



- CHAPTER 8 -

EFFECTS OF PLANTING SEASON ON TRANSPLANT SURVIVORSHIP: SPRING VERSUS AUTUMN INOCULATION

Inoculation was first introduced in the early part of the present century, 'invented', as it is termed, by Mr. Whitworth, of Acre House, Lincolnshire...Inoculation has one great advantage over sowing seeds, namely, that there is no falling off experienced in the third, fourth and fifth year, at least to the extent as is universally admitted occurs when land is laid down to pasture with artificial grasses. Once inoculation 'takes', the grass goes on improving...thus a good pasture is formed more quickly by transplanting turves than by sowing seeds.

Evans M. (1876) Notes on inoculation of grass land, as practised at Kimbolton. *Journal of the Royal Agricultural Society of England* **12**: 230-236.

SUMMARY

1. Key aspects of transplantation methodology are in need of further research, one of which is the influence of seasonality. Planting season may influence establishment success for a number of reasons. Common practice recommends that transplantation of containerised plants is preferable in spring and autumn. Spring growth may establish transplants more quickly and lead to rapid entrenchment conferring greater resistance to broadband mortality risks. In contrast, autumn translocation may take advantage of reducing plant growth, following on to winter dormancy, which may allow transplants greater resilience. Furthermore, the season of inoculation may interact with the ecology of individual species.

2. This experiment was undertaken in order to investigate differences in mortality and performance between spring and autumn implantation. The results from the spring 1994 transplants provide a guide as to the choice of phytometer species to use in the autumn planting. Seven species were selected: *Centaurea nigra*, *Leontodon hispidus*, *Leucanthemum vulgare*, *Lotus corniculatus*, *Malva moschata*, *Primula veris* and *Scabiosa columbaria*. Implantation took place from 22nd October 1996. In each subplot, three planting rows were established on either side of the central area used in the **Chapter 7** experiment. Exactly as for the spring 1994 planting experiment, 30-cm, 15-cm and 0-cm diameter gaps were applied. Two sizes of transplant were used: 9-cm pot, and 2-cm seedling plugs. However, unlike the spring cohorts, the planting rows were spaced at 50-cm intervals, and transplants inserted at 60-cm intervals. In all, 1008 transplants of the 7 species were planted, 252 in each plot and 84 in each subplot. The autumn 1996-99 results are discussed throughout in comparison with the spring 1994-97 findings (first three years).

3. Of the initial input of 1008 transplants inserted into the four treatment plots in October 1996, three years later (36 months), 298 (29.6%) of the transplants were still alive. Autumn implantation led to higher overall survivorship (29.6%) than spring (21.7%), and autumn survivorship was higher for all species except *Malva moschata*. The outstanding species-differential was that of *Centaurea* with a very significantly higher survival than for the spring cohort. As with the spring, all autumn censuses recorded higher pot survivorship than seedling-plug, though mostly not at a significant level. The autumn gap results also generally accord with that of the spring planting, where gap size did not markedly influence transplant survival.

4. In terms of productivity factors, autumn survival correlated significantly (positive) with subplot gradient, and negatively with phosphorous and peak phytomass. No significant interactions with management treatment could be detected in transplant survivorship. Significant correlations between transplant survival and species richness of the receptor swards suggest that this parameter is a good means of predicting the resistance of a sward prior to enrichment.

5. The findings indicate that most transplant species will establishment most successfully when planted in early autumn as soil moisture deficit is low, and light and temperature conditions are still sufficient for plants to establish strong root systems in preparation for droughty conditions during the following summer.

6. Irrespective of season, what transplantation does not seem to achieve is the absolute avoidance of competitive exclusion under productive conditions. Apart from very robust species such as *Primula veris*, *Malva moschata* and *Geranium pratense*, mortality risk is not so much avoided as postponed.

Keywords: transplant, seasonality, spring, autumn, implantation, pot, plug, survivorship, productivity, phosphorus, phytomass, species richness, soil moisture deficit.

INTRODUCTION

The main problems apparently hindering restoration of grasslands which have been subjected to agricultural ‘improvement’ are residual soil fertility (Marrs 1985; Marrs & Gough 1989; Tallowin *et al* 1995), the species-poverty of the improved grassland communities both in the above-ground vegetation and seed bank (Hutchings & Booth 1996; Bekker *et al* 1997), and the lack of local unimproved species-rich grassland to act as propagule emigration sources (Gibson *et al* 1987; Jones & Haggard 1994; Hopkins *et al* 1995). Additionally, Anderson (1995) suggests grassland restoration requires careful management to reduce dominance and inter-specific competition and the availability of colonization gaps. In order to accelerate the restoration of species diversity, it may be requisite to introduce transplants (Wells 1983; Fenner & Spellerberg 1988; Buckley 1989; Howell & Jordan 1989; Wells *et al* 1989; Davies *et al* 1996; Kline 1997; Davies *et al* 1999; Hopkins *et al* 1999). Enrichment of species-poor swards with container-grown plants has been suggested as an effective way of enriching depauperated grasslands (Fenner & Spellerberg 1988; Wells *et al* 1989; Kendle 1992; Luscombe & Scott 1994; Anderson 1995).

It is evident that there are still key aspects of transplantation methodology that are in need of further research (Wells *et al* 1989), one of which is the influence of seasonality on enrichment success (Cavers & Harper 1967; Wells 1983; Fenner & Spellerberg 1988; Howell & Jordan III 1989; Kendle 1992; Morgan 1997; Davies *et al* 1999). Research into the phenological parameters involved in plant species recruitment (Smith & Tallowin 1995; Hitchmough *et al* 1996; Eriksson & Eriksson 1997) suggests that seasonal effects may also have an important influence on the efficacy of transplantation. Planting season may influence relative establishment success for a number of reasons. For instance, standard horticultural practice recommends that transplantation of containerised plants can be carried out at any time of year, but preferably in spring and autumn when there is more likelihood of moist soil conditions thus reducing desiccation and associated mortality risks (Johnson 1984; Bisgrove & Dixie 1994; Luscombe & Scott 1994). While both spring and autumn are widely accepted as preferable planting seasons, the relative merits of spring compared to autumn planting are a further important question. Spring growth may establish transplants more quickly and lead to rapid entrenchment conferring greater resistance to broadband mortality risks. However, as spring is the season of commencement of plant growth and greatest

competition for limiting resources (Howe & Snaydon 1986), this would suggest spring has higher intrinsic mortality risk than autumn, with the added factor of higher soil moisture demand and greater unpredictability in water supply (Al Mufti *et al* 1977; Bakker 1980; Oomes & Mooi 1981; Vermeer & Berendtse 1983; Dunnett *et al* 1998). In contrast, autumn translocation may take advantage of reducing plant growth, following on to winter dormancy, which may allow transplants greater resilience to predation and pathogens. Autumn, however, as suggested by **Chapter 7**, may have its own mortality risks, possibly associated with lower tissue replacement rates leading to reduced compensation for grassland management damage, predation by invertebrates such as molluscs (Hanley *et al* 1995), and lower immunity to pathogens, exacerbated by potential soil water logging (Morgan 1997).

The season of inoculation may interact more acutely with the ecology of individual species, such that while certain species may be relatively insensitive to season of planting such as those with high relative growth rates and tall stature (Grime *et al* 1988), others may be significantly affected. For example, transplant species that need to form deep taproots may find it more difficult to establish in spring than autumn due to the shorter development period before the onset of drier soil conditions. Once established, these species are usually considered drought tolerators (Al Mufti *et al* 1977; Grime *et al* 1988; Dunnett *et al* 1998). Other factors in transplant ecology may also interrelate with season such as transplant size and artificial gap occlusion dynamics. For instance seedling-plugs may require the greater entrenchment time afforded by autumn planting before onset of competition in the spring (Howe & Snaydon 1986; Hodgson 1989). The advantages and disadvantages of gap creation may also partly depend on time of year in which the gaps were created (Hillier 1990; Bullock *et al* 1994; Hitchmough *et al* 1996). Wells *et al* (1989) found that with autumn (October) applications, sprayed areas were visible for up to six months, whereas occlusion was much faster, approximately 2 months, for spring (April) gaps.

The above review suggests that the investigation of *seasonality* on transplant survivorship is an important aspect of transplant ecology (Kendle 1992). In applied terms, properly conducted research evidence as to which season - spring or autumn - is generally preferential in terms of herbaceous transplant inoculation success, may

significantly inform restoration investment risk. Such data may lead to reduced mortality, when attempting to diversify floristically depauperated swards (Wells *et al* 1989; Davies *et al* 1996; Davies *et al* 1999). Working within this context, this chapter presents an evaluation of seasonality in transplant mortality risk, as well as providing verification of the findings from the spring cohort.

METHODS

Phytometer species

The vegetation history of the site is described in full in **Chapter 2**. For direct comparison, the same inoculation methodology was used as for the 1994 spring enrichment experiment, as described in **Chapter 7**. However, because of lack of resources, including implantation space in the subplots, only seven species were selected for use in this experiment. The survivorship results from the spring 1994 cohorts provided a guide as to the sensitivity of each species to the level of agricultural improvement i.e. the higher the sensitivity to grassland productivity effects, generally the lower the survivorship. The choice of species used in the autumn planting was based on selecting a spectrum of species exhibiting apparent survival *thresholds*.

Table 8.01 Comparative characteristics of phytometer species.

Phytometer species	Life-span	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	CSR(1.1)	3	2	1.2	6.9 Intermediate
<i>Leontodon hispidus</i>	P	S(0.1)	2	3	3.4	3.5 Intermediate
<i>Leucanthemum vulgare</i>	P	C/CSR(1.2)	3	2	3.6	0.7 Marginal
<i>Lotus corniculatus</i>	P	S/CSR(0.6)	2	2	2.7	6.9 Intermediate
<i>Malva moschata</i>	P	CSR(1.1)	4	2	2.7	29.9 Core
<i>Primula veris</i>	P	S/CSR(0.6)	2	2	1.7	34.0 Core
<i>Scabiosa columbaria</i>	M/P	S/SR(0.6)	1	2	3.2	0 Extinct

¹Ecological profiles and ²responsiveness scores from Hodgson, Colasanti & Sutton (1995) and Hodgson, Grime *et al* (1995);

³Survival categories from **Chapter 7**.

Life-span: P= polycarpic perennial, M/P=monocarpic perennial

Established strategy includes scores referring to growth rate potential; 0.6 lowest & 1.2 highest

Canopy height; 1=shortest, 5=tallest; Lateral spread potential; 1=least, 5 =most

Responsiveness index = level of responsiveness to vegetational change, the higher the score, the more responsive

Table 8.01 lists the phytometer species used in the present experiment, along with ecological classifications (Hodgson & Grime *et al* 1995), Index of Responsiveness scores (Hodgson, Colasanti & Sutton 1995), and survivorship levels for spring 1994 cohorts censused in September 1999, including survivorship categories (see **Chapter 7**). Hodgson *et al's* (1995) Index of Responsiveness was developed for aiding the monitoring of habitat change using indicator species.

Figure 8.01 Survivorship curves for spring 1994 cohorts of phytometer species.

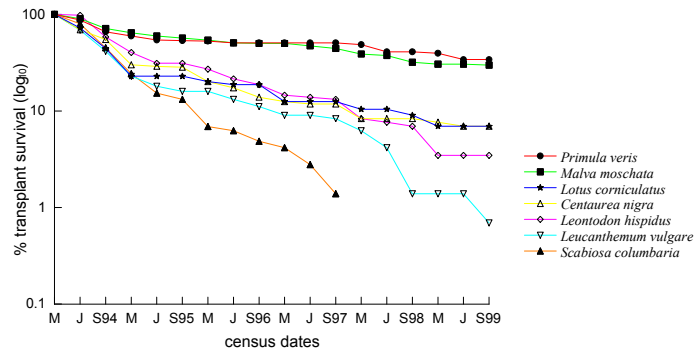


Figure 8.01 sets out the survivorship curves for the selection of indicator species. A visual appraisal suggests that the species fall into three broad categories. The first category includes *Malva moschata* and *Primula veris*, which are ‘top’ survivors, in that they demonstrated themselves capable of establishing relatively successfully across the gradient of grassland improvement. The second stream contains *Lotus corniculatus*, *Centaurea nigra*, *Leontodon hispidus*, which are species that have managed to establish small populations, though variably distributed across the plots. The survivorship of all three species was much lower than expected considering both *Centaurea* and *Lotus* are generally viewed as relatively robust transplant species (Bisgrove & Dixie 1994; Luscombe & Scott 1994), and *Centaurea* even occurs naturally in Plot 3. The third group includes *Leucanthemum vulgare* and *Scabiosa columbaria*, which are nearly extinct, and extinct respectively, in all plots, though probably for markedly different reasons. *Filipendula vulgaris* was to be included in this experiment as its survivorship in the original spring planting scheme showed the opposite features of *Centaurea nigra*, in that it was expected to have a very low survivorship, but in fact established relatively successfully, better than *Centaurea*, even though it is a low growing rosette species, and only naturally found on old, unimproved, species-rich grassland (Stace 1991). Unfortunately, after several attempts, including artificial vernalization not enough seed could be germinated within the required time-scale, and *Thalictrum flavum* was substituted as another ‘wild-card’, though the survival results for this species are not evaluated here.

The research was established within the experimental layout as described in **Chapter 3**. As stated in **Chapter 7**, within each subplot the corners of the internal 12-m x 25-m inoculation areas were marked with short softwood posts. In the initial experimental structure allowance had been made for further enrichment experiments by providing

expansion border areas either side of the posts. However, in order to include a comparable number of replicates, and incorporate the direct seed sowing experiments (see **Chapter 10**), unlike the *core* experiment described in **Chapter 7**, 60-cm planting positions were used instead of the 1-m distances between transplants. However, this was a greater nearest-neighbour distance than used by Wells *et al* (1989) (2 transplants m²). Thus, three rows were established on either side of the central area. The ends of the planting rows were located 50-cm apart using cord marked out at the required 60-cm planting intervals, and the ends of the rows were then permanently denoted with blue plastic water piping knocked in to ground level. In addition, the grass around each pipe was removed by spraying with glyphosate so that relocation was made easier. The spray gaps around the pipes were maintained throughout the project.

Field preparation for the autumn planting experiment was started after hay cut and removal in late July 1996. Exactly as for the spring 1994 planting experiment, 30-cm, 15-cm and 0-cm diameter gaps were applied. Glyphosate herbicide and stencils with the appropriate diameters were used to create the gaps. Spraying was completed by late August 1996, and planting undertaken between the 22nd and 28th October. The gap and size distributions were also randomised on a subplot rather than a row basis. The planting scheme was also stratified-random, with each row containing all the species and replicates (12 individuals per species) in a randomised sequence. In all, 1008 transplants of the 7 species were planted, 252 in each plot and 84 in each subplot. One-third of each species (4 individuals) were introduced into each gap diameter type. Because in the spring 1994 experiment it was not possible to get plug plants for *Leontodon hispidus*, for direct comparison, only pot transplants for this species were also used in this experiment. Otherwise, for the other 6 species, half of the transplants (6) were of each size.

Grassland management treatments

The autumn transplant cohorts were inserted into swards already under the influence of two-and-a-half years of sward management regimes instituted in 1994, the systems of which are described in **Chapter 3**. However, to summarise, three management treatments were randomly allocated among the three subplots within each of the experimental plots. The management followed the traditional hay meadow system used in Somerset before World War II involving spring and autumn grazing with a mid-July

hay cut (Tanner 1857). The sheep grazing was conducted using a local breed (Wiltshire Horn) and the cattle grazing were undertaken using lactating cows (Friesian x Holstein) from a neighbouring farm. The mowing regime was carried out with a rotary mower and grass box, mimicking grazing by cutting the grass to 5-cm twice in the spring and three times in the autumn.

As for the spring 1994 cohorts, transplant survivorship was recorded during censuses in March, June and September of each year. For each census, each planting position was surveyed and the survival state (alive/dead) of the transplant recorded. In addition, notes were taken on any apparent damage to the transplants, and if dead, causality factors. Performance parameters for each transplant were recorded in the June and September censuses. In the June census plant height and number of individual flowering modules (depending on species), were recorded, if present. In the September census, rosette diameters were also measured. The performance parameters are analysed in **Chapter 9**.

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 proved to be the most useful as grassland management treatments have so far had 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 7 (phytometer) species planted in the autumn were used. 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.

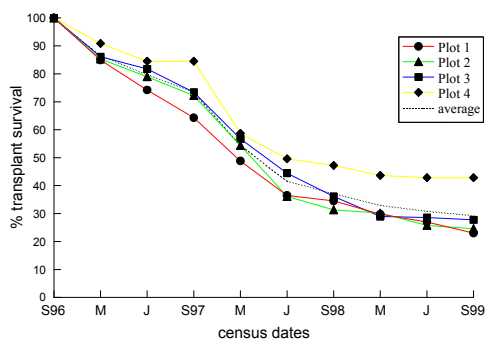
The primary analyses had to be calculated on transformed data, as most of the datasets were composed of simple plant counts and thus considered as not *normally* distributed (Fowler & Cohen 1990). It was therefore necessary to normalize the data using logarithmic ($\log_{10}x$) transformation, as the 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, one was added to each data point ($x + 1$). Analysis of independent pairs of data (<30 observations) was undertaken using the independent samples *t*-test (Fowler & Cohen 1990), specifically for analysis of individual species survival observations. One-way Analysis of Variance was applied to data where there was requirement for comparison of more than two samples, specifically to test for differences between-plot transplant survival. 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. Because of the multicollinearity of the explanatory variables (Jongman *et al* 1995), further regression analysis was undertaken using stepwise multiple least-squares regression in order to compare the predictive value of all the key explanatory variables (Norušis 1998). All statistical analyses were conducted using SPSS ver 9.0 (1998) and MVSP ver 3.0 (Kovach 1998).

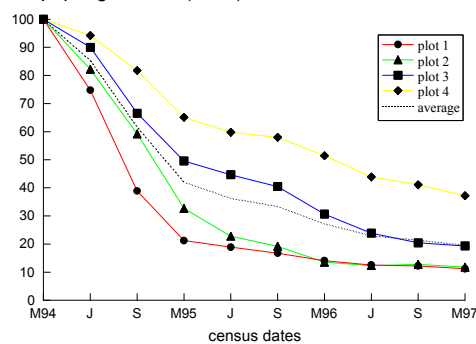
RESULTS

Of the initial input of 1008 transplants inserted into the four treatment plots in October 1996, three years later (36 months), 298 (29.6%) of the transplants were still alive. **Figure 8.02a** shows the survivorship curves for the four plots over the monitoring period, and includes the mean curve for comparison.

Figure 8.02 Survivorship curves for three year plot data.
a) autumn cohorts (1996)



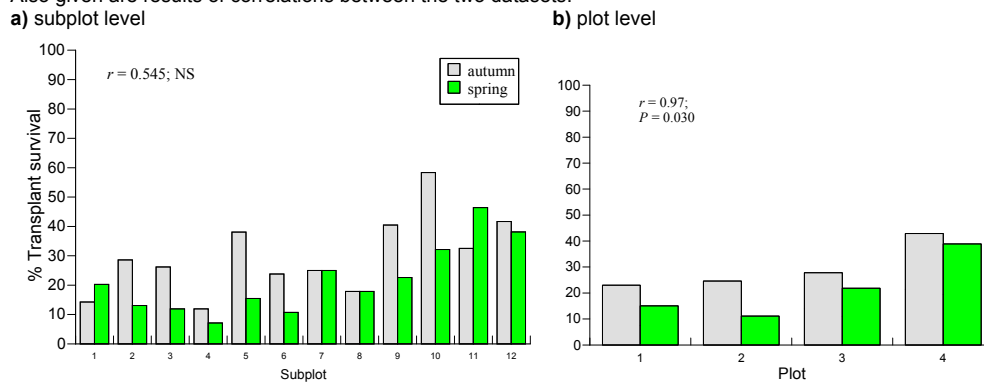
b) spring cohorts (1994)



Although Plot 4 clearly stands out as having higher transplant survival than the other plots, unlike for the spring planting (see **Chapter 7; Table 7.01**), the results of one-way ANOVA show that this division was not statistically significant at any point in the research period ($F_{3,31} = 1.18$; NS). However, when survival is compared at the between subplot level using ANOVA and Tukey HSD, Subplot 10 emerges as the only grassland

presenting demonstrably different transplant survivorship, having significantly ($F_{11,71} = 3.46$; $P = 0.01$) higher survival than subplots 1, 4, 6 & 8. **Figure 8.02b** shows the survivorship curves for the spring cohorts, but only for the first three years so as to serve as a direct comparison with the three years of the autumn survival data. While the mortality risk for the spring inoculation over the first year seems much higher than for autumn, the plot rankings are very similar, as are the final survival percentages. **Figure 8.03**, on the whole, shows that for the seven indicator species, autumn implantation led to higher overall phytometer survivorship (29.6%) than spring (21.7%).

Figure 8.03 Charts comparing survivorship of autumn and spring transplant cohorts. Also given are results of correlations between the two datasets.



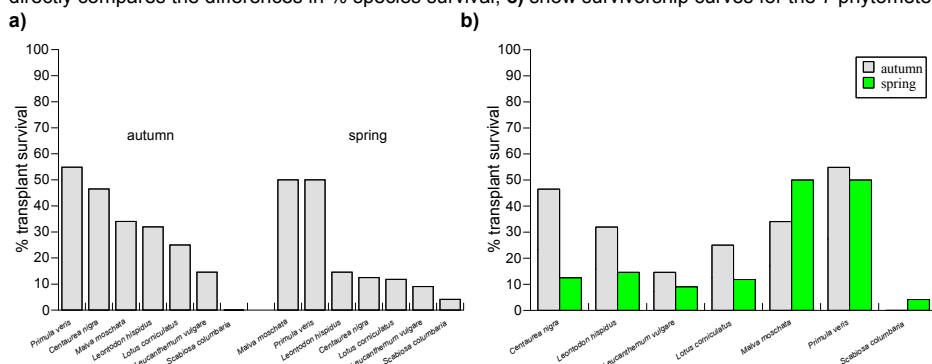
However, **Figure 8.03a** shows that at the subplot tier, the pattern of survival for both seasons was not significantly similar, though a number of subplots show markedly different mortality risks, notably subplots 5, 9 and 10. In contrast, the survival levels of subplots 7, 8 and 12 were virtually the same. Clearly there was high within-plot variation. Nevertheless, when the same data are analysed at the Plot level (**Figure 8.03b**) a different picture emerges. This comparison shows a significant similarity between the two seasonal datasets. The lack of correlation in **Figure 8.03a** may indicate that management treatments and weather may lead to greater variation at the subplot level, whereas at the plot level grassland productivity may still exert the overriding influence.

While no spring cohort species were extinct after three years, by September 1999, all autumn cohort *Scabiosa columbaria* plants were dead. Most of the depletion occurred in the winter of 1997-98, when virtually all the *Scabiosa* died, even in Plot 4, where survivorship and performance had been high during the previous summer. The almost total mortality was possibly due to winter waterlogging of the soil after record wet

weather in the late winter and early spring. Wells *et al* (1989) observed a similar pattern in their species enrichment trials. Otherwise, the other six species were still maintaining populations across the plots. The charts of **Figure 8.04** display comparative aspects of the species survival data. The ranked survivorship levels of **Figure 8.04a** shows a distinct difference in relative dominance, with the spring cohorts having greater dominance due to the higher survivorship levels for *Primula* and *Malva* compared to the other species (Simpson’s $D = 0.76$). In comparison, the autumn survivorship levels are more evenly distributed ($D = 0.81$), even with the complete extinction of *Scabiosa*.

The outstanding species-differential between the autumn and spring datasets is the survival of *Centaurea nigra*. All charts of **Figure 8.04**, **Figure 8.05a**, and **Table 8.02** show that *Centaurea* survival for autumn planting was very significantly higher than for the spring cohort.

Figure 8.04 Chart **a**) is a comparison between the ranked survival data from autumn 1999 and spring 1997 cohorts; **b**) directly compares the differences in % species survival; **c**) show survivorship curves for the 7 phytometers.



c)

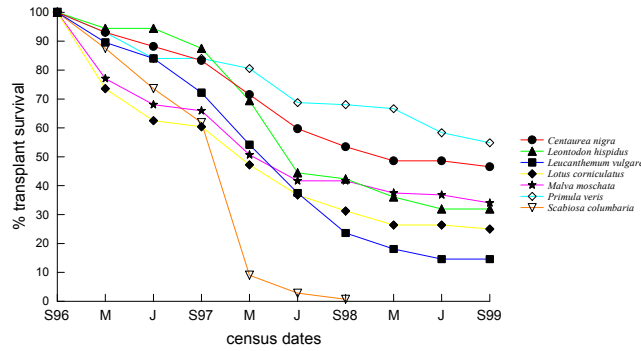
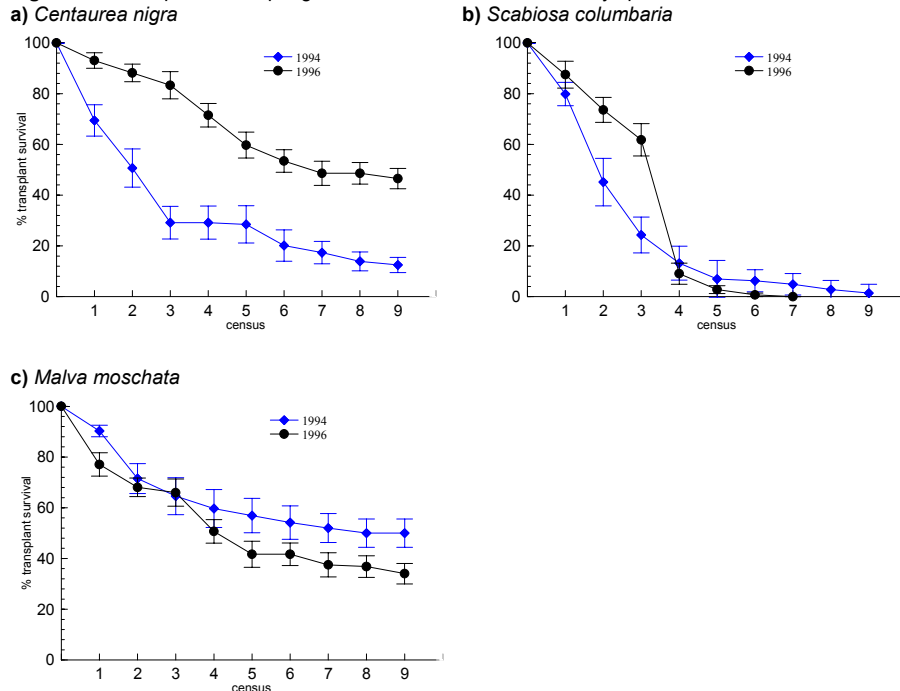


Table 8.02 Comparison of species % survival results for autumn and spring cohorts. Independent *t*-test, two tailed: $P < 0.05^*$; $P < 0.001^{***}$

Species	Autumn cohort	Spring cohort	<i>t</i> -score
<i>Centaurea nigra</i>	46.5	12.5	4.56***
<i>Leontodon hispidus</i>	39.1	14.6	1.81
<i>Leucanthemum vulgare</i>	14.6	9.03	0.93
<i>Lotus corniculatus</i>	25.0	11.8	1.81
<i>Malva moschata</i>	34.0	50.0	2.31*
<i>Primula veris</i>	54.9	50.0	0.56
<i>Scabiosa columbaria</i>	0.00	4.17	1.20

Figure 8.05 Comparison of spring and autumn cohorts for three key species. Mean % survival; bars = standard error.



Malva moschata survivorship seems to demonstrate the reverse trend to *Centaurea*, with higher survivorship for the spring cohort, even though *Malva* mortality was still relatively low for both seasons (**Figure 8.05c**). Otherwise **Table 8.02** shows that survivorship was higher for autumn cohorts for all the subordinate transplant species,

except for *Scabiosa columbaria*, which is nevertheless now extinct throughout all the inoculation experiments (**Figure 8.05b**).

Comparison of the survivorship totals for the two sizes of transplant

Six species (out of seven) were inserted as two sizes: mature pot and seedling plug transplants. Of the 432 pot transplants inserted in 1996, 164 (37.9%) were still alive in 1999, this compares with 95 (21.9%) plug plants remaining, and pot transplants suffered significantly less mortality along the improvement gradient ($t = 3.07$; $P = 0.006$; two-tailed; see **Figure 8.06**). In order to explore this relationship in greater detail, transplant survivorship curves for both sizes for each plot are given in **Figure 8.07**, as well as charts showing comparative curves for the 1994 spring cohort (selection of the same six species over the first three years after inoculation).

Figure 8.06 Illustration of significant differential between pot and plug survival along the subplot gradient. Dataset from 9/99 census.

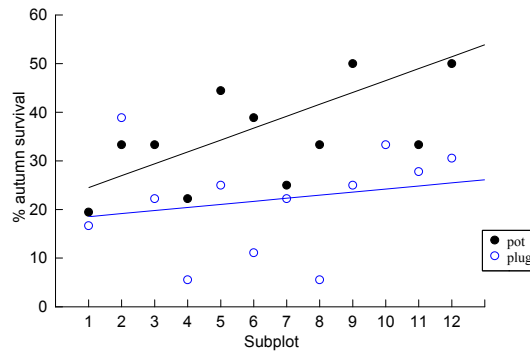
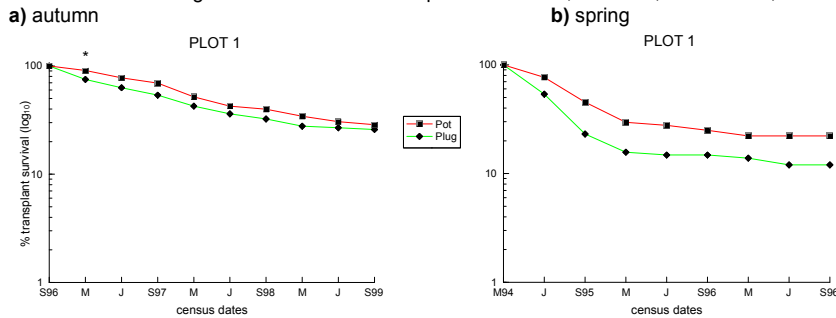
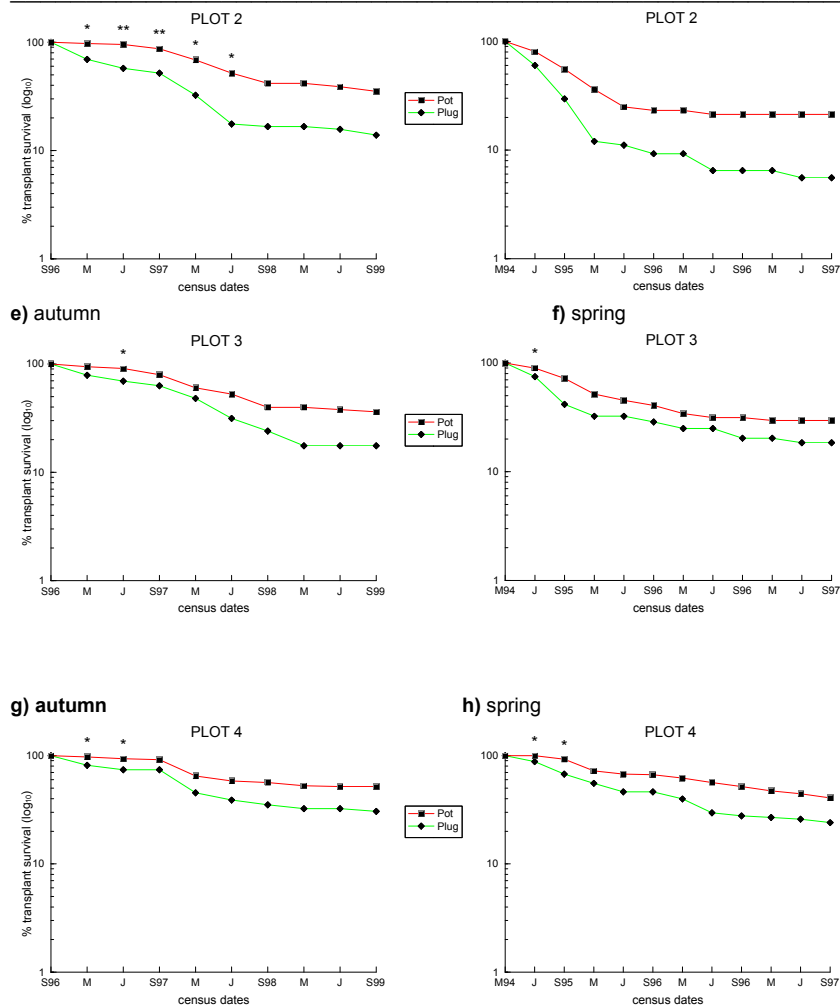


Figure 8.07 Comparisons of survivorship curves for pot and plug plants for each of the experimental plots for both autumn and spring implantations. Curve data points are subplot totals combined to form plot totals. Statistical analyses were conducted using the *t*-test for unmatched pairs: ** $P < 0.01$; * $P < 0.05$; two-tailed P , corrected for ties.



c) autumn

d) spring

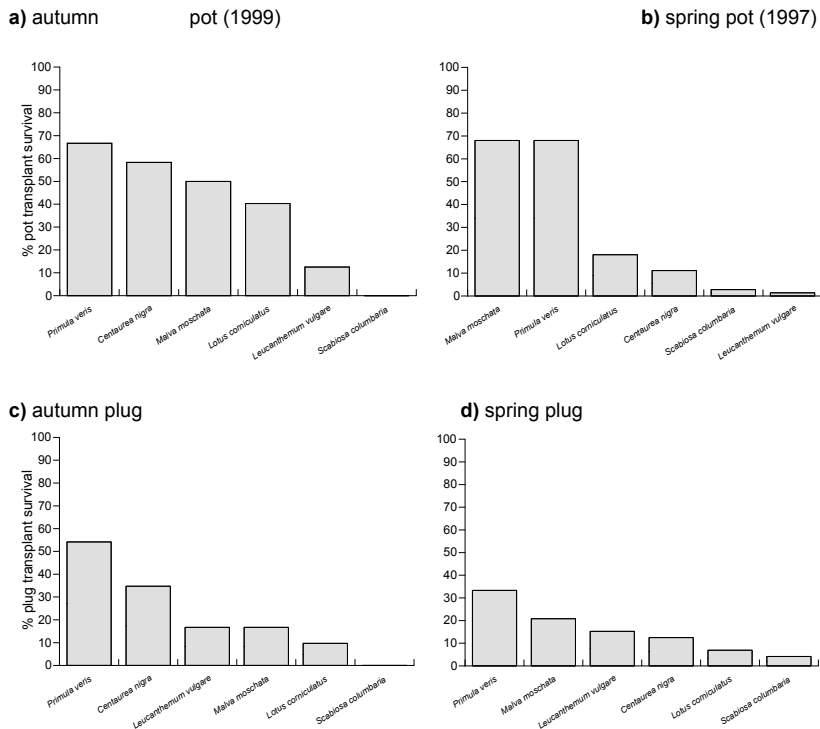


While clearly, throughout all plots, pot transplant survival was greater than plug, unlike for the subplot totals, it is apparent that none of the plots maintained a significant difference between the two sizes over the research period i.e. there was a convergence between the relative mortality risks over time. Further appreciation shows that there were fewer significant differences in pot/plug survival for the indicator spring cohort than autumn. However, only Plot 2 for the autumn cohort shows a succession of more than two contiguous censuses with a significant ($P < 0.05$) difference between pot and plug survival. On reflection, Plot 2 is also notable in that the spring implantation (all species) stands out with an almost continuous significant disparity between transplant sizes up to, and including the 1999 census (**Chapter 7; Figure 8.05**).

None of the species at the pot size, for either spring or autumn, reached over 70% survival for the first three years, and the round threshold was lower for plug transplants

at 60%. **Figure 8.08** compares the survival levels for the two transplant sizes for the two seasonal cohorts. Application of Simpson’s (*D*) diversity index (Kovach 2000) to the same datasets amplifies the visual interpretation. For pot survival (**Figures 8.08a-b**), transplant species dominance was less for the autumn cohort than for spring (autumn: 0.725; spring 0.661). In comparison, overall plug survivorship was higher for the autumn cohort than spring (**Figure 8.08c-d**), while dominance was only marginally lower for the spring (0.769) than autumn cohort (0.766).

Figure 8.08 Comparison of rankings of species survival for the two sizes of transplant, and two plantation seasons.



The two sizes of transplant for the autumn cohort were also compared at the species level. **Table 8.03** presents the statistical results, showing that half of the transplant species; *Centaurea*, *Lotus* and *Malva*, demonstrate a significant difference between inoculant sizes after three years, and only pot plants are foremost. Neither pot sized *Centaurea* nor *Lotus* shows a prominence for the spring cohort (1997). *Malva*, however, developed a similar survival pattern for both seasonal plantings.

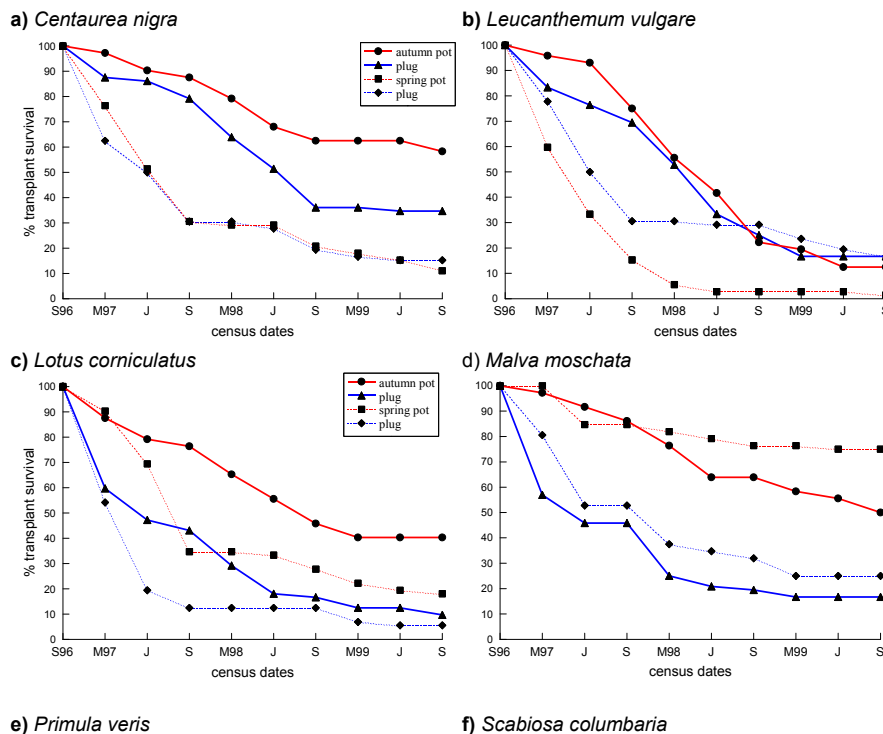
Table 8.03 Comparison of differential survival of pot versus plug transplants. Analysis using independent-pairs *t*-test.

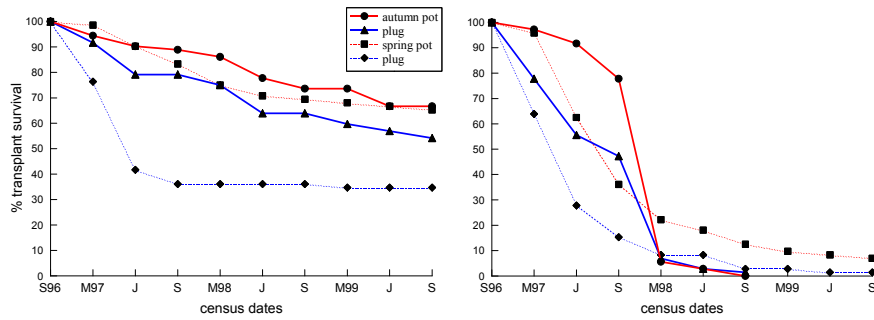
Species	9.97			9.98			9.99		
	% Survival			% Survival			% Survival		
	Pot	Plug	t-test	Pot	Plug	t-test	Pot	Plug	t-test
<i>Centaurea nigra</i>	87.5	71.2	NS	62.5	36.1	2.43*	58.3	34.7	2.17*
<i>Leucanthemum vulgare</i>	75	69.4	NS	22.2	25	NS	12.5	16.7	NS
<i>Lotus corniculatus</i>	76.4	43.0	3.47**	45.8	16.7	2.73*	40.3	9.7	2.87**
<i>Malva moschata</i>	86.1	45.8	3.58**	63.8	19.4	4.65***	50	16.7	3.73**
<i>Primula veris</i>	88.9	79.2	NS	72.2	63.9	NS	66.7	54.2	NS
<i>Scabiosa columbaria</i>	77.8	47.2	2.81*	0	1.39	NS	0	0	NS

***=P<0.000 **=P<0.001 *=P<0.01

The key results presented in **Table 8.03** are put into context in **Figure 8.09**, where pot/plug survivorship curves are graphically compared for the two seasonal cohorts. What is readily apparent for all species is the rapid mortality rate after implantation for the spring cohorts than autumn. Although the autumn curves for the short-lived *Leucanthemum* and *Scabiosa* rapidly converge, for *Centaurea*, *Lotus* and *Primula* the pot curves in particular, trace a very gradual decline. The advantage of autumn planting for *Centaurea nigra* is made very clear in **Figure 8.09a** where both autumn pot and plug survivorships are substantially higher than for spring throughout the monitoring period. Otherwise, both seasonal pot cohorts are ranked above the plug cohorts for *Lotus*, *Malva* and *Primula*.

Figure 8.09 Species comparisons of pot/plug survival curves for autumn and spring cohorts for first three years after implantation. The x-axis follows the autumn census dates, and the actual census dates for the spring curves are not given.

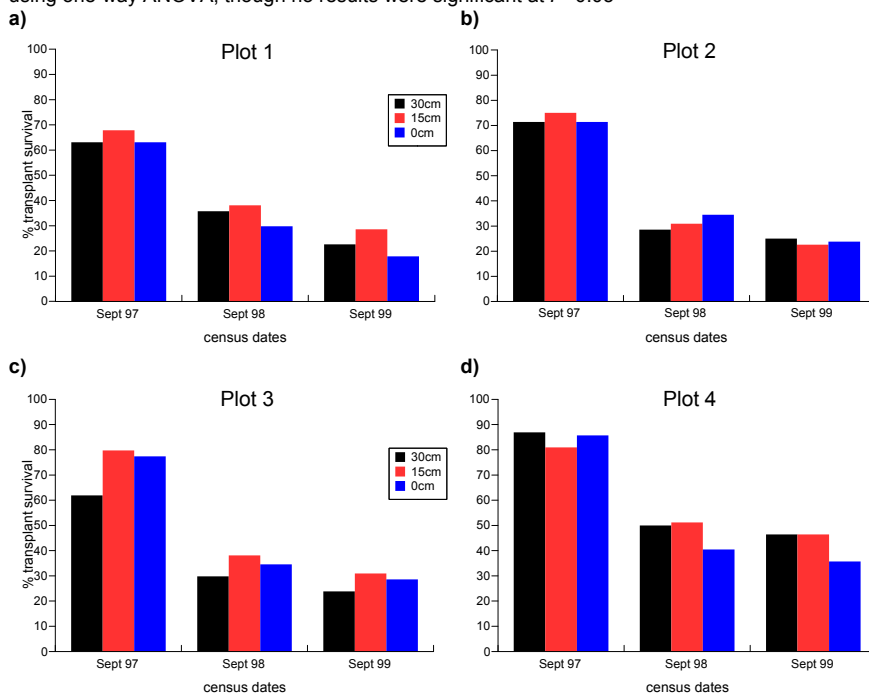




Effects of gap diameter on survivorship

The creation of either a 15-cm or 30-cm diameter competition-free gaps did not appear to have significantly affected transplant survivorship in any of the plots over the research period. Using visual appraisal, **Figure 8.10** shows that survival throughout the plots for the gap sizes was surprisingly even, with no gap diameter showing any clear trend.

Figure 8.10 Charts relating the significance of gap size to total transplant survival for plot data. Data were analysed using one-way ANOVA, though no results were significant at $P < 0.05$



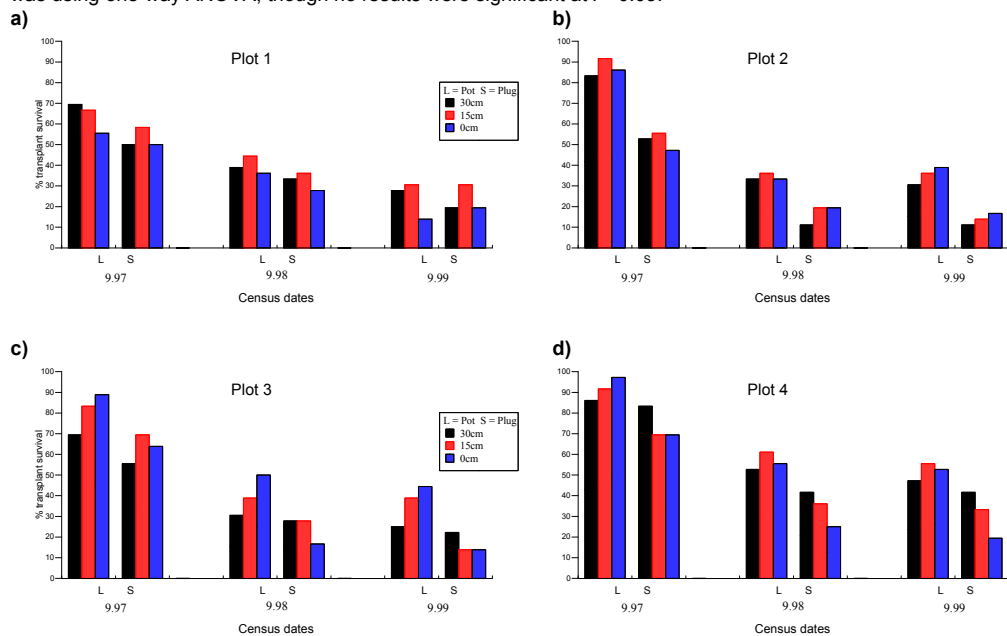
This result generally accords with that of the spring planting (**Chapter 7; Figure 7.07**), where gap size also did not markedly influence transplant survival levels across the plots.

The situation is however different for the spring implantation when the transplants are differentiated into the two sizes classes. **Figure 7.08** (**Chapter 7**) shows that, while pot plants never show a significant difference between gap sizes in mortality risk, all plots

had a least one census where plug plant mortality showed significant variation. In the case of Plot 2, there was a constant trend throughout the research period, where plug plant numbers were significantly higher in the 30-cm gaps. In contrast, **Figure 8.11** shows that, as for the size-undifferentiated results, there were no significant responses for the autumn plant cohorts, either for pot or plug plants. Also, no gap diameter showed any clear trend across the plots, in fact the largest gap size, had marginally the highest mortality risk.

In order to compare like-with-like, the spring planting data were reanalysed selecting only the same species as for the autumn planting, and only using the first three year's data (March 1994-1997). Under this limitation, the results were similar to that of the autumn cohort, with no significant differences between gap size for both total survival and size-differentiated survival across the plots.

Figure 8.11 Charts relating the significance of gap size on survival of the two sizes of transplant for plot data. Analysis was using one-way ANOVA, though no results were significant at $P < 0.05$.

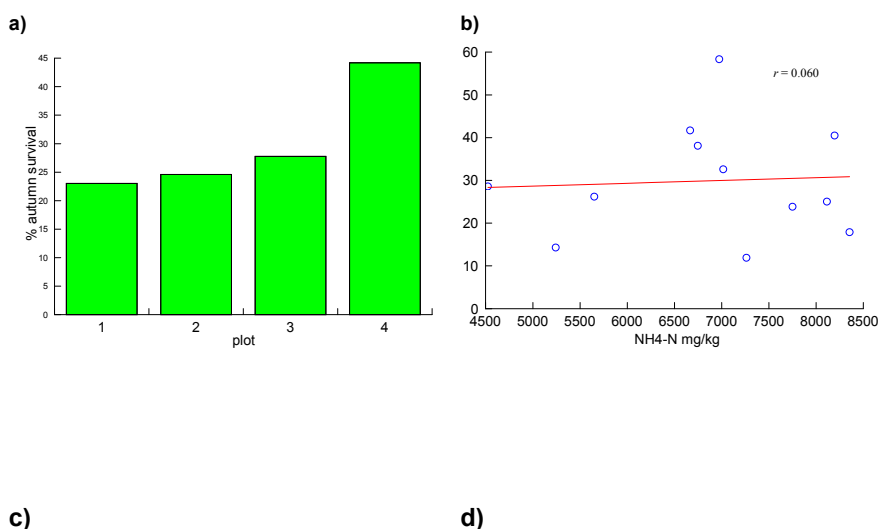


Interactions between transplant survival and productivity factors

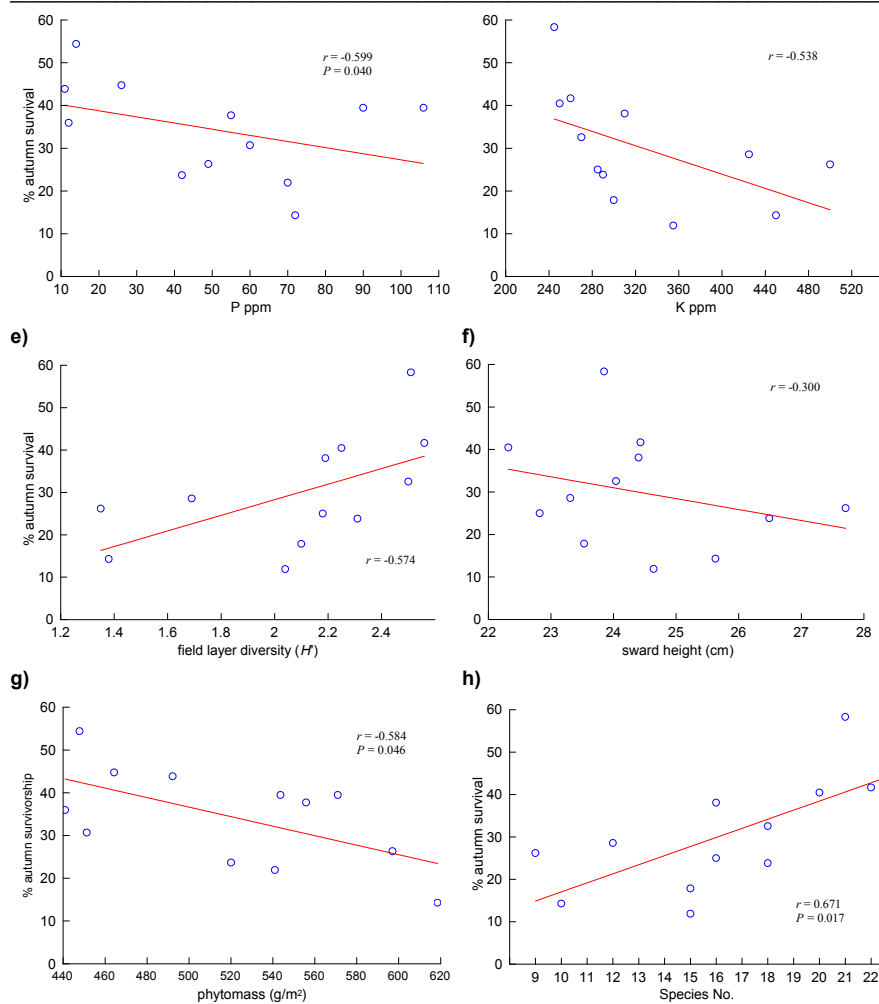
In order to offer further explanatory detail, a range of variables was statistically compared to the survival data. Of the three major nutrients (NPK) quantified from the grassland soils, only phosphorus (**Figure 8.12c**) displayed a significant (negative) relationship with autumn transplant survival. This result is a consistent finding throughout the study, and suggests this macronutrient is the controlling factor in the

productivity and inoculation resistance of these improved grasslands. This aspect is discussed in greater detail in **Chapter 4**. Four related grassland variables were also compared to the transplant survival data: field layer diversity calculated from the 1998 survey data (**Figure 8.12e**); average peak sward height from measurements collected between 1994-9 (**Figure 8.12f**); average peak phytomass collected from 1994-9 (**Figure 8.12g**); and field-layer species-richness derived from the 1998 survey (**Figure 8.12h**). Both diversity and sward height do not show a significant relationship with transplant survival, however, the direct measurement of grassland productivity – phytomass dry weight g/m^2 – produced a significant negative relationship with transplant survival, similar to the result from spring cohort. The comparison between soil phosphorus and autumn survival also showed a negative significant relationship, which may be expected from the results from **Chapter 4** suggesting that P is the major factor controlling peak standing crop. However, the most unexpected regression result was that for species-richness and transplant survival, as this relationship producing the strongest correlation ($P = 0.071$), even though diversity¹, as measured by the Shannon index, proved to have insignificant predictive power. A similar result was found for the spring cohort as well ($P = 0.022$), emphasising that swards with higher species number are likely to those that are more receptive to further species admissions.

Figure 8.12 Trend lines (least-squares linear regression except **8.12a**) showing the relationships between total transplant survivorship; and plot gradient, soil nitrogen, phosphorus, potassium, average sward height (6 years), average peak phytomass (4 years), and sward diversity (1998) Shannon Index. Correlation significance is given when $P < 0.05$.



¹ Shannon vs Spp-richness: 1994 $r=0.994^{***}$; 1998 $r=0.984^{***}$; 2001 $r=0.864^{***}$



Because of the multicollinearity of the explanatory variables, multiple linear regression was applied to compare the set of variables against transplant survival response (Jongman *et al* 1995). When all the above independent variables were *Entered* as one model, together they explained 88% of variation in autumn transplant survival (Norušis 1998). When *Stepwise* variable selection was applied, the variable SPECIE98 was assessed as the best predictor ($R^2 = 0.450$), thus the analysis estimated that species richness of the sward in each subplot was most important variable in explaining the trend in transplant survival. As *species richness*, *subplot* and *diversity* are essentially environmental proxies, their removal allowed for a more accurate evaluation of the environmental factors controlling survivorship. The next model-build, minus the aforementioned variables, again using *Stepwise* selection (**Table 8.04**) presented *P2000*

Table 8.04 Results (model summary statistics) of stepwise multiple linear regression for prediction of transplant survival (dependent variable AUSURV99 = autumn cohorts, September 1999 census) using the above set of independent variables.

Model Summary						
Model	R	R Square	Adjusted R Square	Std. Error of the Estimate		
1	.599	.358	.294	11.1063		
a Predictors: (Constant), Phosphorus 2000 survey						
ANOVA						
Model		Sum of Squares	df	Mean Square	F	Sig.
1	Regression	688.850	1	688.850	5.585	.040
	Residual	1233.500	10	123.350		
	Total	1922.350	11			
a Predictors: (Constant), P2000 b Dependent Variable: AUSURV99						
Coefficients						
Model		Unstandardized Coefficients	Std. Error	Standardized Coefficients	t	Sig.
1	(Constant)	42.766	6.319	Beta	6.767	.000
	P2000	-.254	.108	-.599	-2.363	.040
Excluded Variables						
Model		Beta In	t	Sig.	Partial Correlation	Collinearity Statistics Tolerance
1	N	-.372	-1.272	.235	-.390	.708
	AVBIOMAS	-.333	-.979	.353	-.310	.558
	AVLUX	.310	.731	.484	.237	.375
	K2000	-.001	-.002	.999	-.001	.194
	AVSWDHGT	-.028	-.092	.928	-.031	.785

AVBIOMAS = average phytomass (1994-99); AVSWDHGT = average sward height 1994-99; AVLUX = average sward lux; P2000 = soil P measured 2000; K2000 = soil K measured 2000

soil phosphorus as the best predictor of autumn transplant survival. However, P only explained 36% of the variation in survival. This contrasts with the spring cohort where the single best predictor - field layer phytomass - explaining 64% of survival variation. Introducing further variables to the model in addition to P, using *Enter* selection (Norušis 1998; SPSS 1998), increased explanatory power. The single addition of AVBIOMASS (average phytomass) increased prediction to 42%, however, the only other factor to increase the model further was soil nitrogen ($R^2 = 0.55$). The same environmental factors: species number, sward height, phytomass, and NPK; for both 1995 and 2000 were applied against the 1999 transplant survival levels for both seasonal cohorts, again using stepwise multiple linear regression. The soil phosphorus concentration was selected as by far the best predictor of spring survival ($R^2 = 0.772$; $P = 0.000$). For the autumn cohort, species richness as censused in 1998 was the best predictor of survival ($R^2 = 0.45$). When species richness was removed from the model, soil phosphorus as measured in 2000 was the best predictor ($R^2 = 0.358$; $P = 0.040$), while the 1995 soil phosphorus levels were also significantly correlated ($r = -0.576$; $P = 0.050$)

In order to explore the effects of the above environmental factors on individual species survival, the data were compared using the Pearson correlation coefficient (r). **Table 8.05** presents the significant results for both seasonal cohorts as measured in 1999. For both seasonal cohorts, the same three species show significant interactions with the explanatory variables. Thus, it seems that the survivorship trends for *Centaurea*, *Leucanthemum* and *Malva* do not significantly follow that of the environmental factors. Otherwise, for the spring cohort, as with the regression calculations above, soil phosphorus seems to have the strongest (negative) influence on survival, followed by peak phytomass. Species-richness also positively correlates with *Primula* in particular. This relationship is even more apparent for the autumn cohort, with *Lotus* highly (positively) correlated to species richness. *Lotus* also shows significant results for all three soil nutrients, and positively in the case of nitrogen, posing the contention that *Lotus* may be significantly elevating soil N, though it is more likely that the factors that encourage the growth of other nitrogen fixers such as *Trifolium* spp., also enhance *Lotus* survival.

Table 8.05 Pearson (r) correlations for seasonal cohort survival (1999) for six phytometer species (*Scabiosa* was extinct), compared with the main environmental variables measured in 1999-2000. Only significant results are shown ($P < 0.05$). * = $P < 0.05$; ** = $P < 0.01$

Species	<i>Centaurea nigra</i>	<i>Leontodon hispidus</i>	<i>Leucanthemum vulgare</i>	<i>Lotus corniculatus</i>	<i>Malva moschata</i>	<i>Primula veris</i>
SPRING						
Species98		0.593*				0.729**
AVBiomass		-0.607*		-0.655*		-0.708**
N						
P		-0.745**				-0.855**
K						-0.707*
AUTUMN						
Species98		0.584*		0.819**		-0.615*
AVBiomass						
N				0.582*		
P				-0.707*		
K				-0.801**		

In general, the above results suggest that measuring certain environmental variables may provide a direct means of predicting the survival of certain species. That is, it may be possible to establish soil fertility/productivity thresholds over which these variables have a significant negative effect on transplant survival. Therefore, perhaps the most important question for restoration purposes, is *which environmental factors, measured within the first year of inoculation, most strongly predicted final transplant survival?* To investigate this dimension, **Table 8.06** presents the results for correlations between the same species data and variables as used in **Table 8.05**, except that the explanatory variable data was collected at the beginning of the experiment (1994-5), and the species response data was from the end of the experiment (1999). Thus, significant correlations

may suggest whether the initial environmental records predicted the final transplant depletion outcomes.

Table 8.06 Pearson (*r*) correlations for seasonal cohort survival (1999) for six phytometer species (*Scabiosa* was extinct), compared with environmental predictor variables measured in 1994-95. Only significant results are shown (P <0.05).

Species SPRING	<i>Centaurea nigra</i>	<i>Leontodon hispidus</i>	<i>Leucanthemum vulgare</i>	<i>Lotus corniculatus</i>	<i>Malva moschata</i>	<i>Primula veris</i>	Total spring 1999
Species94							
Phytomass94		- 0.652*		- 0.578*		- 0.623*	-0.736**
Sward height94		- 0.609*				- 0.699*	
N95			- 0.615*				
P95	- 0.646*	- 0.785**		- 0.634*	- 0.646*	- 0.837**	-0.879**
K95					- 0.714**	- 0.860**	-0.710**
AUTUMN							Total autumn 1999
Species94				0.622*			
Phytomass94						- 0.624*	
Sward height94				- 0.696*			
N95							
P95						- 0.620*	
K95				- 0.708*			-0.576*

* = P<0.05; ** = P<0.01

While total spring transplant survival correlated significantly (negatively) with three variables, the total autumn cohort correlated only with one. However, soil phosphorus appears as the linking factor. Also, the results for the spring cohort contrast notably with that of autumn in that all species show at least one significant correlation with the independent variables. Though, once again soil phosphorus is the dominant variable, with five of the six spring cohort species showing significant negativity towards this macronutrient. The second governing variable is peak phytomass, which correlates with four species. Comparable to the results presented in **Table 8.05**, the spring cohorts of *Leontodon* and *Primula* also had the most correlations with the 1994-5 independent variables, though notably, the strongest (negative) correlation with *Primula* was with soil potassium concentration. As for the autumn cohorts, only *Lotus* and *Primula* showed significant correlations. For *Lotus*, soil P measured in 1995 was not a significant factor, though soil K was. *Primula* survival typically correlated significantly with soil P and phytomass. Overall, for both cohorts, in ranked order, the measurement of soil phosphorus was the most significant (negative) explanatory factor in transplant-species survival, followed by peak phytomass, and joint third, soil potassium and sward height.

Management treatments and transplant survival

Although the recipient swards exhibited structural changes due to the three management treatments over the three-year study period (see **Chapter 4**), no significant

effects could be detected in transplant survivorship by the end of the research period. In addition, when data were further stratified, there were no significant differences in survival between management treatments at the within plot level, or at the combined plot level ($F_{2,20} = 0.191$; NS). There were also no significant differences between treatments for individual species. The lack of significant differences in transplant survival due to management treatment may be explained by the fact that all subplots had the July hay-cut in common (see **Chapter 3**). This overall feature of management was perhaps important in moderating/ameliorating any differential effects management regime may have on transplant survival during the spring/aftermath treatment periods, just as management can mediate competitive interactions (Mitchley 1994). It is also probable that the influence of agriculturally elevated soil fertility massively over-rides that of management treatment effects in the initial, and medium-term restoration periods (Oomes & Mooi 1981; Gough & Marrs 1990). As succession and fertility depletion continue, in the *longer term*, it is likely that management will become an increasingly important factor in transplant regeneration and recruitment (Berendse *et al* 1992).

DISCUSSION

The present study was chiefly concerned with looking for divergent trends in mortality risk between autumn planted and spring planted transplants. In addition, by planting the autumn 1996 cohort, it was also possible to test if some of the findings from the earlier spring cohort could be repeated, and thus affirm or deny predictive aspects of this research (van Duren *et al* 1998). Within this context, it is apparent from the above results, that many of the conclusions outlined in **Chapter 7** are consistent with the findings from this experiment: i) transplant survival followed that of the agricultural improvement gradient; ii) mortality risk varied greatly amongst species; iii) the size of transplant, as a whole, did significantly affect survivorship. However, transplant mortality was significantly conditioned at the plot scale by initial size, and the ratio of pot-to-plug survivorship differed between species; iv) artificial gap creation using herbicide did not appear to significantly aid transplant survivorship, and the gap sizes used in this study were seemingly ineffectual in assisting establishment; v) soil

phosphorus emerged as the most significant (negative) explanatory variable in transplant survival.

The results also display differences between the two seasonal cohorts. Although not a statistically significant difference ($P = 0.14$), overall, autumn survival was 8% higher than for spring, which translates into the persistence of 79 more transplants. The survivorship curve for autumn (**Figure 8.02a**) was far less steep than that of spring (**Figure 8.02b**), exhibiting a more recognisable Deevey Type II curve, which is more consistent with natural herbaceous populations (Hutchings 1986). The curve is indicative of an average depletion rate, which is relatively constant and linear over time, rather than the rapid slump in transplant numbers experienced with the spring cohort.

Another difference between the seasons was the lack of significant differences between the plot survival levels for the autumn cohort. Whereas the spring planting levels showed a clear division between the survivorship of the two most improved plots (1 & 2) with the two less improved plots (3 & 4), there was a general convergence of transplant survival in the autumn implantation. Even at the subplot level only Subplot 10 evinced a significantly different survival profile. It is possible that after two and a half years the management treatments, especially the universal July hay cut, had ameliorated the resistances of Plots 1 and 2 to inoculation (Bakker 1989; Bobbink & Willems 1993; Anderson 1995) and thus reduced transplant mortality risk. Certainly the survival level for Plot 4 was least changed, as management-mediation would intuitively have the least impact on the *least* productive grassland environment.

One reason why the autumn cohort had a numerically higher survivorship than spring may be that autumn could be a better season for implantation. An analogous area of interest is tree planting best practice (Brooks 1980; Agate 2000). Arboricultural experience suggests that hardy deciduous trees are best planted before Christmas, and preferably immediately after the top growth becomes dormant in autumn (Agate 2000), as the soil is still 'warm' and also moist, thus encouraging continued establishment root growth in readiness for spring. Tree transplants are quoted as surviving spring

implantation quite adequately, but are more likely to suffer from drought than if planted in the autumn or early winter (Brooks 1980; MacDonald 1986). Evergreen trees are perhaps a better comparison with most perennial herbaceous plants with continuous rosette foliage. Brooks (1980) recommends they are best planted either early or late in the season, though in dry areas early autumn planting is best for most species, to give the trees a chance to become established before spring droughts. Where winter waterlogging is frequent, the suggestion is that spring implantation may avoid this mortality factor. Cell-grown or containerised trees and shrubs are a further comparative to container-grown herbaceous transplants, are, which in theory, are plantable at any time of year. However, Agate (2000) considers that, even for this stock, autumn planting should be the rule, especially during September. Horticultural perception (Johnson 1984), as for forestry, is that for bare-rooted stock, late autumn is the preferable season for transplanting as the plants are shoot-dormant but the soil should be still warm enough for the roots to grow and expand ready for the high system demands of spring and summer. Dixie & Bisgrove (1996) also advise that the best season for planting plug transplants is autumn, as the plants can establish well for the same reasons, and the soft ground conditions also make implantation easier. However, the possibility of heavy frosts during the winter increasing mortality after autumn planting may be a countervailing factor (Watson & Hack 2000). Invertebrate predation, and molluscan predation in particular, may be also less in autumn than spring, as invertebrate activity will lessen with the onset of cooler temperatures in the autumn, and allow transplants to establish with reduced herbivory levels. In contrast, spring inoculation introduces nutritionally enhanced transplant foliage to a mollusc population activated by milder weather (Clear Hill & Silvertown 1994; Hanley *et al* 1996); the transplants are therefore under greater potential threat, and increased mortality risk

Drought is probably the most important mortality factor in initial transplant survivorship (Bisgrove & Dixie 1994; Luscombe & Scott 1994; Dixie & Bisgrove 1996; Gilbert & Anderson 1998; Handa & Jefferies 2000). The most useful common measure of water availability to growing plants is the soil moisture deficit. While the UK Meteorological Office collects this information, it can now be only obtained with substantial cost, even for academic purposes (G. Hood *Met Office pers. com.*). Thus, as a coarser measure of soil moisture content, average rainfall was used; the data were

gratefully received from an amateur meteorological recorder situated 2 miles from Bruton who supplies his data to the Met Office. **Table 8.07** summarises these rainfall statistics for the implantation seasons. Clearly the data indicates that for the local area, autumn is wetter than spring, suggesting lower soil moisture deficit in the autumn months. In turn, most inoculant species will

Table 8.07 Rainfall amounts for implantation periods.

Period	Spring March-May average (mm)	Autumn Sept-Nov average (mm)
1993-1999	60.9	97.8
1994	April (implantation month) 59.8	October (comparison) 131.7
1996	April (comparison) 62.7	October (implantation month) 89.5

probably profit in establishment terms by being planted in early autumn (Dixie & Bisgrove 1996), unless they are particularly susceptible to water-logging induced damping off and other fungal pathogens, e.g. possibly *Scabiosa columbaria* (Grime *et al* 1988; Wells *et al* 1989; Gilbert & Anderson 1998).

Usually, the period with highest mortality risk for natural herbaceous cohorts is considered to be when there is peak sward growth in spring and early summer (Al Mufti *et al* 1977; Bakker 1980; Oomes & Mooi 1981; Vermeer & Berendse 1983; Dunnett *et al* 1998). Surprisingly for the spring cohort, the highest mortality risk was during the winter period; obviously the season with the least active growth. Possible explanations for this phenomenon are advanced in **Chapter 7**. However, for the autumn cohort, the mortality risk is very similar for both six-month periods ($r = 0.981$; $P = 0.000$). Therefore, unlike the spring cohort, mortality risk seems relatively similar throughout the year. This may reflect the better establishment conditions for autumn implantation, thus equalising the bi-annual mortality risk. While these species-categories may seem to be apparent, year-on-year variations in weather for example may greatly affect competitive interactions and transplant establishment (Dunnett & Grime 1999).

As with the spring cohort, *Primula veris* and *Malva moschata* stand out as *Core* transplant species, with substantial survivorship levels across all the plots. These species seem to be relatively insensitive to seasonality in implantation. *Scabiosa* also seems insensitive to season for the opposite reasons. Over the same initial three-year period, the autumn cohort became extinct, and nearly extinct for the spring. While performance parameters were different for each season, this consistent and rapid

depletion (see **Figure 8.05b**) may be due to hostile receptor site conditions, and/or combined with its relatively short life span (Verkaar *et al* 1983; Grime *et al* 1988).

Although the autumn survival values were nevertheless generally higher than for spring 1994 (see **Table 8.02**), only one species - *Centaurea nigra* - had very significantly higher autumn survival. This result strongly suggests that *Centaurea* is best planted in the autumn, and perhaps the other species with notably higher autumn survival levels (*Leontodon hispidus* and *Lotus corniculatus*) should be preferentially planted in autumn as well (Luscombe & Scott 1994). While these species are relatively stress tolerant and can cope with well-drained and dry soils, the transplant establishment phase may impose further environmental stress. All three species are adapted to coping with droughty soil conditions by producing taproots, which penetrate to a considerable soil depth, enabling sustained water supply during summer peak shoot growth (Al-Mufti *et al* 1977; Grime *et al* 1988; Tilman & El-Haddi 1992). In ecological terms (Kendle 1992), it is probably crucial that transplants of these species are able to immediately commence deep root growth in order to establish their water supply and compete with neighbouring grasses (Fenner & Spellerberg 1988). If droughty conditions are prevalent at the time of insertion, as would be more likely in spring than autumn, then these species may not be able to establish effective root systems, and the implants may rapidly fail. With soil moisture deficit lower in the autumn, and therefore water not so limiting, these species may have a better chance to establish tap rooting in preparation for droughty conditions in the following summer (Dixie & Bisgrove 1996).

In terms of seasonality in transplant survival, rainfall amounts are more crucial for spring than autumn. Typically, autumn is wetter than spring, and drought related mortality is a greater possible negative influence on spring implantation (Watson & Hack 2000). Spring cohorts also face the possibility of immediate summer droughts, which diminish neighbour competition, but more importantly undermine effective root establishment. Alternatively, autumn cohorts may benefit from preceding spring and summer droughts, under condition that there is the average autumn soil moisture deficit, and average seasonal decline in temperature, which allow effective establishment conditions. Further monitoring is required to assess whether the differences in autumn

survivorship compared to spring remain, or continuing convergence takes place with on-going depletion.

Importance of initial transplant size on the survivorship of transplants

As with the spring cohort, all autumn censuses recorded higher pot survivorship than seedling-plug. Similarly, the pattern in mortality risk was also consistent across the plots, as all the plot data showed a significant differential between pot and plug survival in the early establishment phase, which continued at a non-significant level until the final September 1999 census. Plot 2 had the longest census string of significant size-differential (until June 1996). The spring cohort (25 species data) suffered a very similar pattern of pot-plug mortality to the autumn data. Plot 2 for the spring cohort also had the longest significant differential trend, up until the final 1999 census. However, when only the spring phytometer species combined-data are analysed, a different picture emerges (**Figure 8.07**). While typically pot survival is higher than plug, only plots 3 & 4 show any statistically significant disparity. This result may be explained by the curves for the spring cohort, which shows such rapid mortality for both transplant sizes, for all species other than *Malva* and *Primula*, that any possible species-specific significance is negated by the overall slump. Nonetheless, the final trend for both seasonal cohorts of the phytometer species is the same; that is, no plot maintained a significant differential for either transplant size. Despite this finding, Luscombe & Scott (1994) identify plugs as more prone to drought in the establishment period than pot stock because of their smaller root systems, especially in existing swards. In addition, Luscombe & Scott (1994) state that the principal advantage of using plugs is price, which can be a third of the cost of a pot plant. Thus, to make economic sense there needs to be a survivorship of more than three plug implants to every pot. **Table 8.08** displays the plug-to-pot ratio for both the spring and autumn cohorts.

Table 8.08 Summary of plug to pot survival ratios. Data for spring taken from 3/97 census; autumn 9/99 census.

Season	Ratio of plugs to pot transplants							
	Plot 1		Plot 2		Plot 3		Plot 4	
Spring	1.8		3		1.5		1.8	
Autumn	1.1		2.5		2.0		1.7	
Transplant size	pot	plug	pot	plug	pot	plug	pot	plug
Ratio spring:autumn	0.77	0.46	0.55	0.47	0.82	1.16	0.91	0.88

These results seem to indicate that, not only did Plot 2 produce the greatest disparity between implant sizes, but also apart from Plot 2, overall, the usage of plug plants makes better economic sense for enrichment schemes. Furthermore, **Table 8.08** also shows the survival ratio comparison between seasonal cohorts. All the results, except for plug plants in Plot 3, suggest that autumn implantation is the more efficient season for inoculation. Plug implants, in particular seem to benefit from autumn planting, possibly as a consequence of their drought-proneness (Luscombe & Scott 1994), and higher soil moisture in the autumn months.

Unlike the combined data, when the data are analysed at the species level, three species of the autumn cohort showed a significant differential in the final census between transplant sizes: *Centaurea nigra*; *Lotus corniculatus*; and *Malva moschata*. Again, three phytometer species of the spring cohort also showed a significant relationship, though two species were different to the autumn implantation: *Leucanthemum vulgare* and *Primula veris*. All of these species, for both cohorts, had higher pot survival than plug, apart from *Leucanthemum*. As with the spring cohort, the autumn *Leucanthemum* cohort had a higher survivorship level for plug than pot transplant, reinforcing the finding that it is probably more effective implanting this species as a seedling than mature plant. The charts of **Figure 8.09** provide an interesting comparison between the seasonal cohorts and the size cohorts. While this is a depletion trial, and all curves decline from 100% survival, the only seasonal curves to show a great disparity are for *Centaurea*, while other species, for one transplant size or the other, display remarkably similar trends, albeit with different margins. For example, the seedling-plug curve for *Malva* is very similar for both seasons ($r = 0.974$; $P = 0.000$). These similarities in survival trend may indicate the relative pressures of environmental factors on the assembly of transplant establishment. For instance, under these eutrophied soil conditions, differences in competitive vigour among sown and unsown grassland species become accentuated, and selection occurs when transplant species deplete and establish at different rates conditioned by soil fertility thresholds, and size of inoculum (Al Mufti *et al* 1977; Wells *et al* 1989).

Effects of competition-free gap diameter on transplant survivorship

Following on from the general findings from **Chapter 7**, this study suggests a more emphatic evaluation, that artificial gap creation before inoculation does not aid survivorship, even within all the experimental parameters such as gap diameter and inoculant size. Autumn planting may negate the main advantages of gap creation such as reduction of neighbour competition induced drought. **Figures 8.10-8.11** show that the gap sizes used in this study were essentially irrelevant to transplant survival, and the influence of the largest gap (30-cm diameter) could not be distinguished from that of no gap at all. The ineffectiveness of the gaps, as posited in **Chapter 7**, may be due the gap creation methodology i.e. use of glyphosate herbicide, rather than say, turf stripping (Luscombe & Scott 1994), or possibly the gap sizes used in the experiment may have been inadequate in terms of reducing either above- or below-ground competition (Morgan 1997; Agate 2000). **Chapter 6** also shows how rapidly the gaps are occluded, thus restricting the effective competition free influence to less than a year. However, the evenness of gap effect i.e. survival was not promoted for either of the spray gap sizes, at a significant level or not; suggests that as autumn is the least competitive period in terms of active plant interference, perhaps gap creation is not relevant. Certainly by summer, the following year, the gaps would have been largely occluded by vegetative infill from species such as *Trifolium repens* and *Holcus lanatus*, to the extent that the gaps are no longer “competition-free”, and perform ineffectually in reducing mortality risk. Looking at the survival trends when the data are split into the two transplant sizes (**Figure 8.11**), there are still no significant comparisons. While pot transplants have never shown a positive survival outcome in response to gap formation either for the spring or autumn cohorts, the lack of impact on the seedling-plugs seems surprising. The findings of **Chapter 7 (Figure 7.08)** show that the 30-cm gap size aided survival in the most productive swards, Plots 1 & 2 for plug implants. No similar trend is apparent in the autumn data, and in pure numerical order, seedling survival was highest in 15-cm gaps for Plot 1, and 0-cm for Plot 2.

It is also possible that the selection of phytometer species used in the experiment were those that least benefit from gap creation anyway. For instance, the suggestion from **Chapter 7** is that species such as *Primula veris* and *Malva moschata* are most

efficiently implanted directly into the receptor sward without gap pre-treatment. That is they are relatively uninhibited by productive sward conditions. *Leucanthemum* and *Scabiosa* experienced such rapid declines that gap creation was superfluous. However, intuition would infer that *Lotus*, *Centaurea* and *Leontodon* would benefit from gaps, in order to aid extensive root systems. However, as droughty conditions seem to impact most on the survival of these transplants, and autumn is a wetter season than spring, gaps do not positively alter autumn soil water deficit. Added to this, there are possible negative effects of gap creation on survival. Large gaps may increase transpiration leading to droughty conditions (Fenner 1985). Clearing larger areas of vegetation may encourage invasion of undesirable weed species such as *Cirsium* spp. or *Senecio jacobea* (Bisgrove & Dixie 1994). Bisgrove (1988) has suggested that gaps provide higher visibility to predators such as molluscs. The 15-cm diameter gap in Plot 2 may have actually increased predation on plug plants. Transplants in large gaps are also more vulnerable to digging animals such as rabbit, fox, badger and foraging corvids (rooks *Corvus frugilegus* in particular), as they are more conspicuous.

Response of transplants to sward and environmental variables

On the whole, a number of easily measured grassland fertility/productivity traits seem to explain most of the variations in transplant mortality risk. For the spring cohort, species-richness, species diversity, soil phosphorus, potassium, and particularly average peak dry phytomass (**Figure 7.09**) showed significant relationships with survivorship, with multiple linear regression estimating phytomass as the best predictor of variation in survivorship. Similarly, for the autumn cohort, species-richness, phosphorus, and phytomass (**Figures 8.12c&g**) were significantly correlated, though the effect of potassium was not significant. Omitting species-richness from the analysis, multiple linear regression advanced P as the most important explanatory variable for autumn cohort survival.

While natural communities have been shown to exhibit the much-discussed *hump-backed* relationship between plant community productivity and species richness (Al-Mufti *et al* 1977; Grime 1973, 1979; Liira & Zobel 2000), it is also widely recognised that grasslands with artificially elevated soil fertility/phytomass are associated with reduced species-richness/species diversity (Vermeer & Berendts 1983; Tilman 1993;

Kirkham *et al* 1996; Bakker *et al* 1998). The evidence presented here also supports the contention that inoculation resistance is also strongly related to peak phytomass, therefore significantly influencing the establishment of transplants (Tilman 1993; Davies *et al* 1999). For both seasonal cohorts, the subplots with the highest survival had maximum phytomass production of less than 500g/m², which compares with Al-Mufti *et al* (1977) and Grime (1979) who have observed that species-impooverishment of herbaceous communities is generally related to a maximum biomass of over 750 g/m² (Hodgson 1989), and Vermeer & Berendse (1983) who suggest >500g/m² for their grassland sites. The work of Tilman (1993) suggests that diversity is lower in productive grasslands because accumulated litter, and possibly lower light penetration inhibit germination and/or survival of seedlings, and thus decrease rates of establishment by new species. However, implantation of container-grown plants should circumvent these constraints on colonisation and establishment. What transplantation clearly does not achieve is the absolute avoidance of competitive exclusion losses under highly productive conditions. Peak phytomass does fluctuate most dramatically on soils that have been eutrophied by standard agricultural management, though in this work it is the average peak standing crop that correlates most closely with transplant survivorship (Dodd *et al* 1994). The contention of Tilman & El-Haddi (1992) that biomass seems to be an indicator of survivability also holds for transplants as for natural populations. Apart from the very robust species such as *Primula veris*, *Malva moschata* and *Geranium pratense*, apparently transplant mortality risk is not so much avoided as postponed (Cavers & Harper 1967; van Duren *et al* 1998; Hopkins *et al* 1999).

Naeem *et al* (2000) present data showing that biomass strongly covaries with soil phosphorus and potassium. Furthermore, Gough *et al* (1994) raise doubts about the overall predictive value of biomass, suggesting that community production has a limited capacity to forecast species richness across a broad range of habitat conditions. Their findings for marshland grassland communities suggest that realized species-richness is controlled primarily by environmental variables such as the soil nutrient base rather than biomass itself. While grassland productivity is usually increased in conventional farming using the synergistic effects of NPK addition (Crofts & Grayson 1999), the main fertility/productivity parameters, most researchers advance soil

phosphorus as the crucial and intransigent arbiter of grassland change through agricultural improvement (Jeffrey & Pigott 1973; Marrs & Gough 1989; Anderson 1995; Willems & van Nieuwstadt 1996; Gilbert & Anderson 1998; Brady & Weil 1999). In their study of lowland meadows, Kirkham *et al* (1996) advocate P as more important than N in determining both biomass and botanical change. In both cases the effects were small when substantial amounts of N and K were applied without P. When P was included biomass increased very significant and species diversity severely reduced. The results from the present research also suggest soil P as the central trait controlling transplant establishment. Multiple linear regression (**Table 8.04**) showed that soil P was the most important predictor of autumn cohort transplant survival, i.e. the higher the soil P, the lower the transplant survivorship. Also, for the spring cohort, although phytomass was the strongest predictor of implant survival, soil phosphorus level was also an important explanatory variable. For conventional agricultural purposes, grasslands are fertilised with P in order to increase root growth and structural dominance of the preferred species, especially grasses (Brady & Weil 1999). This would suggest that transplants are negatively affected by P eutrophication through enhanced neighbourhood root/shoot competition from dominant species (Kirkham & Wilkins 1994; Mitchley 1994; Mountford *et al* 1994). By definition, the transplant species used in enrichment are subordinate or satellite species (Davies *et al* 1999; Hopkins *et al* 1999), which are in natural abeyance to the dominant species, and this relationship is massively exacerbated where inorganic fertilisers are applied (Grime 1998; Willems & Bik 1998).

For practical purposes, it is valuable to be able to identify quantitative measurements, which can be used to predict the success of restoration techniques (van Groenendael *et al* 1998). Certainly, elucidation of the various environmental factors implicated in the respective transplant survivorship quotients can aid effective resource management. Parker (1995) suggests that before restoration is undertaken on a given site, there is a need to measure soil fertility, especially extractable phosphorus and mineralisable nitrogen, in order to be able to estimate whether:

- a) Nutrient levels are low enough that fertility reduction is not needed.
- b) Fertility reduction is needed.
- c) Fertility is so high that there is the question whether fertility reduction can be achieved in a realistic time frame.

Within the present research scheme, the results for both seasonal cohorts suggest a number of factors that if measured before inoculation, will provide a gauge as to inoculation possibilities. Proxies for the underpinning environmental factors, such as species richness and sward diversity (**Figure 8.12a&h**) produced some of the strongest correlations with transplant survival, and are easy to measure before undertaking inoculation with implants. Significant interactions with the species richness of the receptor swards suggest that this parameter in particular, significantly covaries with transplant survival. Thus, ranking and scaling the mortality risks using species richness may be a rough and ready means of predicting the levels of possible transplant losses, and therefore which species are likely to establish and which are likely to fail over the long term. Ironically, the presence of natural populations of transplant species may not be necessarily an infallible measure of potential survivorship. Even though *Lotus* occurs naturally in a diffuse population in the field containing Plot 4, *Lotus* transplants had poor survival in the spring cohort, and though higher for the autumn cohort, not significantly so (Berendse *et al* 1992).

Perhaps the most explicit demonstration of which variables are the best indicators is to explore the before-and-after scheme presented in **Table 8.06**. Here the explanatory variables recorded in 1994-5 at the beginning of the research are compared with the transplant survival outcomes at the end of the research. Using this perspective, species richness recorded at the experimental outset, does not seem to be an important predictor. Phytomass, however, strongly correlates with the spring cohort, though not the autumn. It is possible that the far fewer significant correlations for autumn may be because the experiment has not run long enough (>5 years) to amplify underlying trends. However, once again, measurement of soil phosphorus demonstrates the best potential for predicting survival for both seasonal cohorts. Using the standard agricultural index (MAFF 2000) for P levels is a simplified means of interpreting the sampling results in terms of potential transplant mortality risks². Management decisions can then be made as to whether enrichment is viable, and if so, which particular species are viable components to be added to the restoration scheme. The suggestion here is that only the most robust species should be used where P index levels >2. Only Plot 4

has P levels <2, and Plot 1 has a P index of 5. By this reckoning, enrichment should only be carried out in Plot 4. This is in accord with Dixie & Bisgrove (1996) who state that P readings below 15ppm (index <2) are “ideal for wild flower establishment, but projects can still be successful at phosphorus of 30ppm (index 3)”. However, thorough investigation of precise productivity/fertility thresholds affecting individual transplant-species establishment requires greater depth of data analysis than can be afforded here, further monitoring (Gilbert & Anderson 1998), and extensive detailed controlled experiments using a broader range of phytometer species (Cavers & Harper 1967).

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² Comparing the seasonal data against soil phosphorus index results in significant correlations: spring $r = -0.876^{**}$; autumn $r = -0.653^*$

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