



- CHAPTER 9 -

TRANSPLANT PERFORMANCE AND REGENERATION

The field is very much overrun with worthless weeds, so that nearly half of the area is occupied by them. It does not seem to me possible that any manurial treatment can within a reasonable time convert the field into fair pasture. The weeds are chiefly Ox-eye Daisy, Carnation grass, Hawkbit, Buttercup, Daisy, Self-heal, Mouse-ear chickweed, and moss. It would be well if the field were broken up, and one or two crops of roots were taken off it so as to clean the land, and then if it were re-sown with good and pure seeds.

Acland C. T. D. (1896) Reports upon the society's experiments for the improvement of permanent pasture. *Journal of the Bath & West of England Society* 7: 141-160.

SUMMARY

1. The restoration utility of transplants is based on little more than the longevity of individual plants unless there is recruitment. The objective of this Chapter was to evaluate the inoculation experiments in terms of transplant performance in relation to the establishment treatments, and the biotic and abiotic constraints imposed by the gradient of grassland productivity. Furthermore, analytical emphasis was placed on monitoring vegetative and generative spread, and the prospects for transplant species integration with the receptor grasslands.

2. Because of the number of plants involved in the study, it was only practical to take three simple performance measurements annually. These were rosette width, plant height, and flower number. The rosette size was measured in September when the plants have put up new leaves after the hay cut in July. The plant heights and flower counts were obtained just before the hay cut in July of each year. Clear evidence of second-generation establishment was recorded during each census, though detailed surveys were specifically carried out in the September censuses of 1997 & 1999.

3. Five species showed significant differences between plots in terms of height and rosette performance. *Filipendula vulgaris* and *Lotus corniculatus* demonstrated the strongest difference between performances for both parameters. *Centaurea nigra*, *Leontodon hispidus*, *Leucanthemum vulgare*, *Lotus* and *Malva moschata* rapidly increased rosette diameter above the 9-cm threshold after insertion. The second category includes *Filipendula*, *Geranium* and *Succisa* - species that took at least two years for the rosette average to recover. Thirdly, *Primula veris*, *Scabiosa columbaria* and *Stachys officinalis* rosette performance declined from the insertion size.

4. There were significant disparities in species performance with implantation season. Only for *Leucanthemum* rosette performance did the spring cohort perform significantly better than autumn. In line with overall survival, *Centaurea* performed significantly better for the autumn planted cohorts, most notably in terms of rosette diameter. *Leontodon* and *Lotus* performances were also higher for the autumn cohorts.

5. There were no significant differences between the performances of the two transplant sizes. The inference is that whilst seedling-plugs have an immediate handicap, this disparity is rapidly made up by higher relative growth rate, and/or because pot plants can suffer rapid retardation after implantation.

6. *Lotus* height performance was negatively related to soil K and P, and also sward peak biomass. Of the top survival species *Malva* exhibited the largest number of significant correlations with the performance parameters. On this basis, *Malva* was strongly positively correlated with soil K and P, *Filipendula* correlated positively with species richness of the extant sward. *Geranium* also exhibited strong correlations between mean peak height and P, and sward species richness.

7. Five of the selected species demonstrated significant interactions with management, with only *Succisa* attaining more than one significant response. In terms of peak height, both *Stachys* and *Succisa* attained greatest height under mowing conditions, and least height under cow grazing. Conversely, in terms of flower production, the significant results from both *Lotus* and *Succisa* suggest that cow grazing was promotional. For *Centaurea*, *Filipendula*, and *Succisa*, cow grazing was associated with the lowest rosette sizes, and suppressed growth. Taking into account the non-significant results, overall, it is apparent that mowing seemed to promote rosette expansion better than grazing.

8. For *Centaurea* and *Leucanthemum*, flower production was very significantly higher in Plot 1. In fact, potential seed production was far more in Plot 1 than for all the other plot results put together. Conversely, for *Lotus* and *Succisa*, reproductive effort was significantly superior in Plot 4 compared to the other plots. *Leontodon*, *Leucanthemum*, *Malva* and *Primula* produced offspring, though only the offspring of *Malva* and *Primula* survived to reached adulthood.

Keywords: restoration, transplants, inoculation, recruitment, performance, rosette, height, flower number, implantation, season, management, mowing, grazing, offspring, adulthood.

INTRODUCTION

Because monitoring of restoration schemes using transplants is time consuming and expensive, it is often kept to a minimum, and if included at all, it is usually restricted to the post-insertion phase. Thus, short-term surveillance can often misinterpret acceptable implant survival as ‘successful’ restoration (Ash *et al* 1993; Clark 1997; Dryden 1997; Pywell *et al* 1997 Gilbert & Anderson 1998; Flora Locale 2000). Certainly, in the short-to-medium-term, continued survival of perennial transplant species can enhance grassland species richness, and when robust, long-lived species are used, the effect could conceivably last for decades (Tamm 1956). However, the mere survival of a transplant does not reflect its performance, and it is the performance of each individual, which will ensure a vivid flower display, and more importantly, vegetative and sexual regeneration. Furthermore, it is probably the potential of established transplants to regenerate *naturally* which is the true measure of whether an enrichment programme has been successful or not (Morgan 1997; Hopkins *et al* 1999; Francis & Morton 2001). Wells stated in 1983 that: “Because of the high cost, this method [*inoculation*] may only be applicable to small areas, but little is known about the ability of plants to spread from their islands into the surrounding sward.” Without further recruitment, the restoration utility of a transplant is based on little more than the longevity of individual plants.

The most rudimentary record of transplant survival is binary – either alive or dead. However, whilst death is an unequivocal condition, existence is a continuum, and if resources are available, it requires more sophisticated description. For instance, depending on environmental constraints, implants may decline; remain in stasis; or increase. Population biologists have advanced plant performance description in terms of both calendar dates and age states (Gatsuk *et al* 1980; Hutchings 1986a; Watkinson 1986). Because transplants are by definition *precocious* inoculants to the vegetation, they are perhaps most accurately described in terms of age-state than calendar age. Under productive conditions in particular, **Chapter 4** shows that year-by-year weather can alter sward competitive dynamics, even potentially reverting a flower bearing plant to a purely vegetative state, and thence to terminal decline. A restoration experiment carried out by van Duren *et al* (1998) on degraded fen meadow showed that initial transplant performance can be deceiving. The transplants performed well during the

first year, however the researchers' long-term evaluation ascribed this success to the residual benefits of pre-insertion cultivation under greenhouse conditions. During the second growing season the reserves of the implants became depleted, with a much-reduced population surviving to the third year, most of which were incapable of regeneration.

Just as under natural conditions, transplant survival and reproductive success can be combined under the heading of 'fitness' (Silvertown 1987). The fitness of an individual implant is not a fixed value, but is determined in the context of prevailing ecological conditions. However, perhaps the definitive measure of inoculation success is sustained regeneration from the implants, with species-populations not purely limited by the fitness of first generation survivors (Hutchings 1986; Wells *et al* 1989; Kendle 1992; Pywell *et al* 1997). This is probably the *Rubicon* that restoration needs to cross in order to be judged as fully successful. For example, although many species in Wells *et al's* 1989 experiment flowered, no significant spread into the adjacent grassland except for *Leucanthemum vulgare* and *Ranunculus acris* occurred in three years. Boyce (1994) also recorded 76% survival of 19 species planted 1m apart in a rye-grass sward after five years, though found reduced success where competition with *Trifolium repens* was most intense.

Van Andel (1998) states that *transplant* "survival is a highly discriminative fitness component (either yes or no), while fitness components represented by growth and fecundity parameters can vary by degree." The objective of this chapter is to evaluate the transplant inoculation experiments in terms of the *degrees* of performance of the transplant species in relation to the establishment treatments, and the biotic and abiotic constraints imposed by the gradient of grassland productivity. Furthermore, emphasis was placed on monitoring vegetative and generative spread, and the prospects for transplant-species integration with the receptor grasslands (Boyce 1994).

METHODS

Collecting data on plant performance was deemed an important addition to the basic survivorship censusing (Hutchings, 1986, 1991). Because of the number of plants involved in the study, it was only practical to take three simple measurements annually. These were

rosette width, plant height, and flower production. The rosette size was measured in September when the plants have put up new leaves after the hay cut in July. The plant heights and flower counts were obtained just before the hay cut in July of each year. The height measurements were taken from the tallest part of the plant, for example, from the top of the inflorescence, or if a non-flowering individual, from the tallest leaf. The methodology for the assessment of flowering performance differed, however, between species because each species has a different inflorescence structure e.g. some composed of capitulae (*Knautia arvensis*, *Centaurea* spp. etc), and others composed of cymose inflorescences (*Galium verum*, *Filipendula vulgare* etc). For a number of species with large conspicuous flowers, it was possible to count the number of individual flowers. This category included *Malva moschata*, *Campanula* spp., *Geranium pratense*, *Primula veris*, and *Silene latifolia*. For the other species, different techniques were used. Because *Filipendula vulgaris* and *Salvia verbenaca* naturally only produce a small number of inflorescence spikes, individual inflorescence branches were counted to give an estimate of performance. For *Galium verum* and *Origanum vulgare* the number of panicles were counted, and for the rest of the species - which formed the largest category - the number of ‘flower heads’ was counted (Clapham *et al* 1987).

Table 9.01 Comparative characteristics of phytometer species. Account descriptions see Grime *et al* (1988) and Hodgson *et al* (1995)

Phytometer species	Life-history	Established Strategy ¹	Canopy height	Capacity for lateral spread	Index of responsiveness score ²	% Survival Sept 1999 & transplant survival category ³
<i>Centaurea nigra</i>	P(1)	CSR	3	2	1.2	6.9 Intermediate
<i>Filipendula vulgaris</i>	P(1)	S	-	-	1.4	12.5 Intermediate
<i>Geranium pratense</i>	P(1)	CSR	4	3	2.4	36.9 Core
<i>Leontodon hispidus</i>	P(1)	S	2	3	3.4	3.5 Intermediate
<i>Leucanthemum vulgare</i>	P(1)	C/CSR	3	2	3.6	0.7 Marginal
<i>Lotus corniculatus</i>	P(1)	S/CSR	2	2	2.7	6.9 Intermediate
<i>Malva moschata</i>	P(1)	CSR	4	2	2.7	29.9 Core
<i>Primula veris</i>	P(1)	S/CSR	2	2	1.7	34.0 Core
<i>Scabiosa columbaria</i>	M/P(1)	S/SR	1	2	3.2	0 Extinct
<i>Stachys officinalis</i>	P(1)	S	1	2	1.2	11.1 Intermediate
<i>Succisa pratensis</i>	P(1)	S	1	2	1.2	14.6 Intermediate

¹Ecological profiles from Hodgson *et al* (1995); ²Responsiveness scores from Hodgson (1995). ³Survival category from Chapter 7. P = perennial; M = monocarpic perennial.

Natural recruitment of new individuals to the populations

Clear evidence of second-generation establishment was recorded during each census, for instance new flowering individuals were noted in the spring and summer censuses. However, detailed surveys were carried out in the September censuses of 1997 & 1999. The grassland surrounding each transplant (1m²) was inspected for any juvenile or adult plants of any of the implant species. Because the overall research was dedicated to evaluating the survival and performance of the transplants, unfortunately it was not

possible to relocate and resurvey individual offspring year on year. This obviously limits the value of the data as far as elucidation of population dynamics (Watkinson 1986). However, as the main aim was to assess the effective spread of each species, the data provided proof that regeneration was taking place. And in the case of *Hordeum secalinum* in Plot 1, the population expansion was so great that it was not possible to distinguish between implants and natural spread.

Data analysis

Data were analysed at both subplot and plot scales, depending on which tier seem to produce the best explanatory power. In general, though, as with the results of **Chapter 7**, the plot scale was standard, the use of which was informed by the fact that the grassland management treatments have so far shown little obvious significant impact on transplant survival (Davies *et al* 1999; **Chapter 7**). Because this experiment was set up to directly compare autumn with spring survival, it was also necessary to reorganize the spring data in order to conform to the autumn dataset. Thus, only data for the seven (phytometer) species planted in the autumn were assessed. In addition, rather than using the full dataset (1994-1999), for a more qualified comparison, only the first three years' census data was selected (March 1994 - March 1997), to corroborate with the three years over which the autumn treatment experiment had been running. The primary analyses had to be calculated on transformed data, as most of the datasets were composed of simple plant counts and thus considered as not *normally* distributed (Fowler & Cohen 1990). It was therefore necessary to normalize the data using logarithmic (\log_{10}) transformation, as the variances of the samples were larger than the means (Norušis 1998). Thus, parametric tests could be used within acceptable limits (Fowler & Cohen 1990). In order to integrate and transform zero counts, 1 was added to each data point ($x + 1$). For convenience and analytical power, One-way Analysis of Variance was used throughout. Least-squares linear regression, in combination with the Pearson correlation coefficient (r) (two-tailed) were used to examine the relationships between key environmental variables and transplant survival response. All statistical analyses were conducted using SPSS ver 9.0 (1998).

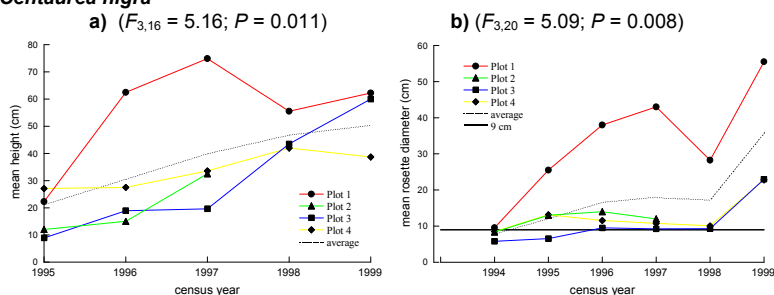
RESULTS

Plot performance comparisons for spring cohort

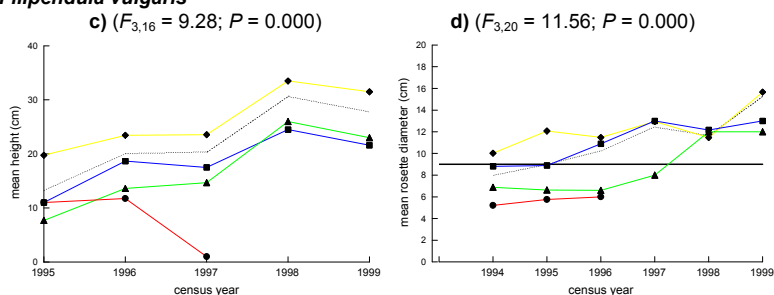
Five species showed significant differences between plots in terms of height and rosette performance. These results are charted in **Figure 9.01** along with the results of one-way ANOVA. *Filipendula* showed the strongest significant difference between performances for both parameters. This result was in part due to the extinction of *Filipendula* in Plot 1 by September 1997, and also its consistently better performance in Plot 4. Similarly, the extinction of *Lotus* in Plot 1, and secondarily in Plot 2, elevated the significance between Plots, with rosettes in Plots 3 & 4 continuing to expand. The converse situation was true of *Centaurea*, whereby the Plot 1 population had outstandingly higher performance, particularly in terms of rosette diameter. The explosive increase in performance was also a feature of *Leucanthemum* in Plot 1. While in Plot 2 the population dwindled early, and remained in relative stasis in Plot 4, the conditions seemed to encourage rapid growth rates in both Plots 3 & 4. However, just as rapidly the population crashed in Plot 3, and performance also fell back in Plot 1.

Figure 9.01 Plot comparisons for each species for mean height and rosette dimensions. Data analysed using one-way ANOVA. Significant results given when $P < 0.05$. The 9-cm line given in the rosette charts is given as a comparison with original pot insertion diameter.

Centaurea nigra

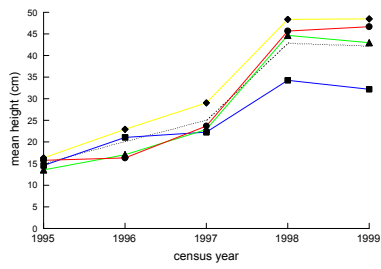


Filipendula vulgaris

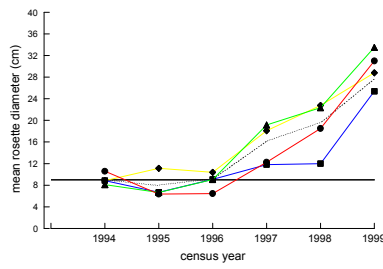


Geranium pratense

e) Not significant

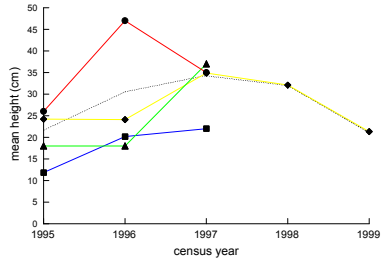


f) Not significant

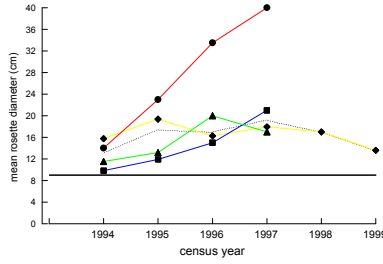


Leontodon hispidus

g) Not significant

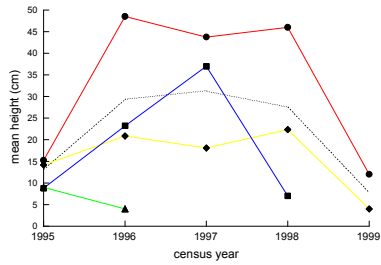


h) Not significant

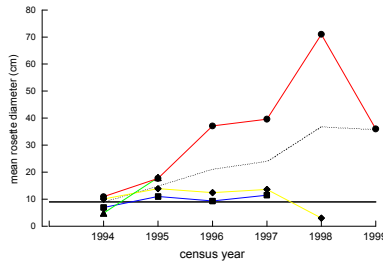


Leucanthemum vulgare

i) ($F_{3,16} = 6.05; P = 0.005$)

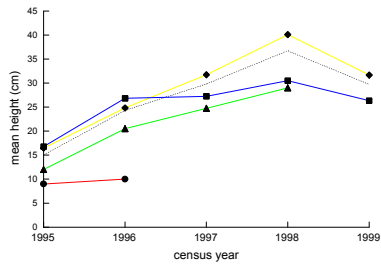


j) ($F_{3,20} = 6.34; P = 0.003$)

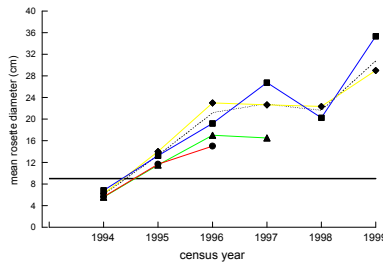


Lotus corniculatus

k) ($F_{3,16} = 6.59; P = 0.004$)

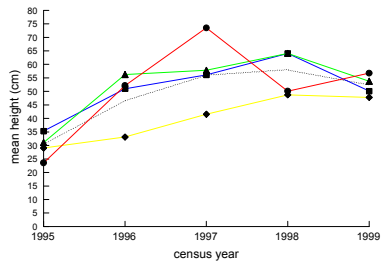


l) ($F_{3,20} = 4.44; P = 0.013$)

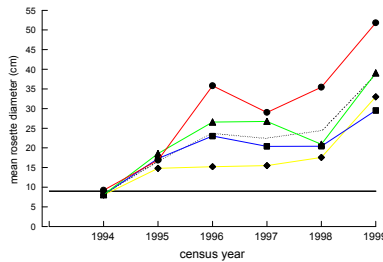


Malva moschata

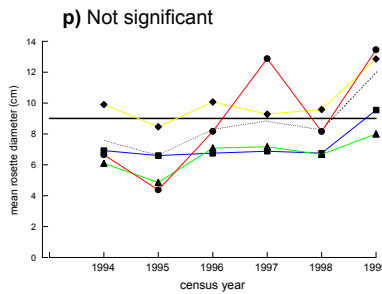
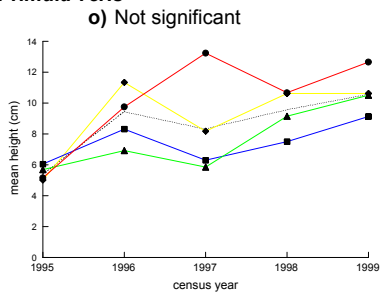
m) Not significant



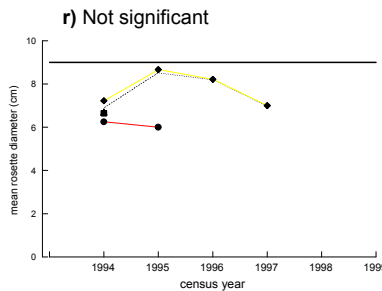
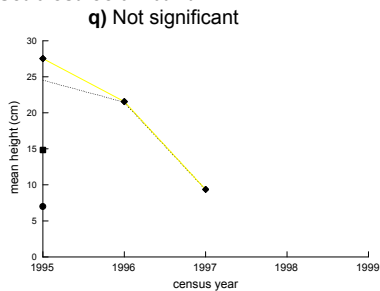
n) Not significant



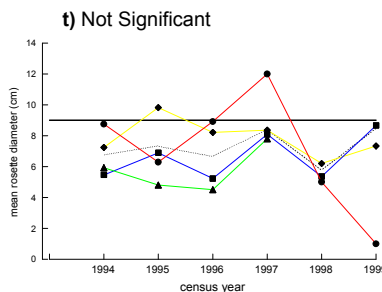
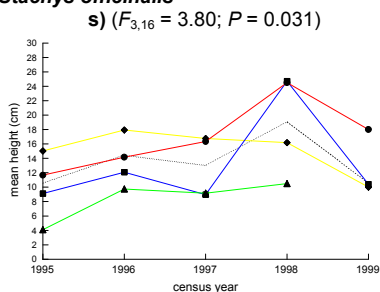
Primula veris



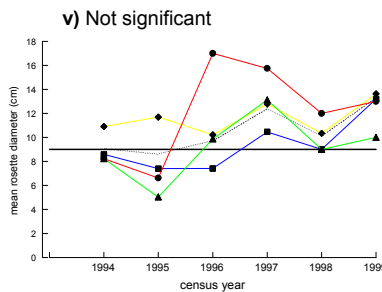
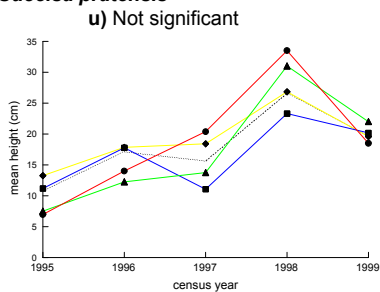
Scabiosa columbaria



Stachys officinalis



Succisa pratensis



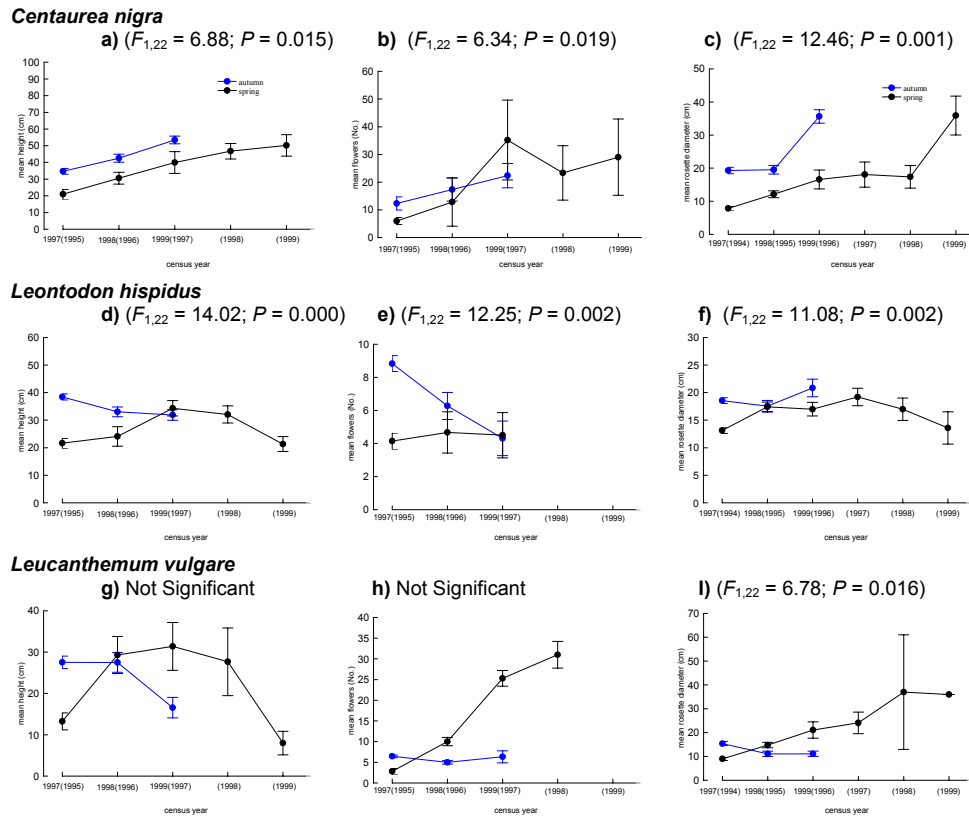
The inclusion of the 9-cm threshold line in the rosette charts gives some impression as to whether each species population managed to attain a greater size than that of the inserted pot transplant. The results combine the data for both transplant sizes – pot and plug - the 9-cm threshold assumes that the seedling-plugs attain the size of mature plants, rather than remain retarded. The relative performances of the two sizes are explored below. However, with regard to plot data, three categories of rosette performance stand out. Following the *average* curve, *Centaurea*, *Leontodon*, *Leucanthemum*, *Lotus* and *Malva* rapidly increased rosette diameter above the 9-cm

threshold after insertion. The second category includes *Filipendula*, *Geranium* and *Succisa*, species that took at least two years for the rosette average to recover, and climb above the implantation size. Of the three, *Geranium* vegetative spread continued to increase steeply up to 1999. Thirdly, *Primula*, *Scabiosa* and *Stachys* rosette performance declined from the insertion size, and in the case of *Scabiosa* the populations never recovered to their pre-insertion containerised proportions.

Planting season and performance

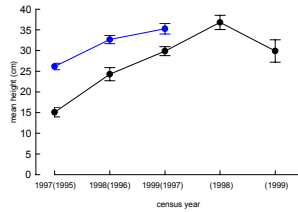
The results presented in **Chapter 8** indicated that there were significant differences in the survival of species in terms of planting season. The results presented below also demonstrate significant disparities in species performance with implantation seasonality.

Figure 9.02 Seasonal comparisons of species' performance parameters. Means for spring and autumn cohorts are given for average height, flower number, and flower number. One-way ANOVA analyses performed on subplot averages for first three years after insertion. Significant results given when $P < 0.05$.

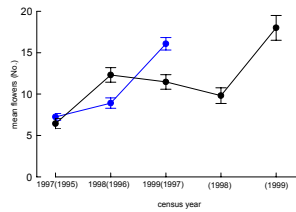


Lotus corniculatus

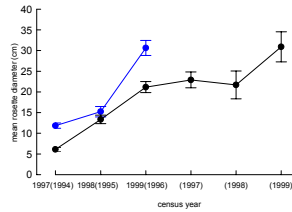
j) ($F_{1,22} = 8.73$; $P = 0.007$)



k) Not Significant

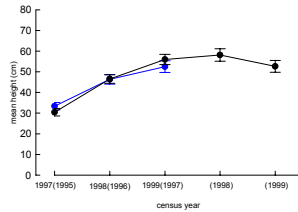


L) ($F_{1,22} = 4.89$; $P = 0.038$)

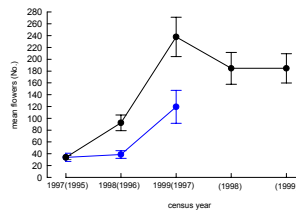


Malva moschata

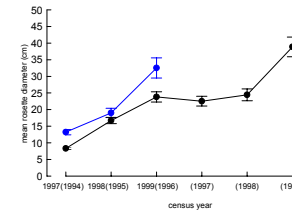
m) Not Significant



n) Not Significant

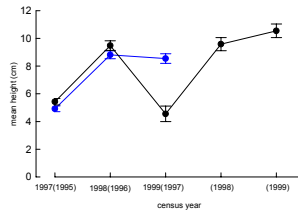


o) ($F_{1,22} = 5.53$; $P = 0.027$)

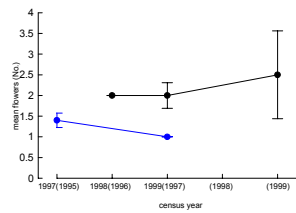


Primula veris

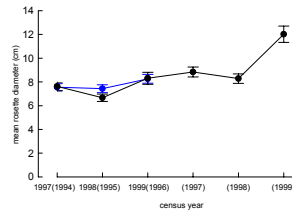
p) ($F_{1,22} = 6.44$; $P = 0.019$)



q) Not Significant

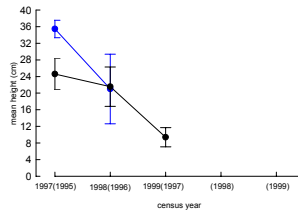


r) Not Significant

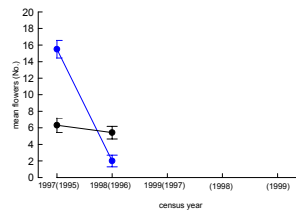


Scabiosa columbaria

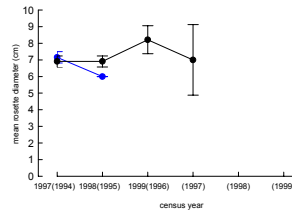
s) Not Significant



t) Not Significant



u) Not Significant



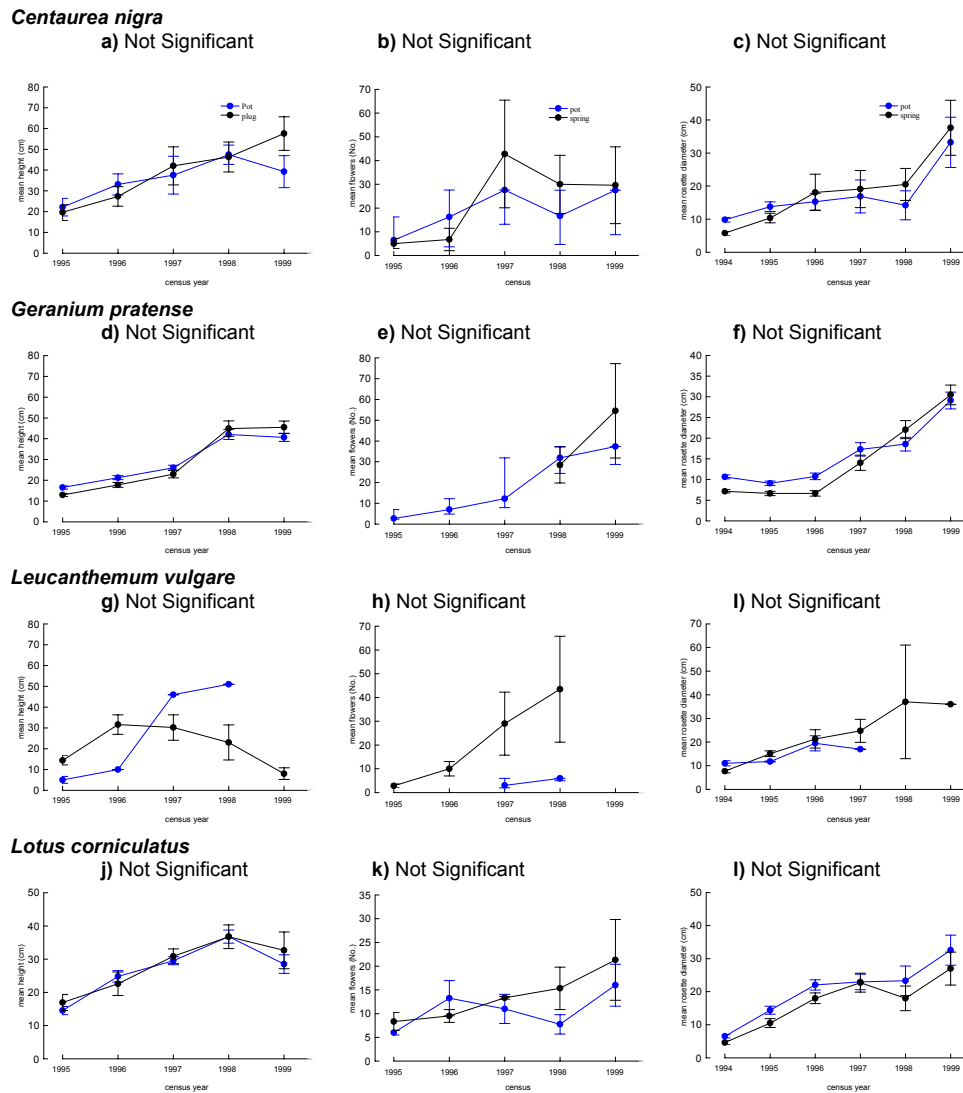
Only for *Leucanthemum* rosette performance did the spring cohort perform significantly better than autumn. In line with overall survival, **Figures 9.02 a-c** show that *Centaurea* performed significantly better for the autumn planted cohorts, most notably in terms of rosette diameter ($P < 0.001$). While *Leontodon* and *Lotus* survival were higher for the autumn than spring cohort - though not significantly so (**Chapter 8; Table 8.02**), height and rosette performances were different, the autumn cohort significantly out performing the spring cohort, at least for the first three years. Otherwise, *Malva* is notable in that survival was significantly better for spring than autumn (**Table 8.02**), and while the

height profiles were almost exactly the same, rosette diameter was significantly greater for autumn than spring cohort.

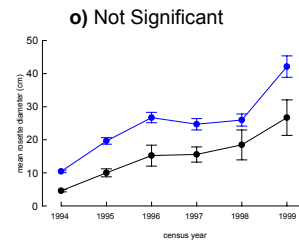
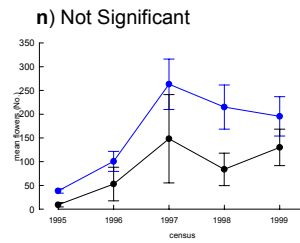
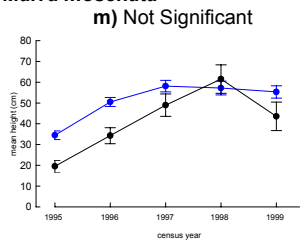
Transplant size and performance

As the spring cohort experiment had been running for five years (1994-99), and the autumn only three (1996-99), performance comparisons between transplant sizes were restricted to the spring cohort due to lack of presentational space and the superior monitoring time-scale. **Figure 9.03** is composed of charts displaying the performance curves for both transplant sizes.

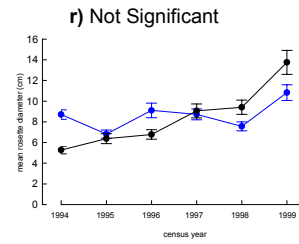
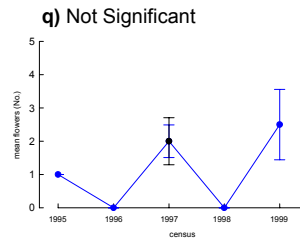
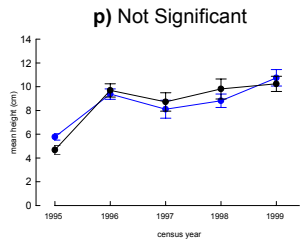
Figure 9.03 Comparisons of species' performance parameters with regards to initial transplant size. Means are given for average height, flower number, and flower number. One-way ANOVA analyses performed on combined plot averages. Significant results given when $P < 0.05$.



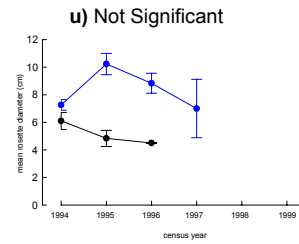
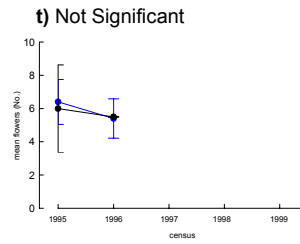
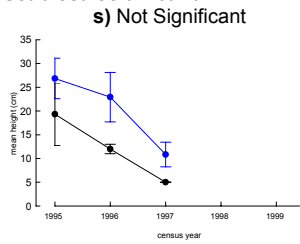
Malva moschata



Primula veris



Scabiosa columbaria



The results are perhaps rather surprising in that none of the selected species showed any significant differences between transplant size performance. **Table 7.02 (Chapter 7)** shows that *Geranium*, *Knautia* and *Malva* maintained a significant differential between transplant size in terms of survivorship up until 1999. While *Knautia* is not analysed in this Chapter, neither *Geranium*, nor *Malva* produced significant performance differentials. The inference is that whilst the transplants have an immediate disparity in growth dimensions, the initial handicap suffered by seedling-plugs is rapidly made up by higher relative growth rate, or pot plants suffer rapid retardation after implantation.

Species performance and productivity factors

The evidence from the previous chapters suggested that there is a set of explanatory variables, which strongly correlate with transplant survival, and therefore might also show significant responses with regards to species performance parameters. These variables relate directly (soil nutrients) and indirectly (e.g. biomass) with the productivity of the swards. The results of Pearson correlation coefficient for each species, for each of the six key explanatory variables, are given in **Table 9.02**, including the division into seasonal cohorts. The results from the autumn cohort is useful for corroborating or rejecting trends found in the spring cohort correlations, that

is, when a significant species response occurs for both cohorts. Clearly not all the species implanted in the spring cohort were planted in the autumn 1996 cohort, and thus the significant correlates for these species could not be backed-up. Of these species, *Filipendula* produced very strong negative correlations with K, P and biomass. Also *Filipendula* correlated positively with species richness of the extant sward. Thus, effectively the performance of this species responded antagonistically to the gradient of agricultural improvement. *Geranium* also exhibited strong correlations between mean peak height and P (strongly negative), and sward species richness (positive). Interestingly, *Stachys* performance did not correlate significantly with soil nutrient status, though correlations were apparent with the sward productivity variables; that is, a negative response between mean rosette diameter and sward height/biomass, and mean plant height and sward height/biomass. As with *Geranium*, the height performance of *Stachys* positively correlated with species richness.

Table 9.02 Correlation matrix comparing species performance parameters with core productivity factors. Pearson correlation coefficient was used for the analysis; only significant results are given. Result is picked out in red when the same correlation is repeated in both cohorts.

Spring rosette							Spring flowers							Spring height							
species	N	K	P	Average height	Average biomass	Spp rich	species	N	K	P	Average height	Average biomass	Spp rich	species	N	K	P	Average height	Average biomass	Spp rich	
Cn	-0.722						Cn							Cn							
Fv	0.598	-0.751	-0.748		-0.655	0.648	Fv		-0.647		-0.619			Fv		-0.821	-0.873		-0.762	0.808	
Gp							Gp							Gp			-0.702			0.597	
Lh							Lh							Lh			-0.629				
Lv	-0.86	0.728	0.58			-0.612	Lv	-0.864	0.822	0.716			-0.72	Lv	-0.641	0.639					
Lc		-0.66	-0.711		-0.824	0.722	Lc				-0.701			Lc		-0.663	-0.718		-0.863	0.72	
Mm		0.745	0.772		0.816	-0.734	Mm						-0.6	Mm							
Pvs							Pvs							Pvs	-0.689						
Sc			-0.652				Sc			-0.61				Sc			-0.666		-0.619		
So				-0.855	-0.654		So							So				-0.740	-0.677	0.624	
Sp							Sp							Sp							
Autumn rosette							Autumn flowers							Autumn height							
species	N	K	P	Average height	Average biomass	Spp rich	species	N	K	P	Average height	Average biomass	Spp rich	species	N	K	P	Average height	Average biomass	Spp rich	
Cn		0.59	0.626				Cn							Cn							
Lh	-0.657						Lh							Lh							
Lv	-0.595						Lv	0.643	0.58	0.626				Lv							
Lc				-0.634			Lc	-0.636					0.676	Lc	0.592	-0.905	-0.805	-0.729	-0.63	0.848	
Mm	-0.721	0.897	0.769		0.69	-0.842	Mm	0.773				0.622	-0.773	Mm							
Pvs	-0.615	0.632					Pvs	-0.74	0.919	0.77	0.601		-0.81	Pvs	-0.755	0.614					
Sc	-0.73						Sc			-0.579			0.626	Sc							

N=soil nitrogen; K=soil potassium; P=soil phosphorus; Av height=mean sward height; Av biomass=mean peak sward production; Spp rich=sward species richness (No.)

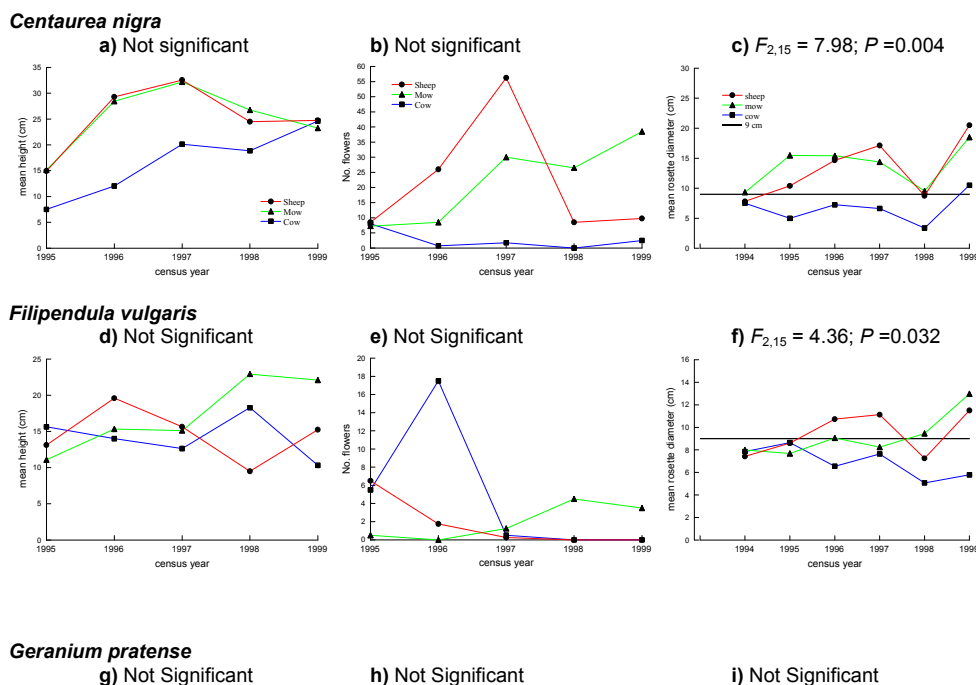
The cells in **Table 9.02** picked out in red show significant correlations that occurred both in the spring and autumn cohorts. Based on these corroborative results, *Leucanthemum* performance in terms of rosette diameter is negatively related to soil N, though flowering seems to be enhanced by soil K and P. *Lotus* height performance is negatively related to soil K and P, and also sward peak biomass, whereas, conversely

Lotus height is strongly positively correlated to sward species richness. Of the top survival species (see **Chapters 7 & 8**), *Malva* exhibits the largest number of significant correlations with the performance parameters. On this basis, *Malva* was strongly positively correlated with soil K and P, though *Malva* flowering was negatively associated with sward species richness. The minor implications for the other species is that *Primula* in terms of peak height may be negatively correlated to soil nitrogen, and *Scabiosa* flower production negatively related to soil P.

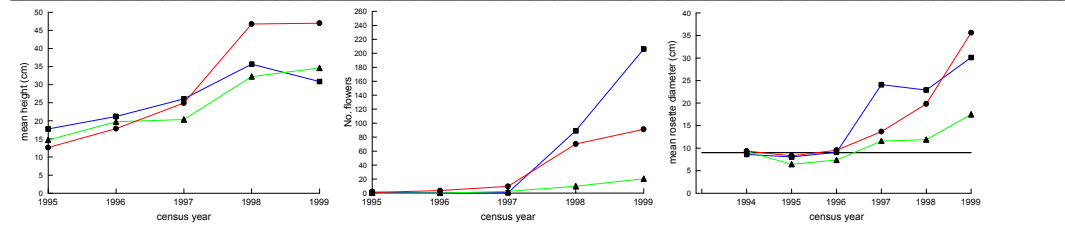
Management treatments

While the results from **Chapters 7 & 8** dealing with transplant survival do not indicate significant responses with the three management treatments, it was worth analysing whether species' performance parameters displayed any interactions, especially as plant height, rosette diameter and flowering are directly impacted upon by the processes of grazing and mowing. Five of the selected species demonstrated significant interactions with management, with only *Succisa* attaining more than one significant response. In terms of peak height, both *Stachys* and *Succisa* as shown in **Figures 7.04ab & ae**, attained greatest height under mowing conditions, and least height under cow grazing.

Figure 9.04 Response of species' height, flower production, and rosette diameter in terms of management treatments. Data analysed using one-way ANOVA; results given when $P < 0.05$.



Chapter 9 - Transplant Performance & Regeneration

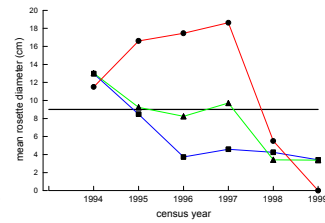
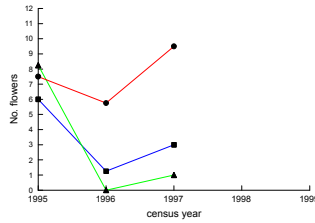
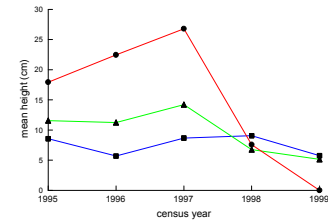


Leontodon hispidus

j) Not Significant

k) Not Significant

l) Not Significant

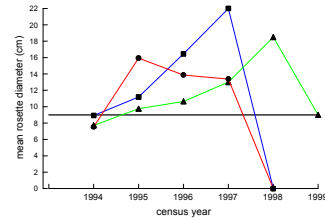
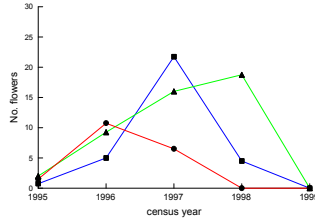
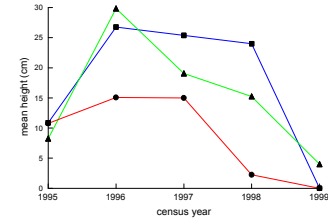


Leucanthemum vulgare

m) Not Significant

n) Not Significant

o) Not Significant

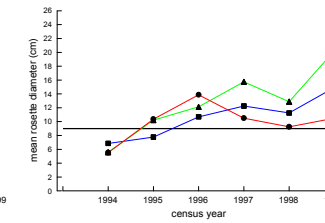
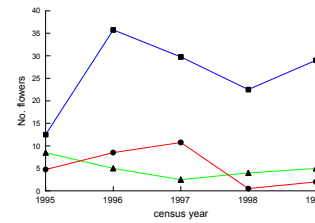
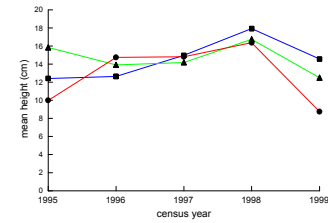


Lotus corniculatus

p) Not Significant

q) $F_{2,15} = 12.43; P = 0.001$

r) Not Significant

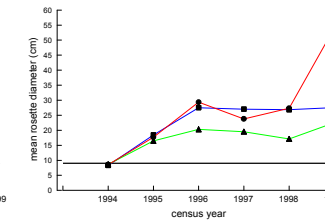
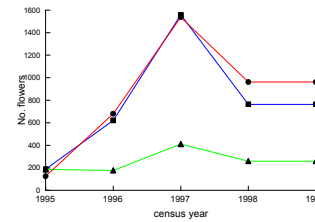
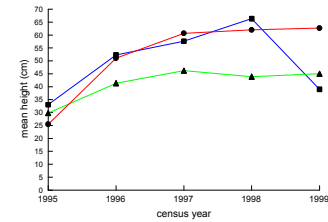


Malva moschata

s) Not Significant

t) Not Significant

u) Not Significant

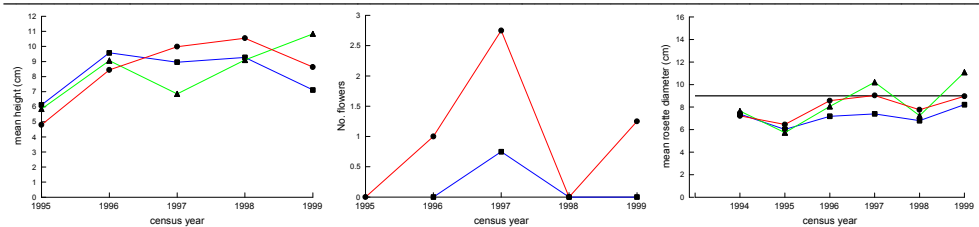


Primula veris

v) Not Significant

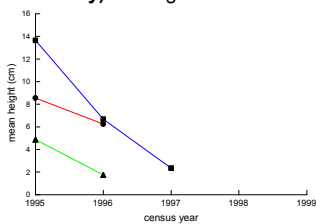
w) Not Significant

x) Not Significant

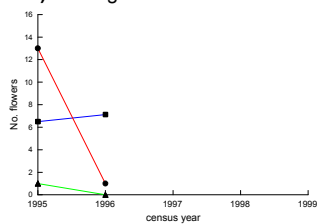


Scabiosa columbaria

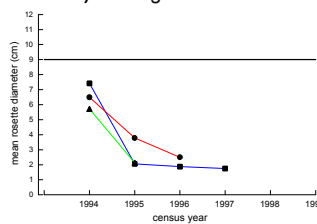
y) Not Significant



z) Not Significant

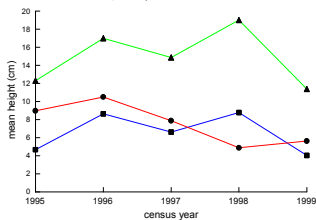


aa) Not Significant

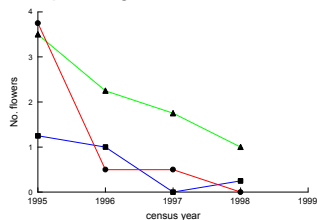


Stachys officinalis

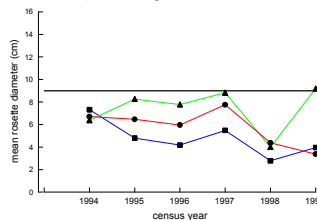
ab) $F_{2,15} = 11.94; P = 0.001$



ac) Not Significant

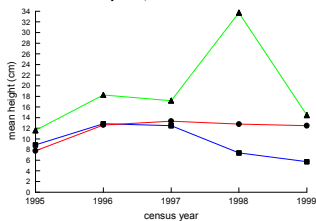


ad) Not Significant

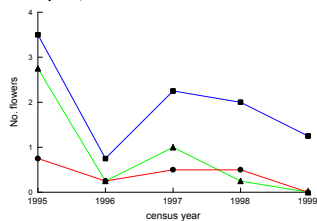


Succisa pratensis

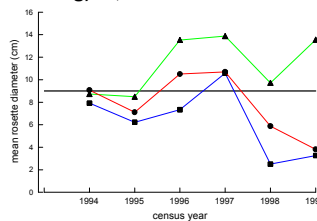
ae) $F_{2,15} = 5.36; P = 0.022$



af) $F_{2,15} = 4.54; P = 0.034$



ag) $F_{2,15} = 4.16; P = 0.036$



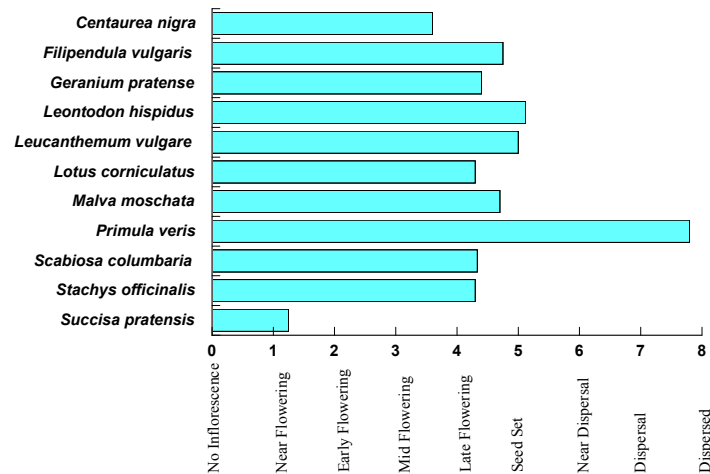
Conversely, in terms of flower production, the significant results from both *Lotus* and *Succisa* suggest that cow grazing promotes, or alternatively, least retards flower production, very strongly in the case of *Lotus* ($P < 0.001$). Because *Primula* is spring flowering and mowing cuts uniformly across the sward, no flowers survive the spring mowing regime, leaving the grazing treatments as the only opportunity for seed set and dispersal, though not a certainty evinced by the non-significant result, as both sheep and cows will selectively eat *Primula* flowers. Comparisons with rosette diameter size and management treatment produced the highest number of significant results, and perhaps the most interesting. For the three species, *Centaurea*, *Filipendula*, and *Succisa*, cow grazing was associated with the lowest rosette sizes, and suppressing growth below the 9-cm threshold. Taking into account the non-significant results,

overall, it is apparent that mowing seems to promote rosette expansion better than grazing.

Reproductive effort and regeneration

The species used in grassland enrichment must have the long-term potential to set seed, and disperse seed before and during hay making, otherwise the populations will be restricted to the longevity of the first generation survivors (Coulson *et al* 2001). **Figure 9.05** provides an impression of what average stage the transplant species have reached just before the hay cut, which is taken usually in late July to early August depending on weather conditions. According to Coulson *et al* (2001), hay cutting has to take place in August for most of these species to stand a chance of shedding ripe seed. Not surprisingly, the earliest flowerer, *Primula veris*, has the potential to shed seed every year. As noted above, seed production and dispersal is largely limited by the imposed grassland management treatments. Otherwise, observations suggest that nearly all the other species are shown to produce a succession of flowers ranging from ‘mid-flowering’ to ‘seed-set’ by the time the swards are cut.

Figure 9.5 Mean developmental stages of inflorescence units of selected species 1996-1999. For descriptions of the specific reproductive units counted see **Chapter 3**.



While the *mid-flowering* stages does not have the potential to produce viable seed, *seed set* does in many cases enable viable seed to be scattered into the sward, facilitated by dispersal through the mechanics of hay making. Certainly this must be the case for *Malva moschata*, where mature seed is usually still enclosed in the papery capsules at the time of haymaking, but easily ruptured by cutting and turning. The only species with phenologies that restrict the possibilities for seed dispersal are *Centaurea nigra*

and *Succisa*, both late season flowerers. In particular, *Succisa* stands out in that it is the only species that has never achieved the stage of seed maturation before the hay is cut.

Only species above certain size thresholds are likely to produce flowers. It is also generally accepted that flower and seed production are closely correlated with the size of the reproducing plant (Waite 1984; Hutchings 1986b). In order to ascertain if the same *fitness* relationship is relevant to the present research, **Table 9.03** shows the results of correlations between each species' flower production and the performance parameters.

Table 9.03 Correlations between (spring cohort) species' flower production, and its height and rosette performances. Analyses using Pearson's correlation coefficient (*r*) (two-tailed): *=*P*<0.05; ***P*<0.01; ****P*<0.001

Species' total flower production	Average species' height	Average species' rosette
<i>Centaurea nigra</i>	0.772**	0.931***
<i>Filipendula vulgaris</i>	0.611*	Not Sig.
<i>Geranium pratense</i>	0.732**	Not Sig.
<i>Leontodon hispidus</i>	0.904***	0.899***
<i>Leucanthemum vulgare</i>	0.777**	0.963***
<i>Lotus corniculatus</i>	0.691*	Not Sig.
<i>Malva moschata</i>	0.796**	0.602*
<i>Primula veris</i>	0.690*	Not Sig.
<i>Scabiosa columbaria</i>	0.918***	0.932***
<i>Stachys officinalis</i>	Not Sig.	Not Sig.
<i>Succisa pratensis</i>	Not Sig.	Not Sig.

As suggested above, overall, average height was the best predictor of flower production (Watkinson 1986). Average rosette diameter was the primary significant correlate for *Centaurea*, *Leucanthemum* and *Scabiosa*. Perhaps surprisingly, *Stachys* and *Succisa* flower production did not correlate with either parameter, though noted above, *Succisa* rarely reaches the stage of peak flowering before the hay is cut, and therefore may not be fully represented by the count of flower buds rather than fully developed inflorescences.

Whilst rosette diameter is a fair descriptor of modular growth, flower production was used as the main descriptor of potential reproductive capacity.

Figure 9.6 Ranking of total potential transplant seed production over the research period 1994-99. Potential seed = total number of flower units produced x averaged seed per unit (from Hodgson *et al* 1995b)

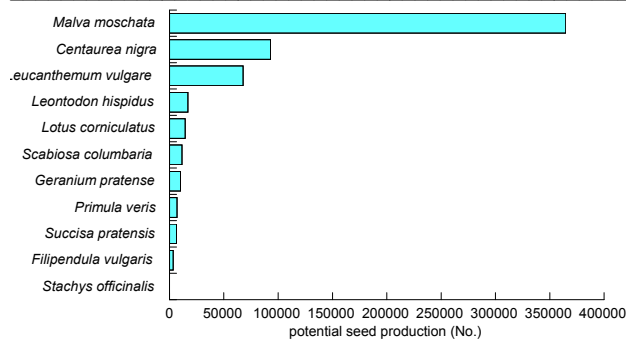
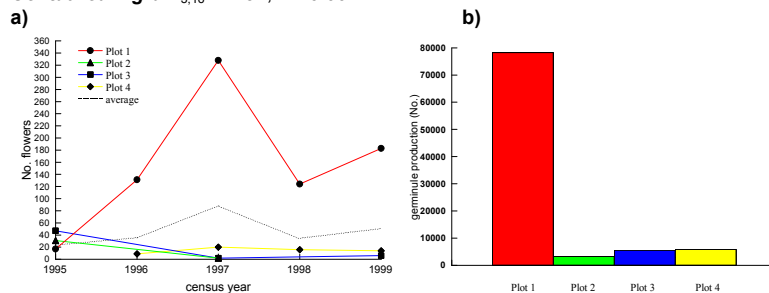


Figure 9.6 presents a rough estimate of the total potential seed that each species could have produced over the research period, although this does not take into account the fact that seed dispersal may not have taken place before hay cut (Coulson *et al* 2001). *Malva* clearly dwarfs the other species in terms of production, followed by *Centaurea* and *Leucanthemum*, both of which owe most of their yield to the few individual plants within Plot 1. To put fine detail on this aspect, the analyses of **Figure 9.07** are included in order to assess whether reproductive potential also differed between plots. The accompanying column charts provide a plot by plot depiction as to how many seeds *in toto* i.e. irrespective of viability, were potentially produced and dispersed into the grasslands over the research period. The significant one-way ANOVA results broadly indicate that most variation in reproductive effort occurred in Plots 1 & 4. For *Centaurea* and *Leucanthemum*, flower production was very significantly higher in

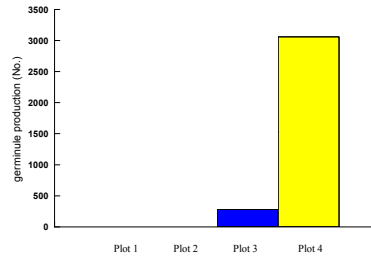
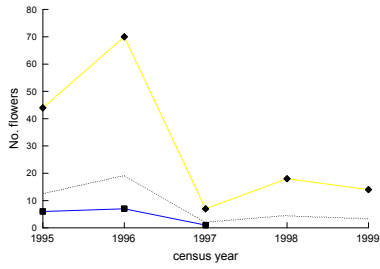
Figure 9.07 Line charts comparing (spring cohort species 1994-99) total flower production plot-to-plot comparisons with one-way ANOVA analysis. Column charts showing the potential total seed production for each of the species within plot: seed production estimates from Grime *et al* (1988), and research observations.

Centaurea nigra $F_{3,16} = 7.57; P = 0.002$



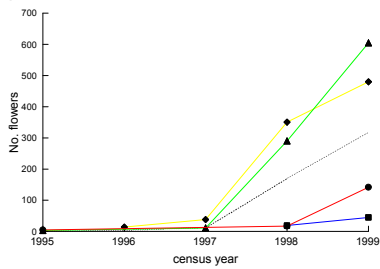
Filipendula vulgaris $F_{3,16} = 24.72; P = 0.000$

c) d)

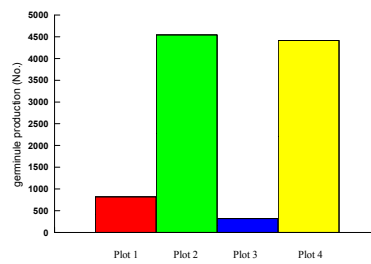


Geranium pratense Not Significant

e)

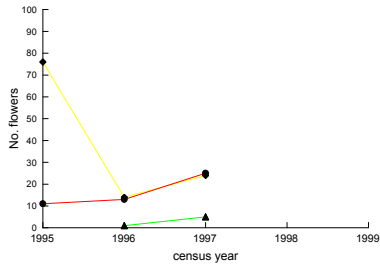


f)

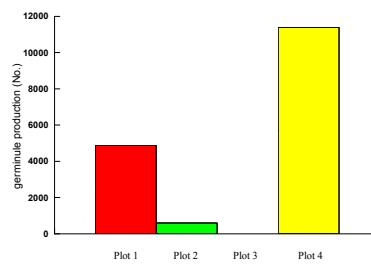


Leontodon hispidus Not Significant

g)

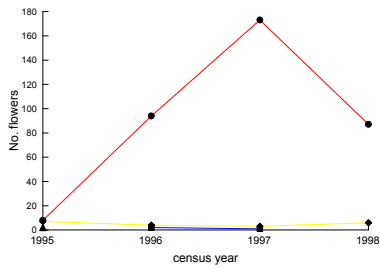


h)

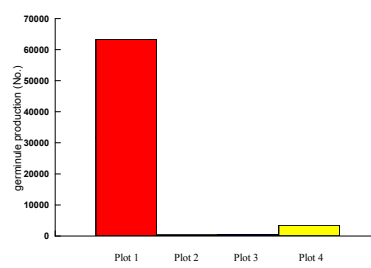


Leucanthemum vulgare $F_{3,16} = 6.84; P = 0.003$

i)



j)

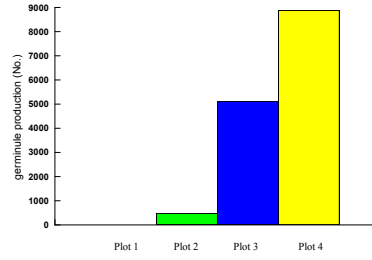
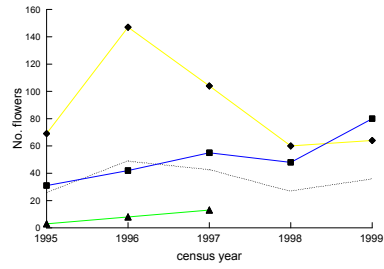


Lotus corniculatus $F_{3,16} = 51.42; P = 0.000$

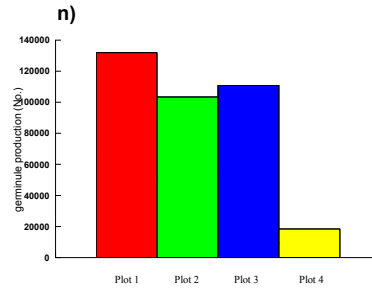
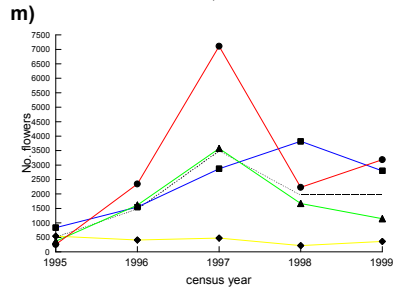
k)

l)

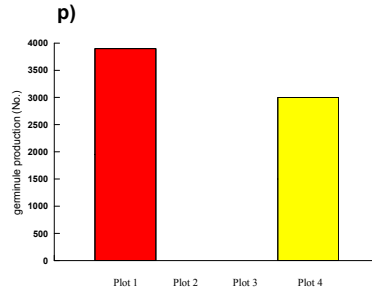
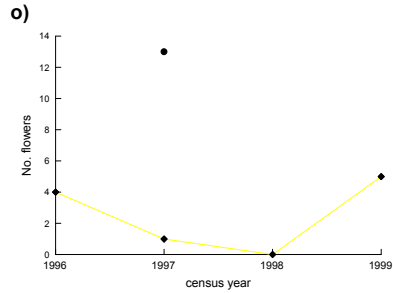
Chapter 9 - Transplant Performance & Regeneration



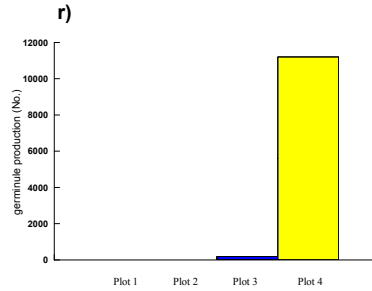
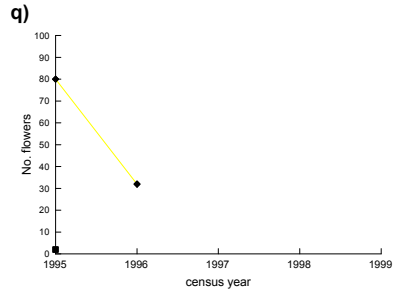
Malva moschata $F_{3,16} = 4.60; P = 0.016$



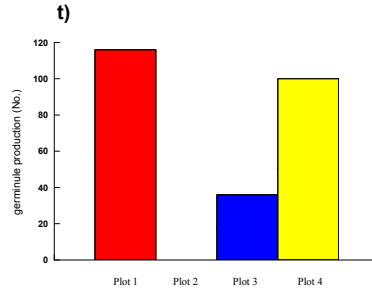
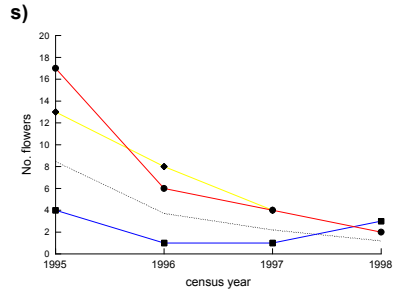
Primula veris Not Significant



Scabiosa columbaria Not Significant

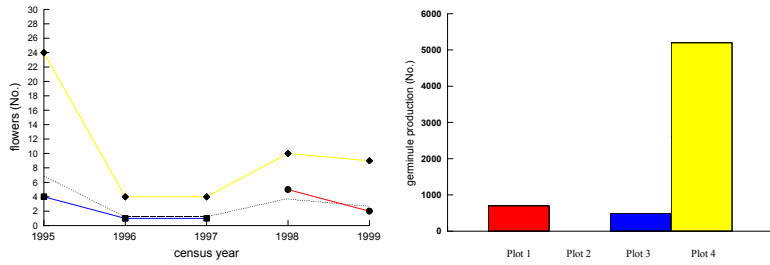


Stachys officinalis Not Significant



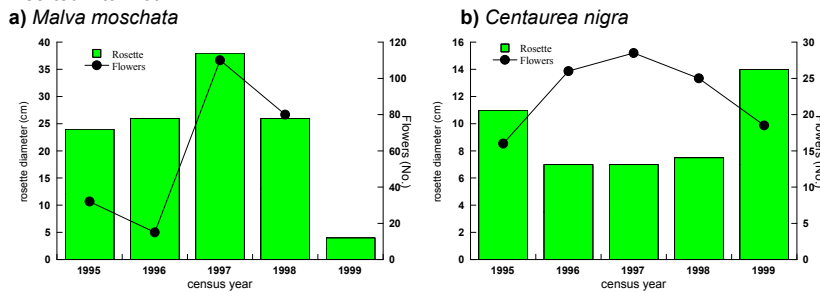
Succisa pratensis $F_{3,16} = 11.70; P = 0.000$





in Plot 1. In fact, potential seed production was far more in Plot 1 than for all the other plot results put together. Conversely, for *Lotus* and *Succisa*, reproductive effort was significantly superior in Plot 4 compared to the other plots. Only for *Malva* is flower and seed production demonstrably lower in Plot 4 than the other grasslands. This is telling, as observations of the age-states (Watkinson 1986) of individual *Malva* transplants shows that some were in stasis (Silvertown & Franco 1993) or even retrogressing (e.g. see **Figure 9.07**).

Figure 9.08 Examples of fluctuations in rosette diameter and flower production for two individual pot transplants inserted into Plot 4.



The true measure of reproductive fitness is of course measured in terms of the production of offspring, and in terms of successful restoration, the expansion of the transplant population away from the initial cohort. Of the 25 species used in the research, only six have managed to produce juvenile and mature offspring. **Table 9.04** shows that *Hordeum secalinum* and *Malva* have been by far the most fecund, with *Hordeum* “going feral”, and becoming a *natural* constituent of the grassland matrix of Plot 1. The population distribution of *Malva* has also become partly feral in Plot 1, though the original transplants are still easily locatable. While *Malva* recruitment has been restricted to the most improved grasslands, in contrast, *Primula* recruitment has been restricted to Plot 4, and subplot 12 in particular. This result, though, may have as much to do with the unpredictable nature of the grazing management treatments as the receptivity of the sward to *Primula* reproduction i.e. the flower heads were clearly not grazed off by the sheep in one or more seasons. Offspring of *Prunella vulgaris* and

Leontodon were also found in Plot 4, though in very low numbers, in keeping with the very low number of surviving transplants.

Table 9.04 Presentation of the species, and abundances of, juvenile and adult offspring recorded in 1999. *Hordeum secalinum* and *Prunella vulgaris*, whilst not included in the above analyses, were included in this section to provide a full report. The term "feral" indicates that a species has become so widespread that it has become too abundant to count individuals.

Species	Subplot	1	2	3	4	5	6	7	8	9	10	11	12
<i>Hordeum secalinum</i>		Feral	Feral	Feral			1						
<i>Leontodon hispidus</i>											2	1	
<i>Leucanthemum vulgare</i>			2	3									
<i>Malva moschata</i>		108	5	77	1	5	1	1					
<i>Primula veris</i>											2	1	44
<i>Prunella vulgaris</i>										2		2	3

DISCUSSION

Differences in performance between plots

(Silvertown & Franco (1993) state that for natural plant populations, the three most important life-history processes are survival, growth and fecundity, and this assertion would seem to be true of transplants as well. While **Chapters 5 & 6** were set out to evaluate the mechanisms of transplant survival, the research of the present chapter was an attempt to use simple performance measurements in order to assess the other two life-history processes - growth and fecundity. The comparisons between plots for transplant height and rosette size over time do show that, not only does survivorship significantly vary along the improvement gradient between species, but also, so do performance parameters, though not necessarily in the ways expected from the survivorship findings. The results from *Lotus* and *Filipendula* fit the general prediction that transplant performance should track a positive trend along the improvement gradient. That is, for these species, performance is significantly better for the two less productive plots than for Plots 1 & 2. However, for two other species, there is a reversal of this trend. Although survivorship for *Centaurea* was higher in Plot 4 than Plot 1, the performance of the plants in Plot 1 was significantly greater in terms of height and rosette expansion. *Leucanthemum* performance was also significantly greater in Plot 1. While not producing a significant ANOVA result, **Figures 9.01m&n** also show *Malva* performance to be far lower for Plot 4 than the other plots.

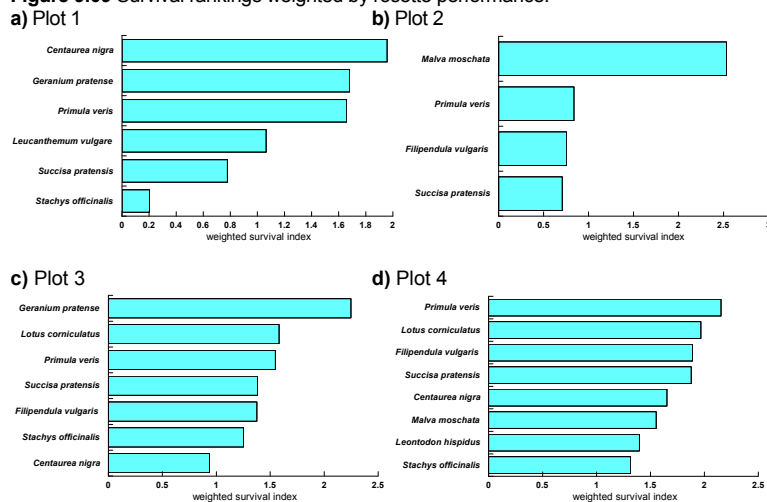
Because not all species survived in all the plots over the research period, it is impossible to compile strictly comparable performance records, though the extinction of a population is fundamentally a total failure in performance. Taking each species and ranking the plots in terms of final average rosette size, including extinction, produces a mixed picture, with no definitive trends. Nevertheless, the correlations from **Table 9.02** help to filter out some of the data attributes. As predicted by the plot comparisons, both *Filipendula* and *Lotus* height and rosette performances react negatively with soil phosphorus and potassium, and average phytomass. *Leontodon*, *Scabiosa*, and *Stachys* also showed significant negative correlations with the same variables. All are essentially stress-tolerators of unimproved grassland (Grime *et al* 1988; Rodwell 1992) and not surprisingly Plot 4 proved to be the best receptor site for these species in terms of performance, as it has the lowest soil P, K and peak phytomass evinced by the highest residual species-richness (Hopkins *et al* 1999). Of the *top-survivor* species, comparisons with productivity factors produced some intriguing results. In terms of rosette expansion, *Malva* performed best on the soils with highest K, P, and phytomass (Plots 1 & 2). *Primula* demonstrated significant positive correlations with K in particular for the autumn cohort, and *Leucanthemum* seemed to thrive on the high soil K and P of Plot 1, though only for the spring cohort.

These results suggest a complex picture where the plot survivorship results can be at variance with performance. The species associated most closely with unimproved grassland conditions do generally seem to perform better in the least improved grassland. However, what of the other species? While hardly species of intensive agricultural swards, *Malva*, *Primula*, and *Leucanthemum* seem to be encouraged by elevated K and P soil fertility, though probably for very different reasons. *Malva* is a tall, branching herb with a strong perennial root system and deep taproot that would seem to be able to perform well on all but highly eutrophied soils (Fenner & Spellerberg 1988; Bisgrove & Dixie 1994; Luscombe & Scott 1994; Hopkins *et al* 1997). Its poor survival and performance on Plot 4 suggests that it may require higher soil P and K for more optimal growth. Certainly it seems to be an effective species in the enrichment of improved grasslands where fertiliser addition has only been recently stopped. To some extent the same explanation may hold for the comparatively extreme performance of *Centaurea* in Plot 1 as well. *Primula* also seems to be able to take advantage of artificially enriched soils as, though relatively short in stature, it avoids peak competitive interference through its semi-vernal habit (Grime *et al*

1988; Ash *et al* 1993). Alternatively, *Leucanthemum* presents weedy life-history characteristics (Grime *et al* 1988), which seems to allow it to take advantage of the relative *gappiness* of Plot 4, and the simplified canopy structure and elevated soil fertility of Plot 1 (Fenner & Spellerberg 1988; Wells 1990).

As suggested above, effective establishment is more than just survival, and equally it is more than the performance of an individual plant. Therefore, as an after-thought, and supplementary to the results section, the plot survivorship results presented in **Chapters 7** were weighted with the rosette performance findings of this Chapter in order to provide a more refined measure of species-enrichment success. The index for the charts of **Figure 9.09** was derived by $\log_{10}(+1)$ transformation of both survival and rosette datasets and multiplying them together.

Figure 9.09 Survival rankings weighted by rosette performance.



While this method does not take account of the relative vegetative expansion potential of each species (Hodgson *et al* 1995a; Hodgson *et al* 1995b), with log transformation smoothing (Fowler & Cohen 1999), between-plot and overall ranking comparisons can be adequately made. For instance, a visual appraisal of the bar charts suggests that with survival and performance combined, Plots 3 & 4 show less dominance in transplant establishment success, evinced by Simpson's diversity scores (Plot 1 0.817; Plot 2 0.730; Plot 3 0.864; Plot 4 0.884)(Kovach 1998). As *Primula* does not have significant clonal expansion ability, rosette performance weighting lowered its overall survival ranking in all the plots, whilst particularly in Plot 1 (**Figure 9.09a**) for *Centaurea* and *Leucanthemum*, and Plots 3 & 4 for *Lotus*, rosette performance raised rankings considerably. Perhaps the most striking impact of weighting is for *Malva* in Plot 4 (**Figure 9.09d**). Whereas for Plots

1-3 *Malva* non-weighted survival and rosette performance have approximately equal rankings, in Plot 4, survival is relatively poor, though rosette performance is very similar to the other plots, thus giving a far higher overall ranking. What these results hopefully show is that more refined calculations using multiple weightings can add further layers of functional description to transplant establishment analysis (Hodgson *et al* 1995a).

Seasonal differences in performance

A number of proposals were advanced in **Chapter 8** as to why some of the transplant species showed significant survival disparities between the spring and autumn cohorts. The key argument was that typically autumn is wetter than spring, and drought related mortality in the immediate establishment phase is a greater possible negative influence on spring implantation (Luscombe & Scott 1994; Agate 2000). Spring cohorts also face the possibility of abrupt summer droughts, which diminish neighbour competition, but more importantly may undermine effective root establishment. The performance comparisons also demonstrate significant disparities between implantation seasons, in some cases corroborating the survival results. Six of the seven species planted both in the spring and autumn seasons presented significant differences. The performances of *Centaurea*, *Leontodon* and *Lotus* conflate with the trends in survivorship in that autumn performance for both height and rosette diameters were significantly better than that for spring, and flowering better excepting *Lotus*. All three species are associates of unimproved grassland, with adaptations to cope with droughty conditions, specifically the possession of deeply penetrating taproots (Grime *et al* 1988). The survival results from **Chapter 8** intimate that an elongated period of root development through moister autumn soils may aid survival for these species, and also, it seems, autumn implantation may also foster vegetative performance.

For *Leucanthemum*, *Malva* and *Primula*, analysis of the performance parameters is less straightforward. *Leucanthemum* rosette growth was higher for the spring cohort, as were height and flower production though not significantly so. *Primula* foliage grew taller for the autumn cohort, but *Malva* performance was probably the most intriguing. All three performance parameters followed the same trend for both seasons, suggesting that *Malva* transplants develop in much the same way irrespective of implantation period. However, rosette expansion was significantly greater for the autumn cohort.

Overall then, autumn cohort performance was better than for spring, though not in all cases. As suggested by the survival results, the species with most to gain from autumn implantation are those that need to establish sufficient root systems to combat spring and summer droughty conditions. Only for *Leontodon*, and particularly *Leucanthemum* are the seasonal trend lines at considerable variance. While the overall survival of *Leucanthemum* was higher in the autumn cohort, clearly performance was much poorer than spring. This result could possibly be due to the wet, mild, autumnal conditions encouraging competition from graminoids against this shallow rooted species (Grime *et al* 1988 Fenner & Spellerberg 1988), therefore leading to continued suppressed performance, though not comparatively reducing survival. Otherwise, the majority of species' trends may signify that despite the fact that performance levels may differ considerably between the seasons, the transplants follow similar stages in development. However, as the autumn experiment had only been running for three years, and the data comparisons were restricted to this period, further monitoring is required to ascertain if the curves remain on similar trajectories.

Transplant size and performance differentials

The unequivocal finding presented in **Figure 9.03** is that none of the spring cohort species demonstrated significant differences between the performance parameters for either inoculant size (Crofts 1999). This contrasts with the survival results offered in **Chapter 7**, that show plug transplants suffering greater mortality than pot plants in all plots, though not necessarily at a statistically significant level. The implication is, therefore, that in terms of transplant size, the performance parameters respond independently from survival i.e. though plugs have higher mortality, they can rapidly attain size parity with pot transplants, which can often remain in stasis after implantation. It is perhaps useful consequently to analyse the charted data in terms of trends rather than purely statistical significance. For instance, it is notable that most of the charts in **Figure 9.03** show rapid convergence between pot and plug. The averaged performance curves show that the plug transplants that survived the establishment phase, went on to entrench, and quickly reach similar performance levels to that of the pot implants (Bisgrove & Dixie 1994). In fact, *Centaurea* and *Geranium* plugs demonstrated marginally better performance than pot transplants. Only the charts of

Malva and *Scabiosa* show pot performance to be apparently better than seedling-plug, though both transplant sizes of *Scabiosa* were extinct by 1998.

Perhaps the only pattern that can be argued from these results is that although pot inoculation does lead to superior survivorship and initial establishment, the seedling-plugs that do survive rapidly converge with pot inoculants in terms of the three measured performance parameters. Accordingly, calculations based purely on survival may be rather misleading. The fact that seedling-plugs can swiftly *catch up* with mature implants adds further weight to the contention that plug transplants are overall more cost effective (see **Chapter 7**) (Allen 1992; Bisgrove & Dixie 1994; Parker 1995; Gilbert & Anderson 1998).

Management treatments and performance

Although in terms of survivorship the management treatments have not so far produced significant divergence, and are unlikely to do so due to the low remaining population levels, the results from this Chapter provide evidence that management can at least affect species performance parameters. The most basic factor is the impact of relatively unselective mowing compared to the selective nature of animal grazing (Ausden & Treweek 1995). Also, unlike mowing with arisings removed, grazing includes nutrient input in the form of urine and dung. The immediate effect of mowing treatment is therefore uniformity (Parish *et al* 1990; Mitchley 1994) whereas grazing generally produces patchiness (Putman *et al* 1991; Gibson & Brown 1992; Crofts & Grayson 1999). Nonetheless, although mowing is unselective in operation, it does have a selective impact in relative terms with regards to the phenology and morphology of each species, particularly as to flowering and seed set (Mitchley 1994; Liira & Zobel 2000). For example, the semi-vernal flowering *Primula veris* was effectively prevented from setting seed by spring mowing in all plots. Species, which produce substantial aerial growth, would presumably also be at a disadvantage under mowing regimes compared to grazing treatments (Ausden & Treweek 1995). The results presented in **Figures 9.04 g-i & s-u** bear out this contention as mowing produced the lowest performance levels for tall forbs *Geranium* and *Malva*. Conversely, in the case of *Stachys*, mowing clearly seemed to produce the highest rosette performance, as with *Filipendula* and *Succisa*, possibly as cutting may induce lateral branching and shoot extension (Arnthórsdóttir 1994). Also, as these species are relatively low growing, with

limited leaf extension properties, the uniformly short sward created under mowing provides comprehensive early season respite from shading (Ausden & Treweek 1995).

Observations on dairy cow grazing suggest that they tend to be selective but coarse foragers, as their large mouthparts and feeding action make them less able to avoid more unpalatable sward components than sheep (see **Chapter 3**). Also, unlike sheep they tend not to select out flowers to eat, thus in the spring grazing treatment, when *Primula veris* inflorescences were grazed off by cows, it was generally incidental (Crofts & Grayson 1999). However, some sward components are assiduously avoided such as *Ranunculus bulbosus* and *acris* (see **Chapter 4**). In contrast sheep are highly selective, though have a wider and more varied foraging capacity. They do not generally create the avoidance patterns of cattle, and their grazing eventually leads to a more evenly defoliated sward (Ausden & Treweek; Crofts & Grayson 1999). Observations suggest that flowers and foliage of less palatable and digestible species were grazed preferentially during different periods (Frame *et al* 1994). For instance, in the spring grazing treatment *Primula veris* flowers were often left standing for a number of days into the treatment, and then all of them were consumed in one go, even though plenty of grass was remaining. This behaviour was not quantified, though it suggests that some sheep acquire a *taste* for particular plants and then attend to selectively eating them. The significance of this behaviour for the reproductive potential of the transplants is that with herbivory by sheep and cattle there is a strong lottery element as to whether in any one year, a species' growth is retarded by selective grazing of its foliage and flowers by sheep in particular, or the deleterious effects of trampling, dung and urine deposition by cows. For instance, rosette performance in *Centaurea* was significantly lower for cow grazed swards than the other two treatments. This trend is also followed in height and flowering. It is difficult to ascertain why this is so without regular detailed monitoring during the treatment periods of the impacts on each transplant individual. Cow grazing on productive grasslands produces more extreme patchiness and sward height differentials due to reinforced avoidance grazing behaviour. These habitats are particularly *size-beneficial* (Begon 1985), and seem to have the most negative effects on low growing rosette species such as *Filipendula*, *Leontodon*, *Stachys* and *Succisa*. Dairy cows are unable and/or reluctant to reduce coarser swards as closely as sheep, or even beef cattle, and thus may not reduce grass

competition sufficiently around these implants to aid performance. Certainly, the rotational grazing management of dairy farms is used in order to stimulate grass growth and retard ingressing forbs (Crofts & Grayson 1999). In addition, dairy cows are very heavy and able to damage vegetation through trampling and poaching, particularly through the wet conditions early and late in the season. Equally importantly, dairy cows have a huge dietary throughput, and redeposit substantial quantities of nutrients as urine and dung, which can clearly alter the local competitive balance in the sward against the low growing, more stress tolerant species (Parish & Turkington 1990). This aspect probably affected *Centaurea* performance, in addition to the fact that its leaves seem to be more palatable to cows than both *Malva* and *Geranium*. Conversely, the eutrophying effects of cow urine (N and K) and dung (P and Mg) and may have led to the significantly higher flower production in *Lotus* (**Figure 9.04q**), which being a legume already enriches the soil with nitrogen.

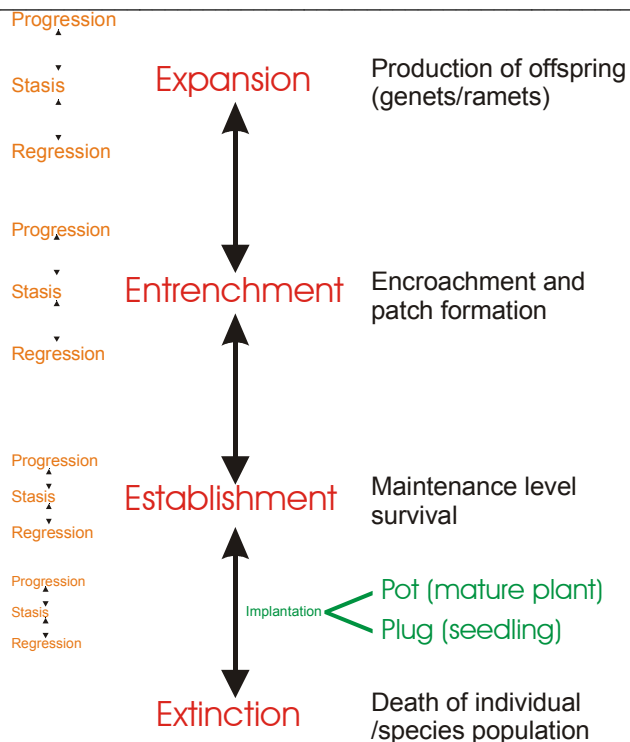
The only significant trend curve to suggest a comparatively positive performance response to sheep grazing was for *Leontodon* (**Figure 9.04 j-l**). Sheep grazing does seem to fit midway between mowing and cow grazing in effect. Unlike cow grazing, but like mowing, sheep can close-crop, and graze relatively evenly across the sward (Crofts & Grayson 1999). Unlike mowing, but like cow grazing, sheep are selective, trample, and deposit fertilising wastes (Ausden & Treweek 1995). Rather than at the individual species level, averaging across species-management trends, sheep grazing seems to encourage higher performance than cow grazing and though not at a statistically significant level, sheep seem to promote the highest performance in *Geranium* and *Malva*. While clearly mowing reduces these species to an average sward level, observations suggest that like cows, sheep avoid these tall herbs. However, unlike cows, they are able to graze intensively around individuals without causing great trampling damage, and at the most positive, this in effect reduces neighbour competition and promotes performance (Silvertown *et al* 1994; Hulme 1996).

Stages of transplant development

Clearly, when seeking to enrich grasslands using transplants, the minimum aim is that the introduced species do not become rapidly extinct (Bisgrove & Dixie 1994; van Groenendael *et al* 1998; Morgan 1999). In order to prevent this happening, the transplant

has to rapidly entrench, that is, produce an effective root system and robust foliage, so that its survival in the short term is secured against unmediated neighbourhood competition (Silvertown *et al* 1994). Beyond these developments, in order that the enrichment process is successful on a species by species basis, the transplants have to undergo expansion and recruitment. This may take the form of the production of genets, ramets and modules (Goldberg & Werner 1983; Bakker *et al* 1989). Davies *et al* (1999) is a presentation of the results from the first three years of this transplant inoculation experiment, and this period of analysis was appropriately described as the *establishment phase*. A further two and a half years on, implant numbers have continued to decline, and the performance of each remaining plant becomes ever more crucial to the restoration scheme. And without the successful recruitment of new individuals to the populations, introducing transplants is fruitless unless the species used are at least robust and long-lived (Grime 1987). Very few data, however, are available on the longevity of herbaceous plants (Tamm 1956; Tamm 1991), and age in terms of calendar date does not necessarily represent a true picture of plant *growth state* (Hutchings 1986). Although a particular transplant species may not at once regenerate effectively, if it is long-lived the chances of future regeneration are high, and the 'effective' enrichment capacity of the species is increased. However, research evaluating transplant age in terms of *age state* has shown that plants, irrespective of time *lived*, can reach maturity and then regress to previous ontogenical phases due to changes in environmental conditions (Gatsuk *et al* 1980; Hutchings 1986b; Watkinson 1986; Silvertown & Franco 1993). A simple scheme (**Figure 9.10**) is presented to summarize the above points.

Figure 9.10 Schematic representation of the life-history stages of transplants.



It is possible that in artificially fertile grasslands ontogenical (Gatsuk *et al* 1980) fluctuations may be amplified, leading to greater flux in age states (Dunnett & Grime 1999). In order to assess the transplants in terms of age state changes, **Tables 9.05-6** have been included as an addendum. While the data are combined rather specific to individual plants, they provide a useful additional level of analysis. **Table 9.05** gives an indication as to the ratio of implants in the generative state (Hutchings 1986a) over the research period, and **Table 9.06** provides an examination of the proportion of implants maintaining or exceeding the vegetative dimensions of the initial pot transplants. A caveat on interpretation is that data for seedling plugs (2-cm diameter) were also included in the calculations, thus results from the first two years may be skewed downwards. Nevertheless, **Table 9.05** indicates that the number of species that had increased in the proportion of generative individuals by 1999 was the same as the number that had regressed proportionately from flowering to vegetative state over the same period. The outstanding species is *Geranium*, which rose from 5% of plants in reproductive state in 1995 to 100% in 1999. Otherwise, *Leontodon* and *Stachys* are also remarkable for the opposite reason in that they present huge reductions in generative state over the course of the study.

Table 9.05 The percentage of plants flowering each year in relation to total surviving plants. *Primula veris* and *Scabiosa columbaria* excluded as management largely prevented *Primula* flower production, and the *Scabiosa* populations rapidly became extinct.

Species	1995	1996	1997	1998	1999
<i>Centaurea nigra</i>	44	44	59	50	70
<i>Filipendula vulgaris</i>	23	20	19	22	12
<i>Geranium pratense</i>	5	6	12	85	1
<i>Leontodon hispidus</i>	93	48	60	0	0
<i>Leucanthemum vulgare</i>	24	52	54	50	0
<i>Lotus corniculatus</i>	50	76	88	73	89
<i>Malva moschata</i>	72	88	87	80	93
<i>Stachys officinalis</i>	74	21	13	14	0
<i>Succisa pratensis</i>	17	7	17	15	13

In terms of vegetative expansion, **Table 9.06** shows that only *Leontodon* rosette diameter declined over the research period. As with the flowering data, without weighting in terms of population size, the results can be marginally misleading, such as for *Leucanthemum*, which from 1997 onwards was represented by only a few individuals. However, clearly for the most populous transplants, taking into account the fact that plugs are included in the analysis, *Centaurea* and *Lotus* have a claim to significant vegetative expansion, whilst the *Geranium* and *Malva* populations have also achieved significant encroachment.

Table 9.06 Ratio of plants with rosette diameter \geq 9-cm to total surviving plants. *Scabiosa columbaria* excluded.

Species	1994	1995	1996	1997	1998	1999
<i>Centaurea nigra</i>	0.40	0.73	0.75	0.70	0.70	1
<i>Filipendula vulgaris</i>	0.46	0.51	0.55	0.73	0.68	0.72
<i>Geranium pratense</i>	0.52	0.39	0.53	0.72	0.82	0.96
<i>Leontodon hispidus</i>	0.86	0.92	0.96	0.95	1	0.60
<i>Leucanthemum vulgare</i>	0.47	0.91	0.81	1	0.5	1
<i>Lotus corniculatus</i>	0.30	0.79	1	1	0.77	1
<i>Malva moschata</i>	0.48	0.80	0.92	0.87	0.89	0.95
<i>Primula veris</i>	0.33	0.27	0.41	0.52	0.41	0.73
<i>Stachys officinalis</i>	0.27	0.36	0.25	0.48	0.22	0.50
<i>Succisa pratensis</i>	0.55	0.48	0.65	0.79	0.77	0.91

Evidently the age state potentiality of transplants is a major consideration in restoration (Silvertown & Franco 1993). Long term expansion of transplant populations is of paramount importance for the success of any restoration (Cottam & Wilson 1966). And yet, under productive conditions, with defoliating management treatments, some species populations e.g. *Leontodon* and *Stachys*, seem to have effectively stalled. Gatsuk *et al* (1980) demonstrate that developmental capacity varies with given age state, with some individuals strongly developed while others become greatly suppressed. The large individuals continue to survive through all age states, and the suppressed ones die without progressing to the next ontogenical phase. However, Cavers and Harper (1967) note that young plants often have the ability to survive for long periods, without putting on weight, a suppressed, but survival state which Chippindale (1948) termed “resistance to inanition”. In contrast, after five-and-a-half-years of this study, individual implants that remained in stasis and/or regressed after implantation, rapidly failed, probably because environmental selection (Wells *et al* 1989) and turnover seem to be amplified under fertile conditions, as evinced by the

survivorship analyses of **Chapters 7 & 8**. Nevertheless, fluctuations in age state also seem to continue amongst the surviving “large” individuals (Gatsuk *et al* 1980). **Figure 9.07** shows that for two species, *Malva* and *Centaurea*, average rosette size and flowering fluctuate noticeably, and are also often out of synch. Weather probably plays a key role in age-state variability, and oscillations in rainfall frequency have been shown to alter the competitive balance within the sward (Grime & Curtis 1976; Silvertown *et al* 1994). For more stress tolerant species, droughty conditions may encourage increased transition to the generative phase (Fowler & Antonovics 1981), whilst increased rainfall pulses may create greater competitive dominance, especially on eutrophied soils (see **Chapter 4**), leading to suppression of subordinates and the regression of individuals back to vegetative states (Novoplansky & Goldberg 2001). Continued monitoring of these individuals and populations will enable more detailed analyses of the dynamics involved in changes in ontogeny (Tamm 1953; Dunnett & Willis 2000).

Local spread and recruitment

Whilst transplant survival is a primary aspect of floristic enrichment, vegetative expansion and the recruitment of new individuals to the population, especially above replacement rates, is the best sign that floristic diversification through inoculation is successful (Hutchings 1986; Begon *et al* 1990; Tilman 1997). For regeneration under relatively environmentally hostile conditions, longevity of individual perennials, especially surviving above maintenance performance, is of paramount import in increasing the chances of sexual regeneration, and year on year vegetative expansion. As Tamm (1991) states: “A long-term balance between death and recruitment implies stability, while a long persistence of individual ramets without replacements of new ones is an expression of inertia rather than stability”. The performance data collected during this research presents a robust though relatively imprecise approach to the analysis of transplant regeneration. Vegetative reproduction was incorporated within the gauge of rosette diameter expansion, and sexual reproduction by the number of flowers produced. As Bazzaz & Ackerly (1992) comment, vegetative reproduction is hard to define as daughter ramets are dependent on the parent for a varying length of time, and without clear physiological separation, it can be difficult to distinguish between growth and reproduction. Equally, the problem with relatively infrequent

monitoring is that little idea can be gained as to the turnover of seedling recruits, and what data is collected comes from censuses, which provide *snapshots* rather than continuous appraisal. As Hutchings (1986) states: “Simple monitoring of population size, however, is insufficient on its own. Even in those populations where the number of individuals remains relatively constant from one census to the next, there may be a rapid flux of births and deaths and a considerable turnover of individuals.” However, for the purposes of estimating present and future regeneration within an enrichment scheme, these analyses were generally well beyond what is usually undertaken (Wells *et al* 1989; Gilbert & Anderson 1998).

Aspects of vegetative reproduction have already been addressed in the above discussion. Rosette diameter expansion may include just transplant growth, but more importantly ramet production, though as noted above, without intimate examination, for most herbaceous species, definition between modules is difficult. Nevertheless, the charts of **Figure 9.01** include *average* rosette diameter curves for each spring cohort species. Overall, only the populations of the extinct species *Scabiosa columbaria*, and the extant *Stachys officinalis* recorded average rosette diameters *under* the pot implantation size of 9-cm. In contrast, the average rosette trends of *Centaurea*, *Geranium*, *Lotus* and *Malva* were all escalating. However, none of these expanding species are stoloniferous or rhizomatous, and only the growth form of *Lotus* provide it with greater potential for extensive patch formation (Grime *et al* 1988). Otherwise, vegetative regeneration is largely restricted to modules separating from the parent plant by trampling of grazing animals (Grime *et al* 1988). Under these limitations, any reproduction will be reliant upon very long-term, light-moderate mechanical disturbance by livestock.

In terms of sexual reproduction, the number of flowers produced by each transplant species was used as a surrogate for propagule production. The phenologies of most meadow species are in phase with traditional hay management and **Figure 9.05** indicates that all species except for *Succisa* had the potential over the five-and-a-half-years to have produced and dispersed at least some viable seed before the hay was cut. And as a number of accounts show, while natural dispersal may not have taken place before hay cut, the process of hay making can effectively liberate seed into the field-

layer (Bakker *et al* 1996; Smith *et al* 1996). In effect, almost all the transplant species had the potential to scatter dispersules into the neighbouring swards. A clearer picture as to the actual rather potential amount of seed shed into the experimental grasslands (Coulson *et al* 2001) required much more detailed analyses than could be afforded. It is expected that with time the transplants that have established enough to entrench and produce seed year-on-year, will build up an ‘inoculation pressure’, whereby the probability of sexual regeneration increases with the continuing input of propagules into the grassland systems. With this premise in mind, the column charts of **Figure 9.07** provide a broad estimate as to the potential quantities of seed dispersed into the neighbouring grassland environments. These extrapolations imply that some species have produced considerable quantities of seed, particularly *Malva*, *Centaurea* and *Leucanthemum*. Where these plants have entrenched successfully, they display the potential to produce very large volumes of propagules, increasing the inoculation pressure for new recruitment. Certainly **Table 9.04** suggests that *Malva* has produced much more offspring than any other species except *Hordeum secalinum*. However, only a few *Leucanthemum* genets have been recorded, and no *Centaurea* recruits. The lack of *Centaurea* recruits may be a function of the immaturity of the capitulae at the time of hay cutting, and/or high seed predation (K. Thompson pers. comm.) The three species, which have successfully expanded their populations; *Malva*, *Hordeum*, and *Primula* – have done so under specific environmental conditions. In general, the charts displaying significant variation in flower production show a marked polarization between Plots 1 & 4. Plainly both *Hordeum* and *Malva* not only performed better in terms of flower production in Plot 1, but also as far as sexual regeneration as well. It would seem that *Hordeum* and *Malva* have responded dramatically to the high soil reserves of phosphorus and potassium in Plot 1, and the populations have shifted from *transplant* to *natural* distributions. While adequate availability of both these mineral nutrients is essential for flowering, fruiting and maturation (Brady & Weil 1999), these species seem to have responded positively to the *luxury supply*. In contrast, the less productive, more open swards of Plot 4 would seem to offer the better regeneration environment for seedling recruitment. The above species, however, had low flower production in Plot 4, and hence potentially low seed production. Conversely, *Filipendula*, *Lotus*, *Primula* and *Succisa* found the conditions of Plot 4 preferential in terms of flowering performance. *Primula* has produced at least 50 offspring, though virtually all in subplot

12 which is sheep grazed. No evidence has been found for the other three species producing offspring, though both *Filipendula* and *Lotus* have produced not insubstantial quantities of seed. As noted above, *Succisa* has not so far been able to produce mature seed before hay cut. Kirkham *et al* (1995) suggest that cutting dates would have to occasionally stretch into September to allow late flowerers like *Succisa* to set seed.

Clearly, substantial quantities of seed have been dispersed by most of the species, though, it seems to little effect. How does the lack of seedling recruitment relate to the concept of the regeneration niche (Grubb 1977)? In the practice of enriching agriculturally improved grasslands, the survival and longevity of individual implants becomes even more important. As many researchers have noted, in systems largely dominated by perennials, such as hay meadows, regeneration from seed is a relatively rare event, and most plant species rely on a *long-term competitive* strategy (Grubb 1976) based on a long life of seed production in order to take advantage of favourable regeneration conditions as and when they occur (Smith & Jones 1991; Rusch & Fernández-Palacios 1995). The experimental grasslands are especially ‘closed turf’ systems; agricultural levels of artificial fertiliser input have effectively *sealed* the swards against the extension of all but the dominant productive species (Fenner 1978). Transplant populations therefore face difficulty in establishment, and outright *hostility* to recruitment. In the early years of a restoration, the conditions seem to be too productive and competitive for transplants to do other than entrench (Davies *et al* 1999). As fertility is reduced by nutrient export through conservation management, competitive dominance should (slowly) reduce, and the ameliorating conditions may provide the opportunity for long-lived plants to produce offspring (Oomes *et al* 1981; van der Woude *et al* 1994). **Chapter 4** indicates, however, that the process of reducing productivity can be a slow one, and transplants may have to contend with years of competitive suppression before conditions have ameliorated sufficiently to allow population expansion. Even with productivity within optimal limits vis-à-vis Grime’s (1979) “hump-back” model, management has to be attuned to creating appropriate regeneration niches for seedling survival and establishment (Bakker *et al* 1980; Oomes & Mooi 1981). Yet, evidently each grassland plot seems to exhibit its own regeneration characteristics. The recruitment successes do seem to have a *habitat based* component

(Begon *et al* 1990). This means that successful recruitment by a few species may be largely restricted to the particular ecological features of each of the plot grasslands, which might be temporary adjustments, rather than signify any increase in the reproductive potential of the species' populations. For example, although Plot 1 has the most eutrophied soil in terms of P and K, the cessation of fertiliser input in 1994, most importantly N, rapidly led to a marked reduction in standing crop, opening up the sward to invasion, and *Malva* and *Hordeum* have so far flourished. A similar phenomenon was observed by Boyce (1994). For his study sites, there was rapid degeneration of perennial ryegrass following the withdrawal of fertiliser inputs which led to the creation of an open sward with reduced competition and increased gappiness, promoting vegetative spread and seedling colonisation. Plots 2-4 have far more complex, closed physiognomies, and without significant reductions in productivity, recruitment may depend on yearly variations in weather. The results of **Chapter 6** show that regeneration gaps, even large artificially created ones, are as a rule rapidly occluded by the dominant species, thus allowing limited opportunity for transplant seeds to reach the gaps, germinate, and seedlings to establish. This points to the fact that regeneration is not only limited by microsite availability (Coulson *et al* 2001), but also the intense competition for these microsites as and when they appear. Different yearly weather conditions, often extremes such as drought, may retard grass growth and provide transplant species the *window of opportunity* to recruit offspring (Waite 1984; Dodd *et al* 1994). Only continued monitoring will provide evidence of how the remaining transplants will perform with respect to the forecasted declines in sward productivity and increases in regeneration niches. In addition, data has to be analysed with respect to species' responses to year-on-year weather conditions (Dunnett & Willis 2000). As Tamm (1991) states: "There is no good substitute for long-term observation series (several years and preferably decades) at the level of the individual ramet. If we wish to understand vegetation changes, the same applies to all studies of plant succession where the environment is dominated by potentially long-lived perennials."

ACKNOWLEDGMENTS

Righteous gratitudes go to Ian and Owen Davies for prodding, peering and encountering molluscs nose to feeler.

REFERENCES

- Agate E.** (ed)(2000) *Tree Planting and Aftercare*. British Trust for Conservation Volunteers, Wallingford, Oxon.
- Allen R. H.** (1992) *The A10 Melbourn Bypass Planting Trial: a Backdrop of Wildflowers*. Unpublished report, High Value Horticulture PLC, Uxbridge.
- Anderson P.** (1995) Ecological restoration and creation: a review. *Biological Journal of the Linnean Society* **56** (suppl.): 187-211.
- Arnthórsdóttir S.** (1994) Colonisation of experimental patches in mown grassland. *Oikos* **70**: 230-240.
- Ash H. J. Bennett R. & Scott R.** (1993) *Flowers in the Grass: Creating and Managing Grasslands with Wild Flowers*. English Nature, Peterborough.
- Ausden M. & Treweek J.** (1995) Grasslands. In: *Managing Habitats for Conservation*, Sutherland W. J. & Hill D. A. (eds), Cambridge University Press, pp. 197-229.
- Bakker J. P., Dekker M. & de Vries Y.** (1980) The effect of different management practices on a grassland community and the resulting fate of seedlings. *Acta Botanica Neerlandica* **29**: 469-482.
- Bakker J. P., Poschod P., Strykstra R. J., Bekker, R. M. & Thompson K.** (1996) Seed banks and seed dispersal: important topics in restoration ecology. *Acta Botanica Neerlandica* **45**: 461-490.
- Bakker J. P., van Andel J. & van der Maarel E.** (1998) Plant species diversity and restoration ecology: introduction. *Applied Vegetation Science* **1**: 5-8.
- Bazzaz F.A. & Ackerly D.D.** (1992) Reproductive allocation and reproductive effort in plants. In: *Seeds - The Ecology of Regeneration in Plant Communities*, Fenner M (ed), CAB International, Wallingford. pp. 1-26.
- Begon M.** (1985) A general theory of life-history variation. In: *Behavioural Ecology*, Sibly R.M. & Smith R.H. (eds), Blackwell Scientific Publications, Oxford, pp. 91-97.
- Begon M., Harper J. L. & Townsend C. R.** (1990) *Ecology: Individuals, Populations and Communities*. Blackwell Scientific Publications, Boston.
- Bisgrove R. & Dixie G.** (1994) Wild flowers: plugging the gap. *Enact* **2**: 18-20.
- Boyce D.** (1994) Survival and spread of pot-grown flowers inserted into a perennial ryegrass ley. In *Grassland Management and Nature Conservation*, Hagger R. J. & Peel S. (eds), British Grassland Society Occasional Symposium **28**, pp. 238-9.
- Brady N. C. & Weil R. R.** (1999) *The Nature and Properties of Soils*. Prentice Hall, New Jersey.
- Cavers P. B. & Harper J. L.** (1967) Studies in the dynamics of plant populations: I. the fate of seed and transplants introduced into various habitats. *Journal of Ecology* **55**: 59-71.
- Chippindale H. G.** (1948) Resistance to inanition in grass seedlings. *Nature, London* **161**: 65.
- Clark M. J.** (1997) Ecological restoration - the magnitude of the challenge: an outsiders view. In: *Restoration Ecology and Sustainable Development*, Urbanska K. A., Webb N. R. & Edwards P. J. (eds), Cambridge University Press, pp. 353-377.
- Cottam G. & Wilson H. C.** (1966) Community dynamics of an artificial prairie. *Ecology* **47**: 88-96.

- Coulson S., Bullock J. M., Stevenson M. J. & Pywell R. F.** (2001) Colonization of grassland by sown species: dispersal versus microsite limitation in responses to management. *Journal of Applied Ecology* **38**: 204-216.
- Crofts A.** (1999) Grassland creation. In: *The Lowland Grassland Management Handbook 2nd Ed*, Crofts A. & Jefferson R. G. (eds), English Nature/The Wildlife Trusts, Lincoln.
- Crofts A. & Grayson B.** (1999) Grazing. In: *The Lowland Grassland Management Handbook 2nd Ed*, Crofts A. & Jefferson R. G. (eds), English Nature/The Wildlife Trusts, Lincoln.
- Davies A. Dunnett N. P. & Kendle T.** (1999) The importance of transplant size and gap width in the botanical enrichment of species-poor grasslands. *Restoration Ecology* **7**: 271-280.
- Dodd M. E., Silvertown J., McConway K., Potts J., & Crawley M.** (1994) Stability in the plant communities of the Park Grass experiment: the relationships between species richness, soil pH and biomass variability. *Philosophical Transactions of the Royal Society of London* **346**: 185-193.
- Dryden R.** (1997) *Habitat Restoration project: fact sheets and Bibliographies*. Horton, P. and Hall. J. (eds), English Nature Research Reports **260**: English Nature, Peterborough.
- Dunnett N. & Grime J. P.** (1999) Competition as an amplifier of short-term vegetation responses to climate: an experimental test. *Functional Ecology* **13**: 388-395.
- Dunnett N. P. & Willis A. J.** (2000) Dynamics of *Chamerion angustifolium* in grassland vegetation over a thirty-nine-year period. *Plant Ecology* **148**: 43-50.
- Dunnett N. P., Willis A. J., Hunt R. & Grime J. P.** (1998) A 38-year study of relations between weather and vegetation dynamics in road verges near Bibury, Gloucestershire. *Journal of Ecology* **86**: 610-623.
- Fenner M.** (1978) A comparison of the abilities of colonizers and closed-turf species to establish from seed in artificial swards. *Journal of Ecology* **66**: 953-963.
- Fenner M. & Spellerberg I. F.** (1988) Plant species enrichment of ecologically impoverished grassland: a small scale trial. *Field Studies* **7**: 153-158.
- Fowler N. & Antonovics J.** (1981) Competition and coexistence in a North Carolina grassland. Patterns in undisturbed vegetation. *Journal of Ecology* **69**: 825-841.
- Frame J., Fisher G. E. J. & Tiley G. E. D.** (1994) Wildflowers in grassland systems. In: *Grassland Management and Nature Conservation*, Hagger R. J. & Peel S. (eds), British Grassland Society Occasional Symposium **28**, pp. 104-114.
- Francis J. L. & Morton A.** (2001) Enhancement of amenity-woodland field layers in Milton Keynes. *British Wildlife* **12**: 244-251.
- Gatsuk E., Smirnova O. V., Vorontzova L. I., Zaugolnova L. B. & Zhukova L. A.** (1980) Age-states of plants of various growth forms: a review. *Journal of Ecology* **68**: 675-696.
- Gibson C. W. D. & Brown V. K.** (1992) Grazing and vegetation change: deflected or modified succession? *Journal of Applied Ecology* **29**: 120-131.
- Gilbert O. & Anderson P.** (1998) *Habitat Creation and Repair*. Oxford University press, Oxford.
- Goldberg, D. E.** (1987) Seedling colonisation of experimental gaps in two old field communities. *Bulletin of the Torrey Botanical Club* **114**: 139-148.
- Goldberg D. E. & Werner P. A.** (1983) The effects of size of opening in vegetation and litter cover on seedling establishment of golden rods (*Solidago* spp.). *Oecologia* (Berlin) **60**: 149-155.
- Grime J. P.** (1987) Dominant and subordinate components of plant communities: implications for succession, stability and diversity. In: *Colonization, Succession and*

- Stability*, Gray A. J., Crawley M. J. & Edwards P. J. (eds), Blackwell, Oxford, pp. 429-453.
- Grime J. P.** (1979) *Plant Strategies and Vegetation Processes*. John Wiley, Chichester.
- Grime J. P. & Curtis A. V.** (1976) The interaction of drought and mineral nutrient stress in calcareous grassland. *Journal of Ecology* **64**: 975-988.
- Grubb P. J.** (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review* **52**: 107-145.
- Grubb P. J.** (1976) A theoretical background to the conservation of ecologically distinct groups of annuals and biennials in the chalk grassland ecosystem. *Biological Conservation* **10**: 53-76.
- Hodgson J. G., Colasanti R. & Sutton F.** (1995a) FIBS (Functional Interpretation of Botanical Surveys). In: *Monitoring Grassland vol 1: The Development of Botanical Monitoring Methods*, Hodgson J. G., Colasanti R. & Sutton F. E. (eds), English Nature Research Report **156**: English Nature, Peterborough.
- Hodgson J. D., Grime J. P., Hunt R. & Thompson K.** (1995b) *The Electronic Comparative Plant Ecology*. Chapman & Hall, London.
- Hopkins A., Pywell R. F., & Peel S.** (1997) *Suitability of wild flower species for introduction on sites targeted for increased biodiversity*. British Grassland Society Fifth Research Conference, Seale Hayne College, British Grassland Society, Reading. pp. 193-194.
- Hopkins A., Pywell R. F., Peel, S., Johnson R. H. & Bowling P. J.** (1999) Enhancement of botanical diversity of permanent grassland and impact on hay production in Environmentally Sensitive areas. *Grass and Forage Science* **54**: 155-162.
- Hulme P. E.** (1996) Herbivory, plant regeneration, and species coexistence. *Journal of Ecology* **84**: 609-615.
- Hutchings M. J.** (1986a) Plant population biology. In: *Methods in Plant Ecology*, Moore P. D. & Chapman S. B. (eds), Blackwell Scientific Publications, Oxford, pp. 377-437.
- Hutchings M. J.** (1986b) The structure of plant populations. In: *Plant Ecology*, Crawley M.J. (ed), Blackwell Scientific Publications, Oxford, pp. 97-136.
- Jones A. T. & Hayes M. J.** (1999) Increasing floristic diversity in grassland: the effects of management regime and provenance on species introduction. *Biological Conservation* **87**: 381-390.
- Kendle A. D.** (1992) The management of man-made habitats. *Aspects of Applied Biology* **29**: 25-32.
- Kirkham F. W. & Tallowin J. R. B.** (1995) The influence of cutting date and previous fertilizer treatment on the productivity and botanical composition of species-rich hay meadows on the Somerset Levels. *Grass and Forage Science* **50**: 365-377.
- Kovach W. L.** (1998) *MVSP - A Multivariate Statistical Package for Windows, ver. 3.0*. Kovach Computing Services, Pentraeth, Wales.
- Liira J. & Zobel K.** (2000) Vertical structure of a species-rich grassland canopy, treated with additional illumination, fertilization and mowing. *Plant Ecology* **146**: 185-195.
- Luscombe G. & Scott R.** (1994) *Wildflowers Work: a Technical Guide to Creating and Managing Wildflower Landscapes*. Landlife, Liverpool.
- Mitchley J.** (1994) Sward structure with regard to conservation. In: *Grassland Management and Nature Conservation*, Hagger R. J. & Peel S. (eds), British Grassland Society Occasional Symposium **28**, pp. 43-53.
- Morgan J. W.** (1999) Have tubestock plantings successfully established populations of rare grassland species into reintroduction sites in western Victoria? *Biological Conservation* **89**: 235-243.

- Morgan J. W.** (1997) The effect of grassland gap size on establishment, growth and flowering of the endangered *Rutidosia leptorrhynchoides* (Asteraceae). *Journal of Applied Ecology* **34**: 566-576.
- Novoplansky A. & Goldberg D. E.** (2001) Effects of water pulsing on individual performance and competitive hierarchies in plants. *Journal of Vegetation Science* **12**: 199-208.
- Oomes M. J. M. & Mooi H.** (1981) The effect of cutting and fertilizing on the floristic composition and production of an *Arrhenatherion elatioris* grassland. *Vegetatio* **47**: 233-239.
- Parish R., Turkington R.** (1990) The influence of dung pats and molehills on pasture composition. *Canadian Journal of Botany* **68**: 1698-1705.
- Parish R., Turkington R. & Klein E.** (1990) The influence of mowing, fertilization, and plant removal on botanical composition of an artificial sward. *Canadian Journal of Botany* **68**: 1080-1085.
- Putman R. J., Fowler, A. D. & Tout S.** (1991) Patterns of use of ancient grassland by cattle and horses and effects on vegetational composition and structure. *Biological Conservation* **56**: 329-347.
- Pywell R., Peel S., Hopkins A. & Bullock J.** (1997) Multi-site experiments on the restoration of botanically diverse grassland in ESAs. In: *Grassland management in Environmentally Sensitive Areas. Occasional Symposium No. 32*. Sheldrick R. D. (ed), British Grassland Society, pp. 160-165.
- Rodwell J. S.** (1992) *British Plant Communities Volume 3. Lowland Grassland and Montane Communities*. Cambridge University Press.
- Rusch G. & Fernández-Palacios J. M.** (1995) The influence of spatial heterogeneity on regeneration by seed in a limestone grassland. *Journal of Vegetation Science* **6**: 417-426.
- Silvertown J.** (1987) *Plant Population Ecology*. Longman Scientific & Technical, London.
- Silvertown J., Dodd, M. E., McConway K., Potts J. & Crawley M.** (1994) Rainfall, biomass variation, and community composition in the Park Grass Experiment. *Ecology* **75**: 2430-2437.
- Silvertown, J. & Franco, M.** (1993) Plant demography and habitat: a comparative approach. *Plant Species Biology* **8**: 67-73.
- Smith R. S. & Jones L.** (1991) The phenology of mesotrophic grassland in the Pennine Dales, northern England: historic hay cutting dates, vegetation variation and plant species phenologies. *Journal of Applied Ecology* **28**: 42-59.
- Silvertown J., Lines C. E. M. & Dale M. P.** (1994) Spatial competition between grasses - rates of mutual invasion between four species and the interaction with grazing. *Journal of Ecology* **82**: 31-38.
- Smith R. S., Pullan S. & Shiel R. S.** (1996) Seed shed in the making of hay from mesotrophic grassland in a field in Northern England: effects of hay cut date, grazing and fertilizer in a split-split-plot experiment. *Journal of Applied Ecology* **33**: 833-841.
- Tamm C. O.** (1991) Behaviour of some orchid populations in a changing environment, observations on permanent plots, 1943-1990. In: *Population Ecology of Terrestrial Orchids*. Wells T. C. E. & Willems J. H. (eds), SPB Academic Publishing, The Hague, Netherlands, pp. 1-13.
- Tamm C. O.** (1956) Further observations on the survival and flowering of some perennial herbs. I. *Oikos* **7**: 273-92.

- Tilman D.** (1997) Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* **78**: 81-92.
- Tilman, D. & El Haddi, A.** (1992). Drought and biodiversity in grasslands. *Oecologia*, **89**, 257-264.
- van Andel, J.** (1998) Intraspecific variability in the context of ecological restoration projects. *Perspectives in Plant Ecology, Evolution and Systematics* **2**: 221-237.
- van Duren I. C., Strykstra R. J., Grootjans A. P., ter Heerdt G. N. J. & Pegtel D. M.** (1998) A multidisciplinary evaluation of restoration measures in a degraded *Cirsio-Molinietum* fen meadow. *Applied Vegetation Science* **1**: 115-130.
- van der Woude, B. J., Pegtel, D. M. & Bakker, J. P.** (1994) Nutrient limitation after long-term nitrogen fertilizer application in cut grasslands. *Journal of Applied Ecology* **31**: 405-412.
- van Groenendael J. M., Ouborg N. J. & Hendriks R. J.** (1998) Criteria for the introduction of plant species. *Acta Botanica Neerlandica* **47**: 3-13.
- Waite S.** (1984) Changes in the demography of *Plantago coronopus* at two coastal sites. *Journal of Ecology* **72**: 809-826.
- Watkinson A. R.** (1986) Plant population dynamics. In: *Plant Ecology*, M. J. Crawley (ed), Blackwell, pp. 137-184.
- Wells T. C. E.** (1990) Establishing chalk grassland on previously arable land using seed mixtures. In: *Calcareous Grasslands - Ecology and Management*, Hillier S. H., Walton D. W. H. & Wells D. A. (eds), Bluntisham Books, Huntingdon, pp. 169-170.
- Wells T. C. E.** (1983) The creation of species-rich grasslands. In: *Conservation in Perspective*, Warren A. & Goldsmith F. B. (eds), John Wiley & Sons Ltd, Chichester, pp. 215-246
- Wells T. C. E., Cox R. and Frost A.** (1989) Diversifying grasslands by introducing seed and transplants into existing vegetation. In: *Biological Habitat Reconstruction*, Buckley G. P. (ed), Belhaven Press, London, pp. 283-297.