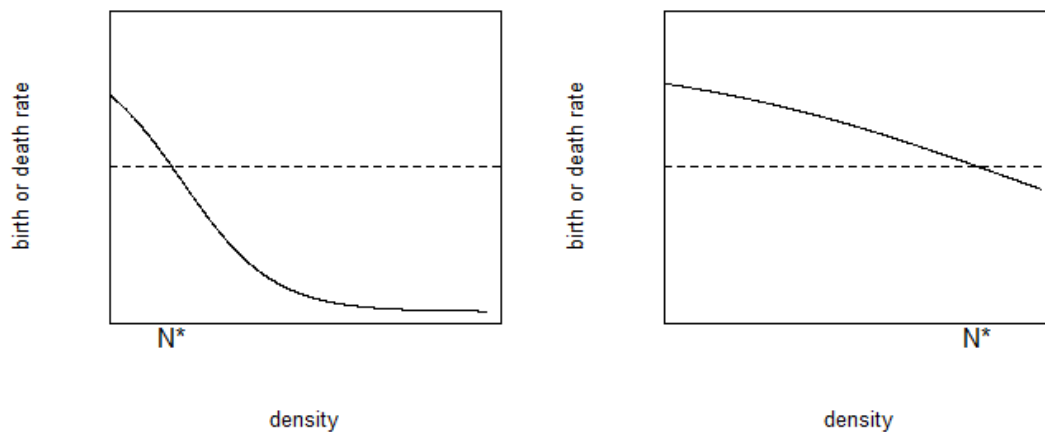


Fig 6.1 Two species with exactly the same values of λ at low density can have contrasting equilibrium population densities (N^*) depending on the nature of the density dependence they exhibit. Left: a low density equilibrium population because the birth rate (solid line) falls rapidly with density. Right: a high density equilibrium population because the birth rate (solid line) falls slowly with density. The death rate is assumed to be density independent, and identical in both cases (dashed line). Equilibrium population occurs when the rates of birth and death are equal (i.e. at the intersection of the solid and dashed lines).

The simplest prediction is that the winner in competition will be the species that produces the greatest biomass in monoculture. The question then arises as to whether peak biomass is density dependent: the law of constant yield suggests not (Harper 1977b), but there are cases of over-compensating density dependence where populations get “stuck” when grown at the highest population densities and produce relatively low biomass, and there are other cases where the species with the lowest R^* does not have the highest biomass (Tilman, 1982).

On the basis of the results of 5 years of monoculture studies (Chapter 2) we might predict the following competitive hierarchies based on peak biomass (mg):

Ornithopus perpusillus (3683) > *Aira praecox* (1104) > *Veronica arvensis* > (979)
Arabidopsis thaliana (888) > *Myosotis discolor* (772) > *Cerastium glomeratum* (721)
 > *Erophila verna* (368). Here (pairs): Op > Md > Ap > Va > Cg > At > Ev

However, there are several ways that species with lower peak biomass might coexist with species exhibiting higher biomass:

- grow earlier in the season and set seed before the other species reaches peak biomass
- grow later in the season once peak biomass has passed
- produce allelochemicals that interfere with the growth of the other species
- harbour a relatively benign pathogen that is virulent to the other species
- live in the spatial gaps in the biomass of the other species
- rely on its own good years in which to do disproportionately well
- prosper on rare spatial heterogeneities within the plots (e.g. nutrient cold-spots, or relatively dry places).

At the start of the study we had no evidence of shared pathogens (except possibly between *Erophila* and *Arabidopsis*) and no evidence of allelopathy for any of the species. The replicated 21 pairs of every possible species combination allow a strong test of the hypothesis that there is consistent competitive superiority between given pairs of species and hence a deterministic hierarchy across the 7 species.

Alternatively, the lack of consistent superiority might imply neutrality but could

equally well be due to heterogeneity of outcome based on local, small-scale contingencies (e.g. micro-climate or density dependence).

The dynamics of each time series are assumed to be driven by “year effects” which are experienced by both species, but which can affect their vital rates (dormancy, germination, growth, survival and fecundity) in different ways. The year effects could also modify the density dependent interactions within and between species. The central issue for this chapter is whether the year effects tend to hasten or to delay competitive exclusion. The model underlying the joint time series is:

$$N_{1,t+1} = F_{1,t} s_{1,t} g_{1,t} N_{1,t}$$

$$N_{2,t+1} = F_{2,t} s_{2,t} g_{2,t} N_{2,t}$$

in which the fecundity (F), survival (s) and recruitment (g) rates are both year-dependent and density dependent, varying with both N_1 and N_2 (e.g. proportional to $(1 - \alpha_{11}N_{1t} - \alpha_{12}N_{2t})$ where the alphas are the absolute per-capita intraspecific (α_{11}) and interspecific (α_{12}) competition coefficients; see Chapter 1). The hypothesis is that redistribution should cause the increase of one species (the putative superior competitor) and the decrease of the other species (putative inferior competitor).

The chapter investigates 6 key questions:

1. Is there a characteristic pattern of density trajectories across years (e.g. a trend towards competitive exclusion of sown species)?
2. How similar are the time series for the same species across replicates?
3. How often is local extinction observed?
4. Are there consistent identity effects in terms of dominance rank (e.g. if $A > B$ and $B > C$ then $A > C$), and can we identify “superior competitors”?
5. How does experimental seed redistribution of seed affect the outcome compared with control replicates?
6. Are the years of peak abundance in paired combinations predicted by the monoculture and/or saturation data?

7. Does seed-redistribution affect either mean population density or population stability?

6.2 Materials and Methods

6.2.1 Site and the plots

The experiment was carried out in the herbivore enclosure at Ashurst Silwood Park, on 250 raised beds laid out in 10 columns of 25 rows.

For the construction of the beds, the soil mixture, seed collection, method of seed sowing, mulch, monitoring of seedling appearances, weeding and other demographic measurements see chapter 2, 2.1. Species pairs were allocated at random to plots, with one replicate in each of four spatial blocks. There were two experimental treatments of each treatment and species-composition (see below).

6.2.2 Seed sowing

Seeds were sown in to 168 of the 250 plots between 25/09/2002 and 04/10/2002 for all species. Species were sown into a 25cm x 25cm quadrat in the center of each raised bed (1m x 1m) lined by railway sleepers. The sowing densities for *Arabidopsis thaliana*, *Erophila verna*, *Cerastium glomeratum* and *Veronica arvensis* were 600 seeds each per plot. The sowing densities for *A. praecox* and *M. discolor* were 250 seeds per plot. For *Ornithopus perpusillus* the sowing density was 125 seeds per plot.

6.2.3 Estimating recruitment

Seedling appearances were monitored following sowing in mid-October until the earliest batch of recruits for one bout of the pair appeared on 06/12/2002. Apart from the first year - when there was only one recruitment (estimate in the spring of 2003 following sowing in mid-October 2002), at least two recruitment estimates were made for all species in subsequent years. Although all the species are ostensibly winter annuals, adult survival from autumn and winter recruitment was very low due to seedling mortality as a result of frost heave and low temperatures. In years when autumn and winter temperatures were mild, for example in 2004/2005, there was some of adults from 10 of the 168 plots, and also in 2006/2007, the mildest and wettest year with 15 of 168 plots having flowering/fruited plants from fall recruitment.

A transparent acetate sheet marked with 30 randomly selected 1cm x 1cm mini-quadrats was laid over the 25cm x 25cm sown area and counts made of both species within each of the 30 mini-quadrats. If all the mini-quadrats provided zero counts, but the species was present elsewhere in the plot, then presence was noted, i.e. the zero count did not mean local extinction in this case other than to indicate low density. Dates of the counts are given in Table 6.1.

Table 6.1 Recruitment count dates for all species in each of the five years. Recruitment count for *Arabidopsis thaliana* was made between 07/10/2004 and 10/10/2004 in fall of 2004.

year	season	recruitment count dates	species
2002/2003	fall	none	all
	spring	15/01/2003 - 07/02/2003	all
2003/2004	fall	23/10/2003 - 14/12/2003	all
	spring	13/03/2004 - 28/03/2004	all
2004/2005	fall	08/09/2004 - 16/09/2004	all
	spring	15/03/2005 - 30/03/2005	all
2005/2006	fall	13/09/2005 - 16/09/2005	all
	spring	10/04/2006 - 26/04/2006	all
2006/2007	fall	12/09/2006 - 21/10/2006	all
	spring	none	all

Recruitment count for *Arabidopsis thaliana* was made between 07/10/2004 and 10/10/2004 in fall of 2004.

6.2.4 Seed redistribution

Half (84) of the plots were allowed to set seeds naturally while the other half had their seeds harvested during the ripening period prior to seed setting at the end of the growing season. This was done by selectively removing whole plants to the base of the main stem (to minimize substrate disturbance). In some species, such as *E. verna*, fruit production was not uniform in that the lower part of an individual plant had ripe fruits while the upper half was still in flower. In this case, ripe fruits were systematically removed using fine scissors on a regular basis and then collected in to paper bags. Each time a harvest was completed for a particular species within each plot, the total fruits were counted and fecundity was calculated using the calibrated seed number per fruit which was worked out at the start of the study (see, Table 2.1). Instead of using the same seeds to redistribute back into the plot, due to the risk of non-fully ripe fruits not producing viable seeds, an exact amount of seeds were weighed out from locally collected freshly ripened seeds for each species. Seeds were sown back into the same plot within a short period of time after fruits were removed to minimize the time gap between natural seed setting and seed redistribution.

6.2.5 Harvesting

At the end of the five years experiment, all species from the quadrats of all pair plots were harvested in the spring and summer of 2007 (see Table 6.2). All plants were sorted in to seven size classes and their dry matter determined. Harvesting biomass, estimating fecundity and allocating adults to size classes were done in the same way as for monocultures (see chapter, 2.4).

Table 6.2 Harvest dates for each of the twenty one pairs are summarized in the table below. Plots on the left-hand side column of the table refer to redistributed plots while those on the right-hand side refer to control plots for each pair. D1sp1=harvest date one for the first species in the pair. D2sp1=harvest date two for the first species in the pair. D1sp2=harvest date one for the second species in the pair. D2sp2=harvest date two for the second species in the pair. Abbreviated species names are: Apat = *Aira praecox* and *Arabidopsis thaliana* pair; cgev = *Cerastium glomeratum* and *Erophila verna*; mdop = *Myosotis discolor* and *Ornithopus perpusillus*; va = *Veronica arvensis*.

pair	d1sp1	d2sp1	d1sp2	d2sp2	plotd1sp1&d1sp2	plotd2sp1& d2sp2
apat	16/06/2007	20/06/2007	28/04/2007	08/05/2007	A25,G23,A10,H8	K23,A23,C1,F8
apcg	16/06/2007	20/06/2007	04/05/2007	16/05/2007	J1,D20,B13,K19	J19,A15,B5,G5
apev	16/06/2007	20/06/2007	14/04/2007	20/04/2007	G6,B9,E17,K17	H15,H6,A4,B23
apmd	16/06/2007	20/06/2007	21/05/2007	02/06/2007	C21,F25,D1,G1	G21,K4,A8,,B20
apop	16/06/2007	20/06/2007	12/07/2007	23/07/2007	G13,E8,E19,F22	K14,A21,C7,H13
apva	16/06/2007	20/06/2007	02/06/2007	15/06/2007	K8,F21,A9,E23	A14,G7,K25,E1
atcg	28/04/2007	08/05/2007	04/05/2007	16/05/2007	F4,B4,J20,D22	G25,C10,G2,B25
atev	28/04/2007	04/05/2007	14/04/2007	20/04/2007	H19,B16,K7,D2	H25,H4,A17,D12
atmd	28/04/2007	04/05/2007	21/05/2007	02/06/2007	C24,H21,B8,H1	J5,H22,B11,C15
atop	28/04/2007	04/05/2007	12/07/2007	23/07/2007	F3,C4,A18,H18	K24,J9,A11,D14
atva	28/04/2007	04/05/2007	02/06/2007	15/06/2007	H20,C17,E12,H11	H16,H3,C22,D4
cgev	04/05/2007	16/05/2007	14/04/2007	20/04/2007	D9,J11,K20,C16	K12,H23,D16,E4
cgmd	04/05/2007	16/05/2007	21/05/2007	02/06/2007	B1,K9,C14,G18	G11,K21,C12,C18
cgop	04/05/2007	16/05/2007	12/07/2007	23/07/2007	J8,D10,H14,D18	K18,K5,D15,E3
cgva	04/05/2007	16/05/2007	02/06/2007	15/06/2007	A3,H2,E20,J25	G16,K6,A24,E7
evmd	14/04/2007	20/04/2007	21/05/2007	02/06/2007	C3,F22,K15,F1	J4,J15,B17,C5
evop	14/04/2007	20/04/2007	12/07/2007	23/07/2007	J13,K16,A20,D5	F23,K11,A12,C20
evva	14/04/2007	20/04/2007	02/06/2007	15/06/2007	K1,B7,C25,H24	G8,A5,D19,G20
mdop	21/05/2007	02/06/2007	12/07/2007	23/07/2007	F5,C11,A16,F20	J23,H7,A6,A22
mdva	21/05/2007	02/06/2009	02/06/2007	15/06/2007	J22,D24,D6,G3	F24,C9,F6,D25
opva	12/07/2007	23/07/2007	02/06/2007	15/06/2007	G19,D17,K13,D7	G9,K22,D11,E16

6.2.6 Statistical analysis

Linear regression of log (counts+1) against time was used to assess the significance of any trend in abundance over time. Linear mixed effects models were used to test the significance of identity effects and treatment effects, with plot and year fitted as

random effects. There are too few sampling occasions to use formal time series analysis models to establish temporal autocorrelation function $N_{t+1} = f(N_t)$. In addition, proportion tests were performed on “no shows” (6 sample comparisons). The trends of mean recruitment abundance over time were analysed using linear model.

6.3 Results

6.3.1 Trends

Table 6.3. Effects of seed redistribution on mean log abundance. In all 7 species, the effect of seed redistribution was to increase mean log (seedling count +1). This was significant as a main effect ($t = 3.88$) but not significantly different across species when all species are modelled together (for separate species analyses, see Table 6. 4). There were more mean seedlings in seed redistributed replicates than there were in control replicates for all species.

	<i>Ap</i>	<i>At</i>	<i>Cg</i>	<i>Ev</i>	<i>Md</i>	<i>Op</i>	<i>Va</i>
control	4.797170	3.094067	3.714358	4.512021	3.442653	2.471237	3.388096
redistributed	5.031195	3.562886	4.085030	4.513986	4.030297	2.564776	3.990713

Fixed effects from the mixed effects model:

	Estimate	Std. Error	t value	
(Intercept)	4.74566	0.12288	38.62	
speciesat	-1.58571	0.16256	-9.75	
speciescg	-1.01449	0.16256	-6.24	
speciesev	-0.40118	0.16256	-2.47	
speciesmd	-1.17771	0.16256	-7.24	
speciesop	-2.39618	0.16256	-14.74	
speciesva	-1.22478	0.16256	-7.53	
levelst	0.33704	0.08689	3.88	**

Table 6.4. Effects of competitor identity and seed redistribution on mean log (seedling count +1). *Arabidopsis thaliana* (At), *Myosotis discolor* (Md) and *Veronica arvensis* (Va) were significantly more abundant following seed redistribution. *Veronica arvensis* (Va) was more abundant when paired with *Arabidopsis thaliana* (At), and individual species-contrasts show that *Arabidopsis thaliana* (At) was significantly less abundant when paired with *Erophila verna* (Ev) than with all species other than *Aira praecox* (Ap), and *Erophila verna* (Ev) was less abundant when paired with *Arabidopsis thaliana* (At) than with *Veronica arvensis* (Va).

Ap

	Estimate	Std. Error	t value
(Intercept)	4.94195	0.27409	18.031
cidcg	0.23597	0.35886	0.658
cidev	-0.31453	0.35886	-0.876
cidmd	-0.19740	0.35886	-0.550
cidop	-0.56427	0.35886	-1.572
cidva	-0.02842	0.35886	-0.079
levelst	0.23403	0.20719	1.130

At

(Intercept)	2.7853	0.3125	8.912
cidcg	0.7148	0.4092	1.747
cidev	-0.6150	0.4092	-1.503
cidmd	0.6290	0.4092	1.537
cidop	0.4678	0.4092	1.143
cidva	0.6558	0.4092	1.603
levelst	0.4688	0.2363	1.984 *

Cg

(Intercept)	3.8316	0.3067	12.493
cidat	-0.1455	0.4016	-0.362
cidev	-0.1990	0.4016	-0.496
cidmd	-0.1135	0.4016	-0.283
cidop	-0.5213	0.4016	-1.298
cidva	0.2759	0.4016	0.687
levelst	0.3707	0.2318	1.599

Ev

(Intercept)	4.707358	0.335985	14.011
cidat	-0.734372	0.439908	-1.669
cidcg	-0.395627	0.439908	-0.899
cidmd	-0.441384	0.439908	-1.003
cidop	-0.018426	0.439908	-0.042
cidva	0.417792	0.439908	0.950
levelst	0.001964	0.253981	0.008

Md

(Intercept)	3.6718	0.2851	12.880
cidat	-0.1739	0.3733	-0.466
cidcg	-0.1984	0.3733	-0.532
cidev	-0.7225	0.3733	-1.936
cidop	-0.2265	0.3733	-0.607
cidva	-0.0535	0.3733	-0.143
levelst	0.5876	0.2155	2.727 **

Op

(Intercept)	2.57041	0.29744	8.642
cidat	0.14234	0.38944	0.366
cidcg	-0.10317	0.38944	-0.265
cidev	-0.18042	0.38944	-0.463
cidmd	-0.41613	0.38944	-1.069
cidva	-0.03767	0.38944	-0.097
levelst	0.09354	0.22484	0.416

Va

(Intercept)	3.30260	0.30610	10.789
cidat	0.92522	0.40078	2.309 **
cidcg	-0.13121	0.40078	-0.327
cidev	-0.09956	0.40078	-0.248
cidmd	-0.05311	0.40078	-0.133
cidop	-0.12834	0.40078	-0.320
levelst	0.60262	0.23139	2.604 **

Table 6.5 Effects of seed redistribution on population stability as measured by the standard deviation of log (seedling count +1). The effect of seed redistribution was to *reduce* population stability in 6 cases out of seven (the one case being *Myosotis discolor*), with significant reductions in stability in 2 cases (*Cerastium glomeratum* and *Erophila verna*).

Ap	-0.23135	0.13401	-1.726	0.091 .
At	-0.006702	0.10658	-0.063	0.95
Cg	-0.27525	0.09947	-2.767	0.00812 **
Ev	-0.26324	0.12239	-2.151	0.0368 *
Md	0.01606	0.10492	0.153	0.879
Op	-0.09693	0.08042	-1.205	0.234
Va	-0.05498	0.09400	-0.585	0.562

Table 6. 6. Year effects on mean seedling counts. For *Aira praecox*, 2004 was the best year and 2006 the worst; for At 2004 and 2003, for Cg 2004 and 2003, for Ev 2004 and 2006, for Md 2005 and 2003, for Op 2004 and 2003, and for Va 2003 and 2006. Thus 2003 was both best and worst, 2004 was best for 5 species and 2005 best for one. For three species, 2006 was the worst year, 2003 was the worst for four species.

	2003	2004	2005	2006
Ap	281.42708	1000.3333	243.67708	235.75000
At	51.16842	204.3299	98.87500	125.78125
Cg	122.25000	238.7917	194.12500	141.56250
Ev	252.66316	1258.4124	248.33333	230.81250
Md	98.18750	119.8958	166.15625	164.14583
Op	17.63542	146.1458	61.08333	61.28125
Va	187.35417	158.4792	106.92708	92.51042

Table 6. 7. Trends in the times series for species in pairs. Four of the species showed significant downward trends in mean abundance (*Arabidopsis*, *Cerastium*, *Erophila* and *Veronica*) but no species showed significant increase over the 5 years. The slopes of the linear regressions and their standard errors (s.e.) were:

species	slope	s.e.	t	p
Ap	-7.844e-07	5.577e-07	-1.407	0.1603
At	-1.628e-06	2.836e-07	-5.740	1.79e-08 ***
Cg	-1.333e-06	3.201e-07	-4.164	3.78e-05 ***
Ev	-2.236e-06	8.230e-07	-2.717	0.00686 **
Md	2.973e-07	2.046e-07	1.453	0.147
Op	3.110e-08	1.629e-07	0.191	0.849
Va	-2.402e-06	2.419e-07	-9.932	<2e-16 ***

The time series showed complex fluctuations around the trend. Here, as illustration, are the data and fitted linear trend for *Veronica arvensis*. There was a decline in mean recruitment abundance over time for this species (Fig 6.2) as was the case for the other 6 species.

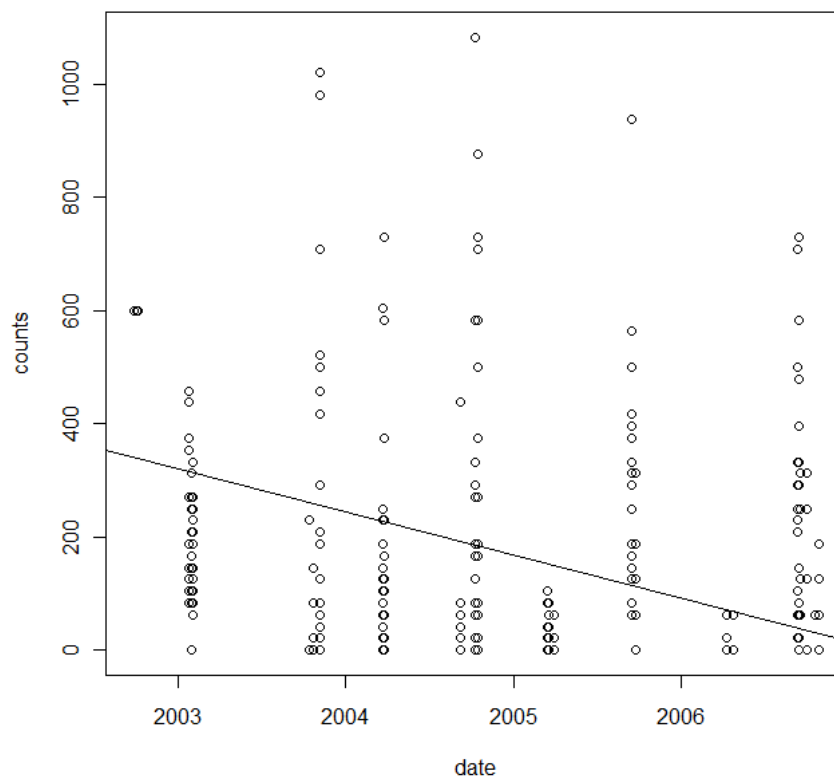
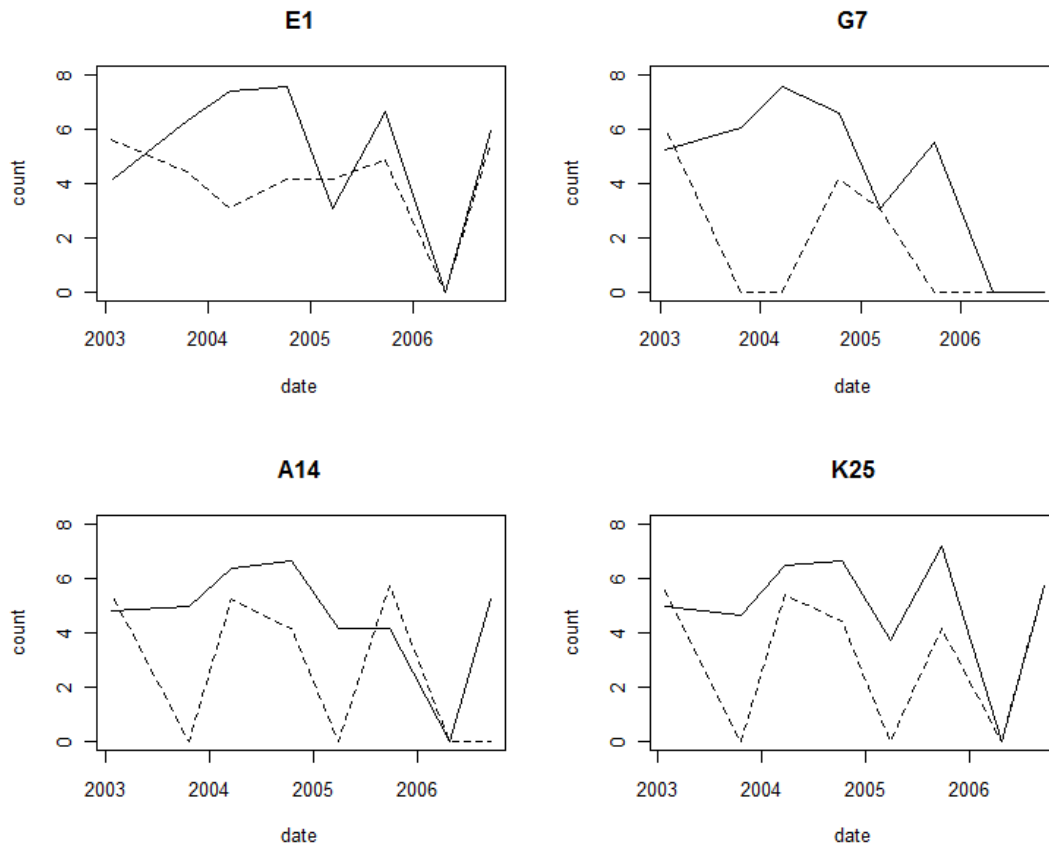


Fig 6.2 Linear trend in mean recruitment abundant over time (from a quadrat, 625cm² in size) for *Veronica arvensis*.

6.3.2 Behaviours of pairs of species

Apva (a)



(b)

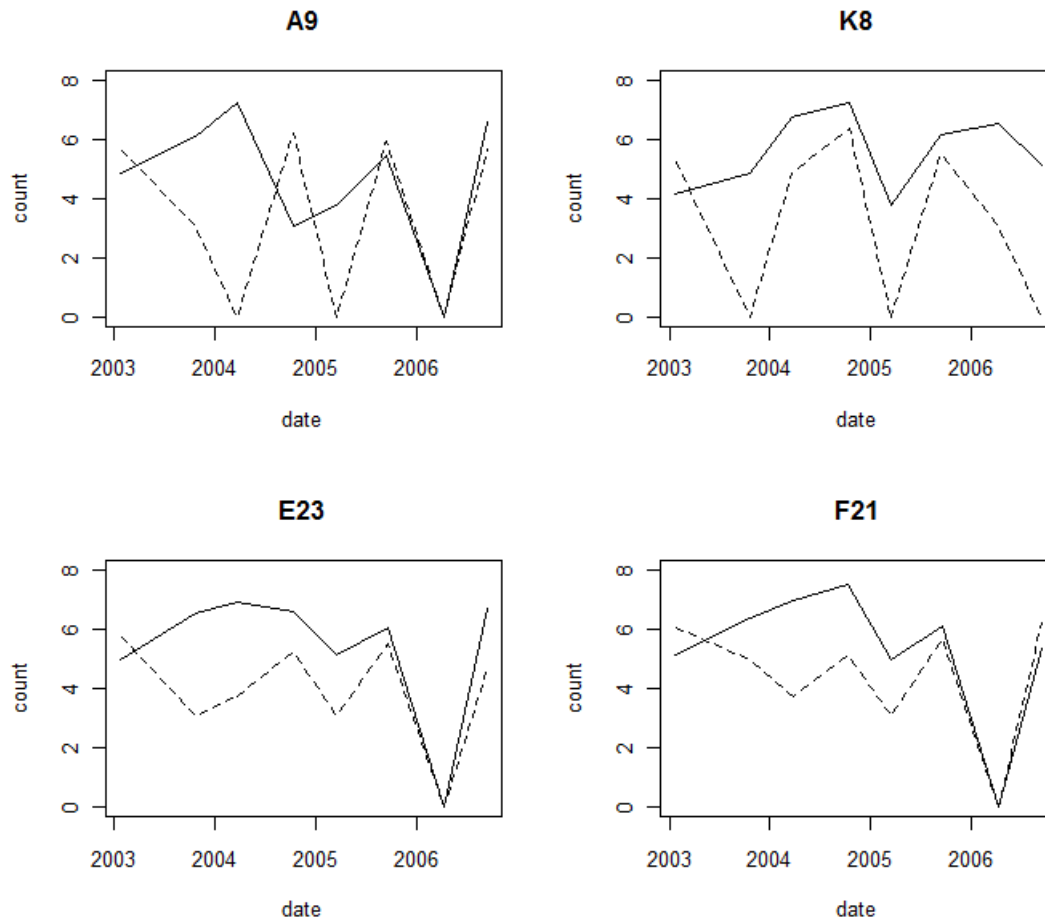
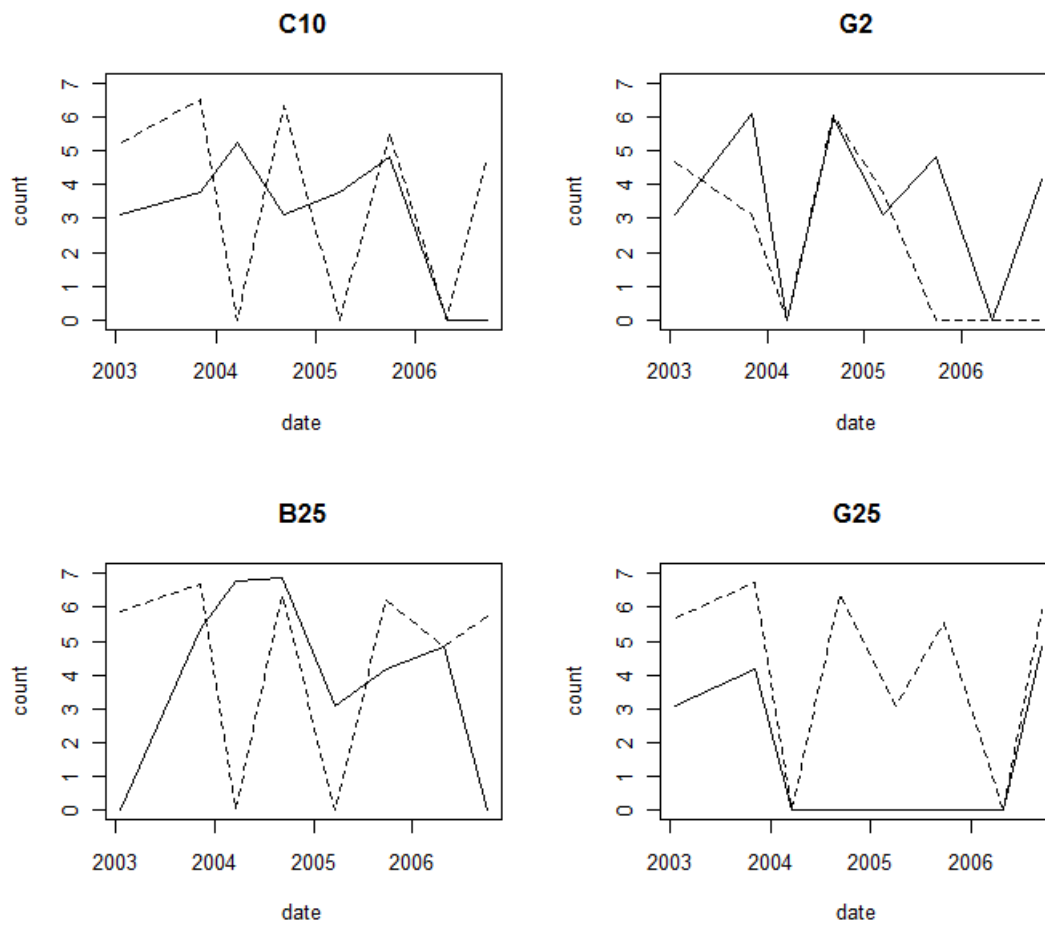


Fig 6.3 (a) Time series of control replicates for *Aira praecox* (solid line) and *Veronica arvensis* (dashed line) pair. The peaks are not synchronous between the two species, or across replicates. (b) Time series of seed redistributed replicates. The peaks are synchronous between the two species in autumn 2006 in 3 of the 4 replicates unlike in the control replicates. Population density of both species went up in 2007 in 3 of 4 replicates in seed redistributed replicates in contrast to control replicates when density went up in 2 of 4 replicates. Each replicate is 625cm² in size.

Both species persisted on all 4 replicates of each treatment. However, *Aira* was consistently more abundant on all replicates, while *Veronica* was less abundant on most replicates. *Aira* showed only one peak recruitment on all replicates in most years, except on control replicate, where there were only 2 peaks between 2004 and 2006. The pair was rather more in synchrony on the treated replicates compared with control ones.

Atcg (a)

(b)

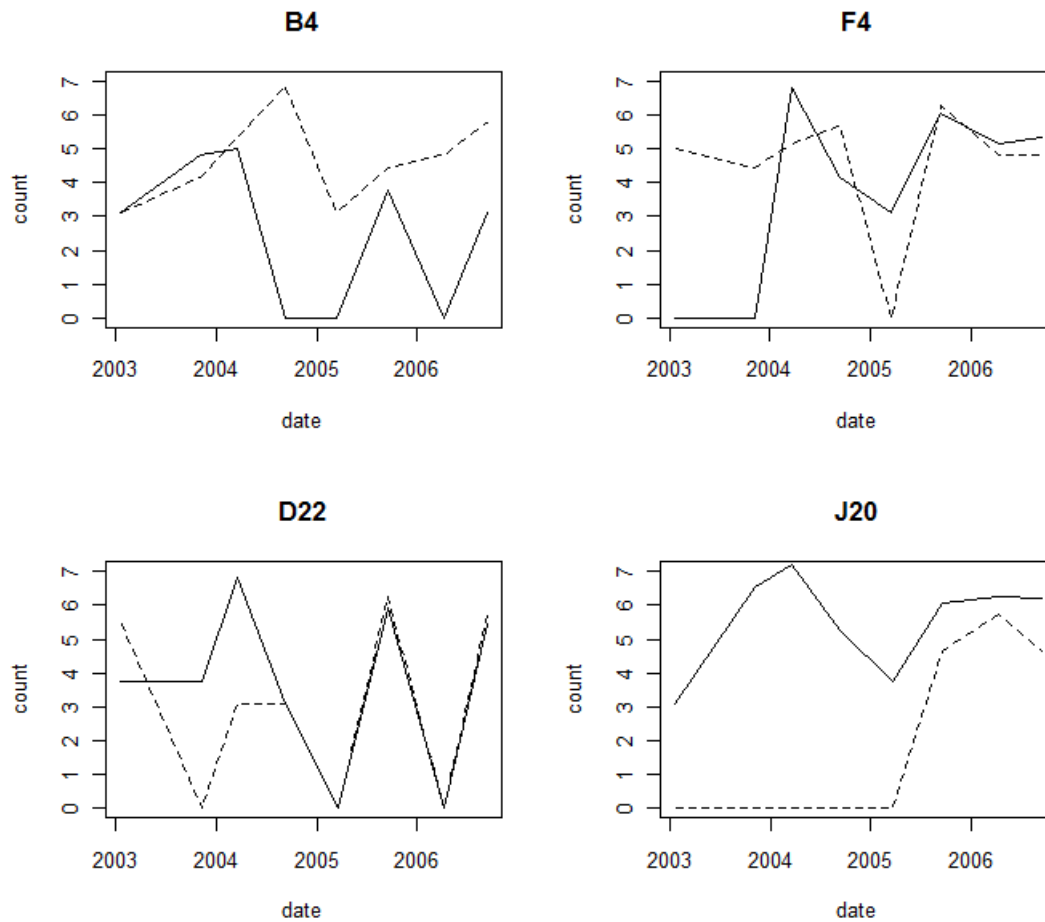


Fig 6.4 Time series of control replicates for *Arabidopsis thaliana* (solid line) and *Cerastium glomeratum* (dashed line) pair. (a) The peaks are not synchronous between the two species, or across replicates. (b) Time series of seed redistributed replicates. The pair was not in synchrony between each other and across replicates. There was less variability in peaks between the two species in 2006 -2007 season, which was not the case in the control replicates. Each replicate is 625cm² in size.

Both species persisted on all replicates. However, *Cerastium* was more abundant on 1 control and 3 treated replicates. *Cerastium* was more abundant on one treated and 3 control replicates. Both species showed abundance on one control replicate.

Both species persisted on all replicates. However, *Cerastium* was more abundant on 1 control and 3 treated replicates. *Cerastium* was more abundant on one treated and 3 control replicates. Both species showed abundance on one control replicate.

The pair was not in synchrony across the 4 replicates, except on 3 seed redistributed replicates in later years. *Cerastium* was more abundant on treated replicates than control replicates.

1) *Aira praecox* and *Arabidopsis thaliana*

Both species persisted on all replicates but one for *Arabidopsis* on treated replicate with no recruitment count in the fifth year and also no adults were recorded. There was no clear effect of treatment for the pair although there were fewer peaks on treated replicates compared with control ones. There was no clear synchrony across the four replicates in each treatment for each species and also between species. *Aira* was more abundant on all plots with year 2004 being a good year for this species but there was no year that was good for *Arabidopsis*, except on 2 treated replicates.

2) *Aira praecox* and *Cerastium glomeratum*

Both species persisted on all replicates. However, *Aira* was consistently the most abundant species except on 1 control replicate. The year 2004 was particularly good for *Aira* but year 2005 was good for *Arabidopsis* on 2 control and 2 redistributed replicates. There was no clear effect of treatment for the pair although there was slightly more fluctuation on control replicates. There was synchrony for the pair after 2004 on 2 control and 2 treated replicates but no species disappeared and then reappeared.

3) *Aira praecox* and *Erophila verna*

There appears to be no clear treatment effect for this pair and, both species persisted on all replicates except on 1 replicate although there were a few adults. *Aira* was more abundant in 2004 on most replicates but year 2006 was poor for both species on all replicate except on 2 control replicates. *Erophila* was more abundant in all redistributed replicates in 2005 compared with control replicates. In addition, the pairs were in synchrony in 3 of the 4 redistributed replicates, unlike in control replicates which were less synchronous.

4) *Aira praecox* and *Myosotis discolor*

Both species persisted in all replicates. The year 2004 was the best for *Aira* on all replicates although it did well in all years. There was no year that was good for

Myosotis on all replicates except on 3 treated replicates in 2006. *Myosotis* was more abundant in redistributed replicates than on control replicates. There was no clear synchrony for the pair apart from on 2 redistributed replicates in 2006. There is an indication of a treatment effect for the pair. In addition, no species disappeared and then reappeared even if there were 0 counts inside the sampling area (30, 1 x 1 square cm) in some seasons.

5) *Aira praecox* and *Ornithopus perpusillus*

Both species persisted on all replicates except on 2 control replicates. *Aira* was consistently abundant on all replicates but *Ornithopus* was very low on all replicates except on 2 control replicates. Moreover, there was synchrony for the pair in only 1 control replicate. *Aira* showed peak recruitment in the fifth year (2006) on all 4 control and 3 treated replicates. There was no clear treatment effect for the pair except on 2 treated replicates in the final year when *Aira* recruitment density increased.

6) *Arabidopsis thaliana* and *Erophila verna*

Both species persisted on all replicates except on 1 treated replicate when both were very low in earlier years. However, *Arabidopsis* was abundant on 2 control and 2 treated replicates unlike *Erophila* which was abundant on all replicates with more than one peak on most replicates. Overall, *Erophila* was more than twice abundant in recruitment density compared with *Arabidopsis*. None of the species were in synchrony across the 4 replicates. However, there were more peaks in recruitment for *Erophila* on all 4 control replicates but with only one peak on treated replicates.

7) *Arabidopsis thaliana* and *Myosotis discolor*

Both species persisted on all replicates. Although there was no clear synchrony for both species across the four treatment replicates except only 1 of 4 control replicates showing synchrony in later years. Year 2004 was always good for both species. Overall, *Arabidopsis* was more abundant than *Myosotis*. There was no clear effect of treatment for the pair.

8) *Arabidopsis thaliana* and *Ornithopus perpusillus*

There was no synchrony across the four replicates for the species apart from 1 treated replicate. In addition, both species persisted on all plots. *Arabidopsis* was more abundant and showed 2 peaks in 2004 and 2006 on 3 treated replicates. However, *Ornithopus* was more abundant on 1 control and 1 treated replicates between 2004 and 2006. Both species were more abundant across the treated replicates than on control ones after 2005, except on 1 control replicate.

9) *Arabidopsis thaliana* and *veronica arvensis*

Both species persisted on all replicates. Moreover, there was synchrony on 2 control and 2 treated replicates for the pair. However, *Veronica* was more abundant on all control replicates compared with the treated ones and, year 2004 was always good for *Veronica* on 4 controls and 1 treated replicates but there was no year that was particularly good for *Arabidopsis*.

10) *Cerastium glomeratum* and *Myosotis discolor*

Both species persisted in all replicates. Moreover, there was no clear synchrony across all the replicates. *Erophila* was more abundant on all replicates with 2004 being a good year for this species on 5/8 plots. On the contrary, year 2006 was good for *Cerastium* on most replicates. However, there was no clear effect of treatment for this pair.

11) *Cerastium glomeratum* and *Myosotis discolor*

Both species persisted on all replicates. In addition, there was synchrony on 2 control replicates in later years and also on 3 of the treated ones for the pair. Moreover, both species were more abundant on most treated replicates than on control ones. One control replicate had very low recruitment density for both species. *Cerastium* showed peak recruitment in 2005 on 2 control replicate. However, peak recruitment on treated replicates occurred in 2006.

12) *Cerastium glomeratum* and *Ornithopus perpusillus*

Both species persisted on all replicates. In addition, the pair was not in synchrony across the replicates except on 3 treated replicates in later years. 2006 was the best year for *Cerastium* in at least 4 of the 8 plots. This species was also more abundant in 6 of the 8 plots. However, *Ornithopus* was abundant only on 3 of all plots with 2005 being the best year for this species on 2 control and 2 treated replicates. In one other replicate, there was no *Ornithopus* recruitment for 4 years in a row but it did appear in the last year.

13) *Cerastium glomeratum* and *Veronica arvensis*

Both species persisted in all replicates except that there was neither recruitment in the fifth year nor adults in 1 control replicate for both species and, similarly, one other treated replicate with no recruitments or adults for *Veronica*. *Cerastium* was more abundant in all plots although year 2005 was good in all control replicates while 2006 was best for 2 of the 4 redistributed replicates. On the other hand, 2004 was a good year for *Veronica* on all treated replicates and 1 control replicate.

14) *Erophila verna* and *Myosotis discolor*

There was neither clear synchrony for the pair on all replicates nor a clear effect of treatment. Both species persisted on all replicates, except for *Myosotis* with neither recruitments record in the fifth year nor adults (treated) and for one control replicate when no recruitment were recorded for three counts consecutively before the last count. *Erophila* was consistently the most abundant species on all plots with year 2004 always being good for this species on 6 of 8 plots but there was no year that was good for *Myosotis* except on 1 treated replicate in 2004 and 2006. The pair showed lower density in 2006 and, thereafter on 3 control replicates compared with treated ones for the same period.

15) *Erophila verna* and *Ornithopus perpusillus*

Both species persisted on all plots, except on 2 replicates with no *Ornithopus* recruitment in the last 3 counts on one control replicate, nor adults, and also none from the other treated replicates in all 5 years. *Erophila* was more abundant in all plots and 2004 was good for this species, where as for *Ornithopus*, 2005 was always a good year for most replicates. The pair was in synchrony on 1 of the 4 control replicates but none on treated ones. There was no clear effect of treatment for this pair.

16) *Erophila verna* and *Veronica arvensis*

Both species persisted on all replicates with *Erophila* being consistently abundant on all replicates especially in 2004, which was always good for this species for most of the replicates but there was no year that was good for *Veronica*. There was no clear synchrony for the pair across the replicates, except on 2 control and 1 treated replicates in later years. Moreover, there was no clear treatment effect for the pair.

17) *Myosotis discolor* and *Ornithopus perpusillus*

Both species persisted on all plots except for *Ornithopus* with neither recruitment records nor adults in the last 3-5 counts in 1 control and 1 treated replicates. Moreover, there was no clear synchrony for this pair, apart from on 1 control replicate after 2004 and 3 treated replicates after 2005. *Myosotis* was consistently abundant on all plots with 2006 being a good year for 6 of 8 plots. There was no clear effect of treatment for this pair.

18) *Myosotis discolor* and *Veronica arvensis*

Both species persisted on all replicates. In addition, they were in synchrony in 3 of the 4 treated replicates and on 2 of 4 control ones with *Myosotis* showing abundance in at least 6 of the 8 plots. Both species showed higher density in at least 2 of the treated replicates compared with the control ones.

19) *Ornithopus perpusillus* and *Veronica arvensis*

Both species persisted on all replicates except *Veronica* on 1 control replicate with neither recruitment nor adults at the last count. For *Ornithopus*, there were no recruitments in the last 2 counts from 1 treated replicate and also from one other control replicate in the last 4 counts (only 1/8 counts), with no adult recorded from both plots. The species were not in synchrony across the replicates except on 1 treated and 1 control replicates. Similarly, there was no clear treatment effect for the pair, apart from 1 treated replicate when both species increased in density after 2004. The year 2006 was good for *Ornithopus* on 1 control and 3 treated replicates. On the other hand, 2004 was a good year for this species on 3 of the 4 control replicates. For *Veronica*, 2006 was good on 6 plots. This species was also abundant in 3 of the treated replicates and on all control ones but *Ornithopus* was abundant on 2 of the 4 treated and on 1 of the control replicates.

6.3.3 Population stability

There were very few significant effects on population stability (log (seedling count+1)). (See Table 6.5 for details of the stability analysis).

6.3.4 Identity effects on biomass

Table 6.8 Identity effects on mean biomass from 2007.

	ap	at	cg	ev	md	op	va
ap	NA	278.5714	213.2	172.1389	156.8611	299.4478	287.2444
at	99.85185	NA	134.1774	122.1	82.26667	134.8421	114.5769
cg	184.1852	173.3571	NA	119.4762	141.1852	246.2692	222.8966
ev	67.69048	36.39474	68.26316	NA	64.15833	101.9756	66.39535
md	811.5116	482.0857	409.0526	564.2353	NA	784.587	686.0526
op	864.7438	1784.469	1580.31	2704.677	845.56	NA	1235
va	209.037	175.0714	324.1765	257.6316	127.2667	178.4	NA

Biomass of *Aira* was significantly less when it was paired with *Myosotis* and also with *Erophila*. Biomass of *Arabidopsis* was significantly more when it was paired with *Ornithopus*. No species has an effect on the biomass of *Cerastium*. Biomass of

Erophila was significantly more when it was paired with *Ornithopus* but it was significantly less when it was paired with *Arabidopsis*. Biomass of *Myosotis* was nearly less significant when it was paired with *Aira*. Biomass of *Ornithopus* was significantly more when it was paired with *Erophila*. Biomass of *Veronica* was nearly more significant when it was paired with *Cerastium* and also with *Erophila*.

Table 6.9 Log biomass of the 6 species when paired with *Aira praecox*. The biomass of *Erophila* and *Myosotis* were significantly less when paired with *Aira*. The biomass of *Cerastium* and *Ornithopus* was marginally more than that of *Aira*.

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	4.95991	0.18801	26.381	<2e-16	***
cidcg	0.04325	0.28044	0.154	0.8776	
cidev	-0.61190	0.28889	-2.118	0.0352	*
cidmd	-0.63252	0.28889	-2.189	0.0295	*
cidop	0.02504	0.27019	0.093	0.9262	
cidva	-0.06917	0.27173	-0.255	0.7993	

Residual standard error: 1.316 on 246 degrees of freedom

Multiple R-squared: 0.04517, Adjusted R-squared: 0.02576

F-statistic: 2.327 on 5 and 246 DF, p-value: 0.04335

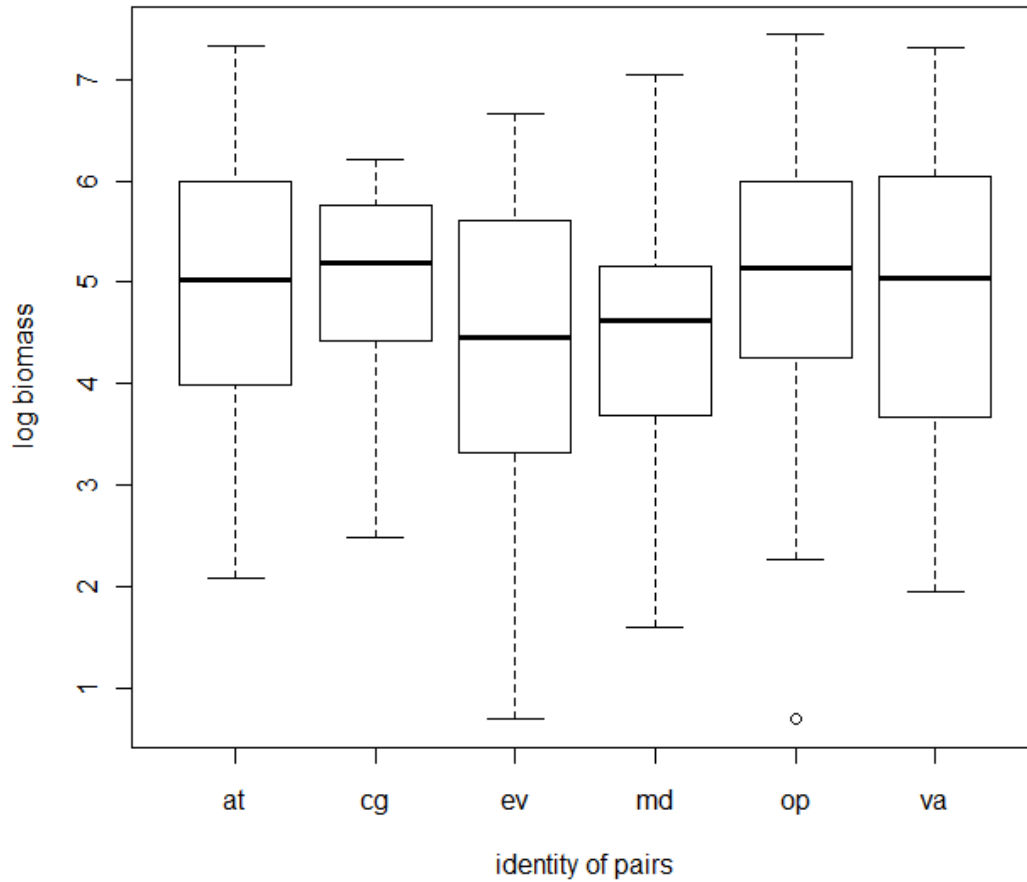


Fig 6.5 Log biomass of *Aira* when it was paired with the other 6 species. The log biomass of *Aira* was significantly less when it was paired with *Erophila* and *Myosotis*. Adult numbers of this species were also less when it was paired with *Erophila* but this was not significant. Quadrat size for biomass = 625cm².

Table 6.10 Log biomass of the 6 species when they were paired with *Erophila verna*.

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	3.76946	0.15950	23.634	<2e-16	***
cidat	-0.50782	0.23142	-2.194	0.0292	*
cidcg	-0.05595	0.23142	-0.242	0.8092	
cidmd	-0.37714	0.23477	-1.606	0.1095	
cidop	0.49743	0.22693	2.192	0.0294	*
cidva	-0.15196	0.22425	-0.678	0.4987	

Residual standard error: 1.034 on 232 degrees of freedom
Multiple R-squared: 0.08928, Adjusted R-squared: 0.06965
F-statistic: 4.548 on 5 and 232 DF, p-value: 0.0005629

Log biomass of *Erophila* was significantly less when it was paired with *Arabidopsis*. However, it has significantly more biomass when it was paired with *Ornithopus* (nitrogen fixing legume).

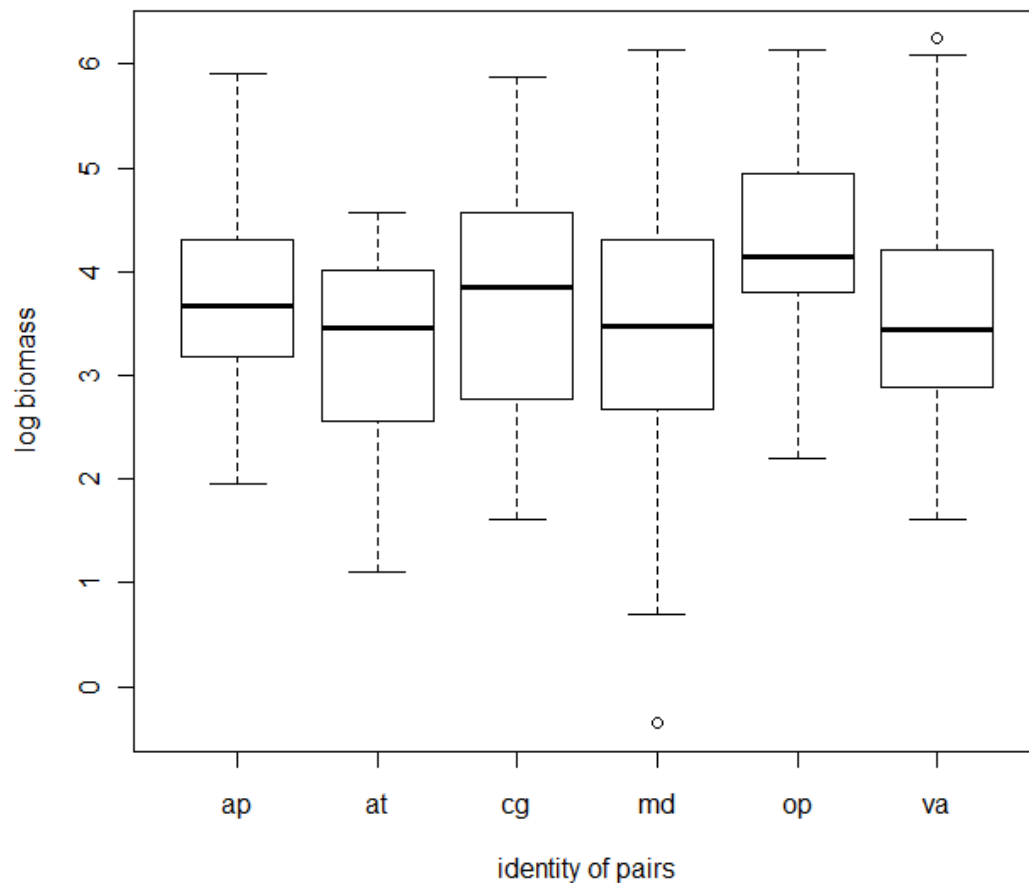


Fig 6.6 Log biomass of *Erophila* when it was paired with the other 6 species. The log biomass of this species was significantly more when it was paired with the legume (*Ornithopus*). Adult numbers of this species were also significantly more when it was paired with the same species. Both crucifers always showed higher adult numbers and biomass in the presence of the legume, as were *Aira* and *Cerastium* perhaps benefiting from nitrogen fixing. The two crucifer species never seem to do well both in recruitment, growth and biomass when they are paired together. Quadrat size for biomass = 625cm².

6.3.5 No-shows and Local extinctions

Some plots were scored as zero counts for one or both of the sown species on certain sampling occasions (these are called “no shows” for non-appearances). Following a non-appearance, if a species was never recorded subsequently from that plot, this is scored as a “local extinction”.

Table 6.11 Non-appearances and local extinction. Species scored zero counts for recruitments out of a total of eight counts over the course of 5 years. There were 64 counts for each species when paired with one other species. A 6-sample test for equality of proportions showed *Arabidopsis* was highly significant (more) when paired with *Erophila* but less when it was paired with *Cerastium*, *Myosotis* and, *Veronica* ($p < 0.01$).

species	<i>ap</i>	<i>at</i>	<i>cg</i>	<i>ev</i>	<i>md</i>	<i>op</i>	<i>va</i>	p -value
<i>ap</i>	NA	9	5	11	9	13	8	0.45
<i>at</i>	28	NA	18	34	17	23	17	0.01
<i>cg</i>	17	20	NA	16	15	22	14	0.59
<i>ev</i>	13	22	16	NA	18	13	10	0.17
<i>md</i>	15	16	17	24	NA	17	16	0.52
<i>op</i>	30	28	30	33	37	NA	30	0.67
<i>va</i>	21	12	21	22	19	22	NA	0.37

Table 6.12 Non-appearance of *Ornithopus* when paired with 6 other species. *Ornithopus* was absent from 9 plots nearly equally split (4:5 ratio) into treated and control replicates. There is no clear association of these non-appearing, but *Ornithopus* never showed a no-show when paired with *Cerastium*.

<i>Aira</i>	<i>Arabidopsis</i>	<i>Cerastium</i>	<i>Erophila</i>	<i>Myosotis</i>	<i>Veronica</i>
2	1	0	2	2	2

Despite being the largest seed size, *Ornithopus* was the most absent species from all the seedling recruitment recordings compared with the other 6 species, either due to seed limitation or competition.

6.4 Discussion

The experiment was designed to test three hypotheses: 1) that competitive exclusion would be observed within 5 years; 2) that the seven species would differ consistently in their competitive abilities; and 3) that this would allow us to predict the identity of a superior competitive in each of the 21 different pair-wise mixtures. It turned out that identifying a superior competitor was much less straightforward than assumed by the simple theoretical models. Certainly, we could rank average biomass across the species, and there were some consistent identity effects (species A performing better when paired with species B than with species C). But these niche differences did not generally lead to increased rates of competitive exclusion, or even to enhanced

downward trends in the population of what might have been thought of as the inferior competitor.

The seed-redistribution part of the experiment tested the hypothesis that increased rates of competitive exclusion of the inferior competitor would follow redistribution of the seeds of the superior competitor. This pattern was not observed for any of the 21 species pairs. In fact, downward-trended fluctuating coexistence was the norm, with most of the replicates behaving in broadly similar ways (Table 6.7). Over the course of five years, 4 species were lost from 4 of the 168 plots in this experiment and 3 species were never lost in any plot. Contrary to the predictions of the hypothesis, the species that we suspected would be the inferior competitor *increased* in abundance following seed redistribution.

Had we had more space and time it would have been interesting to redistribute the seeds of species one at a time on different replicated plots (as well as both and neither as we did here). Then we could have explained the increase in abundance following seed redistribution in terms of relaxed inter- or intra-specific competition.

The pairs experiments were started in 2002 and run for 5 years (unlike the monocultures and saturation experiments, which were begun afresh each year). This means that in the pairs experiment, year effects represent a potentially complex interaction between time-varying drivers (like weather) and the states of the interacting populations (their population densities, size structures, seed banks, as such like). It is instructive, therefore, to compare our conclusions about “good years for species A” across the various experiments. The monoculture and saturation experiments should indicate “pure good years” in environments dominated by intraspecific and interspecific competition respectively whereas the pairs and the fine- and coarse-grained mixtures are responding to historical processes (e.g. nutrient depletion, natural enemies, allelopathic build-up, etc) and population performance over previous years (e.g. densities of fresh and older seed).

Chapter 7

Inter-specific competition in fine-grained mixtures

Abstract

We grew mixtures of seven species of annual plants in replicated plots with and without seed redistribution. We hypothesized that seed redistribution would increase the rate of competitive exclusion, by exposing the inferior competitor to the superior competitor over the entire area (i.e. by removing local spatial refugia from interspecific competition resulting from limited seed dispersal by a putative superior competitor). We did not observe competitive exclusion over 5 years in any of the replicates. Where seed redistribution had significant effects, it was typically an increase in population size and stability of all of the interacting species. This argues against the presence of a seed-limited superior competitor, despite the considerable differences in species biomass when grown in monoculture. There was no evidence of development of spatial heterogeneity within the plots as a result of intraspecific aggregation or interspecific separation.

7.1 Introduction

This chapter concentrates on the outcome of 7-species interspecific competition in replicated plots over 5 generations. Our hypothesis was based on theoretical modelling by Bolker and Pacala (Bolker and Pacala 1997). They reasoned that competitive exclusion should occur more rapidly if seeds were gathered pre-dispersal, then sown at random over the entire study area. The rationale is that limited dispersal (a small seed shadow) by the superior competition would create a spatial refuge for the inferior competitor in which it would benefit from rare species advantage and hence coexist.

The theory for spatially explicit multi-species competition (Chesson 2000a, Murrell and Law 2003) is less well developed than it is for the classical fully-mixed case (Tilman 1994, Levine and Rees 2002) but makes consistent predictions. For instance,

in the limiting case of no dispersal and temporal constancy, the theory predicts competitive exclusion in the fine-grained case, and coexistence in the coarse-grained case, where spatial heterogeneity and niche differences ensure that intraspecific competition is more important than interspecific for all species (Chesson and Neuhauser 2002).

Coexistence could result from any of the four classes of mechanism (Chapter 1) but here we were particularly interested in testing the role of the colonization competition trade-off (Turnbull 1999, Stanton 2002) and the impact of temporal heterogeneity (“kinds of years, Chesson, 2007; Hastings, Tilman, 98). Of course, with only 5 years of field work, we were unlikely to discover the ‘unusual year’ for any one of our species, let alone all seven of them. Equally, it is not obvious that we should expect to observe competitive exclusion of even the least competitive of the species in so short a period of time.

The key questions in this chapter are as follows:

- Is there a characteristic pattern of density trajectories across years (e.g. a trend towards competitive exclusion)?
- How similar are the time series across spatial replicates?
- How often is local extinction observed?
- Are there consistent identity effects in terms of dominance rank (e.g. if $A > B$ and $B > C$ then $A > C$)?
- Are the peak years predicted by the monoculture and/or saturation data?
- Does pattern converge between the fine and coarse-grained series over time?
- How does experimental seed redistribution affect the outcome?

Nevertheless, we embarked on the study in the hope of understanding what we observed to occur, rather than with the expectation of proving unequivocally that one particular mechanism was responsible for coexistence in this system.

7.2 Materials and Methods

We hypothesized that competitive exclusion would occur, and that the rate of exclusion would be related to the relative superiority of the eventual dominant.

7.2.1 *The plots*

The plots were the same design of raised beds as described in Chapter 2, with 1m x 1m interior dimensions within each plot. We carried out a multi-species competition experiment containing all seven species. Different plots experienced one of two levels of seed redistribution (all or none). Within each plot, the spatial scale was 7 times greater than in the pairs experiment (chapter 6) with 7 quadrats arranged in a polygon (Fig 7.1), each of area 625cm².

7.2.2 *Seed sowing*

For the construction of the beds, the soil mixture, seed collection, method of seed sowing, mulch, monitoring of seedling appearances and weeding, see chapter 2.1.

Seeds for seven species were weighed into appropriate batches in the same sowing density as used for saturation plots of intermediate sowing density (see chapter 5). Seeds of each species were divided into seven equal batches before they were sown evenly on 10/10/2002 in each of a sector of the hexagonal quadrats.

7.2.3 *Redistribution*

Seeds were collected pre-dispersal. In control plots, seeds were allowed to ripen and disperse *in situ*. For the redistributed plots, the total crop of seeds of each species was estimated, and fresh seed was sown back at random over the sector from which they were gathered from; the seven sectors were collected and redistributed separately.

7.2.4 Estimating recruitment

Apart from the first year - when there was only one recruitment; estimated in spring 2003 following sowing in mid-October 2002, at least two recruitment estimates were made for all species in subsequent years, one in fall and one in spring. There were 9 sampling occasions over a 5 year period (dates in Table 7.1). For details of recruitment sampling methods, see chapter 6.2.3.

Table 7.1 Recruitment sampling dates for the multi-species experiment in all 5 years for all 7 species. There were 2 counts (spring and autumn) in each except in 2002/2003 when there was only spring counts.

year	count	<i>A praecox</i>	<i>A thaliana</i>	<i>C glomeratum</i>	<i>E verna</i>	<i>M discolor</i>	<i>O.perpusillus</i>	<i>V arvensis</i>
2002/2003	1	NA	NA	NA	NA	NA	NA	NA
	2	17/02/2003	17/02/2003	17/02/2003	17/02/2003	17/02/2003	17/02/2003	17/02/2003
2003/2004	1	29/10/2003	03/11/2003	29/10/2003	03/11/2003	29/10/2003	29/10/2003	03/11/2003
	2	29/03/2004	29/03/2004	29/03/2004	29/03/2004	29/03/2004	29/03/2004	29/03/2004
2004/2005	1	15/09/2004	15/09/2004	15/09/2004	15/09/2004	26/10/2004	26/10/2004	26/10/2004
	2	17/03/2005	17/03/2005	17/03/2005	17/03/2005	26/03/2005	26/03/2005	26/03/2005
2005/2006	1	27/09/2005	17/10/2005	17/10/2005	17/10/2005	17/10/2005	27/09/2005	17/10/2005
	2	14/04/2006	11/04/2006	11/04/2006	11/04/2006	14/04/2006	14/04/2006	14/04/2006
2006/2007	1	18/09/2006	10/10/2006	10/10/2006	10/10/2006	10/10/2006	18/09/2006	18/09/2006
	2	06/03/2007	03/30/207	03/30/207	03/30/207	06/03/2007	06/03/2007	06/03/2007

7.2.5 The final harvest at the end of the 5th year

In the summer of the final year (2007), all seven species were collected from each of the seven sectors during the ripening period, by cutting below the rosette level. The harvest dates for the seven species were: *Aira* on 17/06/2007; *Arabidopsis* on 04/05/2007; *Cerastium* on 07/05/2007; *Erophila* on 23/04/2007; *Myosotis* on 06/05/2007; *Ornithopus* on 15/07/2007; *Veronica* on 10/06/2007. Adult plants were sorted in to seven size classes following their harvest, in the same way as for monocultures (see chapter 2, 2.4) and their biomass determined.

7.2.6 Statistical modelling

There were too few sampling occasions to allow analysis of the counts using formal time-series analysis to estimate autocorrelation and partial autocorrelation functions (Crawley 2005). Instead, we used linear mixed effects models (lmer in R) to treat plot and sampling occasion as random effects, and to remove the temporal pseudoreplication. Species and seed redistribution were incorporated as fixed effects. The response variable y was $\log(\text{seedling counts} + 1)$.

```
lmer(y ~ species * treatment +(1|sample) + (1|plot))
```

The count data were analysed again using Poisson errors in a generalized mixed effects model, but the results were always the same, and are not presented here. Also data analysis was performed on trends in recruitment over time. Proportion test was also carried out to compare no shows between 2 the levels (control against seed redistribution).

7.3 Results

There was no clear pattern of density trajectories across years in the control and redistributed replicates. Peak years for recruitment for some species was low, for others, and also the same species showed recruitment peaks in different years on different replicates of the same treatment which suggests a good year for a particular species doesn't necessarily manifest in all replicates. Some species showed similar recruitment time series in some replicates but not in all, both in control and redistributed replicates. (See below).

Most of the species showed relatively lower recruitment rate in 2007 but there were no recruitment and also adult records for only two species from two control replicates (one species from each replicate). For some species such as At and Ev, low recruitment (near extinction) in one or two years was followed by high recruitment in subsequent years.

7.3.1 Dominance rank by species

Table 7.2 Species ranked based on their dominance in recruitment, adult, survival and biomass from all sectors.

species	Recruitment	adults	biomass
<i>Aira</i>	1	2	3
<i>Arabidopsis</i>	7	7	6
<i>Cerastium</i>	2	6	4
<i>Erophila</i>	3	1	7
<i>Myosotis</i>	5	5	2
<i>Ornithopus</i>	4	4	1
<i>Veronica</i>	6	3	5

Aira is ranked in the top 3 for recruitment, adult survival and biomass. At the other extreme, *Arabidopsis* is last or next to last in the ranking. No species showed identical ranking in all three.

7.3.2 Time series

There was considerable heterogeneity across replicates for the four plots on which seed was spatially redistributed (Fig 7.1).

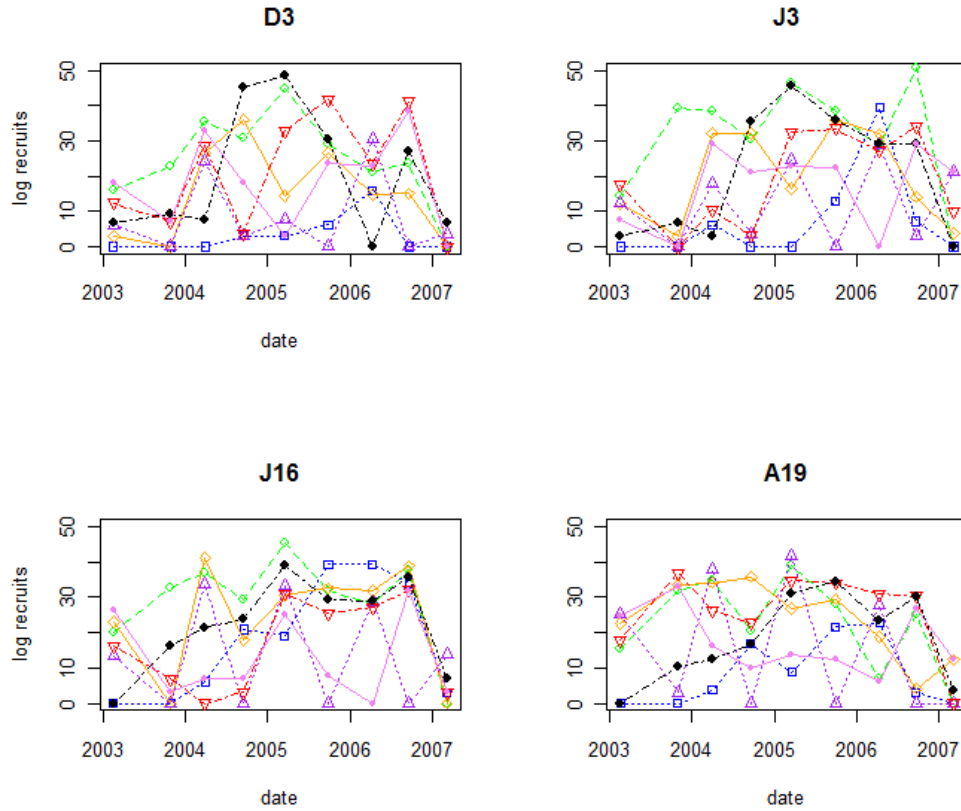


Fig 7.1 Time series in log recruitment for each of the 4 redistributed replicates summed over all sectors (plots D3, J3, J16 and A19) aggregated across all-sectors for each of the 7 species. Colour codes for each of the 7 lines are: *Aira* (green), *Arabidopsis* (blue), *Cerastium* (orange), *Erophila* (purple), *Myosotis* (red), *Ornithopus* (black) and *Violet* (violet). Most of the species showed recruitment peaks in 2005.

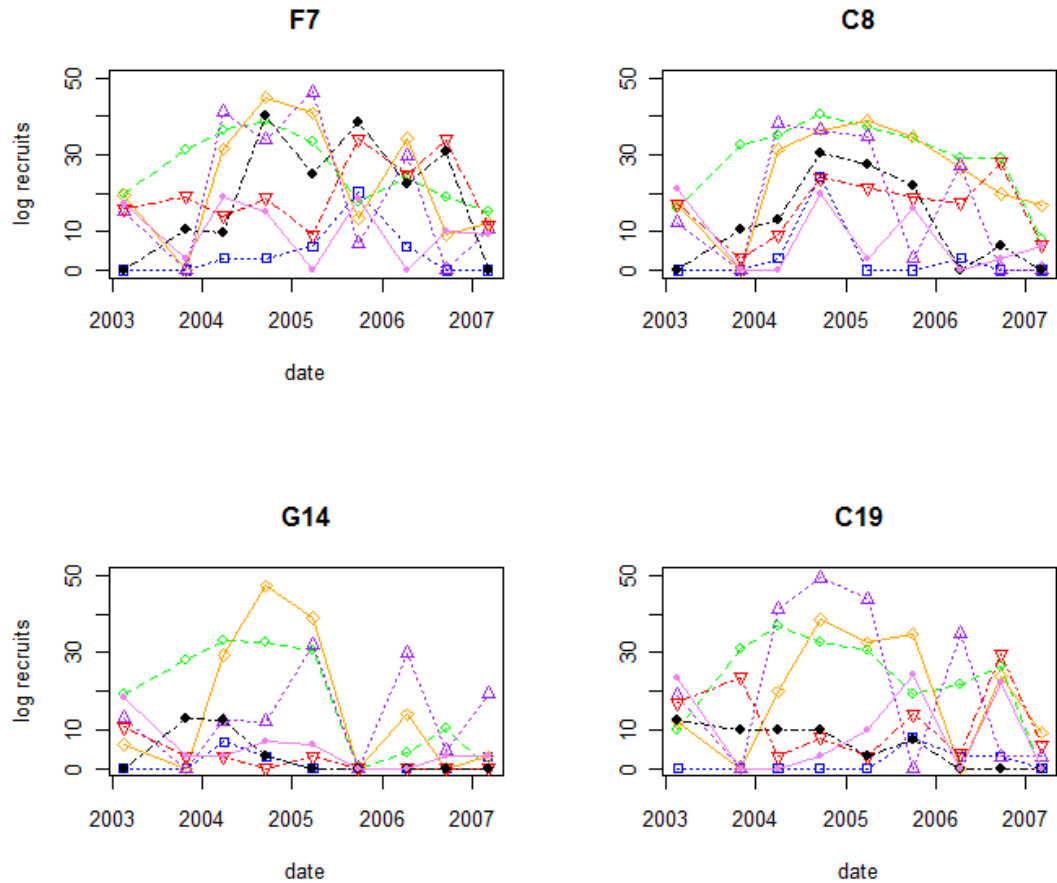


Fig 7.2 Time series in log recruitment for each of the 4 control replicates summed over all sectors (plots F7, C8, G14 and C19) aggregated across all sectors for each of the 7 species. Colour codes for each of the 7 lines are: *Aira* (green), *Arabidopsis* (blue), *Cerastium* (orange), *Erophila* (purple), *Myosotis* (red), *Ornithopus* (black) and *Violet* (violet). Most of the species showed recruitment peaks in 2005, as the the case on the seed redistributed replicates.

Mean density and relative abundance was similar on the plots where seed was allowed to disperse naturally (Fig 7.2). Times of peak recruitment were different from those in monocultures and saturation experiments. For example, *Ap* showed peak recruitment in 2005 in this experiment but in monoculture and saturation experiments, 2004 was the best year for recruitment for this species.

7.3.3 Trends in abundance over 5 years

Table 7.3 Trends in mean log seedling abundance over 5 years.

species	slope	s.e.	t	Sig. level
<i>Aira</i>	-1.478	0.217	6.82	***
<i>Arabidopsis</i>	0.787	0.188	4.19	***
<i>Cerastium</i>	-0.374	0.251	1.49	ns
<i>Erophila</i>	-0.583	0.264	2.21	*
<i>Myosotis</i>	0.530	0.238	2.23	*
<i>Ornithopus</i>	0.445	0.253	1.75	ns
<i>Veronica</i>	0.442	0.214	1.97	*

Log mean seedling densities declined significantly over 5 years in *Aira* and *Erophila* (Table 7.3). Two species showed no significant linear trend (*Cerastium* and *Ornithopus*) and three species showed significant increase over time (*Arabidopsis*, *Myosotis* and *Veronica*).

7.3.4 No shows and extinction

Seed redistribution caused a significant reduction in the number of cases of “no shows (proportion test, $p < 0.00001$). In one species (*Erophila verna*), the number of no-shows was greater on the redistributed plots (Table 7.4). In all the other 6 species, the number of no shows was greater in control replicates.

Table 7.4 The frequency of “no show” counts of seedlings and adults.

species	redistributed	control	No adults/sector	No adults/plot
<i>Aira</i>	48	56	0	0
<i>Arabidopsis</i>	175	225	13	0
<i>Cerastium</i>	82	92	4	0
<i>Erophila</i>	147	118	0	0
<i>Myosotis</i>	87	132	7	1
<i>Ornithopus</i>	90	161	14	2
<i>Veronica</i>	106	170	6	0
Total	735	954	44	3

7.3.5 Treatment effects

Peak mean recruitment for 5 of the 7 species occurred in the redistributed plots compared with the control plots but *Cerastium* and *Erophila* showed highest recruitment in the control plots. *Erophila* was the most abundant species in the control plots while *Arabidopsis* was the least abundant. In the redistributed plots, the picture is somewhat different. *Ornithopus* was the most abundant while *Veronica* was the least abundant.

We found no strong support for our hypothesis that experimental seed redistribution would increase the rate of competitive exclusion. When the 4 replicates of control treatments are compared with the 4 replicates of treated plots within the fine-grained mixture, mean counted seedlings were higher in the treated plots than in the control plots for all species except *Erophila* where there were slightly more mean recruits in the control plots. Again the picture is similar to when fine-grained results are compared with coarse-grained mixtures.

Table 7.5 Effects of seed redistribution on population stability in 7- species fine-grained mixtures. Population stability of *Arabidopsis* was significant ($p < 0.0369$) compared with the other species following seed redistribution.

Ap	-0.1095	0.2268	-0.483	0.646
At	0.7965	0.2981	2.672	0.036911 *
Cg	-0.2342	0.3539	-0.662	0.532775
Ev	-0.3667	0.2323	-1.579	0.165
Md	0.2225	0.12623	1.763	0.128
Op	0.4794	0.2745	1.746	0.131
Va	-0.09267	0.10859	-0.853	0.426

Table 7.6 Effects of seed redistribution on mean log abundance in 7-species fine-grained mixtures. Seed redistribution increased mean recruitment in 6 of 7 species, as shown below.

	ap	at	cg	ev	md	op	va
fgmc	4.065229	0.6518928	3.882548	3.775685	2.603588	2.002111	1.991184
fgmr	4.857690	1.7500905	4.004336	3.121200	4.112872	3.653085	3.528596

Table 7.7 Mixed effects model. The random effects showed temporal variability to be substantially more important than spatial variability. The species effects of redistribution were significant increases in mean log recruitment for *Aira* (the intercept), *Cerastium*, *Myosotis*, *Ornithopus* and *Veronica*, and a significant decline for *Erophila*.

Linear mixed model fit by REML

Formula: $\log(\text{recruitscount} + 1) \sim \text{level} * \text{species} + (1 | \text{plot}) + (1 | \text{factor}(\text{year}))$

Data: data

AIC	BIC	logLik	deviance	REMLdev
15255	15404	-7604	15176	15207

Random effects:

Groups	Name	Variance	Std.Dev.
plot	(Intercept)	0.17990	0.42414
factor(year)	(Intercept)	1.27112	1.12744
Residual		3.59600	1.89631

Number of obs: 3675, groups: plot, 15; factor(year), 5

Fixed effects:

	Estimate	Std. Error	t value
(Intercept)	3.51696	0.54249	6.483
levelfgmc	0.54827	0.33322	1.645
levelfgmr	1.34073	0.33322	4.024
speciesat	-1.80553	0.17133	-10.538
speciescg	-0.25373	0.17133	-1.481
speciescv	-0.36916	0.17133	-2.155
speciesmd	-1.52064	0.17133	-8.875
speciesop	-2.09449	0.17133	-12.225
speciesva	-1.36560	0.17133	-7.970
levelfgmc:speciesat	-1.60781	0.28412	-5.659
levelfgmr:speciesat	-1.30207	0.28412	-4.583
levelfgmc:speciescg	0.07105	0.28412	0.250
levelfgmr:speciescg	-0.59963	0.28412	-2.110
levelfgmc:speciescv	0.07962	0.28412	0.280
levelfgmr:speciescv	-1.36733	0.28412	-4.812
levelfgmc:speciesmd	0.05900	0.28412	0.208
levelfgmr:speciesmd	0.77582	0.28412	2.731
levelfgmc:speciesop	0.03137	0.28412	0.110
levelfgmr:speciesop	0.88988	0.28412	3.132
levelfgmc:speciesva	-0.70845	0.28412	-2.493
levelfgmr:speciesva	0.03650	0.28412	0.128

7.3.6 Year effects

Table 7.8 Effect size is the largest recruitment from all sectors mean divided by the smallest recruitment mean.

species	2003	2004	2005	2006	2007	effect size
<i>Aira praecox</i>	21	323	515	130	245	25
<i>Arabidopsis thaliana</i>	0	13	24	148	24	148
<i>Cerastium glomeratum</i>	23	169	499	154	59	22
<i>Erophila verna</i>	23	204	487	97	15	32
<i>Myosotis discolor</i>	24	62	95	185	138	8
<i>Ornithopus perpusillus</i>	3	28	484	135	71	162
<i>Veronica arvensis</i>	33	54	41	34	81	3

Year effects on recruitment were highest for *Ornithopus* (162 fold) while, *Veronica* showed the smallest year effect (3 fold).

Overall, the species *Aira*, *Cerastium*, *Erophila* and *Ornithopus* had higher mean recruitment in 2005 than in any other year. On the other hand, *Arabidopsis* and *Myosotis* were more abundant in 2006; whereas *Veronica* was more abundant in 2007. *Arabidopsis* and *Erophila* had similar mean recruitment, both in the first and last years.

Peak mean recruitment for 5 of the 7 species occurred in the redistributed plots compared with the control plots. *Cerastium* and *Erophila* showed highest recruitment in the control plots. *Erophila* was the most abundant species in the control plots but *Arabidopsis* was the least abundant. In the treated plots, the picture was different: *Ornithopus* was the most abundant while *Veronica* was the least abundant.

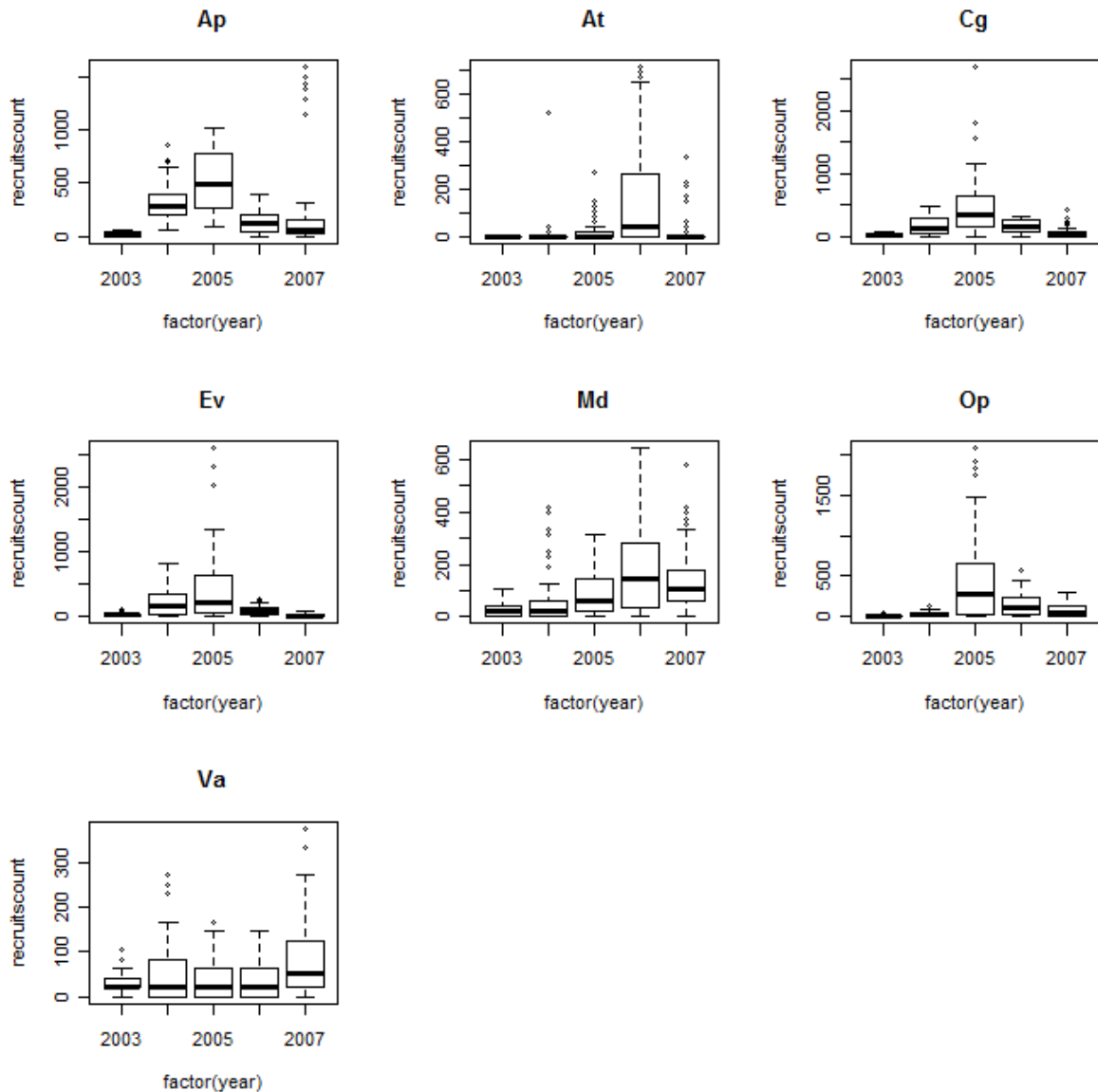


Fig 7.3 Recruitment of the 7 species across 5 years. Total recruitment across years from all sectors shows peak years of 2005 for *Aira*, 2006 for *Arabidopsis*, 2005 for *Erophila* and *Ornithopus*, 2006 for *Myosotis*, and remarkably uniform recruitment across time for *Veronica*. In so far, as *Veronica* had a best year, it was in 2007 when several other species did very badly.

7.4 Discussion

Starting with a uniform spatial mixture of species, we were interested to discover whether spatial pattern would develop over the course of five years (Law, Murrell, 2003; Pacala, 1994), and if so, whether this indicated the relative importance of

limited dispersal, local resource depletion, natural enemy build-up or allelopathy in creating the observed small-scale patterning. As it turned out, the sectors within the fine-grained plots were not significantly different at the end of the 5 years. There was no visual impression of within plot heterogeneity either. The seed-redistribution part of this experiment was designed to test the hypothesis that competitive exclusion would occur more rapidly following dispersal of the seeds of the superior competitor (see also the Pairs Experiment in Chapter 6).

The prediction was that seed redistribution would enhance the dominant species to out compete the inferior competitors resulting in extinction or a very low density. However, results showed this was not the case (species increasing in abundance). If anything, extinction or low recruitment and adult density occurred in either coarse-grained or fine-grained control replicates.

Mean recruitment was higher on redistributed plots than on control plots for all species except for Cg and Ev but there were more mean adult densities for Ap, Cg, Ev in control plots than on redistributed plots. However, Cg, Ev, Md showed more mean biomass in control replicates than on redistributed replicates suggesting, despite having more adults, the biomass was lower but for Md, fewer mean adults in redistributed replicates have higher mean biomass than more adults in control replicates. Mean biomass of Op was more than 15-fold in redistributed replicates compared with control replicates. The overall mean number of adult species between the two experiments was marginal, but biomass was nearly 4 times more in redistributed replicates compared with control replicates.

Chapter 8

Inter-specific competition in coarse-grained mixtures

Abstract

We grew mixtures of seven species of annual plants in replicated plots each divided into 7 equal-area sub-plots that were initiated in 2002 by sowing monocultures of each species within one sector of each plot. Over the next 5 generations, species dispersed from the plots where they were sown initially, and colonized other plots that were previously monocultures of the other 6 species. We predicted that these experiments would converge to the conditions exhibited by plots sown at the same time with fine-grained mixtures of all seven species within each of their 7 sectors. This convergence was observed within 3 generations on all replicates. The initial protection from interspecific competition in the coarse-grained mixture was not associated with any impact on the long-term rates of competitive exclusion (negligible in all treatments) or relative abundance after 5 generations. The results of this experiment with 7 species competition are consistent with the results of the 21 pair-wise competition experiments carried out over the same period: this set of species does not appear to represent a guild in which competitive ability can be ranked in a consistent manner (as required by the competition-colonization model of species coexistence). There is no “superior competitor” which predictably excludes any of the other species.

8.1 Introduction

The aim of this experiment was to determine the effect of initial spatial pattern on the outcome of inter-specific competition over 5 years. In Chapter 7 we saw that replicate fine-grained species mixtures showed no example of complete competitive exclusion over 5 years, but two of the seven species showed significant negative trends in seedling population size.

Our expectation was that populations sown initially in 7 adjacent monocultures (what we call the ‘coarse-grained mixture’) would more or less rapidly become invaded by species from other plots, the boundaries of the initial monocultures would blur, and the resulting larger multi-species population would become more and more spatially homogeneous with time. Again, if there was competitive exclusion, we predicted that it would occur more rapidly on plots that were initially sown as fine-grained mixtures (chapter 7) than on plots sown as coarse-grained mixtures (this chapter).

The theory for spatially explicit multi-species competition (Murrell and Law 2003) is less well developed than it is for the classical fully-mixed case (Chesson, 2002) but in the absence of dispersal it predicts competitive exclusion in the fine-grained case, and coexistence in the coarse-grained case. We predicted that species will disperse at rates predicted by the measured dispersal kernels (i.e. Chapter 3) and that seed limitation will be inversely correlated with mean dispersal differences.

Coexistence could result from any of the four classes of mechanism (Chapter 1) but here we were particularly interested in testing the role of the colonization competition trade-off (Pacala and Tilman 1994). Of course, with only 5 years of field work, we were unlikely to observe competitive exclusion of even the least competitive of the species, but we hoped to observe consistent trends in relative abundance.

This Chapter concentrates on the following questions:

- How long does the system remember its spatial history?
- Do the coarse-grained plots converge towards the fine-grained case?
- If so, how long does this convergence take?
- Did species persist longer in the coarse-grained case?

8.2 Methods

8.2.1 *Seed sowing*

For the construction of the beds, the soil mixture, seed collection, method of seed sowing, mulch, monitoring of seedling appearances and weeding, see chapter 2, 2.1. The materials and methods for coarse-grained mixture are the same as in to the previous chapter (chapter 7), except that there was no seed redistribution.

Seeds of the 7 species were weighed into appropriate batches to obtain the same sowing density as for saturation plots of intermediate sowing density (see chapter 5.2). Seeds of each species were sown on 07/10/2002 in one of the 7 sector of the hexagonal quadrat with each species appearing once in the centre of the hexagon in one of the plots. There were 7 plots in all, differing only in the identity of the species sown into the center plot.

8.2.2 Estimating recruitment

Seedlings were counted in 30 randomly located mini-quadrats (1cm x 1cm) in each of the 7 sectors as described in Chapter 7. Dates of seedling counts are shown in Table 8.1.

Table 8.1 Seedling recruitment sampling dates for the coarse-grained experiment from 2003 to 2007. There were two such dates per year except in 2002/2003 when there was only one count in the spring (count 2) but none in the autumn (count 1).

year	count	<i>A praecox</i>	<i>A thaliana</i>	<i>C glomeratum</i>	<i>E verna</i>	<i>M discolor</i>	<i>O perpusillus</i>	<i>V arvensis</i>
2002/2003	1	NA	NA	NA	NA	NA	NA	NA
	2	17/02/2003	17/02/2003	17/02/2003	17/02/2003	17/02/2003	17/02/2003	17/02/2003
2003/2004	1	29/10/2003	03/11/2003	29/10/2003	03/11/2003	29/10/2003	29/10/2003	03/11/2003
	2	29/03/2004	29/03/2004	29/03/2004	29/03/2004	29/03/2004	29/03/2004	29/03/2004
2004/2005	1	15/09/2004	15/09/2004	15/09/2004	15/09/2004	26/10/2004	26/10/2004	26/10/2004
	2	17/03/2005	17/03/2005	17/03/2005	17/03/2005	26/03/2005	26/03/2005	26/03/2005
2005/2006	1	27/09/2005	17/10/2005	17/10/2005	17/10/2005	17/10/2005	27/09/2005	17/10/2005
	2	14/04/2006	11/04/2006	11/04/2006	11/04/2006	14/04/2006	14/04/2006	14/04/2006
2006/2007	1	18/09/2006	10/10/2006	10/10/2006	10/10/2006	10/10/2006	18/09/2006	18/09/2006
	2	06/03/2007	03/30/207	03/30/207	03/30/207	06/03/2007	06/03/2007	06/03/2007

8.2.3 The final harvest (biomass)

In the summer of the final year (2007), all 7 species were collected from each of the 7 sectors during the seed ripening period, by cutting below the rosette level. The harvest dates for the 7 species were: *Aira* on 17/06/2007; *Arabidopsis* on 04/05/2007; *Cerastium* on 07/05/2007; *Erophila* on 23/04/2007; *Myosotis* on 06/05/2007; *Ornithopus* on 15/07/2007; *Veronica* on 10/06/2007. Adult plants were sorted in to different size classes following their harvest, in exactly the same way as for monocultures (see chapter 2, 2.4).

8.2.4 Statistical modeling

We decided to measure spatial and temporal variability with different metrics, simply for ease of remembering what we were quantifying. We could easily have used the same measures for both, and tests with simulated data show that the different measures perform equally well in most practical circumstances.

We measure temporal variability by the standard deviation of the log of the counts+1 (see Chapter 6 for a justification of this). Transformation involving $\log(\text{count} + 1)$

has recently come in for some bad press (Robert 2010) but we feel that it retains its usefulness for measuring temporal variability in population dynamics.

We measured spatial variability using the coefficient of variation (CV) of the population counts, defined as the ratio of the standard deviation to the mean. This dimensionless number is the inverse of the signal-to-noise ratio. For low values of the mean (close to zero), the coefficient of variation will approach infinity, and hence is highly sensitive to small changes in the mean.

The coarse-grained mixtures start out at sowing time with 6 zeros (the unsown sectors) and one very high number (the intermediate monoculture sowing rate). With *Cerastium*, for instance, we sowed 600 seeds in 625 cm², so the data within one plot are 600, 0, 0, 0, 0, 0, 0; the mean is 85.71, the variance is 51,429, and the CV at the start of the experiment is $226.78 / 85.71 = 2.65$. We expect that this value will decrease to roughly the value observed in the fine-grained mixtures, as species spread out from the sectors in which they were sown and colonize the rest of the plot.

As in pairs and fine-grained mixture, linear model was performed to assess the trend of recruitment for all species over time. In addition, biomass of all species was compared between coarse-grained and fine-grained mixtures with a linear model. Mixed effects model was performed with species and levels as fixed effect, years and plots as random effect to compare mean recruitment, mean adults and mean biomass between coarse and fine-grained mixture for all species.

8.3 Results

Time series plots for all 7 species in each of the 7 replicate plots are shown in Fig 8.1.

8.3.1 Big pattern

(a)

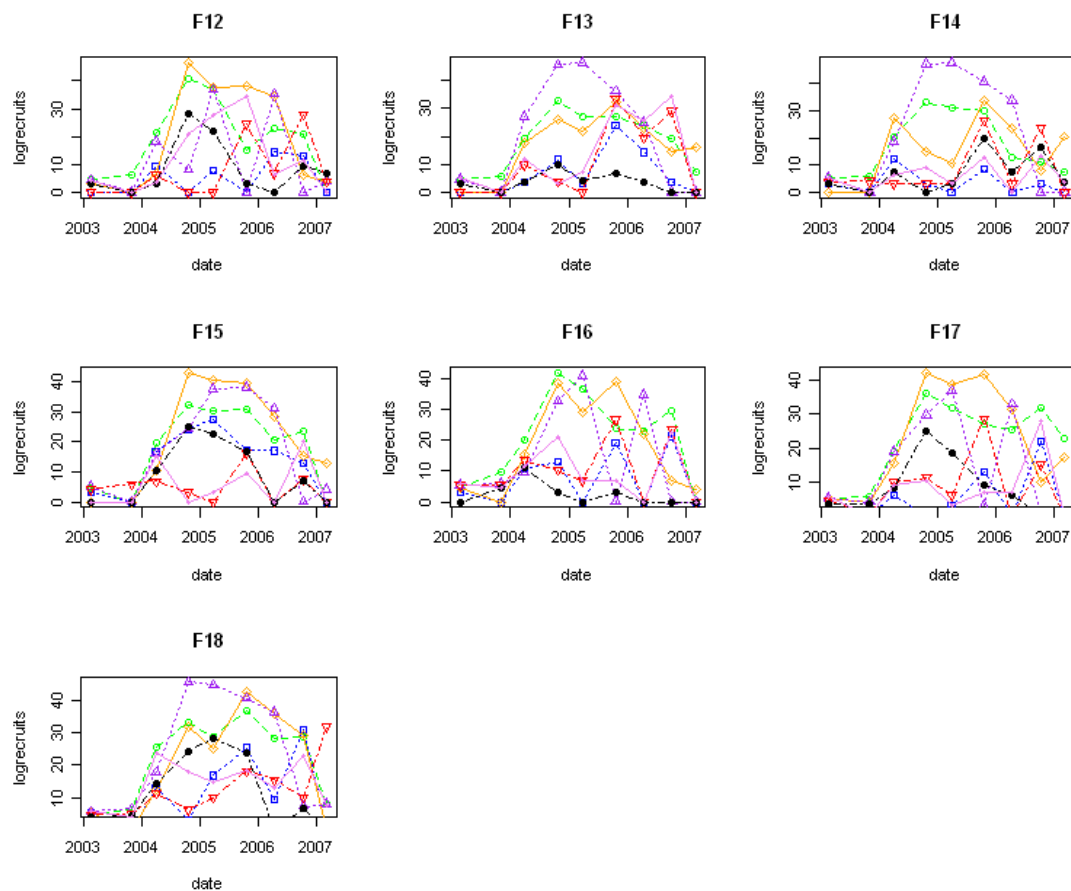


Fig 8.1 Recruitment time series for each species, per plot summed across all sectors for each of the 7 plots with coarse-grained. *Aira* (green), *Arabidopsis* (blue), *Cerastium* (orange), *Erophila* (purple), *Myosotis* (red), *Ornithopus* (black) and *Veronica* (violet).

Aira, *Cerastium* & *Erophila* are the most abundant (highest recruitment) species in most of the 7 plots. *Myosotis*, *Arabidopsis* and *Veronica* are the next abundant (intermediate recruitment) species in most of the plots. *Ornithopus* is the least abundant (low recruitment) species in most plots. As in fine-grained mixtures, most species showed peak recruitments in 2005 than in other years.

8.3.1.1 Trends in recruitments

```
model<-lm(log(recruits+1)~sp*time,subset=(treat=="cgm"))
```

Table 8.2 Trends in recruitment. There was a significant upward trend in seedling numbers of *Aira*, *Arabidopsis*, *Cerastium*, *Myosotis* and *Veronica* ($p = 0.000225$), but no trend in *Erophila* or *Ornithopus*. No species showed a significant down trend in abundance.

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	1.9371468	0.2636947	7.346	2.60e-13	***
spAT	-1.5020470	0.3729206	-4.028	5.77e-05	***
spCG	-0.7579000	0.3729206	-2.032	0.042206	*
spEV	0.4793129	0.3729206	1.285	0.198786	
spMD	-1.7748184	0.3729206	-4.759	2.03e-06	***
spOP	-0.8168239	0.3729206	-2.190	0.028574	*
spVA	-1.2874306	0.3729206	-3.452	0.000563	***
time	0.0007892	0.0002137	3.694	0.000225	***
spAT:time	-0.0002389	0.0003022	-0.791	0.429144	
spCG:time	0.0005736	0.0003022	1.898	0.057745	.
spEV:time	-0.0006912	0.0003022	-2.288	0.022230	*
spMD:time	0.0001810	0.0003022	0.599	0.549137	
spOP:time	-0.0008729	0.0003022	-2.889	0.003891	**
spVA:time	-0.0001551	0.0003022	-0.513	0.607826	

Residual standard error: 2.122 on 3073 degrees of freedom
Multiple R-squared: 0.1375, Adjusted R-squared: 0.1339
F-statistic: 37.7 on 13 and 3073 DF, p-value: < 2.2e-16

8.3.1.2 Biomass

```
model<-lm(biomass~sp,subset=(treat=="cgm"))
```

Table 8.3 Biomass of *Ornithopus perpusillus*. *Ornithopus* showed significantly more biomass than any of the other species, as predicted. This was also true in monocultures.

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	54.54	20.14	2.709	0.00679	**
spAT	-45.66	28.48	-1.604	0.10891	
spCG	-29.30	28.48	-1.029	0.30358	
spEV	-50.58	28.48	-1.776	0.07582	.
spMD	15.80	28.48	0.555	0.57894	
spOP	76.36	28.48	2.682	0.00737	**
spVA	-45.65	28.48	-1.603	0.10904	

Residual standard error: 422.8 on 3080 degrees of freedom
Multiple R-squared: 0.01011, Adjusted R-squared: 0.008186
F-statistic: 5.245 on 6 and 3080 DF, p-value: 2.192e-05

8.3.2 No-shows

The frequency with which each species was recorded as zero in the recruitment assessments are shown in Table 8.4.

Table 8.4 Number of zero recruits from 7 plots, each with 7 sectors, and with 7 seedlings counts for each species (343 sectors). The first year recruitment was not included in the census other than to estimate recruitment for each species in the sector it was sown in. Just under a third of all seedling recruitment recordings have zero records. Unlike in fine-grained mixture, *Veronica* has the highest number of zero records. None of the species went extinct from any of the 7 plots, based on fifth year recruitment and adult data, which was not the case in the fine-grained mixture experiment. However, there were sectors where neither recruitments nor adults were recorded in fifth and final year (2007) except for *Aira*. In doing proportion test, the following proportions of species comparisons for the number of cases when there were no recruitments from 49 sectors in at least the last 2 counts nor adults, were significant ($p=0.05$). 7:0, 8:0, 11:2, 11:0.

<i>species</i>	<i>No recruits</i>	No adults/sectors	Extinction/plot
<i>Aira</i>	39	0	0
<i>Arabidopsis</i>	175	2	0
<i>Cerastium</i>	60	2	0
<i>Erophila</i>	98	2	0
<i>Myosotis</i>	169	7	0
<i>Ornithopus</i>	188	8	0
<i>Veronica</i>	152	11	0
total	881	32	0

8.3.3 Year effects

In this experiment, the good years show a simple pattern:

2005 was best in recruitment for *Aira*, *Cerastium*, *Erophila* and *Ornithopus*, while *Veronica*, *Myosotis* and *Arabidopsis* were more abundant in 2006 (Table 8.5).

Table 8.5 Year effects on mean recruitment for all species, per sector in each of the 5 years.

Species	2003	2004	2005	2006	2007
<i>Aira</i>	50.43	207.14	106.61	44.1	15.31
<i>Arabidopsis</i>	4.69	20.04	36.17	20.88	1
<i>Cerastium</i>	9.58	187.43	227.32	57.03	23.81
<i>Erophila</i>	39.34	289.65	354.19	67.82	4.68
<i>Myosotis</i>	18.31	10.04	40.25	30.02	15.31
<i>Ornithopus</i>	5.55	45.1	39.61	5.13	2.13
<i>Veronica</i>	31.27	22.01	51.28	36.85	2.55

The biggest difference between good and bad years for recruitment was shown by *Erophila* (76 fold differences) in recruitment between 2005 and 2007. The smallest year effects were from *Myosotis*, with only a 4-fold difference between bad and worst (2004 versus 2007).

8.3.4 Dispersal in coarse-grained mixture and convergence to fine-grained

8.3.4.1 Dispersal in coarse-grained mixture

The species ranked as follows in terms of colonization of unsown plots after 1 year:

Aira>*Erophila*>*Cerastium*>*Veronica*>*Arabidopsis*>*Myosotis*>*Ornithopus*

Table 8.6 Dispersal of the 7 species away from where they were originally sown based on seedling recruitment counts from all sectors (42), from the 2nd year (2004) are ranked. When *Aira* was compared with *Ornithopus*, it was more than 11 times likely to invade neighboring sectors. Total recruitment for *Aira* where it was sown was 2.34 times than the 6 sectors combined. By the 5th year, there was more than 6 times recruitment in sectors where this species was not sown, which is nearly 1/7 which means there was an even distribution in all sectors.

species	counts	effect size	rank
<i>Aira praecox</i>	2668	NA	1
<i>Erophila verna</i>	1257	2.1	2
<i>Cerastium glomeratum</i>	923	2.9	3
<i>Veronica arvensis</i>	838	3.18	4
<i>Arabidopsis thaliana</i>	399	6.69	5
<i>Myosotis discolor</i>	377	7.08	6
<i>Ornithopus perpusillus</i>	231	11.55	7

After 5 years, the situation is shown in Table 8.7. Overall, *Erophila* was the most numerous colonist and *Arabidopsis* the least numerous. By the final year (2007), *Ornithopus* had the highest biomass and *Erophila* the lowest (Table 8.7).

Table 8.7 Species ranked by their mean recruitment over the course of 5 years, adults and biomass in the fifth year (2007). *Erophila* was ranked first in an overall recruitment as well as in adult numbers.

species	overall recruits	2007 recruits	adults	biomass
<i>Aira</i>	2	3	2	3
<i>Arabidopsis</i>	7	7	7	6
<i>Cerastium</i>	3	1	5	4
<i>Erophila</i>	1	4	1	7
<i>Myosotis</i>	5	2	6	2
<i>Ornithopus</i>	4	6	3	1
<i>Veronica</i>	6	5	4	5

8.3.4.2 Convergence to fine-grained mixture

Table 8.8 Log seedling recruitment counts from all sectors in each of the three levels for all species and years. Seedling counts between coarse-grained and fine-grained were not significantly different from 2005 onwards. However, there were significant differences in 2003 and 2004 between the two levels as expected because seeds of the coarse-grained mixture were sown in only one of the 7 sectors compared with fine-grained ones which were sown in all sectors. The only difference between coarse and fine-grained in seed sowing is that there were 1/7 of coarse-grained mixture seeds sown in each of the 7 sectors in fine-grained mixtures. Overall, the sectors in coarse-grained mixture became heterogeneous as in fine-grained mixture from the third year onwards.

years	2003			2004			2005			2006			2007		
species	fgmc	fgmt	cgm	fgmc	fgmt	cgm	fgmc	fgmt	cgm	fgmc	fgmt	cgm	fgmc	fgmt	cgm
<i>Aira</i>	2.33	2.37	0.70	4.72	4.86	1.89	4.94	5.12	4.82	2.69	3.79	3.56	1.92	2.46	2.15
<i>Arabidopsis</i>	0.00	0.00	0.29	0.23	0.29	0.73	0.66	1.28	1.16	0.72	3.53	1.66	0.11	0.85	1.09
<i>Cerastium</i>	1.95	2.18	0.36	2.01	3.05	1.12	5.69	3.75	4.56	2.83	3.97	4.75	1.69	1.58	1.68
<i>Erophila</i>	2.13	2.04	0.74	2.37	2.08	1.46	5.15	2.04	5.35	2.34	2.07	3.96	0.72	0.75	0.24
<i>Myosotis</i>	2.18	2.28	0.46	1.40	2.08	0.83	1.57	2.93	0.65	2.02	4.35	2.24	2.08	2.69	1.76
<i>Ornithopus</i>	0.44	0.36	0.35	1.60	1.55	0.72	2.49	5.11	2.18	1.61	3.78	1.02	0.66	2.50	0.51
<i>Veronica</i>	2.89	2.74	0.65	0.50	2.30	0.92	1.15	2.15	1.51	1.05	1.70	1.75	1.02	2.90	1.67

Table 8.9 Comparison of mean biomass from all sectors and the effect size between coarse-grained mixture and fine-grained mixture for the fifth and final year.

species	cgm	fgm	effect size (fgm/cgm)
<i>Aira praecox</i>	61	36	0.6
<i>Arabidopsis thaliana</i>	12	10	0.9
<i>Cerastium glomeratum</i>	32	38	1.2
<i>Erophila verna</i>	5	8	1.5
<i>Myosotis discolor</i>	91	101	1.1
<i>Ornithopus perpusillus</i>	131	249	1.9
<i>Veronica arvensis</i>	11	27	2.3

Cgm = coarse-grained mixture, fgm = fine-grained mixture

Except for *Aira* and *Arabidopsis*, all species had more biomass in fine-grained mixture with the highest effect shown by *Veronica*, in contrast with *Myosotis* which is only marginal. The difference in biomass between the 2 mixtures is minimal.

The interesting contrast between coarse-grained mixture and fine-grained mixture experiment is that, except *Arabidopsis*, the mean counted seedlings in the final year was marginally higher in fine-grained mixture for 6 species. The prediction had been that there would fewer recruits of most species (the “inferior competitors”) and more of one species (the “superior competitor”).

Table 8.10 Mean biomass (mg) comparisons of Coarse-grained mixture replicates between sectors for each species with their effects sizes. The effect size in mean biomass was substantially high for *Myosotis* and *Ornithopus*.

species	Sectors							total	effect size
	1	2	3	4	5	6	7		
<i>Aira</i>	59.18	48.86	56.01	63.32	41.99	54.04	58.38	381.78	1.51
<i>Arabidopsis</i>	13.49	5.33	9.27	4.90	8.63	9.43	11.08	62.14	2.75
<i>Cerastium</i>	27.78	30.19	17.88	16.51	39.05	11.58	33.68	176.67	3.37
<i>Erophila</i>	8.53	3.13	1.97	3.67	2.48	4.68	3.30	27.75	4.34
<i>Myosotis</i>	141.53	35.96	13.32	2.69	86.10	157.56	55.26	492.41	58.56
<i>Ornithopus</i>	385.74	348.69	4.21	25.26	35.10	28.97	88.34	916.30	91.72
<i>Veronica</i>	8.20	19.90	3.05	2.71	6.32	18.57	3.50	62.25	7.33

8.3.4.3 *Mixed-effects model*

Mean recruitment, adults and biomass as response variables were modeled against levels (coarse or fine-grained) and species as fixed effects, with plots and years as random effects. In comparing fine-grained with coarse-grained mixtures for recruitment, adults and biomass, *Myosotis* and *Ornithopus* have significantly more mean recruitment in fine-grained mixture ($p = 0.05$). There were no significant differences in mean adult numbers between the two levels. *Aira* had significantly higher mean biomass in coarse-grained mixture compared with fine-grained mixture ($p = 0.05$). Comparing the three levels (coarse-grained, fine-grained control, fine-grained seed redistributed), *Veronica*, *Arabidopsis*, *Ornithopus* and *Myosotis* have significantly more mean recruitments in seed redistributed replicates compared with control replicates. In addition, *Myosotis* and *Ornithopus* have also significantly more biomass in fine-grained plots compared with coarse-grained mixtures. *Veronica* showed significantly more adults in seed redistributed plots compared with control replicates and also compared with coarse-grained mixture plots (0.05). *Aira* have significantly more biomass in control replicates of fine-grained mixture compared with coarse-grained mixtures ($p = 0.05$). *Ornithopus* showed significantly more mean biomass in seed redistributed replicates compared with control ones and also compared with coarse-grained mixtures. *Veronica* showed significantly more mean biomass in seed redistributed replicates compared with coarse-grained mixtures ($p = 0.05$).

8.3.4.4 *Coefficient of variation in grained mixtures time series*

Convergence

The time course of convergence of the coarse-grained plots towards the condition of fine-grained plots, is shown in Fig 8.2 and Fig 8.3.

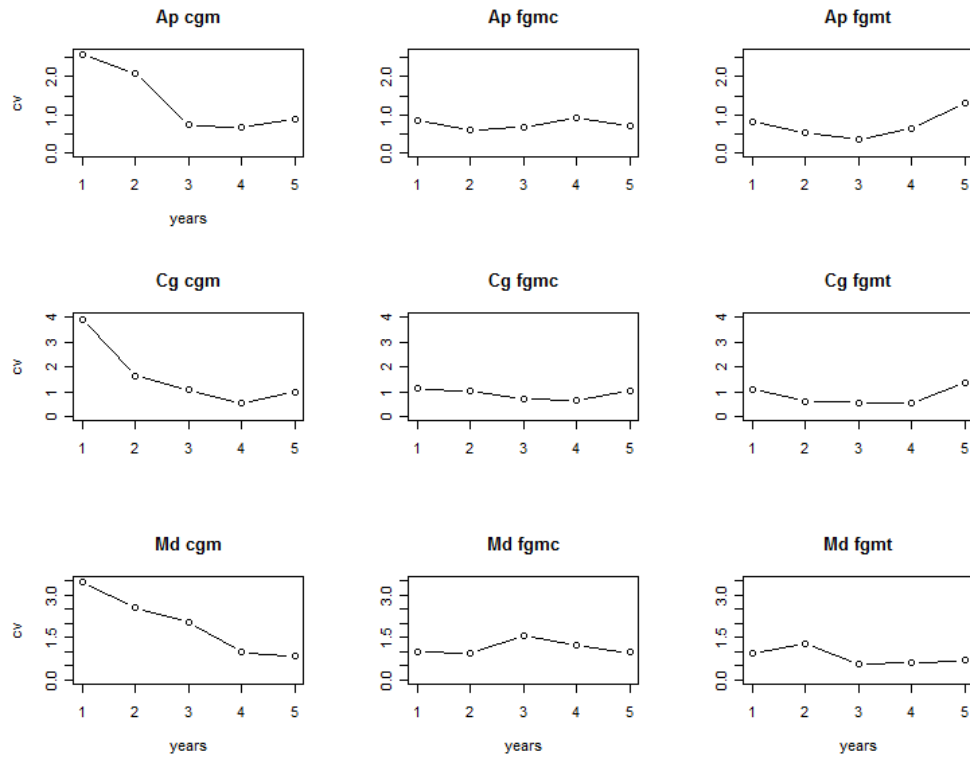


Fig 8.2 Spatial coefficient of variation (CV) in seedling recruitment for 3 species (*Aira praecox*, *Cerastium glomeratum* and *Myosotis discolor*) for each of the 3 levels (cgm, fgmc and fgmt). By year 3, the coefficient of variation between coarse-grained and fine-grained mixtures were almost identical. cgm = coarse-grained, fgmc = fine-grained-mixture (control), fgmt = fine-grained mixture (seed redistributed). CV = sd/mean. Year 1 - 5 = 2003 – 2007.

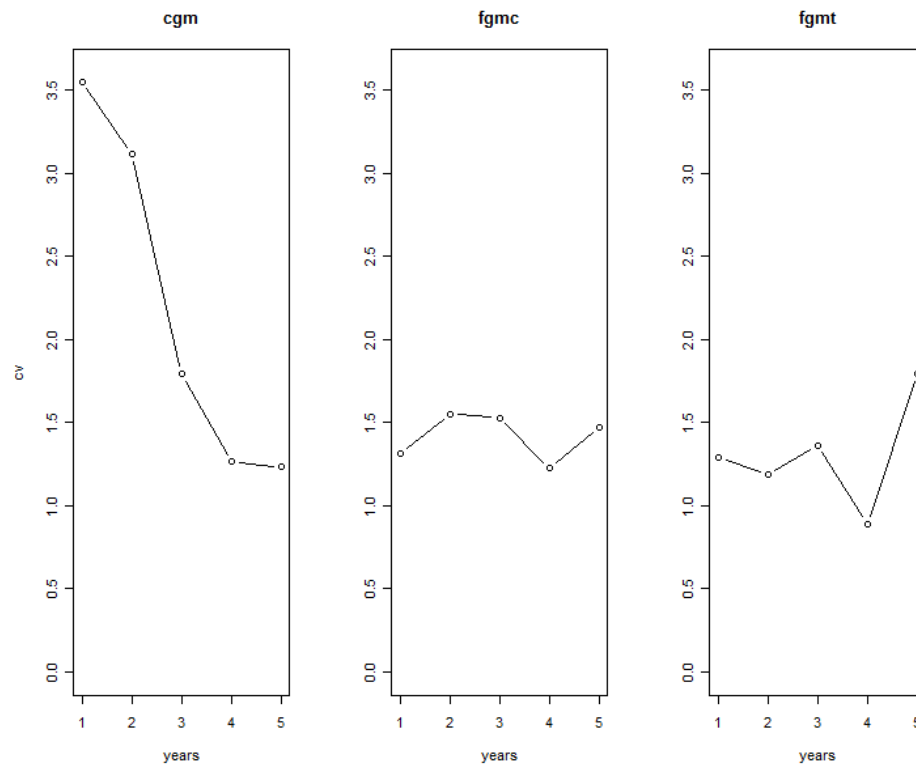


Fig 8.3 Spatial coefficient of variation plotted against years in each of the 3 levels. Prior to year 3, CV was much higher in cgm compared with fgm. cgm = coarse-grained mixtures, fgmc = fine-grained-mixture (control), fgmt = fine-grained mixture (seed redistributed). CV = $sd/mean$. Year 1 - 5 = 2003 – 2007.

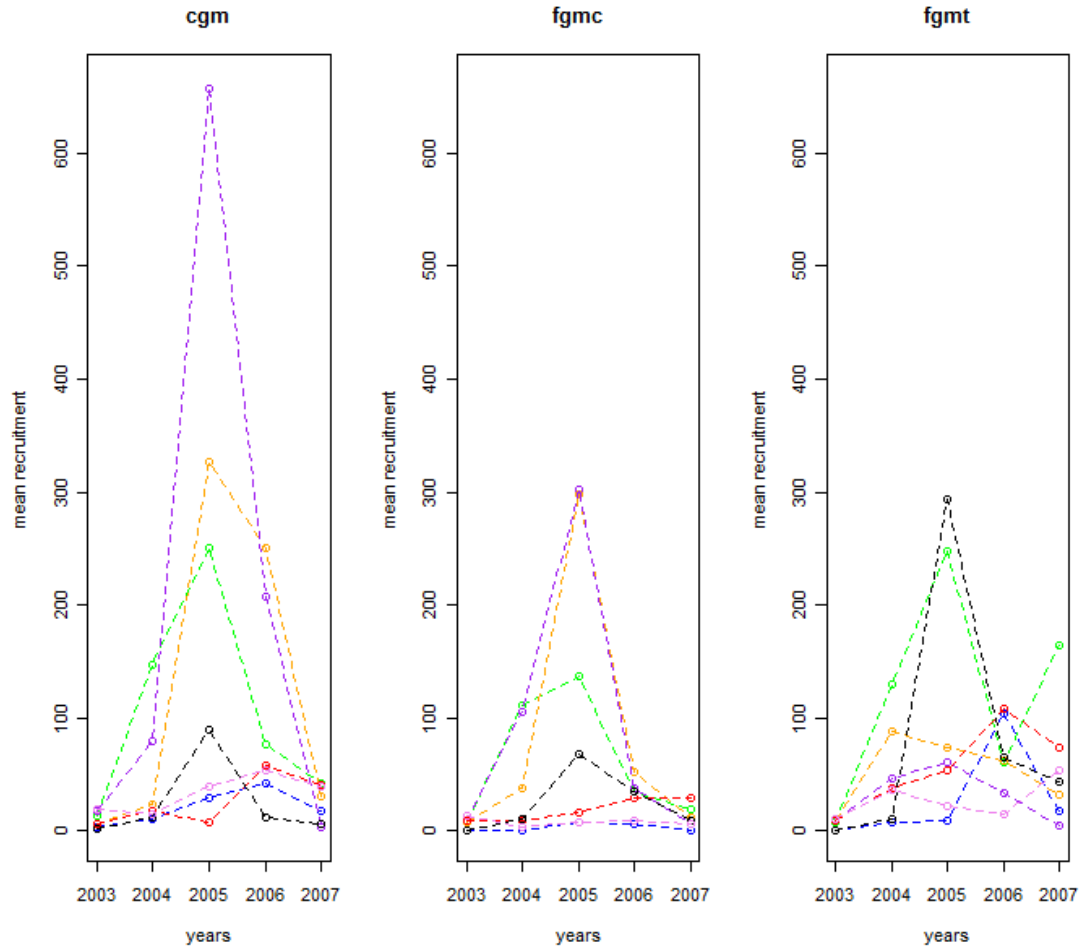


Fig 8.4 Mean recruitment per plot (from 7 quadrats = 625 cm² in size) of the 7 species plotted against years for coarse and fine-grained mixture. Four of the species (*Erophila verna*, *Cerastium glomeratum*, *Aira praecox* and *Ornithopus perpusillus*) had their peak recruitment in 2005 for coarse-grained mixture and for fine-grained mixture (control). In fine-grained mixture two of the four species had their peak recruitment. *Aira praecox* (green line), *Arabidopsis thaliana* (blue line), *Cerastium glomeratum* (orange line), *Erophila verna* (purple line), *Myosotis discolor* (red line), *Ornithopus perpusillus* (black line), *Veronica arvensis* (violet line). Cgm = coarse-grained mixture, fgmc = fine-grained mixtures control, fgmt = fine-grained mixtures seed redistributed.

8.3.5 Stability in recruitment

Table 8.11 Population stability between fgm and cgm. There were small differences in population stability between the fine (fgm) and coarse-grained mixtures (cgm) at the whole-plot scale (i.e. averaged across sectors within plot). The species are significantly different (*Arabidopsis* and *Myosotis* are less variable than the other 5 species; $p < 0.05$) but there is no significant difference between fine and coarse-grained mixtures.

sp	cgm	fgm
<i>Ap</i>	2.278551	2.068725
<i>At</i>	1.760086	1.743738
<i>Cg</i>	2.449016	2.299688
<i>Ev</i>	2.753515	2.424259
<i>Md</i>	1.895131	2.186275
<i>Op</i>	1.766274	2.326056
<i>Va</i>	1.950965	1.966180

8.4 Discussion

The coarse-grained plots conform to the main predictions, in that their structure converged to that of the fine-grained plots within 3 years. The order of species colonization, however, was not as predicted by the dispersal kernels (*Aira* was best, not worst). *Myosotis* and *Ornithopus* showed significant differences in mean adult numbers between sectors of coarse-grained mixture from 2 replicates each and *Arabidopsis* from 1 replicate. *Ornithopus* was the only species which showed significant differences in recruitment between polygons on one control plot (G14, fine-grained control). This particular replicate was peculiar compared with the other 3 control replicates. Mean recruitment, adult density and biomass were much lower for most of the species in most of the sectors in most of the years. *Ornithopus* was highly variable between sectors compared with the other species. This could be due to the build-up of allelopathy in the soil.

Species are ranked based on recruitment counts in the 2nd year, following 1st year recruitment, away from where they were originally sown (Table 8.6):

Aira>*Erophila*>*Cerastium*>*Veronica*>*Arabidopsis*>*Myosotis*>*Ornithopus*

Species are ranked by their mean dispersal distance from seed dispersal experiment:

Cerastium>*Erophila*>*Veronica*>*Myosotis*>*Arabidopsis*>*Aira*>*Ornithopus*

Ornithopus showed significant differences between sectors of coarse-grained mixtures in at least one replicate while *Arabidopsis* in at least 4 replicates.

We were also interested to discover whether monocultures of certain species were more invisable, and if so, whether the identity of their immediate neighbours was consequential in determining the rate of invasion.

In general, most of the sectors were invaded by the 2nd year but in some subplots there was no recruitment in the first year following sowing mainly those dominated by *Ornithopus* (slow growing sp). By the end of the experiment (5 years), subplots had all 7 species. In the last year of seedling count, there were no subplots without any of the 7 species (no complete extinction). On average there were 6.49 species per plot (out of 7) by the end of the fifth year (2007).

After two years, the initially coarse-grained sub-plots were indistinguishable from the fine-grained mixtures both in spatial pattern and in species' relative abundances for most of the species. There was no evidence that an initial period during which intraspecific competition outweighed interspecific competition was either a benefit or a hindrance to invasion. There was a ranking in terms of invasibility as measured in the second year after sowing as the proportion of all recruits belonging to species other than the sown ones (see Table 8.6).

Adults and biomass abundances in coarse-grained mixture, ranked by adult density from the most abundant to least abundant:

$Ap > E > Op > At > Cg > Md > Va$

Ranked by biomass from largest to the smallest:

$Op > Md > Ap > Cg > At > Va > Ev$

There was a significant difference in mean abundance between coarse-grained and fine-grained mixtures for all species (more abundant in coarse-grained). However, spatial heterogeneity in abundance (CV) was significant only for *Veronica*.

Chapter 9

Overall discussion

This combination of experiments throws light on several issues bearing on coexistence in this guild of 7 annual plants species. Perhaps most importantly, all species passed the invasion criterion when sown at low and medium densities in the experimental universe we had created in the raised beds. It would have been possible that we had mis-designed the soil mixture by making it, for example, too nutrient-poor or insufficiently water-retentive. This sets the scene for detecting the factors associated with competitive exclusion.

The plots turned out to be reasonably similar both internally and across blocks within the Ashurst experimental area. We saw little evidence in any of the experiments of the kind of within-plot spatial heterogeneity that might be assumed to be a cause of coexistence (e.g. in the fine-grained 7-species mixtures, we saw no evidence of spatial clumping, even after 5 years (Murrell 2003). There were consistent differences between the four blocks at Ashurst (Fig 2.2) with the sunny, drier south-west quarter having consistently lower densities of *Ornithopus* and *Veronica* than the shaded, moister north-east quarter, but competitive exclusion was not routinely observed in any of the four blocks.

Overall, in fact, competitive exclusion was very seldom observed, either in time series experiments with two species or all seven species, or in saturation experiments that were started *de novo* each year. Whatever the coexistence mechanisms might be, they are clearly highly effective, at least over periods of five years.

Biomass effects were revealing in the contrast of monocultures (intra-specific competition) and interspecific competition plots (saturation experiments, pairs and multi-species plots). Simple models predict that the biomass of a mixture will be equal to the biomass of the superior competitor (contest competition) or to the average of the two monoculture biomasses (scramble competition). Departures from these simple model expectations point to more interesting dynamics involving, for instance, some form of synergy (e.g. over-yielding or under-yielding; Loreau & Hector, 2001).

One of the most interesting findings from the monoculture experiments was the generally low prevalence of density thresholds below which plant performance was density independent. We found that plants were experiencing intraspecific competition even at very low shoot densities. This finding was reinforced during weeding, when we would routinely find that individuals with very small shoot systems (say 2cm tall) would have very extensive root systems (of order 10cm radius). Clearly, these plants were competing mainly for soil resources, as the design of the plots had intended, although we have no way of knowing the relative importance of competition for mineral nutrients like nitrogen and phosphorus and competition for water. The existence of large year effects in plant performance argues for the importance of some weather effects, and some of these might be resource related (e.g. the timing and intensity of rainfall), but others are clearly more direct in their effects on plant demography (the prevalence of killing frosts, and episodes of soil-heave during winter that could up-root tiny seedlings).

As discussed in the preceding chapters, there are four mechanisms of coexistence: colonization competition trade-off (Pacala and Tilman 1994), Janzen-Connell density dependent attack by natural enemies (Pacala and Crawley 1992), spatial heterogeneity (Chesson 2000a) and temporal heterogeneity with a storage effect and sub-additivity (Chesson 1994). All of these are based on one or more niche differences that can produce the necessary rare species advantage by which all coexistence is to be understood (the celebrated Lotka-Volterra coexistence criterion).

One of the most important traits affecting dispersal and establishment is seed size (Turnbull et al 1999). Across our seven species, we observed a very clear correlation between seed size and seed number (Fig 9.1): the species with the largest seeds showed the lowest annual seed production per individual. This is potentially important in several coexistence mechanisms, but perhaps most clearly in the competition-colonization trade-off.

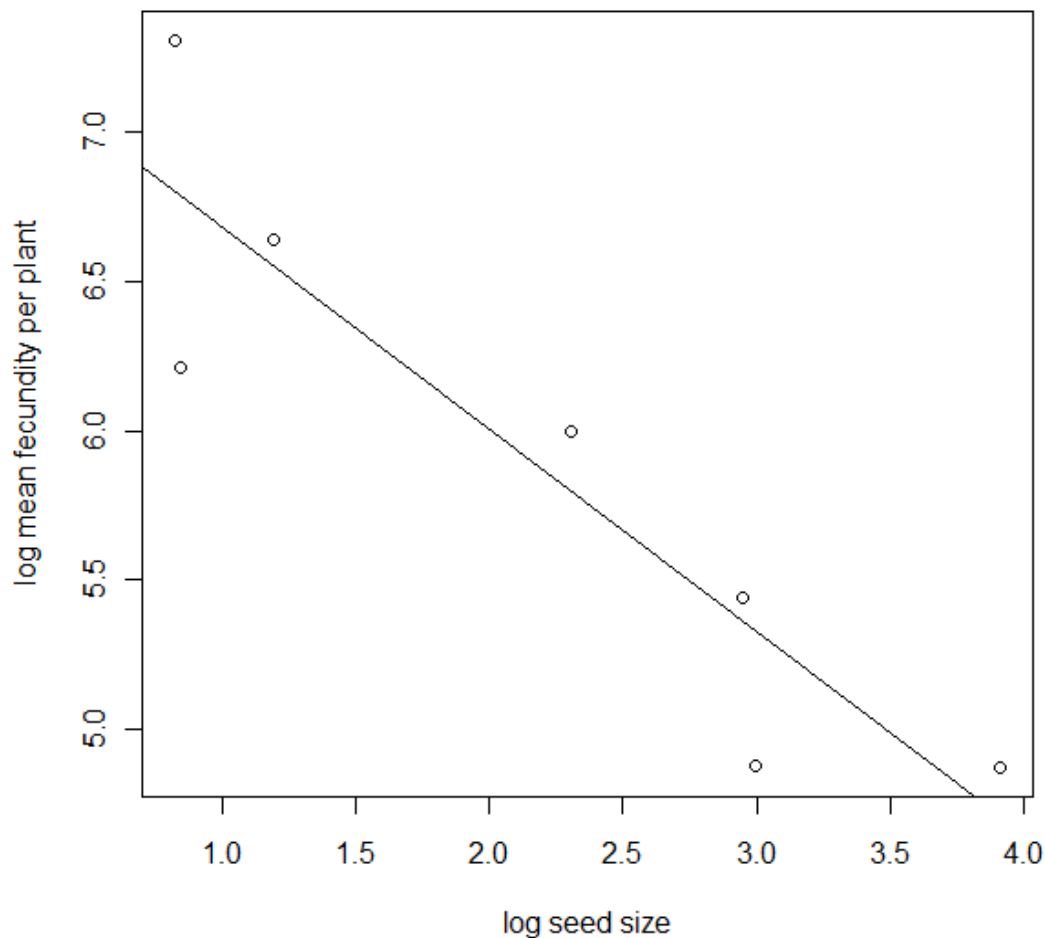


Fig 9.1 Mean log seed number per plant plotted against log seed size (fresh weight mg) for the 7 species. There is negative correlation between seed size and mean seed number per plant (fecundity). *Ornithopus perpusillus* has the largest seed size and the fewest seeds per plant. As seed size increases, seed number decreases significantly (slope=-0.7, $p<0.005$). This is in line with the competition-colonization trade-off (seed size versus seed number) which is one key element for species coexistence.

It is much less obvious whether one would expect a relationship between seed size and biomass, but again, our species show a very clear pattern with biomass increasing with seed size (Fig 9.2). Our species fall into three broad categories: species with very small seeds and very low biomass (*Arabidopsis*, *Erophila* and *Cerastium*); species with medium-sized seeds and intermediate biomass (*Aira*, *Myosotis* and *Veronica*); and *Ornithopus perpusillus* with very large seeds and very high biomass. On the basis of Fig 9.2 one would predict a competitive hierarchy based on mature plant biomass,

which ought to be able to identify a superior competitor (*Ornithopus perpusillus*) and inferior competitors (*Arabidopsis*, *Erophila* and *Cerastium*), and this in turn, leads to predictions about the outcome of pair-wise competition experiments.

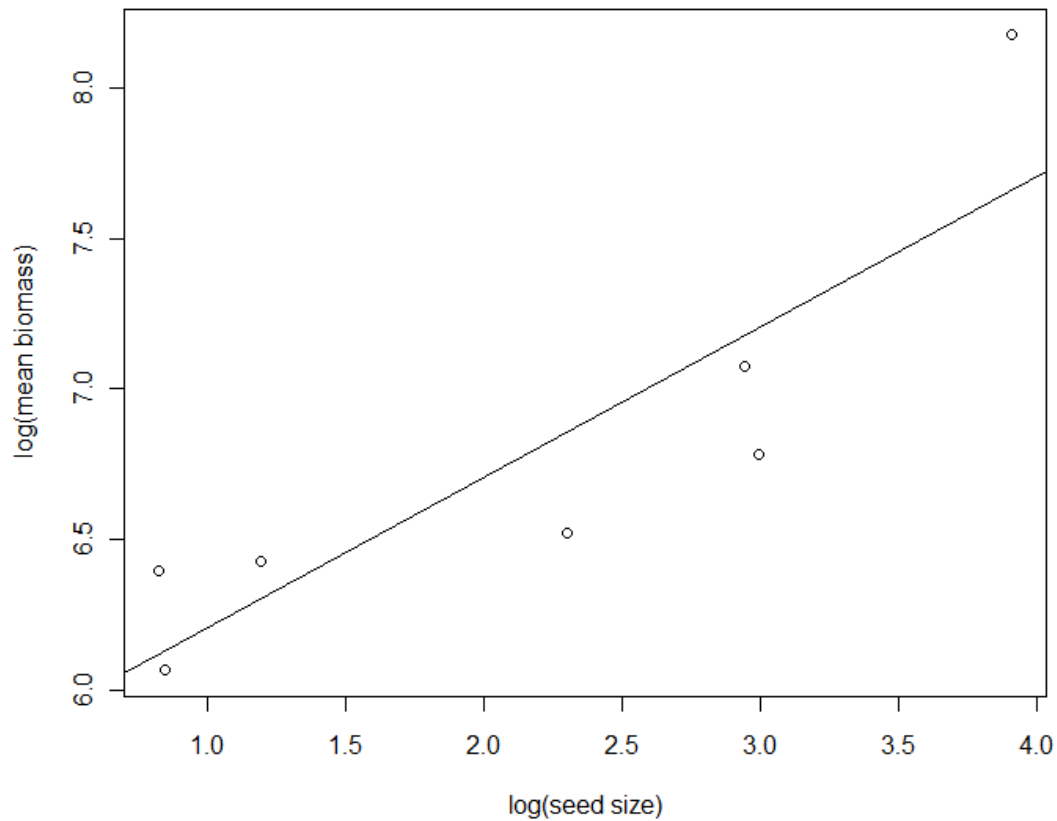


Fig 9.2 Log (mean biomass (mg) per 25cm x 25cm quadrat) plotted against log (seed size (fresh weight in mg)); slope = 0.5; $p < 0.01$). *Ornithopus perpusillus* has the largest seeds and the highest biomass compared with the other 6 species. See text for details.

There has been substantial progress in understanding the relative importance of the four mechanisms in recent years. When this research was in the planning stage (Ratcliffe 1999), the colonization competition trade-off was the most fashionable of the mechanisms (Pacala and Crawley 1992, Pacala and Tilman 1994, Bolker and Pacala 1999, Chesson 2000a), and there is a substantial literature on experiments that lend some support to this mechanism. For instance, at high density, large-seeded species outcompete small seeded species (Coomes et al. 2002a). On seed limited sites, the addition or introduction of seeds will lead to the establishment of the more competitive species, whereas establishment in new patches will favour the colonizing

species (Turnbull et al. 2000). Although evidence from studies within functional groups suggests that seed size does trade-off against seed number and dispersal of these seeds, and that seed size is correlated with competitive ability among seedlings, the available evidence suggests long-term coexistence is unlikely without other forms of niche differentiation (Coomes and Grubb 2003, Turnbull et al. 2004).

Other studies report that the seed-size seed-number trade-off alone is not sufficient for coexistence among species, but depends on growing conditions (Paul-Victor and Turnbull 2009). A seed sowing experiment showed that in unsown areas, small seeded species tend to do better than large seeded species; however large seeded species tend to win when they come in contact with small seeded species (Turnbull 1999). Density dependent mortality of seedlings was commonly observed in our experiments, especially in large-seeded species at the highest sowing densities (e.g. *Myosotis* and *Ornithopus*), pointing to an important role for intraspecific competition between newly-germinated seedlings for these species relative to smaller-seeded species such as *Arabidopsis* and *Cerastium*. This is one possible mechanism, amongst others, for the coexistence of the 7 species. Similar findings were reported in other experiments involving agricultural wild plant species (Wassmuth et al. 2009).

Spatial and temporal heterogeneity have received considerable attention as potential mechanisms favouring coexistence. In temperate grassland communities, invasion of resource-rich and pathogen-free sites are some of the important biological drivers of community assembly (Petermann et al. 2010). Annual species in the Sonoran desert were able to adapt to climate changes through changes in phenology and phenotypic plasticity, and also through photosynthetic resource-use efficiency as well as demographic variability (Angert et al. 2007, Angert et al. 2010). On the other hand, species abundance can depend on geographic range position and on demographic variability of the species (Gerst et al. 2011). Spatial processes may slow down competitive exclusion and hence promote coexistence even in the absence of evident trade-offs or frequent disturbances. Weak competitors have been found to increase their fitness when grown in the neighbourhood of conspecifics, and that for the weakest competitors, species identity is not important and *all* other species are best avoided through intraspecific aggregation (Stroll 2005). The importance of spatial

pattern for competitors might not only depend on the position within the hierarchy but also on the identity of neighbour species, species characteristics, below ground interactions and other non-spatial factors (Monzeglio 2005).

Niche differentiation amongst plant communities for coexistence is clearly more likely than neutral theory (Silvertown 2004, Turnbull et al. 2005, Aarssen et al. 2006, Purves and Turnbull 2010). However, a neutral outcome is possible where seed mass affects survival rather than competition; otherwise exclusion is likely (Turnbull et al. 2008b).

Functional trade-offs (morphological and physiological differences, differences in resource up-take and allocation between species) have the ability to determine species coexistence via the storage effect (Angert et al. 2007, Angert et al. 2009). Most of our species showed non-identical timing in recruitment, flowering and seed production. For example, *Erophila* was always much earlier in recruitment and flowering compared with the next most closely related species (*Arabidopsis thaliana*) which was at least a week behind in these traits, although when the two species came into contact, one but not both of them typically did well (although *which* species performed better was idiosyncratic). One reason could be that one or both of them release allelopathic compounds during germination and/or recruitment, which can be harmful both for the same species, when densities are very high, or against the other species. Another reason might be that *Arabidopsis thaliana* might invest in defensive compounds against predators at the expense of weakened growth (Paul-Victor et al. 2010).

There is a debate as to whether relative growth rate (RGR) of plant species is one measure of the outcome of plant competition. Perhaps this is a useful metric in considering the potential rate of population increase in empty habitats, however, plant growth analysis is likely to be a better way of understanding underlying differences in species' phenology (Turnbull et al. 2008a, Rees et al. 2010). We did not make any within-season plant size measurements.

In some annual-plant species, year-to-year environmental variations exert major influences on population sizes and spatial structures (Coomes et al. 2002b). Some of

our species (for example, *Cerastium glomeratum*) showed high density in recruitment and adults survival in some years in monocultures, but quite the opposite in other years (what we call “year effects”). Of course, year effect might interact with plant density and other factors, or climatic differences alone could result in significant year-to-year differences in performance.

Colonization-competition trade-off. During the pilot studies for this project (Ratcliffe 1999) there was a clear expectation that the competition colonization trade-off would be an important component of coexistence. That is why we designed explicit tests of seed dispersal and seed-limitation into the work. Despite our initial expectations, and the findings of several other recent studies (Levine and Rees 2002, Stanton 2002, Turnbull 2004, Cadotte et al. 2006), we found little compelling evidence to support the hypothesis that competition-colonization processes were of central importance. First and foremost, we found no evidence on which to identify a superior competitor, let alone to rank all seven species by their interspecific competitive ability (as required by the simplest colonization-competition models for coexistence; Pacala and Tilman 1994). Moreover, our seed-sowing experiments indicated that recruitment was seed-limited for all species, even at the highest densities (at least in terms of seedling numbers; some species showed overcompensating density dependence in final adult biomass). Our seed redistribution work with pairs and seven-species mixtures was focused directly on testing the competition-colonization model. If this mechanism was important then the superior competitor would be strongly seed limited, and redistributing its seed should lead to an increase in its population, and a commensurate decline in the population(s) of the other species (the inferior competitor(s)). In the minority of cases, where we did find a response to seed redistribution, it was typically the case that *both* species increased in abundance following redistribution of their seed (rather than one increasing and the other decreasing).

There is no *a priori* reason to expect a relationship between seed size and biomass. For a given biomass, plants would be expected to trade off seed size against seed number, and that is certainly what our seven species do (Fig 9.1). It turns out, however, that there is a highly significant correlation between seed size and adult biomass for our seven species (Fig 9.2). This, in turn might lead to a prediction that

seed size would be correlated with competitive ability, and that the largest-seeded species would outcompete any of the others by dint of having the highest biomass. The likely reason that peak adult biomass is not correlated with interspecific competitive ability for our seven species, is that they differ so greatly in phenology. For instance, the peak biomass of the smallest species (*Erophila* and *Arabidopsis*) occurs well before the peak in biomass of the largest species (*Ornithopus*).

Based on our direct measurements of the dispersal kernels, it should be *Aira* that is the most seed limited, and hence the most likely to be the superior competitor, with *Cerastium* as the least seed limited, and hence the least likely to be the superior competitor. As it turned out, *Aira* showed itself to be the *best* medium range (plot-to-plot) disperser, not the worst (as predicted by the small scale measurements of dispersal kernels within plots).

Spatial heterogeneity. It is possible that there was within-plot spatial heterogeneity, despite our best efforts at homogenizing the initial substrate. It is highly likely, however, that within plot heterogeneity developed rapidly in those experiments that were not started afresh each year (the pairs and the fine- and coarse-grained mixtures). Of course, we had no control over this spatial heterogeneity, so it is impossible to ascribe a relative importance to spatial heterogeneity and temporal heterogeneity in these long-running, time-series treatments.

Janzen Connell effect. There were no herbivore or pathogen exclusion treatments in any of our experiments, so we have no direct way of assessing the importance of this mechanism for coexistence. It would make an ideal topic for future research, especially for the closely related taxa (e.g. *Erophila* and *Arabidopsis*). From our knowledge of the shoot systems of the seven species, it is likely that if selective distance-dependent herbivory is important in coexistence, that it is mediated by below-ground natural enemies rather than by shoot-feeders or granivores.

Temporal heterogeneity. Year effects such as the timing and intensity of rainfall, high temperature or low temperature (the prevalence of killing frosts or frost heave of the topsoil) will interact with density dependence, and might weaken interspecific competition between species, enhancing the likelihood of coexistence. In addition, the prevalence of seed banks over several years coupled with a storage effect and also the existing of differing seed dispersal distances can have a stabilizing effect among

species. Phenological differences and physiological growth differences among species, and in recruitment and flowering (early in *Erophila verna* and *Arabidopsis thaliana*, intermediate in *Cerastium glomeratum*, *Myosotis discolor* and *Aira praecox*, and late in *Veronica arvensis* and *Ornithopus perpusillus*), might lead to less competition and the coexistence of multiple species. In addition to year effects, history effects and the interactions between history and year effects (e.g. the size of the seed bank, its dormancy composition and competitor identity effects) are feasible only in the time series experiments, but can all promote coexistence.

The saturation experiment provided convincing evidence that the predictions of the Pacala and Rees model do not apply to this guild of seven species. We did not observe competitive exclusion of any “inferior competitors” when seed of a “superior competitor” was sown in excess. There were always enough survivors, and these survivors managed to produce enough seed, for the species to pass the invasion criterion ($\lambda > 1$) even under the most extreme interspecific competition as seedlings.

The seed bank work reinforced our view that seed banks are likely to play an important role in coexistence, by acting as an insurance against total failure of one or more cohorts in a row. The seed banks did not appear to be especially long-lived (we got no seedlings five years after sowing) but they are probably long-lived enough.

Another form of rescue effect can occur through immigration of seed. Perhaps the most striking result of our detailed work on dispersal kernels was how hopeless these were at predicting longer-distance dispersal. The weeding data from Ashurst provide a uniquely detailed record of plant immigration at a scale of 1m to 10m. While the species that was the worst plot-to-plot disperser (the big-seeded legume *Ornithopus perpusillus*) was perfectly predicted from the dispersal kernel work, the other 6 species were not. It is likely that variation in the number of seeds produced is at least as important (if not more important) than the probability density function for the dispersal distance of any one seed. Our work reinforces what many workers have said before us that understanding the tails of the dispersal kernel (the rare long distance events) is paramount.

The pairs experiments introduced time series dynamics to the picture. Now, it is not just year effects that are important but history effects and the interactions between history and year effects. Thus the size of the seed bank, its dormancy composition and

competitor identity effects can all interact with processes that might be expected to exhibit trends through time: resource depletion, natural enemy build up, accumulation of allelochemicals, and so on. The most striking results from the pairs experiments were the paucity of strong identity effects (there clearly is no universally superior competitor in this guild of seven species, despite the overwhelming biomass superiority of the legume *Ornithopus perpusillus*). The manipulative part of the pairs experiment, seed redistribution to test Bolker and Pacala's hypothesis, had subtle and slightly counter-intuitive results. Redistribution of seed did not hasten competitive exclusion as predicted, but instead (where it had any effect at all) tended to increase the abundance of both species (rather than increase one – the putative seed-limited superior competitor - and reduce the other - the putative inferior competitor).

The seven species interspecific competition experiments were important in assessing the prevalence of emergent spatial patterning in explaining coexistence (Law et al, Murrell et al; 2003, 2004). Would initially homogeneous communities develop spatial clumps of species in which intraspecific competition was relatively more important than interspecific competition? When we created spatial heterogeneity *de novo* then how long would this spatial structure last, and would it delay the onset of competitive exclusion? We did not observe any tendency towards the emergence of spatial clumping, and the sectors within our fine-grained plots were remarkably uniform in total and relative abundance of species. The coarse grained structure that we created experimentally disappeared within the first two years, so that by year 3 there was no significant difference between the coarse and the fine-grained plots.

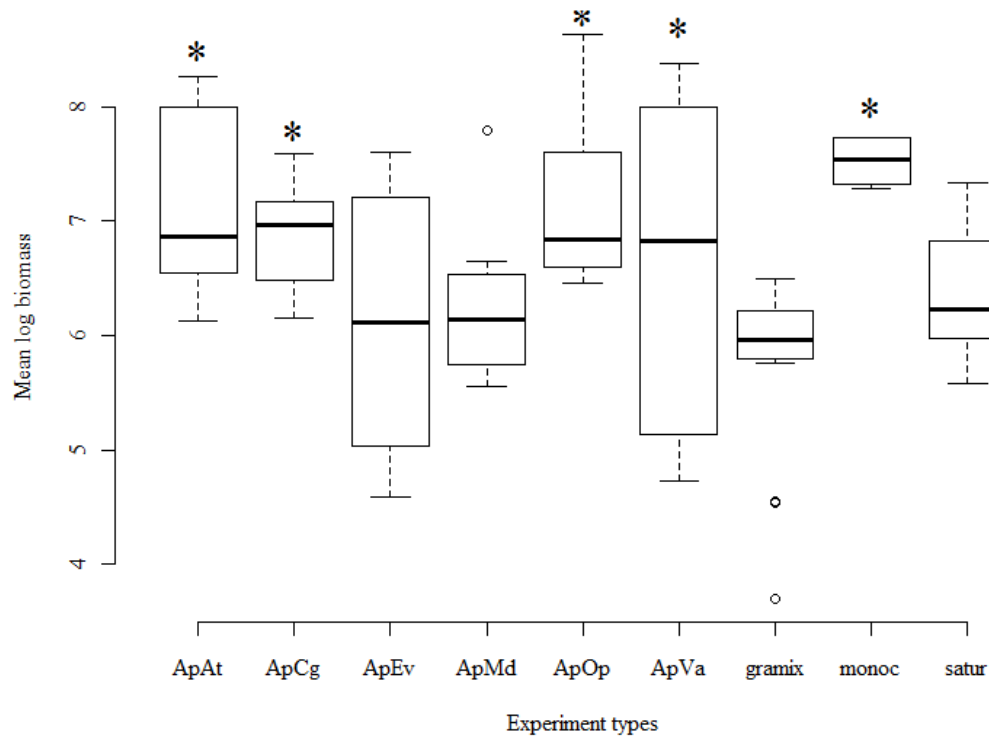


Fig 9.3 Box plots showing log biomass for *Aira praecox* in comparison with the other 6 species in mean monoculture biomass from intermediate sowing, mean saturation biomass from intermediate sowing, mean pairs biomass (2007 data) and mean fine-grained mixtures biomass (2007 data). Abbreviations: ApAt = *Aira* paired with *Arabidopsis*, ApCg = *Aira* with paired *Cerastium*, ApEv = *Aira* paired with *Erophila*, ApMd = *Aira* paired with *Myosotis*, ApOp = *Aira* paired with *Ornithopus*, ApVa = *Aira* paired with *Veronica*, gramix = *Aira* in both grained mixtures, monoc = *Aira* monoculture, satur = *Aira* in saturation sowing. Df (degree of freedom) = 81 (4+14+15+48). Boxes show the interquartile range with the median shown as a solid line. Whiskers extend to the smallest and largest observations or 1.5 times the interquartile range, whichever is the smaller (Crawley 2002), n=81. Asterisks indicate the level of significance: $p < 0.05 = *$. $DF = 8$ and 72. Mean biomass (average per 625cm² quadrat) of *Aira praecox* was significantly higher when paired with *Arabidopsis*, *Cerastium*, *Veronica* and *Ornithopus*, and lower with *Erophila* and *Myosotis*. Not surprisingly, mean biomass of *Aira praecox* was highest when it was grown in monoculture.

Table 9.1 Comparison of mean biomass (mg/625cm²) between monoculture sowing (5 years average) and saturation sowing (5 years average) and also between pairs species and 7 species mixture (fine-grained), both of which are time series experiments with one year only data. The ratio of monoculture over saturation is higher 2 to 10 fold for 5 of the 7 species. Similarly, the ratio of pairs over fine-grained mixture is higher in only 1 species and also marginally higher in 2 species. Abbreviations: m=monoculture, s=saturation, p=pair, f=fine-grained.

species	Monoculture	saturation	m/s ratio	pairs	fine-grained	p/f ratio
<i>Aira</i>	521.025	543.446	0.958	235.740	284.742	0.827
<i>Arabidopsis</i>	599.7	56.998	10.521	112.161	69.591	1.611
<i>Cerastium</i>	452.643	349.753	1.294	182.377	265.857	0.685
<i>Erophila</i>	698.466	67.7683	10.306	62.357	52.210	1.194
<i>Myosotis</i>	3478.66	831.564	4.183	523.894	709.511	0.738
<i>Ornithopus</i>	1325.95	661.455	2.004	1642.99	2243.180	0.732
<i>Veronica</i>	834.55	834.41	1.000	191.104	187.610	1.018

One would expect to observe more adults and/or biomass per species in monocultures compared with pairs, and also more biomass per species in pairs compared with a 7-species mixture. This was the case for some species, such as *Arabidopsis*, but for other species, biomass was either the same or even marginally lower; in some cases total biomass increased with an increase in species number. There is a substantial literature about some forms of resource complementary in species mixtures, leading to increased productivity with increased species richness (Naeem et al. 1996). The species with the highest biomass in monoculture does not always exhibit the highest biomass in a species mixture, as influenced by the identity of its competitor(s) (Hector 1998), and performance of a species in monoculture is not always a good predictor of its relative performance in mixtures (Roscher et al. 2007). It is not clear how exactly this complementarity, when it exists, is operating or what other mechanisms might be involved. One possible explanation for a better performance of a species in mixtures compared with monoculture is niche differentiation and resource partitioning in space and time (Tilman et al. 2001), for example via differing rooting depths or phenologies (Berendse 1982), amongst other mechanisms. It is plausible that there are other mechanisms, and these would reward testing in any related future work.

Table 9.2 Mean biomass (mg/625cm²) comparisons between four experiments from one year data (2007) for each species. *Aira*, *Arabidopsis* and *Erophila* have always more biomass in monocultures compared with the other three multi-species experiments. However, the two supposedly superior competitors, *Myosotis* and *Ornithopus*, showed more biomass in the presence of other species compared with when in monoculture. *Cerastium* has less biomass in pairs compared with when in monoculture but showed more biomass in saturation sowing and grained mixture. *Veronica* has more biomass when it was sown with the 6 other species compared with when it was a monoculture. However, it has less biomass when it was paired with any of the 6 species.

species	monoculture	saturation	Pairs	grained mixture
<i>Aira</i>	1782	1204	234	476
<i>Arabidopsis</i>	110	46	102	93
<i>Cerastium</i>	215	534	182	310
<i>Erophila</i>	622	47	62	56
<i>Myosotis</i>	413	1682	524	842
<i>Ornithopus</i>	1051	1297	1643	2183
<i>Veronica</i>	241	318	191	172

Table 9.3 Number of species (out of 7) showing best and worst seedling recruitment in each of 2 seasons for 5 years.

Year	best spring/autumn								worst spring/autumn							
	monoculture		saturation		pairs		grained		monoculture		saturation		pairs		grained	
	bs	ba	bs	ba	bs	ba	bs	ba	ws	wa	ws	wa	ws	wa	ws	wa
2003	2	0	1	0	2	0	1	0	0	0	1	0	2	0	6	0
2004	2	0	0	0	5	0	0	0	1	5	2	7	0	5	0	4
2005	2	2	0	3	0	5	5	4	3	1	4	0	4	0	0	1
2006	1	0	0	4	0	2	1	2	3	1	0	0	1	0	1	1
2007	0	5	6	0	0	0	0	1	0	0	0	0	0	2	0	1

Every year was both the best and the worst for at least one parameter of one species. In just one case (worst autumn recruits in saturation in 2004) was the same year the worst for all 7 species. Abbreviations: bs = best spring, ba = best autumn, ws = worst spring, wa = worst autumn, grained = Coarse and fine-grained combined. The table summarizes scores of best spring, best autumn or worst spring, worst autumn for each experiment type in each year. The column values under the headings: bs, ba, ws and wa add up to 7 as they are scores coming from the 7 species. For example: in 2007, autumn was best for recruitment with a score of 5 for 5 of the 7 species compared with saturation with 0 score, pairs with 0 score and grained mixture with 1 score. In 2004, autumn was worst for recruitment in saturation experiment with a score of 7 out

of 7 compared with a score of 5 each in monoculture and pairs, and with a score of 4 in grained mixtures. There is no clear pattern where a particular season is best or worst for all species in all 4 experiments due to year effects.

Table 9.4 Spatial and temporal heterogeneity in the first year percentage recruitment from 4 different experiments. *Aira* showed the highest recruitment in all 4 experiments with the highest percentage coming from seed dispersal experiment (this is partly because seedling recruitment was higher than estimated fecundity in some years on some replicates as a result of continuous fruiting following initial estimate). On the other hand, *Arabidopsis* has the lowest recruitment compared with other species. Seed sowing for the seed banks and monocultures are not identical. Seedling recruitment from the seed dispersal experiment was from naturally set seeds and hence is estimated rather than counted.

first year % recruitment species	seed bank		seed dispersal	monoculture
	Pound Hill	Ashurst	Walled garden	Ashurst
<i>Aira praecox</i>	15	74	100	36
<i>Arabidopsis thaliana</i>	2	6	13	8
<i>Cerastium glomeratum</i>	1	35	68	24
<i>Erophila verna</i>	3	25	38	15
<i>Myosotis discolor</i>	3	63	72	50
<i>Ornithopus perpusillus</i>	12	13	48	44
<i>Veronica arvensis</i>	1	38	42	29

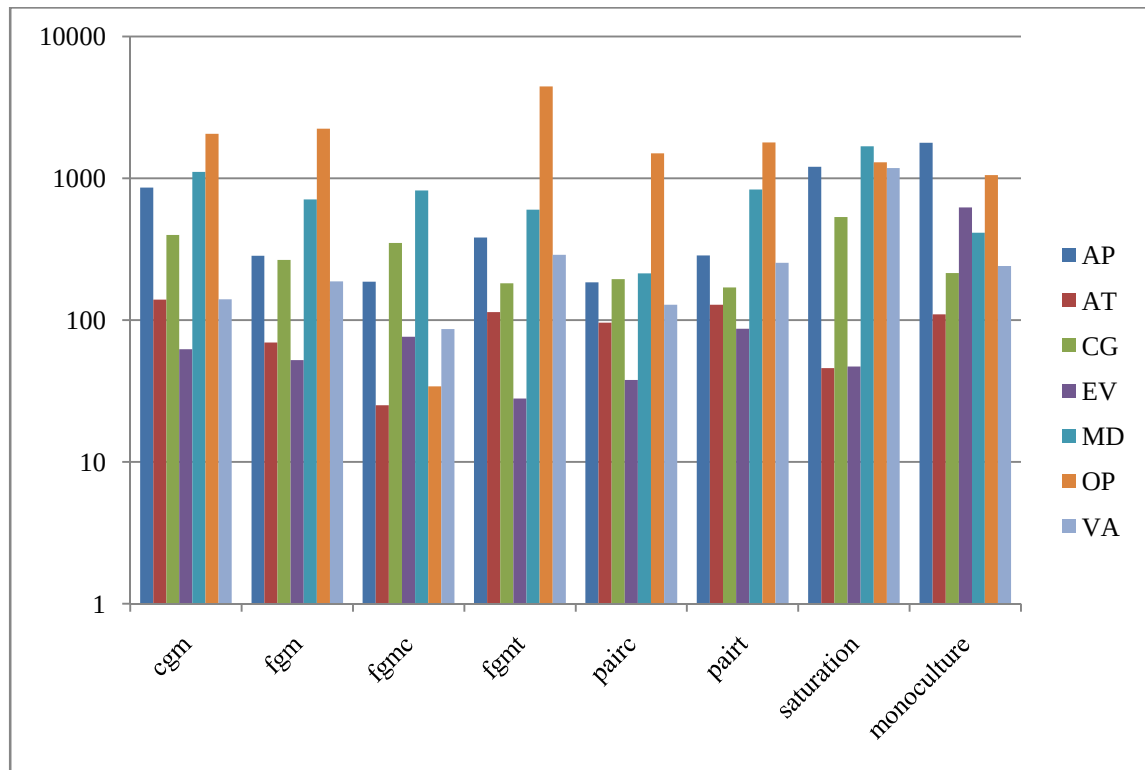


Fig 9.4 Biomass (mg) in 2007 across all the experiments (on a log scale) for 25cm x 25 cm quadrats for each of the seven species (colour coded as indicated in the legend). Contrasting monoculture and saturation plots shows the expected reduction in biomass under intense interspecific competition for three species, but *Ornithopus* is unaffected (orange bar) and three species *Cerastium* (green), *Veronica* (mauve) and *Myosotis* (blue) actually had *higher* biomass on the saturation plot. For the pairs, there was a general increase in biomass of most species following seed redistribution (pairc vs. pairt), but this pattern was not repeated in a comparison of the seed redistributed fine-grained plots (fgmc vs. fgmt). The coarse-grained plots tended to have higher biomass for most species than the fine-grained plots (cgm vs. fgm). Cgm = coarse-grained mixtures, fgm = fine-grained mixtures, fgmc = fine-grained mixtures (control), fgmt = fine-grained mixtures (seed redistributed).

Comparisons with Ratcliffe (1999)

Mapping turned out to be immensely time consuming in pilot trials (Ratcliffe 1999). While it would have been good to have maps identifying the specific identity and size of the neighbours of every individual, it is not obvious that we would have learned a great deal more about the kinds of density dependence that were important than we got from plot-level counts or destructive biomass sampling. Although there is an advantage in mapping using an automated mapping device of every individual plant from recruitment to adult so that a detailed demography is recorded, when the density of some species is likely to be very high this is likely to be difficult to do. The use of 30 mini-quadrats within the 25cm square experimental unit proved to be satisfactory

in estimating seedling densities and was a tremendous time-saver when seedling densities were very high (i.e. many thousands per quadrat).

She found that intraspecific competition was more important in regulating fecundity of her species, while interference from other species played a more important role in regulating survival (Ratcliffe 1999). Most of the species in our study were identical to hers, and our findings in the saturation experiment were in line with her findings in terms of interspecific competition. In her results over 3 years, seed establishment, seedling survival and seed production were subject to major “year effects”, and we observed a similar pattern from our 5 years study of the 7 annual species. She reported that *Aira praecox* and *Myosotis discolor* were good competitors, while *Veronica arvensis* flowered much later than most of the species. *Cerastium* and *Arabidopsis* were highly fecund. The only important difference we found was that *Erophila verna* showed low fecundity in Ratcliffe’s experiment, whereas in our experiments, this species was as fecund and competitive as the other species. In general, however, most of the findings from the two sets of experiments were in agreement especially in terms of the relative importance of the four mechanisms of coexistence in our experimental annual plant species.

9.3 The ideal next experiment

Would we use the same species again? The species were all well-behaved and easy to work with. The only important problem was the tendency of *Ornithopus perpusillus* to keep growing and to delay fruiting and senescence when conditions permitted, which meant that fecundity was difficult or impossible to measure for this species in certain years before the plots had to be dismantled and rebuilt for the next growing season. In such cases, we had to be content with shoot biomass as a measure of performance for that species. Also, the tendency of *Ornithopus perpusillus* to form an unrooted but dense mat above the plot gave certain species that could tolerate, or possibly even benefit from a nurse effect, an advantage over others that were intolerant of the shade cast and/or more humid microclimate created.

Was the plot size appropriate? The use of 25cm square sample areas within a 1.5m square plot worked well in terms of access, total plant numbers and reproducibility. The design of the plots, using wooden railway sleepers was effective, and the sleepers formed a convenient edge for kneeling on during monitoring or for standing on during weeding.

Would it be worth mapping all the individuals? Mapping turned out to be immensely time consuming in pilot trials. While it would have been good to have maps identifying the specific identity and size of the neighbours of every individual, it is not obvious that we would have learned a great deal more about the kinds of density dependence that were important than we got from plot-level counts or destructive biomass sampling.

The use of 30 mini-quadrats within the 25cm square experimental unit proved to be satisfactory in estimating seedling densities and was a tremendous time-saver when seedling densities were very high (i.e. many thousands per quadrat). With hindsight, it is obvious that we should have counted all the seedlings in the 25cm quadrat when counts in the 30 mini-quadrats fell below some threshold value (say, five individuals in total), and we recorded as zero a number of populations that were clearly not locally extinct.

Is it useful to redistribute the seeds of all the species, or should the redistribution be done one species at a time? One species at a time would be more informative, but requires more space and man power than we had available.

What about the substrate and the nutrient supply? The very low nutrient supply proved to be ideal in that plants were small and population sizes were correspondingly high. It is likely that some of the species (e.g. *Arabidopsis thaliana*, *Cerastium glomeratum*) are capable of attaining much greater size than they achieved in these experiments (e.g. when they grow as arable weeds), but the other five species were the same size as one is used to seeing in other circumstances. In any event, all of the species comfortably passed the invasion criterion with the prevailing nutrient supply, and grew large enough to compete with one another even at low sowing densities.

Was the gravel mulch a problem or a benefit? The benefits of the gravel mulch in terms of protection of the soil surface from erosion, enhanced water retention and reduced need for weeding were very substantial. The down-side was the potential for negative impacts on the youngest seedlings. It is possible that a seedling germinating immediately beneath the centre of one of the stones might not have had the carbohydrate reserves to allow it to grow out from underneath. However, there is nothing to suggest that seedlings lacked the hydraulic strength to escape or that they were crushed by the weight of the stones. It is possible that the stones acted to impose density dependence on seedling recruitment, by restricting the surface area through which shoot extension was possible (i.e. in the gaps between the stones). If this was a partial cause of the observed density dependence in seedling recruitment, then it certainly did not prevent the appearance of very high densities of seedlings of all of the species. The seedlings overtopped the gravel mulch within a week or so of appearance, and it is unlikely that the mulch had any subsequent impact on plant performance.

We know from other work in Silwood Park that some plant species do spectacularly well when protected from certain enemies (e.g. *Festuca rubra* when protected from soil pathogens by fumigation). The experimental system is ideally suited to the implementation of a factorial exclusion experiment in which fungicides, insecticides, nematicides and molluscicides are employed in a fully-crossed design at the whole-plot scale. It might be sensible in such an experiment to exclude birds with a netting roof and walls, and to try to exclude rodents with metal barriers. We suffered interference from grey squirrels on certain plots in some years, but birds (mostly jackdaws) were the most consistent nuisance.

Some of the species might have been substantially more competitive if freed from their herbivores by selective exclusion of fungal pathogens, nematodes, mollusc or insects using pesticides. *Veronica arvensis* suffered from a smut fungus in one particular year (2005) and this could have had an impact on fecundity and its ability to compete with the other species. Similarly, *Erophila* siliques suffered from bird and insect predation in 2 of the five years.

Controlling the development of bryophytes on damper plots in years 4 and 5 would have been good if this could have been achieved without soil disturbances (mechanically) or without effects on the experimental plots (using moss-killing herbicides). This is one example, where problems can arise in long-term field experiments.

9.4 Conclusions

The answers to the questions posed in Chapter 1 are as follows:

Chapter 2 Monocultures

How does seedling recruitment vary with seed density across species and years?

Very substantially, and in many more cases than we expected, in a density dependent manner.

How does seedling survival vary with seedling density across species and years?

In a consistently density dependent manner, but with substantial year-to-year variation in the mean.

How do mature plant size and biomass vary with plant density across species and years?

The classic size hierarchy (many small individuals and a few large ones) developed at the highest sowing densities in all species. At lower densities, the size distribution was much less skew, approaching a normal distribution at the lowest densities sown.

How does fecundity vary with mature plant size across species and years?

The per-unit-biomass seed production was systematically more variable than expected, and fecundity was typically a decelerating non-linear function of biomass

for most species and most years. The text-book pattern of a linear relationship between seed production and shoot biomass was not commonly found for these species.

How does total seed production vary with biomass across species and years?

Substantially, both in mean fecundity and in the slope of the allometric relationship between fecundity and biomass.

How does lambda (λ = net multiplication rate, calculated as seed output/seed input) vary with seed input across species and years?

The pattern of density dependence in lambda varied with species and with years. The existence of a threshold density below which lambda was density independent was observed in a minority of years for most species. Some species continued to pass the invasion criterion even at the highest sowing densities we used. There was no evidence of Allee effects (low density density-dependence) in any of our species.

What plant traits are associated with density-dependence and year-dependence in lambda?

None. All of the species showed similar variability in density dependence.

Chapter 3 Seed banks

What is the time course of seedling appearance across years and with season within years?

Seeds stopped appearing from the seed bank after about 4 years. The time course typically did not follow the classic exponential decay predicted by simple models.

How do these patterns differ with species?

Rather little, but there is a clear ranking of species in terms of maximum delay between sowing and seedling appearance.

Is there any immigration to unsown blank plots that might be mis-interpreted as recruitment from seed bank?

Not at Pound Hill where we did the main seed bank experiment, but certainly at Ashurst where we repeated it.

Chapter 4 Dispersal

How do dispersal kernels differ across years and species across four (presumably different) years?

Consistent differences in mean, mode, maximum and percentiles of dispersal distances across species. Some species showed very little year to year variation in kernel (e.g. *Aira*) others showed massive variation (e.g. *Arabidopsis*).

Is there a parametric model that best describes these dispersal kernels across species and years?

Apparently not. All species showed initial increases in seedling density with distance along transects, and the degree of skew and kurtosis were substantial across species.

How does appearance of seedlings relate to estimated seed crop with species and years?

Very much in *Arabidopsis*, not at all in *Aira*.

Are there any special adaptations for seed dispersal in our species (e.g. tumbleweeds)?

Cerastium glomeratum turns out to be an outstandingly effective tumbleweed, and by far the best disperser of the 7 species.

In multi-year population studies, does immigration of seed from adjacent plots contribute to coexistence (e.g. a rescue effect?)

The weeding data from Ashurst indicate a clear hierarchy of candidates for the rescue effect, from strong in *Aira* to negligible in *Ornithopus*.

Chapter 5 Saturation sowing

Which of the 7 species could be said to be the ‘superior competitor’?

Our prediction that the species with consistently the highest biomass (*Ornithopus*) would exclude the other species turned out to be clearly wrong. These experiments provide a convincing demonstration that for these 7 species, there is no single superior competitor. Coexistence appears to be the norm and competitive exclusion was seldom if ever observed.

What is the relative performance across years of species sown at saturation densities, and does this provide evidence for over-compensating density dependence?

There was little evidence of over-compensating density dependence for most species, but there were some dramatic year effects where this was observed.

Is there a difference in demographic performance between first sowing and last sowing for the species sown at saturation density?

It was uncommon for a consistent difference attributable to sowing order to be observed.

Does the performance of a species that is sown at low density depend upon the identity of the species sown at saturation density, and does this vary with years?

Significant identity effects were far less commonly observed than we expected at the outset. There were strong year effects in the outcome of saturation sowing.

Do any species suffer competitive exclusion within a growing season in any of the years or in any of the replicates within years?

No.

How does the distribution of plant sizes at maturity vary with sowing density across species and years?

Most species showed the classic high-density L-shaped size distribution in the saturation experiments. There was often massive mortality of seedlings of the species sown at saturation densities.

Chapter 6 Two-species time series

Is there a characteristic pattern of density trajectories across years (e.g. a trend towards competitive exclusion of one of the two species)?

Most species showed fluctuating abundance with significant negative trends in most cases. Whether these negative trends represent the early stages of competitive exclusion, or rather the result of gradual (e.g. successional) changes in the environment provided by the plots cannot be separated on the data available.

How similar are the time series for the same species across replicates?

Not very similar at all in most cases.

How often is local extinction observed?

Very rarely.

Are there consistent identity effects in terms of dominance rank (e.g. if $A > B$ and $B > C$ then $A > C$)?

No.

How does experimental redistribution of seed affect the outcome compared with control replicates, where seed is naturally dispersed (presumably in clumps around adult plants)?

In the minority of cases where significant effects were observed, one of the pair of species increased following seed redistribution but the other species did not decline in abundance.

Are the years of peak abundance in paired combinations in time series predicted by the monoculture and/or saturation data for the same years?

Seldom. Year effects were often different in the time series experiments and the one-off yearly experiments.

Chapter 7 Seven-species time-series sown as fine-grained mixtures

Is there a characteristic pattern of density trajectories across years (e.g. a trend towards competitive exclusion of one or more species)?

No.

How similar are the seven parallel time series across spatial replicates?

Not very.

How often is local extinction observed?

Seldom if at all. We would have expected some “no shows” by chance alone, especially if species drifted to low densities.

Are there consistent identity effects in terms of dominance rank (e.g. if $A > B$ and $B > C$ then $A > C$)?

No.

Are the peak years of species abundance by the behavior of predicted by the monoculture and/or saturation data for the same years?

Yes and no. It varies with species.

How does experimental seed redistribution affect the outcome?

It does not affect the outcome in terms of coexistence, but redistribution had significant effects on population density (some positive, some negative).

Chapter 8 Seven-species time-series sown as coarse-grained mixtures

How long does the system remember its spatial history (i.e. which species were sown where)?

For two years. The initial heterogeneity was undetectable by year 3 of the experiment across all replicates.

Do the coarse-grained plots converge towards the fine-grained case?

Yes, rapidly.

If so, how long does this convergence take?

Three years.

Did species persist longer in the coarse-grained than in the fine-grained case, as predicted by the Lotka-Volterra criterion?

There was no difference in persistence.

Finally we re-assess the four mechanisms of coexistence for these 7 species in Silwood Park.

Which of the four classes of coexistence mechanism appear to be important in this 7-species system?

1. *Spatial heterogeneity with resource partitioning*: very little evidence of spatial heterogeneity effects, not least because the plots were constructed to be as internally homogeneous as possible. There was no evidence of intraspecific aggregation leading to spatial pattern formation in either the pairs or the 7-species time series. It is very likely that there was resource partitioning based on differences in root system structure but we have no data on this. There was plenty of evidence of phenological niche partitioning across the seven species (*Erophila verna* consistently first to ripen seed, *Ornithopus perpusillus* last).

2. *Colonization competition trade-off*: extensively investigated but little evidence of it, either from seed redistribution experiments, dispersal kernels or seed bank experiments. Despite huge differences in mean biomass, there was no clear competitive hierarchy, and no clear correlation between seed-limitation and competitive ability.

3. *Selective herbivory acting in a frequency dependent manner; e.g. spatial density dependence in regeneration niche (the so-called Janzen-Connell effect)*: no evidence, but shared soil pathogens might explain some of the patterns in the interactions between the two crucifers, *Erophila verna* and *Arabidopsis thaliana*.

4. *Temporal variability in recruitment combined with a storage effect and sub additivity*. Abundant evidence that year effects are all-pervasive and, most interestingly, that the nature of the year effects can be context specific (e.g. the same years had different effects in intraspecific competition (monocultures) and interspecific (saturation sowing) settings. Also, year effects can be expressed differently in time series studies (where historical effects add to, and interact with weather effects) than in one-off studies restarted every year. There was little or no evidence on sub-additivity (this is exceptionally tricky to demonstrate in field experiments), but there was convincing evidence of storage via the seed bank and through rescue effects deriving from immigration of seed.

References

- Aarssen, L. W., B. S. Schamp, and J. Pither. 2006. Why are there so many small plants? Implications for species coexistence. *Journal of Ecology* 94:569-580.
- Angert, A. L., J. L. Horst, T. E. Huxman, and D. L. Venable. 2010. Phenotypic plasticity and precipitation response in sonoran desert winter annuals. *American Journal of Botany* 97:405-411.
- Angert, A. L., T. E. Huxman, G. A. Barron-Gafford, K. L. Gerst, and D. L. Venable. 2007. Linking growth strategies to long-term population dynamics in a guild of desert annuals. *Journal of Ecology* 95:321-331.
- Angert, A. L., T. E. Huxman, P. Chesson, and D. L. Venable. 2009. Functional tradeoffs determine species coexistence via the storage effect. *Proceedings of The National Academy of Sciences of The United States of America* 106:11641-11645.
- Armstrong, R. A., McGehee, R. 1976. Coexistence of species competing for shared resources. *Theoretical Population Biology* 9:317-328.
- Baskin, C. C. and J. M. Baskin. 1998. Seeds: ecology, biogeography, and evolution of dormancy and germination. *Seeds: ecology, biogeography, and evolution of dormancy and germination*:xiv + 666 pp.
- Baskin, C. C. and J. M. Baskin. 2004. Determining dormancy-breaking and germination requirements from the fewest seeds. *Ex Situ Plant Conservation: Supporting Species Survival in the Wild*:162-179.
- Baskin, J. and C. Baskin. 1987. Physiology of dormancy and germination in relation to seed bank ecology. *American Journal of Botany* 74:634-635.
- Baskin, J. M. and C. C. Baskin. 1989. Role of Temperature in Regulating Timing of Germination in Soil Seed Reserves of *Thlaspi-Arvense* L. *Weed Research* 29:317-326.
- Baskin, J. M., Baskin, C.C. 1989. Physiology of dormancy and germination in relation to seed bank ecology. *Ecology*. In *Ecology of Soil Seed Banks*, ed. MA Leck, VT Parker, RL Simpson, pp. 53-66. New York: Academic.53-66.
- Bates, D., M. Maechler, and B. Bolker. 2011. lme4: Linear mixed-effects models using Eigen and R classes. R package version 0.999375-38. <http://CRAN.R-project.org/package=lme4>.
- Begon, M., J. L. Harper, and C. R. Townsend. 1996. *Ecology : individuals, populations and communities*. *Ecology : individuals, populations and communities*:xii + 1068 pp.
- Berendse, F. 1982. Competition between plant-populations with different rooting depths .3. Field experiments. *Oecologia* 53:50-55.
- Bergelson, J. 1991. Competition between plants, before and after death. *Trends in Ecology & Evolution* 6:378-379.
- Bewley, J. D. B., M. 1982. *Physiology and biochemistry of seeds in relation to germination*. Vol.2. Viability, dormancy, and environmental control.
- Bolker, B. and S. W. Pacala. 1997. Using moment equations to understand stochastically driven spatial pattern formation in ecological systems. *Theoretical Population Biology* 52:179-197.
- Bolker, B. M. and S. W. Pacala. 1999. Spatial moment equations for plant competition: Understanding spatial strategies and the advantages of short dispersal. *American Naturalist* 153:575-602.
- Brown, N. A. C. a. J. v. S. 1997. Smoke as a germination cue: a review. *Plant Growth Regulation* 22:115-124.
- Bullock, J. M. and R. T. Clarke. 2000. Long distance seed dispersal by wind: measuring and modelling the tail of the curve. *Oecologia* 124:506-521.
- Bullock, J. M., K. Shea, and O. Skarpaas. 2006. Measuring plant dispersal: an introduction to field methods and experimental design. *Plant Ecology* 186:217-234.
- Cadotte, M. W., D. V. Mai, S. Jantz, M. D. Collins, M. Keele, and J. A. Drake. 2006. On testing the competitioncolonization tradeoff in a multispecies assemblage. *American Naturalist* 168:704-709.

- Cain, M. L., B. G. Milligan, and A. E. Strand. 2000. Long-distance seed dispersal in plant populations. *American Journal of Botany* 87:1217-1227.
- Chesson, P. 1994. Multispecies competition in variable environments. *Theoretical Population Biology* 45:227-276.
- Chesson, P. 2000a. General theory of competitive coexistence in spatially-varying environments. *Theoretical Population Biology* 58:211-237.
- Chesson, P. 2003. Quantifying and testing coexistence mechanisms arising from recruitment fluctuations. *Theoretical Population Biology* 64:345-357.
- Chesson, P. and C. Neuhauser. 2002. Intraspecific aggregation and species coexistence - Comment from Chesson and Neuhauser. *Trends in Ecology & Evolution* 17:210-211.
- Chesson, P. L. 1985. Coexistence of competitors in spatially and temporally varying environments - a look at the combined effects of different sorts of variability. *Theoretical Population Biology* 28:263-287.
- Chesson, P. L. and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* 117:923-943.
- Chisholm, R. A. and H. C. Muller-Landau. 2011. A theoretical model linking interspecific variation in density dependence to species abundances. *Theoretical Ecology* 4:241-253.
- Clark, C. J., J. R. Poulsen, and V. T. Parker. 2001. The role of arboreal seed dispersal groups on the seed rain of a lowland tropical forest. *Biotropica* 33:606-620.
- Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* 80:1475-1494.
- Cohen, D. 1968. A general mode of optimal reproduction in a randomly varying environment. *Journal of Ecology* 56:219-228.
- Coomes, D. A. and P. J. Grubb. 2003. Colonization, tolerance, competition and seed-size variation within functional groups. *Trends in Ecology & Evolution* 18:283-291.
- Coomes, D. A., M. Rees, P. J. Grubb, and L. Turnbull. 2002a. Are differences in seed mass among species important in structuring plant communities? Evidence from analyses of spatial and temporal variation in dune-annual populations. *Oikos* 96:421-432.
- Coomes, D. A., M. Rees, L. Turnbull, and S. Ratcliffe. 2002b. On the mechanisms of coexistence among annual-plant species, using neighbourhood techniques and simulation models. *Plant Ecology* 163:23-38.
- Corkidi, L., E. Rincon, and C. Vazquezayanes. 1991. Effects of light and temperature on germination of heteromorphic achenes of *bidens-odorata* (Asteraceae). *Canadian Journal of Botany-Revue Canadienne De Botanique* 69:574-579.
- Crawley, M. 2002. Statistical computing. An introduction to Data analysis using S-plus. Wiley, Chichester, England.
- Crawley, M. J. 2005a. The Flora of Berkshire. Brambleby Books, Harpenden.
- Crawley, M. J. 2005b. Species invasions - Insights into ecology, evolution, and biogeography. *Science* 310:623-624.
- Crawley, M. J. 2007. The R Book.
- Crawley, M. J., S. L. Brown, M. S. Heard, and G. R. Edwards. 1999. Invasion-resistance in experimental grassland communities: species richness or species identity? *Ecology Letters* 2:140-148.
- Crawley, M. J., A. E. Johnston, J. Silvertown, M. Dodd, C. de Mazancourt, M. S. Heard, D. F. Henman, and G. R. Edwards. 2005. Determinants of species richness in the park grass experiment. *American Naturalist* 165:179-192.
- Crawley, M. J. and R. M. May. 1987. Population dynamics and plant community structure: competition between annuals and perennials. *Journal of Theoretical Biology* 125:475-489.
- Debeaujon, I., K. M. Leon-Kloosterziel, and M. Koornneef. 2000. Influence of the testa on seed dormancy, germination, and longevity in *Arabidopsis*. *Plant Physiology* 122:403-413.
- Dennis, B. and M. L. Taper. 1994. Density dependence in time series observations of natural populations - estimation and testing. *Ecological Monographs* 64:205-224.

- Don, R., J. Bartz, G. F. M. Bryant, A. Vangeffen, G. Lunn, P. Overaa, and A. M. Steiner. 1990. Germination and tetrazolium testing of treated barley seed samples from glyphosate treated crops in 7 ista stations. *Seed Science and Technology* 18:641-651.
- Donohue, K., M. S. Heschel, G. C. K. Chiang, C. M. Butler, and D. Barua. 2007. Phytochrome mediates germination responses to multiple seasonal cues. *Plant Cell and Environment* 30:202-212.
- Elton, C. S. 1927. *Animal Ecology*. Sidgwick & Jackson, London.
- Eriksson, O. and J. Ehrlen. 1992. Seed and micro-site limitation of recruitment in plant-populations. *Oecologia* 91:360-364.
- Falster, D. S., A. T. Moles, and M. Westoby. 2008. A general model for the scaling of offspring size and adult size. *American Naturalist* 172:299-317.
- Gause, G. F. 1934. *The Struggle for Existence*. Waverly Press, Baltimore.
- Gerst, K. L., A. L. Angert, and D. L. Venable. 2011. The effect of geographic range position on demographic variability in annual plants. *Journal of Ecology* 99:591-599.
- Goodwin, N. B., A. Grant, A. L. Perry, N. K. Dulvy, and J. D. Reynolds. 2006. Life history correlates of density-dependent recruitment in marine fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 63:494-509.
- Hardin, G. 1960. The competitive exclusion principle. *Science* 131:1292-1297.
- Harlan, H. V., Martini, N. L. 1938. The effect of natural selection on a mixture of barley varieties. *Journal of Agricultural Research* 57:189-199.
- Harper, J. L. 1977a. *Population Biology of Plants*, Bangor.
- Harper, J. L. 1977b. *Population biology of plants*. Population biology of plants.:892pp.
- Hassell, M. P. 1975. Density-dependence in single-species populations. *Journal of Animal Ecology* 44:283-295.
- Hastings, A. 1980. Disturbance, Coexistence, History, and Competition for Space. *Theoretical Population Biology* 18:363-373.
- Hector, A. 1998. The effect of diversity on productivity: detecting the role of species complementarity. *Oikos* 82:597-599.
- Hector, A., J. Joshi, M. Scherer-Lorenzen, B. Schmid, E. M. Spehn, L. Wacker, M. Weilenmann, E. Bazeley-White, C. Beierkuhnlein, M. C. Caldeira, P. G. Dimitrakopoulos, J. A. Finn, K. Huss-Danell, A. Jumpponen, P. W. Leadley, M. Loreau, C. P. H. Mulder, C. Nesshoover, C. Palmborg, D. J. Read, A. S. D. Siamantziouras, A. C. Terry, and A. Y. Troumbis. 2007. Biodiversity and ecosystem functioning: reconciling the results of experimental and observational studies. *Functional Ecology* 21:998-1002.
- Inouye, R. 1980. Density-dependent germination response by seeds of desert annuals. *Oecologia* 46:235-238.
- Kot, M., Lewis, M. A. , et.al. 1996. Dispersal data and the spread of invading organisms. *Ecology* 77:2027-2042.
- Law, R., D. J. Murrell, and U. Dieckmann. 2003. Population growth in space and time: Spatial logistic equations. *Ecology* 84:252-262.
- Levin, S. A., H. C. Muller-Landau, R. Nathan, and J. Chave. 2003. The ecology and evolution of seed dispersal: A theoretical perspective. *Annual Review of Ecology Evolution and Systematics* 34:575-604.
- Levine, J. M. and M. Rees. 2002. Coexistence and relative abundance in annual plant assemblages: The roles of competition and colonization. *American Naturalist* 160:452-467.
- Linhart, Y. 1976. Density-dependent seed-germination strategies in colonizing versus non-colonizing plant species. *Journal of Ecology* 64:375-380.
- Loreau, M., Hector, A. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72-76.
- Lotka, A. J. 1925. *Elements of Physical Biology*. Williams & Wilkins company, Baltimore.
- Marquard, E., A. Weigelt, C. Roscher, M. Gubsch, A. Lipowsky, and B. Schmid. 2009. Positive biodiversity-productivity relationship due to increased plant density. *Journal of Ecology* 97:696-704.

- Monzeglio, U., Stroll, P. 2005. Spatial patterns and species performance in experimental plant communities. *Oecologia* 145:619-628.
- Murdoch, W. W. 1994. Population regulation in theory and practice. *Ecology* 75:271-287.
- Murrell, D. J., U. Dieckmann, and R. Law. 2004. On moment closures for population dynamics in continuous space. *Journal of Theoretical Biology* 229:421-432.
- Murrell, D. J. and R. Law. 2003. Heteromyopia and the spatial coexistence of similar competitors. *Ecology Letters* 6:48-59.
- Naeem, S., K. Hakansson, J. H. Lawton, M. J. Crawley, and L. J. Thompson. 1996. Biodiversity and plant productivity in a model assemblage of plant species. *Oikos* 76:259-264.
- Nathan, R. 2006. Long-distance dispersal of plants. *Science* 786-788.
- Nilsson, P., T. Fagerstrom, J. Tuomi, and M. Astrom. 1994. Does seed dormancy benefit the mother plant by reducing sib competition. *Evolutionary Ecology* 8:422-430.
- Okubo, A., Levin, S.A. 1989. A Theoretical Framework for Data Analysis of Wind Dispersal of Seeds and Pollen. *Ecology* 70:329-338.
- Pacala, S. W. and M. J. Crawley. 1992. Herbivores and plant diversity. *American Naturalist* 140:243-260.
- Pacala, S. W. and M. Rees. 1998. Models suggesting field experiments to test two hypotheses explaining successional diversity. *The American Naturalist* 152:729-737.
- Pacala, S. W. and D. Tilman. 1994. Limiting Similarity in Mechanistic and Spatial Models of Plant Competition in Heterogeneous Environments. *American Naturalist* 143:222-257.
- Palmblad, I. G. 1968. competition in experimental populations of weeds with emphasis on the regulation of population size. *Ecology* 49:26-34.
- Palmblad, I. G. 1969. Population Variation in Germination of Weed Species. *Ecology* 50:746-748.
- Passarge, J., S. Hol, M. Escher, and J. Huisman. 2006. Competition for nutrients and light: Stable coexistence, alternative stable states, or competitive exclusion? *Ecological Monographs* 76:57-72.
- Paul-Victor, C. and L. A. Turnbull. 2009. The Effect of Growth Conditions on the Seed Size/Number Trade-Off. *Plos One* 4.
- Paul-Victor, C., T. Züst, M. Rees, D. J. Kliebenstein, and L. A. Turnbull. 2010. A new method for measuring relative growth rate can uncover the costs of defensive compounds in *Arabidopsis thaliana*. *New Phytologist* 187:1102-1111.
- Pearson, T. R. H., D. Burslem, C. E. Mullins, and J. W. Dalling. 2002. Germination ecology of neotropical pioneers: Interacting effects of environmental conditions and seed size. *Ecology* 83:2798-2807.
- Petermann, J. S., A. J. F. Fergus, C. Roscher, L. A. Turnbull, A. Weigelt, and B. Schmid. 2010. Biology, chance, or history? The predictable reassembly of temperate grassland communities. *Ecology* 91:408-421.
- Pons, T. 1989. Breaking of seed dormancy by nitrate as a gap detection mechanism. *Annals of Botany* 63:139-143.
- Purves, D. W. and L. A. Turnbull. 2010. Different but equal: the implausible assumption at the heart of neutral theory. *Journal of Animal Ecology* 79:1215-1225.
- Ratcliffe, S. E. T. 1999. Competition and coexistence in experimental annual plant communities. PhD thesis. Imperial College, London.
- Rees, M. and M. J. Long. 1992. Germination biology and the ecology of annual plants. *American Naturalist* 139:484-508.
- Rees, M., C. P. Osborne, F. I. Woodward, S. P. Hulme, L. A. Turnbull, and S. H. Taylor. 2010. Partitioning the Components of Relative Growth Rate: How Important Is Plant Size Variation? *American Naturalist* 176:E152-E161.
- Robert, B. O., Kotze, D.J. 2010. Do not log-transform count data. *Methods in Ecology and Evolution* 1:118-122.
- Roberts, H. 1986. Seed persistence in soil and seasonal emergence in plant-species from different habitats. *Journal of Applied Ecology* 23:639-656.

- Roscher, C., J. Schumacher, W. W. Weisser, B. Schmid, and E. D. Schulze. 2007. Detecting the role of individual species for overyielding in experimental grassland communities composed of potentially dominant species. *Oecologia* 154:535-549.
- Shmida, A. and S. Ellner. 1984. Coexistence of plant species with similar niches. *Vegetatio* 58:29-55.
- Silvertown, J. 2004. Plant coexistence and the niche. *Trends in Ecology & Evolution* 19:605-611.
- Skarpaas, O., R. Auhl, and K. Shea. 2006. Environmental variability and the initiation of dispersal: turbulence strongly increases seed release. *Proceedings of the Royal Society B-Biological Sciences* 273:751-756.
- Skarpaas, O. and K. Shea. 2007. Dispersal patterns, dispersal mechanisms, and invasion wave speeds for invasive thistles. *American Naturalist* 170:421-430.
- Stanton, M. L., Palmer, T.M., T. P. Young, T.P. 2002. Competition-colonization trade-offs in a guild of african acacia-ants. *Ecological Monographs* 72:347-363.
- Thompson, K., Ooi, M.K.J. 2010. To germinate or not to germinate: more than just a question of dormancy. *Seed Science Research*. 20:209-211.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey.
- Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2-16.
- Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294:843-845.
- Titman, D. 1976. Ecological competition between algae: experimental confirmation of resource-based competition theory. *Science* 192: 463-465
- Tonsor, S. J., C. Alonso-Blanco, and M. Koornneef. 2005. Gene function beyond the single trait: natural variation, gene effects, and evolutionary ecology in *Arabidopsis thaliana*. *Plant Cell and Environment* 28:2-20.
- Turchin, P. and A. D. Taylor. 1992. Complex dynamics in ecological time-series. *Ecology* 73:289-305.
- Turnbull, L. A., D. Coomes, A. Hector, and M. Rees. 2004. Seed mass and the competition/colonization trade-off: competitive interactions and spatial patterns in a guild of annual plants. *Journal of Ecology* 92:97-109.
- Turnbull, L. A., Coomes, D. , et.al. 2004. Seed mass and the competition/colonization trade-off: competitive interactions and spatial patterns in a guild of annual plants. *Journal of Ecology* 92:97-109.
- Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* 88:225-238.
- Turnbull, L. A., Crawley, M. J. , et.al. 1999. Seed mass and the competition/colonization trade-off: a sowing experiment. *Journal of Ecology* 87:899-912.
- Turnbull, L. A., L. Manley, and M. Rees. 2005. Niches, rather than neutrality, structure a grassland pioneer guild. *Proceedings of the Royal Society B-Biological Sciences* 272:1357-1364.
- Turnbull, L. A., C. Paul-Victor, B. Schmid, and D. W. Purves. 2008a. Growth rates, seed size, and physiology: Do small-seeded species really grow faster? *Ecology* 89:1352-1363.
- Turnbull, L. A., M. Rees, and D. W. Purves. 2008b. Why equalising trade-offs aren't always neutral. *Ecology Letters* 11:1037-1046.
- Vanwaes, J. M. and P. C. Debergh. 1986. Adaptation of the tetrazolium method for testing the seed viability, and scanning electron-microscopy study of some western-european orchids. *Physiologia Plantarum* 66:435-442.
- Venable, D. L. and J. S. Brown. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *American Naturalist* 131:360-384.

- Volterra, V. 1926. Fluctuations in the abundance of a species considered mathematically. *Nature* 118:558-560
- Wassmuth, B. E., P. Stoll, T. Tschardt, and C. Thies. 2009. Spatial aggregation facilitates coexistence and diversity of wild plant species in field margins. *Perspectives in Plant Ecology Evolution and Systematics* 11:127-135.
- Weidenhamer, J. D. 1996. Distinguishing resource competition and chemical interference: overcoming the methodological impasse. *Agronomy Journal* 88:866-875.
- Weiner, J. and R. P. Freckleton. 2010. Constant Final Yield. *Annual Review of Ecology, Evolution, and Systematics*, Vol 41 41:173-192.
- Wood, S. N. 2006. Generalized additive models: an introduction with R, Bath.
- Yaklich, R. W. and M. M. Kulik. 1979. Evaluation of vigor tests in soybean seeds - relationship of the standard germination test, seedling vigor classification, seedling length, and tetrazolium staining to field performance. *Crop Science* 19:247-252.
- Yoda, K., Kira, T., Ogawa, H. and Hozumi, K. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology* 14:107-129.