



- CHAPTER 7 -

ENRICHMENT OF AGRICULTURALLY IMPROVED GRASSLAND USING TRANSPLANTS: ANALYSIS OF SURVIVORSHIP

There are grasslands in Gloucestershire] in the “extreme of neglect. Their surfaces hid, and in a manner occupied, by restharrow and the anthill fescue: a stage of distemper which nothing but the plow can cure. An oak-wood may be an object of pride to its owner; and grows venerable as it grows old: but a rough grass-ground is an eye-sore; a scab which disfigures the face of a country; and grows offensive with age.”

Mr Marshall (1789) *The Rural Economy of Gloucestershire*. Gloucester, pp. 170-195.

SUMMARY

1. Restoring agriculturally improved grasslands purely by sympathetic management and relative proximity to species-rich sites is nowadays unlikely to be successful. Nevertheless, for sound reasons it is often preferable to try to enrich improved grasslands rather than to destroy them and start again. Therefore it may be necessary to inoculate grasslands with transplants. Enrichment using container-grown transplants has been found to be an effective way of introducing or reintroducing plant species.

2. Twenty-five species were used in the research. Three hundred were inserted into each subplot, amounting to 3600 transplants in total. Fifteen of the species were planted as dual-size transplants (9-cm pot and 2-cm plug). In addition, three diameters (30-cm, 15-cm, 0-cm) of competition-free gap were created using herbicide. A third of each of the transplant sizes was inserted into each of the gaps. After implantation, the transplants were treated with three management regimes: mowing; cow grazing; sheep grazing; including a collective hay cut in July of each year. Evaluation of species enrichment success was achieved by monitoring the survivorship of the transplants over a five-and-a-half year study period.

3. Of the initial input of transplants inserted into the four treatment plots, by September 1999 only 271 (7.53%) of the transplants were still alive. Over 50% of all the transplants died during the first year after implantation. From the initial cohorts of the 25 transplant species, six species were completely extinct. *Campanula glomerata* 6/96, followed by *C. rotundifolia* and *Scabiosa columbaria* (3/98), *Silene latifolia* (9/98), *Briza media* (6/99), and *Plantago media* (9/99). In contrast, three species - *Geranium pratense*, *Primula veris* and *Malva moschata* - have maintained highest survivorship throughout the study period.

4. The size of transplant, as a whole, did not significantly affect survivorship, though, of 1080 pot transplants inserted in 1994, 149 (13.8%) were still alive in 1999, compared to only 66 (6.11%) plug plants remaining. However, transplant mortality was significantly affected by initial size at the plot scale, though the gap between pot and plug survivorship was only relatively constant in Plot 2 throughout the study period. The ratio of pot-to-plug survivorship also differed markedly between species.

5. In general, artificial gap creation did not appear to significantly aid transplant survivorship. When comparing total transplant survival in each of the four plots for the three gap sizes, there were only two censuses where there was a significant difference in survival. With respect to transplant size, gap creation did not significantly contribute to pot transplant survival in any of the plots over the study period. However, there were instances from all the plots when plug survival was significantly affected by gap formation, though only in Plot 1 was this consistent up until the final census.

6. Overall transplant survival (positively) followed the gradient of agricultural improvement, though mortality risk varied greatly between species. Transplant survival was strongly negatively correlated with soil P and K concentrations, and peak biomass. There was no evidence that the three management treatment regimes had a significant impact on transplant survival i.e. no treatment was preferential.

7. On the basis of survivorship, the transplants could be classified into Core species (highest survival), Intermediates, Marginals and Extinct species. In addition *Hordeum secalinum* went Feral. In terms of size, the categories were: a) species with higher survivorship for pot than plug transplants; b) species which established significantly better as plug than as pot transplants; c) species which suffered equally high mortalities as either pot or plug transplants.

Keywords: agriculturally improved grassland, enrichment, inoculation, competition free gap, transplant, pot, plug, survivorship, establishment, biomass, management.

INTRODUCTION

Intensive agricultural management over the last fifty years has resulted in extensive loss of species-rich, semi-natural grassland in Britain (Fuller 1987; Hopkins *et al* 1995; Mitchley 1998; SSDC 1998). This decline has led to interest in methods of recreating floriferous grasslands (Wathern & Gilbert 1978; Wells *et al* 1981, 1989; Parker 1995; Crofts 1999a), and also in techniques to reverse the effects of agricultural intensification in suitable extant grasslands (Oomes & Mooi 1981; Wells 1983; Bakker 1987; Berendtse *et al* 1992; Frame *et al* 1994; Tallowin *et al* 1995; Hopkins *et al* 1999). 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). In addition, Anderson (1995) proposes that achieving a diverse sward is dependent on careful management, low competition and the availability of colonization gaps. However, because areas of species-rich, unimproved grasslands are often rare and fragmented (Strykstra *et al* 1998; Crofts 1999b), trying to restore agriculturally improved grasslands purely by sympathetic management and relative proximity to a diverse source of propagules, is generally still unlikely to be successful (Berentse *et al* 1992; Willems & Bik 1998). Though, for sound ecological, conservation and economic reasons it is often preferable, where appropriate, to try to enrich improved grasslands rather than to destroy them and start again (Wells *et al* 1989; Bisgrove & Dixie 1994).

In order to increase the speed of species diversification, it may be necessary to inoculate grasslands with seed or 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-depauperate swards with container-grown transplants has often been found to be an effective way of introducing or reintroducing plant species, but the implications for the long-term functioning of the system have not always been explored in detail, and there still remains a paucity of research from which to draw firm conclusions (Wells *et al* 1989; Kendle 1992; Anderson 1995). Certainly, there are a number of key advantages to using transplants rather than

sowing seed or relying on natural recruitment of new species. Transplanting by-passes the critical and complex early stages of (re)colonisation, and provides the possibility for rapid establishment of populations of species that may take a very long time to invade by natural processes (Gibson & Brown 1991; Hutchings & Booth 1996; Kline 1997; Francis & Morton 2001). It is also a technique that makes the most efficient use of those species with low rates of seed production or complex germination and establishment requirements (Ehrlén & van Groenendael 1998). Also, the use of transplants allows for greater control of the density and spatial organisation of plants than sowing seed (Handa & Jeffries 2000).

It is apparent that there are key aspects of transplantation methodology, which are in need of further research (Wells *et al* 1989). Species selection, for example, is one of the most critical parameters, though some authorities argue that even the genetic strain of each wild species is a critical parameter (Allen 1992; Everett 1999). The relative establishment and survivorship of species is, however, primarily related to an amalgamation of site-specific biotic and abiotic environmental factors, acting on the transplant, with those species most suited to the site conditions performing most successfully (Jones & Hayes 1999). Wells *et al* 1989 suggested the term “environmental sieving” to describe this process, and can perhaps also be referred to ironically as *un-natural selection* due to the impact of human intervention in modern agricultural grassland system. Hopkins *et al* (1999) established that in their trials inoculating species-depauperate grasslands with plug transplants, the most successfully establishing species were those with wide ecological amplitudes, tall growth habits and strong perennial root systems. Certainly, the present work is applied to the question of whether or not there is a level of soil fertility at which the productivity of the existing sward, and the competitive dominance of grass species in particular, may be too great to permit the introduction of more desirable stress-tolerant species (Al-Mufti *et al*, 1977; Marrs & Gough, 1989; Berentse *et al*, 1992; Mountford *et al* 1994; Kirkham *et al* 1996). Thus comparing survivorships over time may produce a repeatable hierarchy of species (Silvertown & Dale 1991), or re-assembly inventory (Pywell *et al* 1997), relating to the degree of agricultural improvement. Also, a crucial question for all attempts at species enrichment is the determination as to which management techniques will promote the greatest survival of the pioneer individuals and which will ultimately foster the

establishment of their progeny (Bakker *et al* 1980; Anderson 1995; Gilbert & Anderson 1998).

Initial size of transplant is another parameter, which may be a determinant of enrichment success (Davies 1987; Fenner & Spellerberg 1988; McLellan *et al* 1997; Davies 1999). It would seem intuitive that the larger the transplant, the better in terms of competitive capacity, or at least ability to withstand competitive exclusion pressures (Silvertown & Dale 1991). In turn, initial transplant size could effect establishment and longer-term regenerative potential. However, tree-planting studies suggest that transplant size can be a complex issue. Thus, while a 2-m tall whip may be better at coping with immediate neighbour competition from weeds than a 20-cm specimen (Kendle 1992), the more extensive root system of the 2-m transplant may be subject to greater establishment stresses, possibly reducing survivorship and retarding relative growth rates (Parker 1995). Similarly, for herbaceous transplants, seedling-plug transplants may have lower survivorship due to short stature and small root volume, but once past the “crunch” phase of early establishment (Weins 1977; Kendle 1992), they may quickly attain the size of a mature specimen, thus negating the efficacy of using more expensive pot-grown transplants (Bisgrove & Dixie 1994).

Inserting transplants into artificial gaps is another way in, which the restorationist can attempt to aid transplant establishment (Fenner & Spellerberg 1988; Anderson 1995; Davies *et al* 1996; Gilbert & Anderson 1998; Jones & Hayes 1999). The theory is that by killing off the vegetation from the immediate vicinity of the transplantation site, neighbourhood competition is reduced favouring higher survivorship and better establishment (Davies 1987; Hitchmough *et al* 1996; Pywell *et al* 1997; Agate 2000). These gaps may circumvent the stresses and other mortality factors involved in natural recruitment such as competition for light, water, nutrients and the stochasticity of natural gap formation (Cavers & Harper 1967; Silvertown & Smith 1988; Hitchmough *et al* 1996; Morgan 1997; Agate 2000). However, species are not all equally gap-sensitive (Fenner 1978), and Burke & Grime (1996) assert that the “identity of the invader and its associated functional attributes are crucial in determining how resistant a community is to invasion.” Clearly the size of gap (Goldberg & Werner 1983; Bisgrove & Dixie 1994; Bullock *et al* 1995; Pakeman 1998), and method of gap creation (Bakker *et al* 1980; Wells *et al* 1989; Burke & Grime 1996; Pywell *et al* 1997;

Agate 2000) are of major interest, and these aspects are addressed in more depth in **Chapter 6**.

The aims of this Chapter are to compare the survivorship of pot-grown adult transplants and seedling-plug transplants over a three year establishment period when inserted into grasslands with differing agricultural productivities - and by implication - differing inoculation resistances (Cavers & Harper 1967; Burke & Grime 1996; Naeem *et al* 2000). In addition, the effects of planting into artificial competition-free gaps on the survival and establishment of the above transplants were also studied. The present write-up centres on transplant survivorship data, whilst analyses of the performance and recruitment of the same transplants are presented in **Chapter 9**.

METHODS

Study site and experimental design

The study was undertaken on an 11-ha private nature reserve in Somerset, UK. The vegetation history of the site is described in full in **Chapter 2**. The study grasslands have been used for pasture and hay production over the last century, and over the last 50 years they have been subjected to varying degrees of fertilizer input and ploughing/reseeding. The experimental plots were established on four areas of relatively homogeneously structured grassland, forming a succession of improvement, from the most improved (Plot 1), to the least improved (Plot 5). As Plot 5 was already species-rich, this site was used as a reference community only (White & Walker 1997) and not subjected to treatments.

Each plot had dimensions 60-m x 30-m, the angles of which were marked out with softwood posts. The initial vegetation was described in each plot in 1994, and initial soil analyses for total nitrogen, potassium, phosphorus, organic matter and pH were completed in 1995 (as summarised in **Chapter 2**). Ordination and cluster analyses justified the preliminary observations that the swards were significantly different in species structure. The results of the soil analyses also affirmed these observations, showing that there were significant differences in soil fertility for P and K, with the highest levels in Plot 1 and lowest in Plot 5. The total N levels followed the trend of

soil organic matter content, with the highest level in Plot 3, which was the only agriculturally improved plot not to have been ploughed in the last 50 years

The research was established within the experimental layout as described in **Chapter 3**. The four experimental plot areas were given an initial cut in April using a tractor powered “Rotaflail” silage cutter and the arisings raked and taken off site. This was undertaken to level the sward, which had grown up during the winter to approximately 10-cm, so that the 12-m x 25-m planting areas within the subplots could be more accurately measured, and transplants inserted. The corners of these internal areas were marked with short softwood posts. The ends of the 1-m-spaced planting rows were located using cord marked out at the required 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. The internal implantation areas were mown again, prior to spraying, to a height of 5-cm using a domestic rotary mower. The arisings were again raked and removed.

The planting scheme was planned on paper copy in the form of a matrix representing each plot of 36 rows, divided into subplots of 12 rows. This allowed for the transplant species to be randomised within each row, meaning that each species had equal frequency throughout the subplot (i.e. each row contained a representative of each species). In all, 3600 transplants were planted, 900 in each plot and 300 in each subplot. The gap and size distributions were randomised on a subplot rather than a row basis. One-third of each species (4 individuals) were introduced into each gap diameter type. Unfortunately, it was only possible to get plug plants for fifteen¹ of the species used, therefore of these fifteen, half of the transplants (six) were of each size. The row-by-row planting commenced on the 27th April 1994, and paper copies of the planting schemes were subsequently used as recording forms.

Transplant species, size and gap width

The four experimental treatment plots (plots 1-4) were each divided into three subplots, and into these were inserted 12 individuals of 25 perennial grassland species, amounting to 300 transplants per subplot. The species were chosen as a representative

spectrum of life histories/established strategies (Grime 1979; Stace 1991), with the majority occurring in unimproved, species-rich grasslands in the local area (Green *et al* 1997). *A priori* assessment of the ecology of each species (Grime *et al* 1988) meant that they might be used as indicators (phytometers *sensu lato* Cavers & Harper 1967) of the resistance of grasslands with different agricultural improvement levels to invasion, colonisation, and in this specific context, as the degree of resistance to restoration. Thus, at one end of the scale, *Primula veris*, *Malva moschata* and *Geranium pratense* were chosen for their apparent robustness in competitive swards (Bisgrove & Dixie 1994), and *Scabiosa columbaria* and the two *Campanula* spp. for their relatively high sensitivity to, and intolerance of, fertile grassland situations (Grime *et al* 1988).

In order to further assess the importance of key variables on establishment, the effect of transplant size was evaluated. Equal numbers of two sizes of transplant for 15 of the 25 species were used: mature 9-cm potted plants with root volumes of 300-ml; and 2-cm seedling plugs with root volumes of 22-ml. The pot transplants were approximately 10 months old and of reproductive size. The plug transplants were between 2-4 months old. By using these two sizes of plant, a comparison could be made between the relative mortality rates suffered by adult plants as opposed to juveniles when inserted into productive-competitive grassland.

To evaluate the importance of reducing neighbour competition on transplants, three artificial 'competition-free' gap diameter types were applied in the experiment. Gaps of 30-cm, 15-cm, and 0-cm (i.e. no gap), were created to assess their efficacy in improving transplant survival and establishment. These were formed using glyphosate herbicide (Agate 2000) sprayed over plastic stencils with the required diameters. The transplants were inserted when mineral soil became exposed. The experimental plots were set up in the winter of 1994, and gaps created in early February. The transplants were inserted into the subplot swards in late March/April 1994 at spacings of 1-m. Each row of transplants contained one representative of all of the 25 species, and the species positions were randomly allocated within each row. Transplant size and gap size were distributed randomly throughout the whole subplot.

¹ Kindly supplied by High Value Horticulture, Colne House, Oxford Road, Uxbridge.

Management treatments

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 conducted with a rotary mower and grass box, mimicking grazing by cutting the grass to 50-mm twice in the spring and three times in the autumn.

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, possible mortality 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 analyses

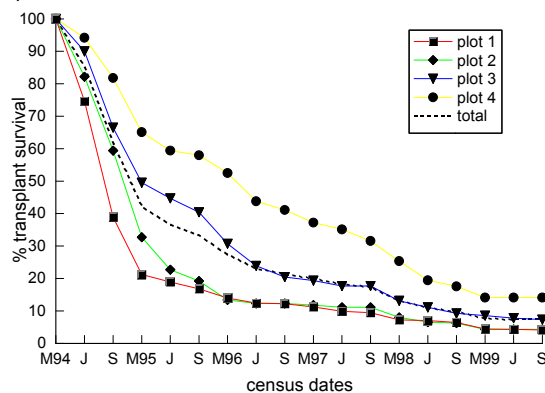
Data were analysed at both subplot and plot scales, though primarily at the plot scale as grassland management treatments seemed to have little identifiable impact on transplant establishment (Davies *et al* 1999). Shannon (H') diversity index and % similarity cluster analysis were used to describe aspects of the survival data (Kovach 1998). 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 (Norusis 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) was used to examine the relationships between key environmental variables and transplant survival. Further elucidation of the findings from the paired linear regressions were explored with stepwise multiple regression in order to directly compare the predictive validity of all the key environmental variables (Norušis 1998). All statistical analyses were conducted using SPSS ver 8.0 (1998) and MVSP ver 3.0 (Kovach 1998).

RESULTS

Of the initial input of 3600 transplants inserted into the four treatment plots in March 1994, five-and-a half years later (66 months), only 271 (7.53%) of the transplants were still alive. **Figure 7.01** shows the survivorship curves for the four plots over the monitoring period, and includes the combined-plot (total) curve for comparison.

Figure 7.01 Survivorship curves for all transplants over the five and a half year study period.

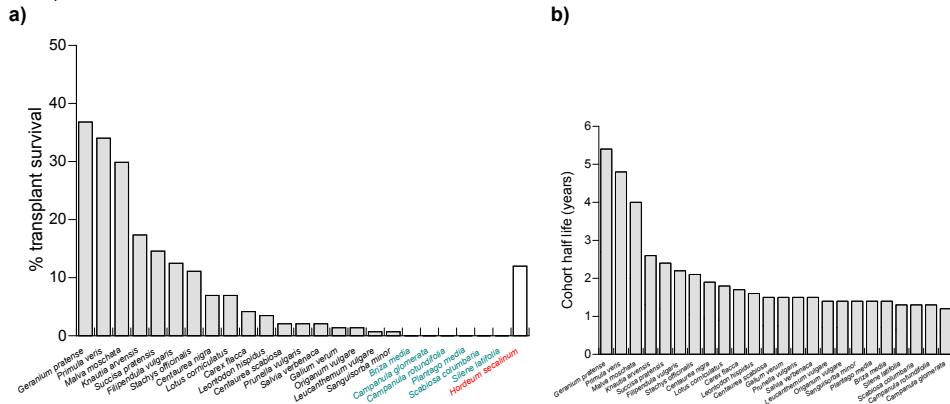


What is readily apparent from these curves is the huge mortality suffered by transplants in the early establishment period in plots 1-3. The curve for *total* transplants shows that over 50% of all the transplants died during the first year after implantation. After this rapid cull, from 1995 onwards, the mortality rates began to decrease, though losses continued up until the final census. The overall curve profile fits the Deevey Type III classification where in natural populations young plants suffer a high mortality risk, which declines with age (Hutchings 1986). The survival curves also fit in with the *a priori* ranking of improvement (see **Chapter 2**), with the most improved sward Plot 1 experiencing - at least initially - the highest mortality, and Plot 4 the lowest. However, while plots 3 and 4 have maintained their survival rank throughout the experiment, transplant depletion has led to levels converging for Plots 1 and 2.

Unexpectedly, the autumn and winter months between 1994 and 1995 continued the trend of high mortality even though this relatively dormant period would usually be considered the least difficult for the survivorship of transplants due to the low level of growth-related competitive interference (Dodd *et al* 1994). However, the effects of damage through hay cutting in July, and defoliation by management treatments in the aftermath period may have led to the death of small and weakened individuals during the winter months.

From the initial cohorts of the 25 transplant species, by September 1999, six species-cohorts were completely extinct. *Campanula glomerata* was the first species to be lost from all the plots by the summer of 1996 (Figure 7.02), followed by *C. rotundifolia* and *Scabiosa columbaria* (3/98), *Silene latifolia* (9/98), *Briza media* (6/99), and *Plantago media* (9/99).

Figure 7.02a Ranking of total transplant species survival from September 1999 census. Includes 'extinct' species (green), and notably *Hordeum secalinum* (red), which has expanded from its inoculation sites and become 'wild' in its distribution in Plots 1, 2 & 4 (see Chapter 9). **7.02b** Half life calculations for surviving species cohorts (Watkinson 1986).

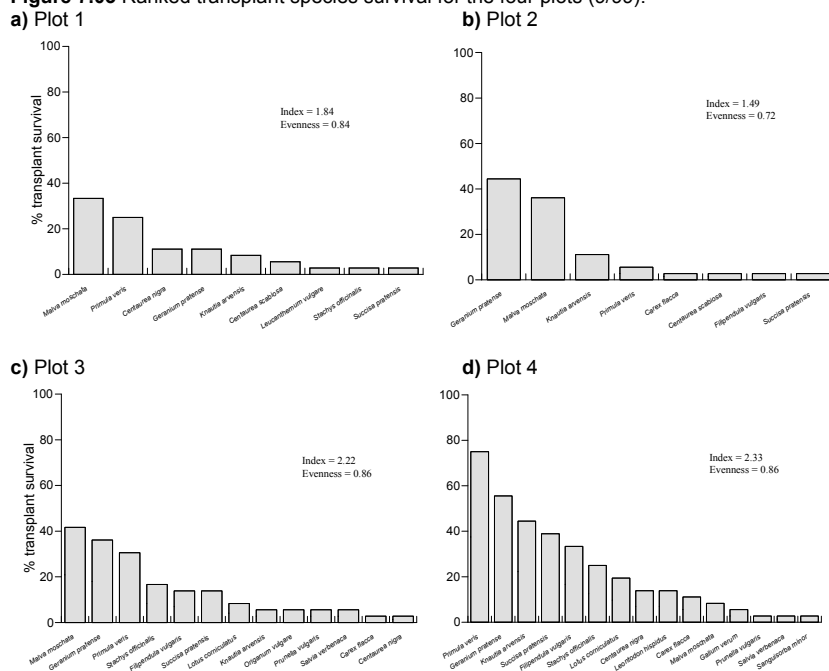


Surprisingly, the survival of *Leucanthemum vulgare* was very poor even though it is a common constituent of semi-improved grasslands (Rodwell 1991). On the research site as a whole, *L. vulgare* is restricted to one headland of the meadow containing Plot 3 (Paddock), and is a widespread, and expanding component of the field containing Plot 4 (Clayground). *Prunella vulgaris*, which is a relatively ubiquitous species, with more weedy characteristics comparative to *L. vulgare* (Grime *et al* 1988), was similarly severely depleted over the research period.

The outstanding species at the opposite end of the survivorship spectrum are *Geranium pratense*, *Primula veris* and *Malva moschata*. These three species have remained

highest ranking throughout the study period, though within this *survivor's caucis* the rankings have frequently fluctuated, especially at the within-plot scale. Calculating the mean rankings for each species from the pot and plug survivorship datasets, these species have overall rankings of 2.25, 2.5 and 3.75 respectively. The nearest survivorship rival to these species is *Knautia arvensis* with an average rank of 4.75. **Figure 7.03** provides a plot-by-plot description of the survivorship rankings, with inset Shannon Index (H') diversity scores. Probably the two biggest surprises as far as overall species survival is concerned, is the relatively low survivorship of the fairly widespread, and one may infer, robust transplant C-S-R strategist *Centaurea nigra* (Grime *et al*1988), compared to the relatively high survivorship for the most ecologically restricted stress-tolerator, *Filipendula vulgaris* (Green *et al* 1997).

Figure 7.03 Ranked transplant species survival for the four plots (9/99).



The diversity index scores show the least improved swards to be far more conducive to a wider range of transplant species establishment than the simplified assemblages of species still surviving in Plots 1 and 2. **Table 7.01** summarises the results of one-way ANOVA applied to the year-by-year survival data in order to show the significance of differences between plots, and how these relationships change over the course of the project. Clearly there is an overall highly significant difference of transplant survival across the plots, which is maintained up until and including the final census. However,

as transplant depletion continued, there is convergence, and the overall difference across the plots has become less significant over time. As for individual plots, the ranking from the 9/94 census fits with the *a priori* assumption, with Plot 1 and Plot 4 at each end of the survival gradient (see **Figure 7.04**). Tukey HSD shows that the transplants of Plot 1 suffered significantly higher early mortality than the other three plots. However, by September 1997 the Tukey tests show the status of the plots to have formed three strands, which continued until the final census in September 1999. Plot 4 still stands out as having significantly higher survivorship than Plots 1 & 2, and has less than 40% similarity with the other three plots (**Figure 7.04**). Plot 3 seems to partially bridge this cleavage, as its transplant levels are not significantly different from either Plots 1 & 2, or Plot 4, though the cluster analysis shows it grouped with Plots 1 & 2.

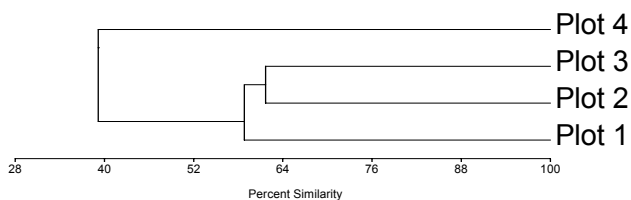
Table 7.01 Results of one-way ANOVA comparing the mean transplant survival rates of the four plots.

	9/94	9/95	9/96	9/97	9/98	9/99
ANOVA	13.76***	13.22***	10.60***	9.65***	5.49**	4.155**
Tukey HSD	Plot 1 ^{bcd} Plot 2 ^a Plot 3 ^a Plot 4 ^a	Plot 1 ^{cd} Plot 2 ^{cd} Plot 3 ^{ab} Plot 4 ^{ab}	Plot 1 ^d Plot 2 ^d Plot 3 ^d Plot 4 ^{abc}	Plot 1 ^d Plot 2 ^d Plot 3 ^d Plot 4 ^{ab}	Plot 1 ^d Plot 2 ^d Plot 3 ^d Plot 4 ^{ab}	Plot 1 ^d Plot 2 ^d Plot 3 ^d Plot 4 ^{ab}

*** = $P < 0.000$ ** = $P < 0.01$

For Tukey HSD multiple comparisons letters indicate significant ($P < 0.05$) differences ^a=Plot 1 ^b=Plot 2 ^c=Plot 3 ^d=Plot 4

Figure 7.04 Percentage similarity of Plot transplant composition (UPGM % similarity cluster analysis; Kovach 2000).

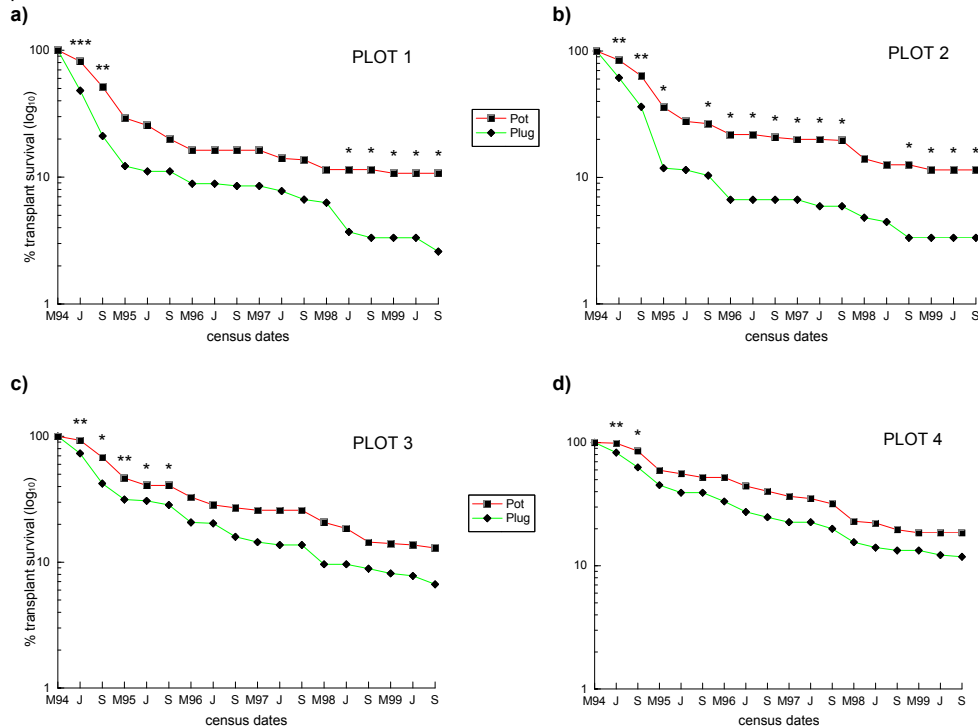


Comparison of the survivorship totals for the two sizes of transplant

Of 1080 pot transplants inserted in 1994, 149 (13.8%) were still alive in 1999. This compares with only 66 (6.11%) plug plants remaining. When compared at the subplot tier, the survival differential between the two sizes is significant ($t = 3.72$; $P = 0.001$; two-tailed; equal variances) indicating that enrichment using pot-sized plants does have survival superiority over using seedling-plugs. In order to explore this relationship in greater detail, transplant survivorship curves for both sizes for each plot are given in **Figure 7.05**. The graphs indicate a more complex picture, with the only clear trend

ensuing from the initial period after planting - the early establishment phase – in which all plots showed significantly higher plug mortality levels than pot transplants.

Figure 7.05 Comparisons of survivorship curves for pot and plug plants for each of the experimental plots. Curve data points are subplot totals combined to form plot totals. Statistical analyses were conducted using the *t*-test for unmatched pairs. *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; two-tailed *P*, corrected for ties.



However, convergence of mortality for both transplant sizes developed for plots 3 & 4 two years after implantation. The gap between pot and plug survivorship was only relatively continuous in Plot 2 throughout the study period. However Plot 1 probably features the most interesting pattern. In accordance with the other three plots, Plot 1 showed a significant distinction between pot and plug survival in the early establishment period, though this difference rapidly became insignificant by the second year. However, within the final two years of the experiment, the significant difference between pot and plug transplants was reaffirmed.

Figure 7.06 shows the rank of survivorship for the two transplant sizes according to species. What is notable is that, as with total survivorship, the same species are the top three for both inoculant sizes - *Primula veris*, *Malva moschata* and *Geranium pratense* – though in differing rank order. The most apparent differences in composition are that the only *Centaurea scabiosa* plants are from pot stock, and the only *Leucanthemum*

vulgare from plugs. By analysing the survival of individual species, further interesting differences between the survivorship of pot and plug plants become clear.

Figure 7.06 Comparison of rankings of species survival for the two sizes of transplant.

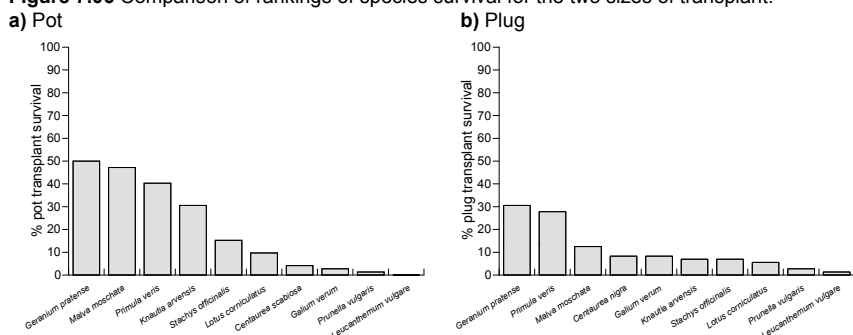


Table 7.02 is a summary of the statistical comparison of the differential survivorships of pot and plug transplants for each of the fifteen species for which two sizes were planted. In the initial post-insertion period (1994 censuses), ten species suffered significantly higher plug mortality than pot mortality; though after this early phase there was rapid convergence. For only three of the species, *G. pratense*, *M. moschata* and *K. arvensis*, has the mortality rate remained significantly higher for pot than plug transplants throughout the five-and-a-half year study period. The only species to show

Table 7.02 Comparison of differential survival of pot versus plug transplants. Analysis using independent-pairs *t*-test.

Species	9.94			9.95			9.96			9.97			9.98			9.99		
	Pot	Plug	<i>t</i> -test	Pot	Plug	<i>t</i> -test	Pot	Plug	<i>t</i> -test	Pot	Plug	<i>t</i> -test	Pot	Plug	<i>t</i> -test	Pot	Plug	<i>t</i> -test
<i>Campanula glomerata</i>	39	18	NS	6	3	NS	0	0		0	0		0	0		0	0	
<i>Campanula rotundif.</i>	42	7	3.53**	3	0	NS	1	0	NS	1	0	NS	0	0		0	0	
<i>Centaurea nigra</i>	51	50	NS	29	28	NS	15	13	NS	11	13	NS	8	10	NS	6	8	NS
			6.91**															
<i>Centaurea scabiosa</i>	67	14	*	32	4	3.33**	21	1	2.78*	17	1	2.72*	4	1	NS	4	0	NS
			3.91**															
<i>Galium verum</i>	78	35	*	40	11	3.19**	32	6	3.74**	28	6	3.91***	3	0	NS	3	0	NS
<i>Geranium pratense</i>	97	81	2.72*	75	61	NS	64	40	2.24*	61	32	2.69*	50	24	2.50*	50	24	2.50*
			4.34**															
<i>Knautia arvensis</i>	82	40	*	64	26	2.68*	50	17	2.91**	42	13	3.29**	38	6	3.52**	31	4	3.03**
<i>Leucanthemum vulgare</i>	33	50	NS	3	29	3.88***	3	19	2.93**	1	15	3.42**	0	3	NS	0	1	NS
			5.97**															
<i>Lotus corniculatus</i>	69	19	*	33	13	NS	19	6	NS	18	6	NS	13	6	NS	10	4	NS
			4.02**															
<i>Malva moschata</i>	92	54	*	79	35	4.20***	75	25	5.59***	68	21	5.65***	50	14	3.77**	47	13	3.09**
			7.16**															
<i>Primula veris</i>	90	42	*	71	36	3.53**	68	35	3.36**	68	33	3.65**	50	32	NS	40	28	NS
<i>Prunella vulgaris</i>	42	61	NS	11	40	2.56*	3	25	3.08**	1	21	3.06**	1	7	2.15*	1	3	NS
<i>Scabiosa columbaria</i>	63	28	2.51*	18	8	NS	8	4	NS	3	4	NS	0	0		0	0	
<i>Silene latifolia</i>	72	63	NS	32	24	NS	15	11	NS	8	0	2.17*	1	0	NS	0	0	
			4.95**															
<i>Stachys officinalis</i>	92	49	*	47	25	2.19*	32	18	NS	31	10	2.37*	15	10	NS	15	7	NS

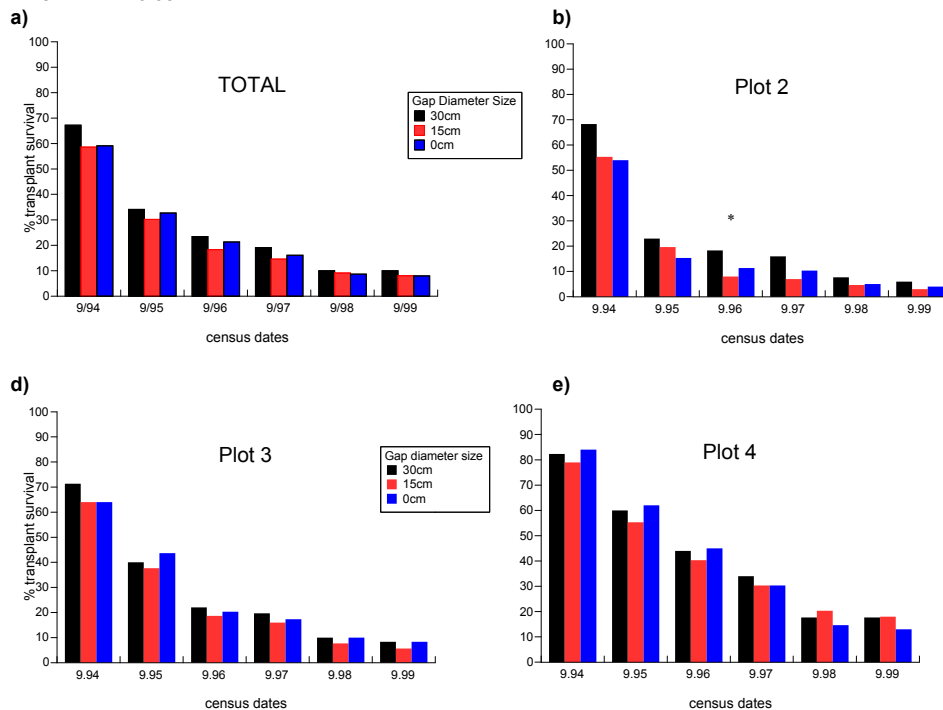
***=P<0.000 **=P<0.001 *=P<0.01

higher plug than pot survival were *L. vulgare* and *Prunella vulgaris*, though this difference was dissipated by 1998. *Centaurea nigra* is the only surviving species, which has not shown a significant difference between the survivorships of the two transplant sizes throughout the study.

Effects of gap diameter on survivorship

When comparing total transplant survival in each of the four plots (see **Figure 7.07**) for the three gap sizes, there were only two instances where there was a significant difference in survival: Plot 1 in 1995 and Plot 2 in 1996, with 30-cm diameter gaps showing higher survival than 15-cm or 0-cm gaps. However, such differences were short-lived.

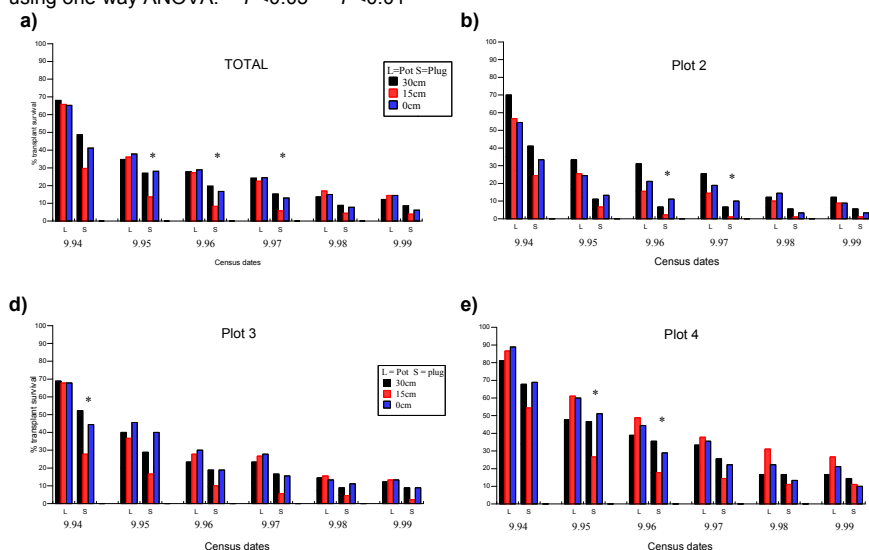
Figure 7.07 Charts relating the significance of gap size to total transplant survival for plot data. Analysis using one-way ANOVA: *= $P < 0.05$



The creation of either a 15-cm or 30-cm diameter competition-free gaps did not appear to have significantly affected pot transplant survivorship in any of the plots over the total research period (see **Figure 7.08**). The results, however, are far more complex for plug transplants. **Figure 7.08a** shows that for the *total* account between 1995-97, plug inoculants suffered highest mortality risk in 15-cm diameter gaps than either 30-cm or, for that matter, no gap at all. This composite picture represents two trends. Plug transplant survival was significantly higher in 30-cm diameter gaps in Plot 1 than for the 15-cm and 0-cm gaps for most of the study period, with highly significant differences between 1995-97 (see **Figure 7.08b**). This positive effect of the large gap size on competition-related mortality was the most expected result because of the productive nature of the Plot 1 sward. In contrast, the trend in Plot 2 suggests a situation

in which the 15-cm gap, which is in fact not sufficiently large enough to ameliorate the effects of neighbourhood competition, may have a negative impact on survivorship. The 1996 and 1997 censuses for Plot 2 show a significant negative effect of the 15-cm diameter gap on plug transplant survivorship. Plots 3 & 4 also show shorter periods in which the 15-cm gaps are significantly higher in mortality risk.

Figure 7.08 Charts relating the significance of gap size on survival of the two sizes of transplant for plot data. Analysis using one-way ANOVA: *= $P < 0.05$ **= $P < 0.01$



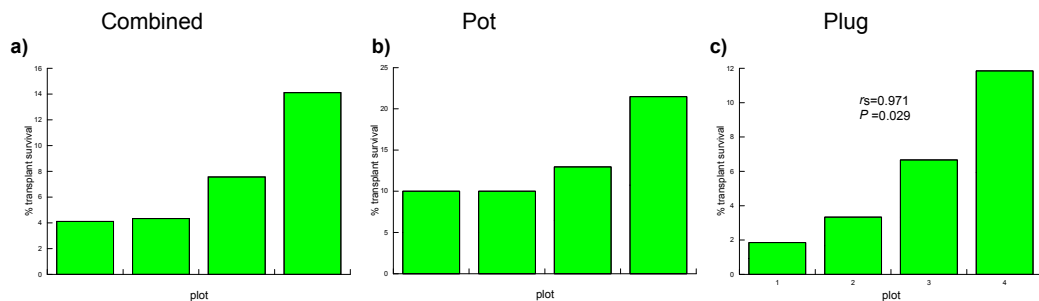
Interactions between transplant survival and productivity factors

In order to offer further explanatory detail, a range of variables was statistically compared to the percentage survival data (see **Figure 7.09**). **Figures 7.09a-c** show that the plot gradient of agricultural improvement generally accords with transplant survival, and the plug transplant data shows a significant positive relationship. Soil potassium and phosphorus in particular, also both display very significant (negative) relationships with transplant survival. This has been a consistent finding throughout the study, and suggests these two macronutrients are the controlling factors in the productivity and inoculation resistance of these improved grasslands. This aspect is discussed in greater detail in **Chapter 4**. In direct comparison, plotting nitrogen against transplant survival produces no significant trends, though this result is consistent for N with all previous analyses (Davies *et al* 1999). Four interrelated grassland explanatory variables are also compared to the transplant survival data: average peak sward height (**Figures 7.09m-o**); average peak phytomass (**Figures 7.09p-r**); grassland diversity

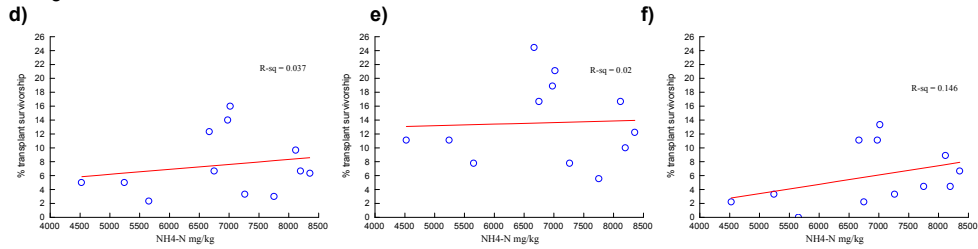
(Figures 7.09s-u); and grassland species richness (Figures 7.09v-x). While sward height does not show a significant relationship with transplant survival, the direct measurement of grassland productivity – phytomass – produced an equally strong (negative) significance with transplant survival, to that of soil phosphorus, which is perhaps a logical outcome considering these factors are so intimately related. The diversity measurements, which are however an indirect description of the improvement gradient, also demonstrate significant (positive) relationships with survival, thus suggesting that swards already with higher species levels, are also less resistant to the ingress of further species.

Intuition would suggest that seedling plugs would overall, be more susceptible to competition elevated by higher productivity than larger pot plants, and thus suffer greater mortality risk. The regression results support this contention, as when the two sizes of transplant are compared with the key environmental variables, there is clear evidence that plug plants have a stronger negative association with the soil and sward productivity factors than pot transplants. This is demonstrated by the results for potassium (Figures 7.09g-i) where there is an overall (total) significant negative correlation ($P = 0.023$), and for plug survival ($P = 0.008$), but pot survival is not significantly related ($P = 0.082$).

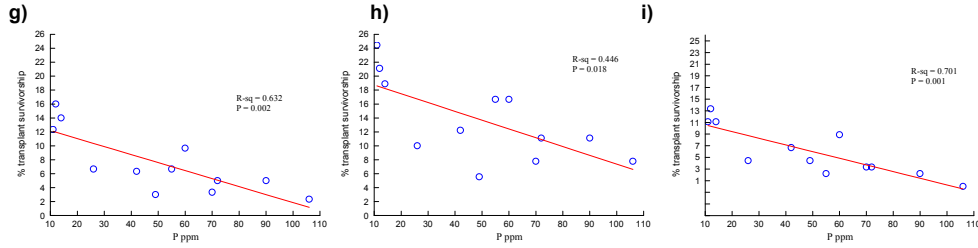
Figure 7.09 Trend lines (least-squares linear regression) showing the relationships between a) total; b) pot; c) plug; transplant survivorship and: plot gradient (column charts only); soil NPK; average sward height (6 years); average (4 years) peak phytomass; sward diversity (1998) Shannon Index; and sward species richness (1998). The coefficient of determination (r^2) is given as well as significance when $P < 0.05$.



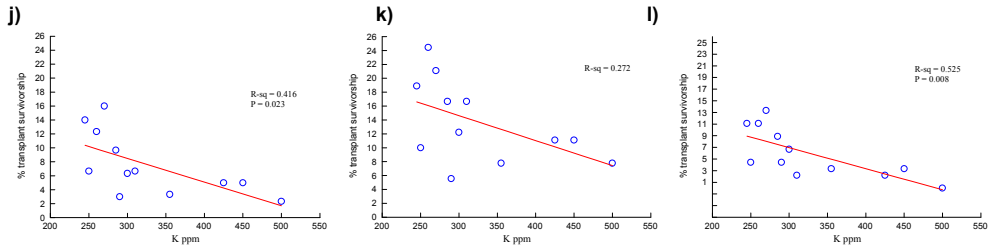
Nitrogen



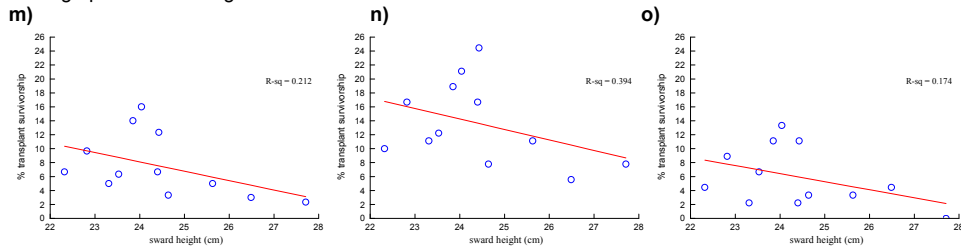
Phosphorus



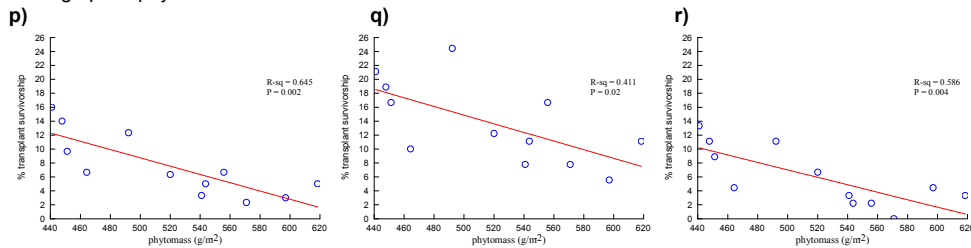
Potassium



Average peak sward height



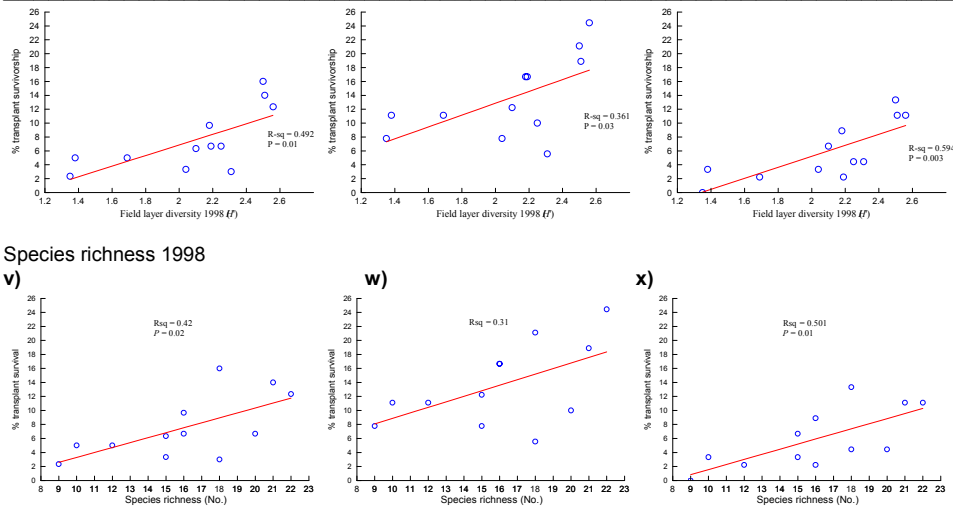
Average peak phytomass



Grassland diversity 1998



Chapter 7 - Enrichment Using Transplants: Analysis of Survivorship



To further elucidate the above findings, stepwise multiple linear regression was applied to the dataset. The only model produced by the analysis (**Table 7.03**) promoted peak phytomass as the chief predictor of transplant survival, explaining 64% of the observed

Table 7.03 Results (model summary statistics) of stepwise multiple linear regression for prediction of transplant survival (dependent variable SPSURV99) using the above set of independent variables.

Variables Entered/Removed

Model	Variables Entered	Method
1	AVBIOMAS	Stepwise

Model Summary

Model	R	R Square	Adjusted R Square	Std. Error of the Estimate
1	.803	.645	.609	2.8082

a Predictors: (Constant), AVBIOMAS

ANOVA

Model		Sum of Squares	df	Mean Square	F	Sig.
	Regression	143.243	1	143.243	18.165	.002
	Residual	78.859	10	7.886		
	Total	222.102	11			

a Predictors: (Constant), AVBIOMAS

b Dependent Variable: SPSURV99

Coefficients

Model		Unstandardized Coefficients	Std. Error	Standardized Coefficients	t	Sig.
1	(Constant)	38.446	7.300		5.267	.000
	AVBIOMAS	-5.942E-02	.014	-.803	-4.262	.002

a Dependent Variable: SPSURV99

Excluded Variables

Model		Beta In	t	Sig.	Partial Correlation	Collinearity Statistics Tolerance
1	SPECIE98	.213	.838	.424	.269	.567
	P2000	-.467	-2.169	.058	-.586	.558
	K2000	-.164	-.601	.562	-.197	.511
	AVLUX	-.249	-1.346	.211	-.409	.957
	AVSWDHGT	.203	.752	.471	.243	.508
	FLINDX98	.284	1.107	.297	.346	.529
	N	-.235	-1.114	.294	-.348	.781
	SUBPLOT	.429	1.471	.175	.440	.374

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; FLINDX98 = field layer diversity 1998; Specie98 = sward species richness 1998.

variability. Adding P to the model increased this to 77%, though entering all variables increased the coefficient of determination to 0.97, thus altogether the selected variables could not explain only 3% of the variability in transplant survival. Using the *Enter* regression method to add variables to the core model of AVBIOMASS and P2000 one by one, soil nitrogen increased R^2 the most, by 12%. Secondly, soil potassium increased R^2 from 0.767 to 0.824.

Management treatments and transplant survival

Although the recipient swards exhibited structural changes due to the three management treatments over the three year study period (unpublished data), no significant effects were apparent in transplant survivorship by the end of the research period (one-way ANOVA: $F_{2,56}$; $P=0.824$). When the surviving transplants were sorted into either pot ($F_{2,29}=0.299$; $P=0.744$) or plug ($F_{2,26}=0.037$; $P=0.064$) there were again no significant management effects. 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. This overall feature of management was perhaps important in moderating any differential effects management regime may have on transplant survival during the spring/aftermath treatment periods. It is also probable that the influence of soil fertility over-rides that of management treatment in the initial restoration period when macro-nutrient levels are still high (Oomes & Mooi 1981; Gough & Marrs 1990). Additionally, by the end of the research period, overall transplant numbers were so low – especially as far as individual transplant species - as to possibly make treatment effects statistically undetectable (see **Chapter 2**). However, in the longer term, it is likely that management will be an increasingly important factor in transplant regeneration and recruitment (Berendtse *et al* 1992).

DISCUSSION

Since the 1994-97 dataset was published in Davies *et al* (1999), transplant numbers have continued to decline in line with the already high transplant mortality compared to similar studies (Fenner & Spellerberg 1988; Wells *et al* 1989; Bisgrove & Dixie 1994; Luscombe & Scott 1994; Hopkins *et al* 1995). Although these changes have altered some of the published findings, the same general trends in the data remain. The results

of this study have shown that over the research period: i) transplant survival followed the gradient of agricultural improvement; ii) because a spectrum of plants with different primary life-history strategies was used (Grime *et al* 1988, see **Chapter 3**), mortality risk varied greatly amongst species; iii) the size of transplant, as a whole, did not 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 markedly between species; iv) in general, artificial gap creation did not appear to significantly aid transplant survivorship, and the gap sizes used in this study were, overall, ineffectual in assisting establishment except within the bounds of specific factors such as plug plants in Plot 1.

As noted previously, the pattern of transplant mortality risk seems to show similar features to the Deevey Type III model, with an early period of very high mortality, mortality risk then declining with age, and only a few individuals attaining long life-spans (Hutchings 1986). Apparently, the best-documented examples of Type III curves exhibited by real populations come from tree species (Hutchings 1986). Thus, while herbaceous species often show evidence of Deevey Type II curves with a constant, linear, exponential depletion of individuals over time (Sarukhán 1973; Waite 1984), transplanted herbaceous cohorts show a marked difference in population ecology (Kendle 1992). However, removal of the crucial, but artificial first year data (1994 censuses, and the survival curve is much closer to that of Deevey Type II, with a relatively constant death rate (Watkinson 1986; Steve Waite pers comm.).

Even with sympathetic management, there was great resistance from the established grassland swards to the infiltration of new plant species. Clearly, mortality risk and depletion trends are amplified by the artificiality of the initial establishment period, and the high productivity/competitiveness of the recipient agricultural grasslands. In natural populations regenerative attributes are crucially important in determining species distribution and abundance in plant communities (Burke & Grime 1996), whereas the use of transplants circumvents these regenerative controls. It is a recognised phenomenon that reduced species-diversity is often associated with increasing productivity/biomass (Al-Mufti *et al* 1977; Grime 1973, 1979; Vermeer & Berendse 1983; Kirkham *et al* 1996). Sward competitiveness, as measured in relation to

resistance to botanical enrichment (inoculation resistance), shows that peak-phytomass can strongly influence establishment of transplants (Tilman 1993). Al-Mufti *et al* (1977) and Grime (1979) have observed that species-impoverishment of herbaceous communities is generally related to a maximum biomass of over 750 g m⁻² (Hodgson 1989). Vermeer & Berendse (1983) suggest >500g/m² for their grassland sites. **Figures 7.09p-r** indicate that a similar mechanism may also be operating for transplant survivorship. Survival was generally highest in subplots with peak phytomass of <500g/m². In addition, the multiple regression results (**Table 7.03**) indicate biomass as the most predictive factor explaining 64% of variation in transplant survival. Gough *et al* (1994), however, are less sure about the predictive value of biomass, suggesting that community production has a limited capacity to predict species richness across a broad range of habitat conditions. Their findings for marshland communities suggest that realized richness is controlled primarily by environmental variables rather than biomass. Certainly in this study the macronutrients P and K, which covary with biomass (Naeem *et al* 2000), show highly significant negative relationships with transplant survival (see **Figures 7.09g-l**), but do not add greatly to the explanatory power of the multiple regression model.

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). It is worth noting for these transplant cohorts that the highest mortality risk is, perhaps surprisingly, during the winter period, obviously the season with the least active growth. This could be explained by the survey methodology, as this is the longest interval between censuses (September- March), and thus a comparatively greater period for plants to die. However, it may also indicate that direct neighbour competition effects such as physical interference and resource capture during peak sward phytomass, are not immediate in killing the inoculants. Observations suggest that the exceptionally mild winters over the 1990s, possibly induced by global warming, have extended dominant grass growth (competition) and mollusc grazing (predation) well into late autumn and early spring. Parasitic and fungal pathogens may also become more virulent (BIODEPTH 2000). Thus, perhaps these phenological changes have also amplified mortality in what was previously a relatively dormant period (Grime 1989; Hanley *et al*

1995; Dunnett & Grime 1999). Only a more intensive monitoring programme, with far shorter intervals between censuses would have revealed a more fine-grained picture of seasonal mortality risk (Hutchings 1986).

Species-specific survival

Much of the mortality that has taken place among the transplants throughout the plots has to do with the effects of what Wells *et al* (1989) broadly term ‘environmental sieving’, perhaps otherwise known as *natural selection*. Although the transplants have been artificially introduced into the grassland habitats, they are rapidly affected by ecological interactions controlling natural populations. Within these biotic and abiotic constraints, a range of ecological abilities to infiltrate the grasslands has become apparent among the transplant species. Interpretation and comparison of the species survival data is however complicated by the fact that two sizes of transplant were not available for all species. In order to attempt further categorical elucidation, **Figure 7.10** displays the ranked distribution of **Figure 7.02** with the species grouped into five categories. Superficial appropriation of Grime’s (1987) dominant-subordinate, and core-satellite (Gibson *et al* 1999) conceptual schemes for community assembly, is useful in classifying the ranking of transplant species, though including the categories of *extinct* and *feral* species:

1) *Core* species: in terms of survival, this category is self-selecting, clearly comprised of *Geranium pratense*, *Primula veris* and *Malva moschata*, which make up 17% of the remaining species but 54% of total transplant survival. These seem to be species that are able to establish moderately successfully as long as intensive agricultural management has ceased. For restoration of agriculturally improved grasslands, they are also the core species, with relatively broad environmental tolerances (Luscombe & Scott 1994). Even though planted as two sizes, these species established and entrenched at levels significantly higher than all the other species. The elevated growth-forms of *G. pratense* and *M. moschata* encourage the production of aerial photosynthetic surfaces, which is an adaptation to life in tall-sward environments and intense light competition (Goldberg & Werner 1983) aiding survival under productive conditions. The relatively low mortality risk of *Primula veris* may be due its partially vernal phenology (Grime *et al* 1988), as it completes most of its main growth period before the grassland reaches peak biomass. This seems to have provided an advantage to both adult and seedling transplants. Grime

Campanula spp. are also apparently very susceptible to mollusc predation (Wells *et al* 1989). Unlike the *Campanula* species, *Scabiosa columbaria*, and particularly *Silene latifolia* managed to maintain reasonable populations until the third year. However, most of the *S. latifolia* plants seemed to have been in stasis, though *S. columbaria* did manage to flower and set seed in Plot 4. Both species are considered to be naturally short-lived monocarps (Grime *et al* 1988), and without recruitment from seed, were unlikely to persist for more than a few years irrespective of the hostile sward conditions.

5) Ferals: Although a number of species have produced sexually generated offspring, only *Hordeum secalinum* has become truly feral in its distribution. In Plot 1 *Hordeum* has become one of the more abundant species. In Plots 2 and 4, the transplanted *Hordeum* originals are now dead, though seed-derived plants are scattered throughout the swards. It is now not possible to assess its survival and performance in relation to the original transplant cohorts. These aspects are further discussed in **Chapter 9**.

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). For example, drought seemed to affect many of the transplants in the immediate post-planting period. High competition for soil moisture can be a critical factor in the failure to establish, especially when the plant is attempting to extend its root system outside of the growing medium (Bisgrove & Dixie 1994). The high mortality of species such as *Centaurea nigra*, *Lotus corniculatus*, *Leontodon hispidus* and *Sanguisorba minor* (which all occur in Plot 5), may be due to failure in establishing deep root systems, particularly if a tap-root has to be formed rapidly. This may have made them unable to compete effectively for moisture with the shallow-rooted grasses, and therefore vulnerable to desiccation (Al-Mufti *et al*, 1977). Planting in the autumn may reduce the losses attributed to drought (see **Chapter 8**). The impact of shoot competition, particularly on plug transplants in grasslands with high biomass production is probably as important, if not more so, than root competition. The tallest, most dense swards by far were in Plots 1 & 2. Low growing species such as the *Campanula* spp., *Scabiosa columbaria* and *Galium verum* are at a great disadvantage when attempting to establish in such conditions, especially during the spring and summer when there is maximum standing crop, intense dominance from species with high relative growth rates and therefore a high level of light

competition (Al Mufti *et al*, 1977). It is not surprising then that the top survivors such as *Geranium pratense* and *Malva moschata* have tall and erect life forms, and are perhaps more adapted to active foraging (Grime *et al*, 1989).

Importance of initial transplant size on the survivorship of transplants

All the graphs of **Figure 7.05** indicate that plug transplants suffered greater mortality than pot plants in all plots, though not necessarily at a statistically significant level. This disparity in mortality risk was, however, statistically significant for all plots in the first two months after insertion. This was due to the very rapid deaths of seedling plugs of species most susceptible to competition and mollusc predation such as *Campanula* spp. and *Scabiosa columbaria*. The likely causes of seedling mortality were probably low light caused by the relatively enormous surrounding adult plants; a dense sod of roots and rhizomes which prevents root penetration, nutrient and water take-up; long, hot droughty summers; damping off and other fungal pathogens; and herbivory from small mammals. The small rooting media volume of the plugs may have also contributed to high mortality, as it can rapidly desiccate and shrink under the droughty conditions experienced in summer 1994, causing problems of contact between the roots and the surrounding soil (Macdonald 1986; Bisgrove & Dixie 1994; Luscombe & Scott 1994). After this initial period, however, site-specific factors seem to become more important.

Plot 2 was the only grassland to maintain a significant differential between pot and plug throughout most of the study period, including the final census in September 1999. However the pot transplant populations experienced two *crunches* (Weins 1977), in 1995 and 1997-98, when the gap between the sizes dramatically converged, though the differential was reinstated with further plug plant losses. Plot 1 is apparently the most hostile environment in terms of competition from the established sward due to the highly productive conditions. Although pot transplants suffered an initially lower mortality rate, the survivorship levels quickly converged after the first year. Nevertheless, taking the full study period of 5.5 years, the pot/plug survival pattern for Plot 1 takes on a curious twist. It was not until the June 1998 census that the gap between pot and plug again became once again significant – pot transplant survival remained relatively constant, whereas plug numbers again plunged. Because of the

small numbers of individuals remaining (68 plants in June 1998), this event may be a function of chance. However, it may also reflect the final depletion of plug plants, which have been *hanging on* for over four years. This provides further support for the value of longer-term monitoring (Tilman *et al* 1994; Dunnett *et al* 1998; Davies *et al* 1999). Plots 3 and 4 exhibited rapidly converging survivorship rates similar to Plot 1, but probably for the opposite reasons. These plots are the least productive of the sequence, and although there is an initial significant gap between pot and plug survivorship, the plug mortality rate began to level-off, comparatively, by the second year. This initial disparity was probably due to the fact that, although the populations of the most sensitive species failed irrespective of initial size, the pot transplants took longer to succumb than the plug plants and therefore exhibited a lagged mortality.

Overall perhaps three conclusions stand out concerning the survivorship of the sizes of transplant used. Firstly, overall, pot plants suffered significantly less mortality than plugs, and this translated to the two highly productive grasslands (Plots 1 & 2), suggesting that it is most expedient (excepting cost) to use larger transplants in such grasslands. However, it is worth noting that pot transplants do seem to be more susceptible to damage by wild mammals. In the first few months after insertion, some pot plants were used as nesting sites for voles. In addition, foxes and badgers targeted the pot transplants as possible sources of invertebrate food. However, rabbits made by far the greatest impact, as they found the pot compost to dig, and therefore destroyed any plant that was regularly encountered. Species with dense root systems seemed to be less affected than those where the compost was less firmly bound. Plot 3 was particularly badly affected by rabbit disturbance, and the close-grazed sheep treated sites were especially preferred. Secondly, size did not seem to have a significant influence over survival in the two less productive grasslands (Plots 3 & 4), perhaps signifying that under these conditions transplant size is a relatively unimportant factor in enrichment success. Thirdly, the fact that a significant differential opened up between transplant sizes in Plot 1 late in the study suggests that short term monitoring can give premature results (Fisher *et al* 1996).

An interesting additional result from census results of 1997 was achieved by correlating species abundance/distribution data (see **Chapter 3**) with pot and plug survivorship (Davies *et al* 1999). There was no significant relationship with pot transplant

survivorship and number of tetrads occupied, but a significant positive correlation ($r_s = 0.5714$; $P = 0.026$) with plug transplants. This result was construed as a possible link between transplant age-state and regenerative constraints on distribution (Burke & Grime 1996) as seedling plugs may be more prone to mortality factors, which determine the abundance of natural populations (Ellenberg 1986). However, by 1999, this correlation was nullified by continuing pot transplant losses.

Transplant size-species interactions

Although analyses of the plot-combined data shows that initial transplant size has a lasting effect only on the survivorship of the most improved grasslands, **Table 7.02** clearly reveals that the size-effect is even more complex at the species level. Under conditions of high residual soil fertility, differences in competitive vigour among species may become accentuated, and particular species are unable to establish over certain soil fertility thresholds, irrespective of initial size (Al Mufti *et al* 1977; Wells *et al* 1989). Since publication of Davies *et al* (1999), the differential between plant sizes has altered, however, the fifteen dual-size species used in the study may still be placed into four general categories:

1) No significant difference between transplant sizes: This is the largest category, made up of longer-term survivors that, in the final analysis, show no significant difference between pot and plug survivorships, although there may have been periods, in the establishment stage when they showed significantly higher survivorship as pot plants. This has been true of *Centaurea scabiosa*, *Galium verum*, *Lotus corniculatus*, *Primula veris* and *Stachys officinalis*, where continued depletion has led to convergence between sizes. In 1997 *Primula veris* had significantly higher survivorship for pot than plug plants. However, by 1999 this differential had ended, though *P. veris* continues to be the third highest survivor of all species. *Centaurea nigra* is notable in that the plug and pot mortality rates have never been significantly different throughout the three years of the study. This may be due to the combined effects of susceptibility to drought; especially affecting the pot plants in the initial year, and mollusc predation, which seems to have affected both transplant sizes equally.

2) Species for which pot was more successful than plug: *Malva moschata*, *Geranium pratense* and *Knautia arvensis* are ‘top’ survivors, with 50%, 30% and 47% survival rates for pot transplants respectively. Even so, plug mortality was still comparably less than for the other species used in the experiment. This may be accounted for by the robustness of this group of species. Hodgson *et al* (1995) classify *G. pratense*, *K. arvensis* and *M. moschata* and as C-S-R strategists. Their growth-forms encourage the production of aerial photosynthetic surfaces, which is an adaptation to life in tall-sward environments and intense light competition (Goldberg & Werner 1983). This may explain why adult pot plants have survived significantly better than plugs as they have an immediate height advantage

3) Species for which plug survival was greater than for pot: For over four years of the project, two species, *Leucanthemum vulgare* and *Prunella vulgaris* had significantly higher survivorship for plug than pot transplants (Davies *et al* 1999). This may have been because both species may be less well adapted to *ex-situ* cultivation in that they suffer from some constraint or physiological change, such as a premature start of reproductive development, that makes pot transplants less effective at establishment (Luscombe & Scott 1994). They are also considered to be relatively short-lived perennials (Grime *et al* 1988), and the higher pot plant losses may also be a consequence of age-related mortality. By the end of the study, however, there was eventual convergence between the sizes, as plug numbers continued to decline, to the point where there is only one *L. vulgare*, and four *P. vulgaris* left alive from all cohorts. This suggests that the plugs also eventually suffered age-related mortality.

Effects of initial competition-free gap diameter on transplant survivorship

This study provides evidence that competition-free gap creation around a transplant can aid survivorship, but only under specific conditions. The charts of **Figure 7.08** show that gap creation did not significantly contribute to pot transplant survival in any of the plots over the study period, and only plug plants demonstrated an impact from the treatments. There were instances, though, from all the plots when plug survival was significantly helped, or hindered, by gap formation, but only in Plot 1 was this consistent up until the final census. In Plot 1 the 30-cm gaps are clearly related to lower plug mortality risk. While the magnitude of this effect has decreased, it is still apparent

from the 1999 census. Interestingly, the 15-cm gaps have suffered the highest mortality, and this is also clearly evinced in Plot 2, where between 1996-97 the 0-cm gaps actually seemed to promote survival over gap formation. The evidence for creating artificial herbicide gaps, therefore, seems equivocal. The difference between competition reduction in large than small gaps may simply be differences in timing of the commencement of resumed interference from the neighbouring (Gurevitch *et al* 1990). The suggestion is that that the effectiveness of the gap creation strategy is only significant in very productive swards such as Plots 1 & 2, for seedling plugs only, inserted into 30-cm gaps. Gap sizes less than 30-cm may in fact have a negative effect on survival. It is possible that the gap sizes used in the experiment may have been inadequate in terms of reducing either above- or below-ground competition (Morgan 1997). In the analogous situation with tree transplants inserted into grasslands, the evidence suggests that drought stress induced by the neighbouring sward is the major establishment mortality factor when the planting-gap is not sufficiently large (Bradshaw *et al* 1995; Agate 2000). The findings of Hitchmough *et al* (1996) propose, though, that 20-cm gaps are adequate for the establishment of *Bulbine bulbosa* in vigorous swards of *Festuca arundinacea* on a productive site. However, this was contingent on maintaining the competition-free gap rather than applying a one-off treatment, as is the case with the present study. The recommended approach for tree planting and aftercare is to create a one metre weed-free zone around the implant, and for grassland situations, this gap should be maintained for at least five years (Agate 2000). Further extrapolating the *arboricultural* approach, placing the equivalent of tree-shelters around each transplant may be highly beneficial to survival and growth, but along with maintaining the weed-free gap, such care is probably only merited with transplantation of rare species. It could also be argued, in line with tree planting, that much larger gap sizes, perhaps of 50-cm or 100-cm diameters (Morgan 1997), would significantly improve survivorship of transplants. However, from a practical point of view, such gaps are hard to apply in the field, and unacceptably large areas of the recipient sward are destroyed when hundreds of transplants are inserted. Clearing larger areas of vegetation may also encourage invasion of undesirable weed species such as *Cirsium* spp. or *Senecio jacobea* (Bisgrove & Dixie 1994). In less competitive swards, gaps may have negative effects that outweigh any advantages. For example, 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, as they are more conspicuous.

In general, gap creation can aid plant survival in the initial post-insertion stage, but transplant losses may continue for many years, and one-off gaps are transient. The results from **Chapter 6** suggest that herbicide-created gap occlusion in the two most agriculturally improved grasslands (Plots 1 & 2), over a period of a year, was very high, with as little as 6% (average 14%) of the gap-space remained un-recolonized, and the majority of colonists were dominant and subordinate species for which the gaps were created to retard. Perhaps using other methods for gap creation may be more effective such as turf removal (Hopkins *et al* 1995). However, within the limitations of this experiment, inoculating with transplants of pot size does not seem to benefit from gap creation, whereas gaps of 30-cm may reduce plug-plant mortality risk, though further work is required to disentangle any significant interactions between transplant species, transplant size and gap size. For grasslands of lower competitive vigour, simply inserting a robust species such as *Geranium pratense*, as either a pot or plug transplant, directly into the sward may be just as effective in survivorship and establishment terms as placing it in an artificial gap.

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