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# Short-term variability of plant populations within a regularly disturbed habitat

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**Abstract.** The changing populations of weeds during 13 years of the Broadbalk continuous wheat experiment were analysed to investigate the extent of differences in short-term variability of cover between species. The data were from two sections of the experiment where winter wheat was grown continuously under herbicide treatment for 13 and 6 years respectively. Logistic regressions were fitted to the data. *Equisetum arvense* showed significant long-term increases on both sections; long-term trends were also detected in the longer data run for *Agrostis stolonifera, Cirsium arvensa, Poa trivialis, Ranunculus arvensis* and *Vicia sativa*, and for *Medicago lupulina* on the shorter data run. Variation around long-term trends was low in the case of *Equisetum*, and, in the longer data run, for *Cirsium* and *Tussilago farfara*, and high for *Poa* spp. and *Vicia.* Cover values on the two sections were positively correlated for *Alopecurus myosuroides, Equisetum, Poa annua* and *Tripleurospermum inodorum.* There was a weak correlation between C-S-R strategy and short-term variability; the more competitive species displayed less variability than the ruderal species. Furthermore, species regenerating from persistent seed banks were more variable in the short term than those regenerating from short-lived seed or bud banks. This can be explained by differences in response to year-to-year variation in environmental conditions, those species with persistent seed banks being typically more sensitive to annual fluctuations in the environment than those without.

**Key words:** Plant population dynamics – C-S-R strategy – Seed banks – Weed populations

The typical approach to modelling the dynamics of plant populations involves decomposing the life-history into a series of stages, and parameters are estimated which describe transitions between stages either as fixed or density-dependent probabilities obtained from experimental or survey data (e.g. Sarukhan and Gadgil 1974; Watkinson 1980). Once the life-cycle model is parameterised, then it can be cycled forward to provide forecasts.

Deterministic models based on this approach have explanatory value (e.g. Firbank and Watkinson 1986), but are unlikely to provide accurate forecasts because the parameters are all subject to variation through factors external to the model (e.g. Firbank et al. 1985). If the model is to be used for prediction, then either the error distributions of these parameters should be determined, or their relationships with other driving variables must be elucidated. Both approaches require substantial experimentation and/or data collection if the full range of likely parameter values is to be sampled. Fortunately, this level of detail is not always necessary. Time-series models based on regular population counts can be used to describe gross population changes without requiring each life-history stage to be addressed individually. The variability in population behaviour between time periods appears as the error term around the model. The extent of variation can be detected at different time-scales according to the choice of modelling approaches.

If the objective is to make short-term forecasts of population size, then species which respond most strongly to short-term changes, such as fluctuations in weather, or rapidly changing habitat quality, will be more difficult to forecast than those which track longer-term environmental signals, such as climate change. These situations can be distinguished by comparisons of error terms around a time-series model describing longer-term fluctuation; the greater the error term, the greater the short-term variability. While there are always dangers in extrapolating any model into the future, it would be valuable to know whether some species are intrinsically less variable between time periods, and thus more predictable in the short term.

There are few long-term data sets suitable for such comparative plant population studies (Silvertown 1991). One difficulty is that different plant species have different life spans, making comparisons of population changes difficult. This problem is reduced in weed-crop systems, in which cultivation imposes a powerful annual rhythm on the entire system. The best known long-term weed data set comes from the Broadbalk experiment at Rothamsted (Thurston 1969). While the experiment itself has continued for over a century, the collection of weed data has not been continuous, and there have been periods of fallow. However, the 13 years of data published by Thurston (1969) are suitable for a comparative analysis of above-ground weed populations, with the proviso that cover rather than density estimates were recorded.

An initial analysis of three of the Broadbalk weeds indicated that they differ in short-term variability (as displayed by phase diagrams); the year-to-year changes in cover were much smaller for *Cirsium arvense* than for *Ranunculus arvensis* (Firbank 1991). However, the *Cirsium* numbers were far from being constant across the period of the data; the populations were in long-term decline, presumably because of regular control by herbicides introduced at the start of the period (Thurston 1969).

In this paper the analysis is extended to the 12 most common weeds at Broadbalk during this period. Long-term population changes are accounted for by fitting a regression to the data, with time as the independent variable; short-term variation is then estimated from the residual mean square around the model. The analysis is repeated for a shorter data series from within the same period from another section of the Broadbalk experiment. In this way, the following questions can be addressed: are there differences in short-term variability of population behaviour between species at one location, and are these differences repeated at a nearby location? There is also a subsidiary question; if species do differ in short-term variability, is it possible to explain these differences in terms of their ecology?

## Methods

The Broadbalk experiment dates back to 1843, when a continuous wheat crop was divided into large plots and was used to answer the question as to whether plants obtain nitrogen from the air or from the soil. As time went on, the nature of the experiment and of the data collected evolved (Woiwod 1991). The most readily available data set on the weeds of Broadbalk is provided by Thurston (1969). She reported the changing levels of cover of the most abundant weeds on two areas of the experiment, I and V, during the 1950s and 1960s. Sections I and V were both split into subsections A and B after fallowing in 1955 and 1962 respectively to contrast a herbicide-continuous wheat system (Sections IA and VB) with a no-herbicide, occasional fallow system (although herbicides were not applied to IA in 1955 and 1956). The herbicide-continuous cereals parts of the field provide rare long-term weed data, of 13 years for Section IA and 6 years for Section VB.

Thurston (1969) aggregated the data over all treatments within the sections for her results, which are presented in terms of cover per plot on a 0–5 scale, summed over 18 plots for Section IA (giving a maximum score of 90) and 17 plots for Section VB (maximum score 85). These values subsume much variation in fertiliser treatment [see Johnston and Garner (1969) for details of methods and management]. It should be noted that seed banks were substantially larger in Section V in the year before the data began than in IA for *Medicago lupulina*, *Papaver* spp., *Tripleurospermum inodorum* and *Alopecurus myosuroides*: data for *Papaver rhoeas* and *P. argemone* are combined (Thurston 1969).

For this analysis, any long-term trends (relative to the extent of the data) for each species on each section were accounted for by fitting to the cover values a logistic regression of the form

$$\ln[c/(1-c)] = a + bt \qquad (1)$$

where $a$ and $b$ are fitted parameters, $t$ is time in years, and

$$c = (n+1)/n_{\max} \qquad (2)$$

where $n$ is the total count of cover values, and $n_{\max}$ is 90 for Section IA and 85 for Section IB. Equation 1 was chosen as it cannot generate values beyond 0 and 100% cover, and the fitting is on a logarithmic rather than linear basis, so that the errors are proportional to the mean. The value 1 was added to each observation to remove zero cover values. The standard error of the sampled mean, $s$, (i.e. the square root of residual mean square around the model), was adopted as the measure of short-term variability. Note that significant trends were easier to detect for the longer Section IA data run than for Section VB, and also that the suitability of $s$ for the purpose of this paper was not affected by the statistical significance or otherwise of the trend model. By ranking the species by $s$ values for each section, and adding the ranks, an overall rank order of short term variability was produced. The degree of correlation between cover on the two Sections for each species was also determined to reveal the extent of synchrony of population changes on the two sites.

## Results

Inspection of the residuals revealed that Eq. 1 provided a good summary of long-term trends, except for two cases. The Section IA fit for *Poa trivialis* was strongly influenced by zero cover values in the first 2 years, and so the model was re-fitted excluding these points. For the same section, the *Agrostis* values rose and then declined, implying population changes between the time scale of interest and that removed by the model fitting. Therefore Eq. 1 was re-fitted to the data with a quadratic time term. Cover values of *Tussilago farfara* never exceeded 1 in Section V, so no fitting was attempted; for the comparison of rank order of $s$, its rank order on Section IA was simply doubled.

Only for *Equisetum* was there a significant (at $P < 0.05$) long-term trend (an increase) on both parts of the experiment; *Medicago* decreased on Section VB but not on IA; *Cirsium*, *Poa annua*, *Ranunculus* and *Vicia* displayed long-term trends on IA only and *Agrostis* rose and then declined on IA (Fig. 1; Tables 1 and 2).

Some species, notably *Poa* spp., displayed high $s$ values on both sections regardless of the significance level of the long term-trend; *Equisetum* displayed low $s$ values on both sections. However, any correlation of $s$ values on the two Sections of the experiment across all species was weak [$r = 0.45$, 9 *df*, $P$ (1-tailed) $= 0.08$, using revised models for *Agrostis* and *Poa*]. *Tripleurospermum*, *Alopecurus*, *Poa annua*, *Ranunculus* and *Equisetum* displayed synchronous changes (at $P < 0.05$) in cover between the two sections of the field (Table 2).

## Discussion

There do appear to be differences in short-term variability between species within this data set; the data suggest that predictions on the basis of Eq. 1 would be more accurate for *Cirsium* and *Equisetum* than for *Vicia* or *Poa annua*. Incidentally, the same holds true if polynomial, rather than logistic, trend models are fitted. The weak correlation between standard error values $s$ on the two sections gives little guidance as to how consistent levels of variability would be for particular species under different conditions; more data, from a wider range of environments, are needed to address this issue.

Why should some species display greater variability than others? Many animal ecologists would invoke $r$-$K$

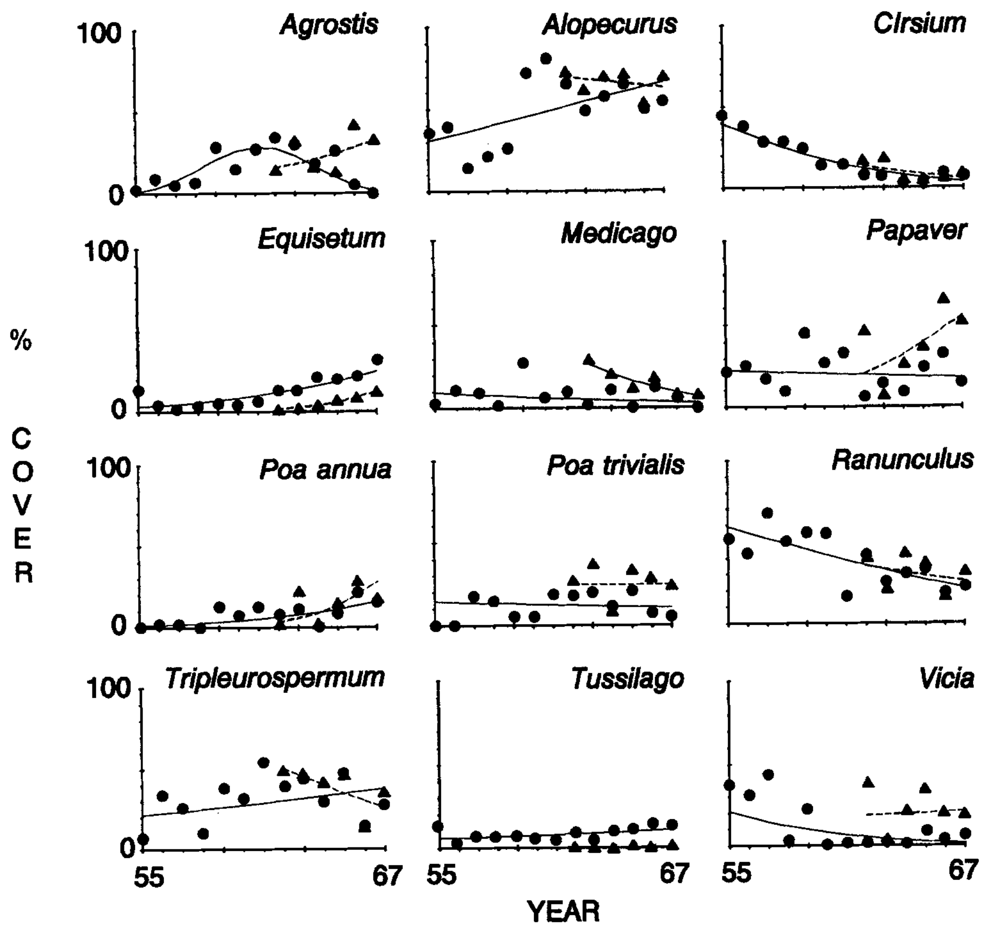

**Fig. 1.** Changes in percentage cover of 12 weed species on Sections IA (●) and VB (▲) of the Broadbalk experiment from 1955 to 1967. The lines show Eq. 1 fitted to Section IA (—) and VB (– –) data; parameter values are given in Tables 1 and 2. Data from Thurston (1969)

**Table 1.** The results of fitting logistic regressions to changes in weed cover through time in Section IA of the Broadbalk experiment.

| Species | Model | $P$ | $r^2$ | $s$ |
|---|---|---|---|---|
| *Agrostis stolonifera* | $-2.25+0.032t$ | 0.74 | 0.01 | 1.26 |
| Quadratic model | $-5.12+1.182t-0.082t^2$ | 0.00 | 0.73 | 0.63 |
| *Alopecurus myosuroides* | $-0.89+0.125t$ | 0.06 | 0.28 | 0.81 |
| *Cirsium arvense* | $-0.17-0.216t$ | 0.00 | 0.83 | 0.40 |
| *Equisetum arvense* | $-3.25+0.170t$ | 0.00 | 0.61 | 0.56 |
| *Medicago lupulina* | $-2.05-0.080t$ | 0.28 | 0.10 | 0.95 |
| *Papaver* spp. | $-1.15-0.024t$ | 0.65 | 0.02 | 0.70 |
| *Poa annua* | $-3.94+0.178t$ | 0.03 | 0.35 | 0.97 |
| *Poa trivialis* | $-3.28+0.141t$ | 0.08 | 0.25 | 1.00 |
| Excluding years 1 & 2 | $-1.68-0.026t$ | 0.67 | 0.20 | 0.60 |
| *Ranunculus arvensis* | $0.54-0.137t$ | 0.00 | 0.55 | 0.51 |
| *Tripleurospermum inodorum* | $-1.31+0.066t$ | 0.26 | 0.11 | 0.75 |
| *Tussilago farfara* | $-2.65+0.049t$ | 0.14 | 0.18 | 0.42 |
| *Vicia sativa* | $-1.06-0.204t$ | 0.05 | 0.31 | 1.24 |

The models are of the form $\ln[c/(1-c)]=a+bt$, where $a$ and $b$ are fitted parameters, $t$ = time in years, coding 1955 as year 1; and $c=(n+1)/90$ where $n$ is the cover value out of a maximum of 90 (see text for details). Three measures of fit are indicated; $P$, the significance level of the model; $r^2$ and the standard error of the sampled mean $s$. Two models gave poor fits by inspection; *Poa trivialis*, where two zero values in the first 2 years distorted the model; and for *Agrostis stolonifera*, where a non-linear relationship was apparent. In both cases, an alternative model is given

strategy theory at this point; species which experience large local variation in population size often have associated life-history characteristics, such as short life cycle and high reproductive rate, which are in turn adaptations to fluctuations in habitat quality over space and time (e.g. Southwood 1977). The conceptually similar C-S-R classification of Grime (1977; Grime et al. 1988) also relates life-history and growth characters to habitat. Different strategies are expected to predominate in different environments; competitors in predictably high-quality

**Table 2.** The results of fitting logistic models to changes in weed cover through time in Section VB of the Broadbalk experiment

| Species | Model | $P$ | $r^2$ | $s$ | $r$ |
|---|---|---|---|---|---|
| *Agrostis stolonifera* | $-1.80+0.183t$ | 0.29 | 27 | 0.63 | −0.65 |
| *Alopecurus myosuriodes* | $0.93-0.057t$ | 0.56 | 9 | 0.37 | 0.81* |
| *Cirsium arvense* | $-1.59-0.175t$ | 0.30 | 26 | 0.62 | 0.55 |
| *Equisetum arvense* | $-4.05+0.27t$ | 0.00 | 98 | 0.10 | 0.93* |
| *Medicago lupulina* | $-0.66-0.296t$ | 0.01 | 83 | 0.28 | 0.22 |
| *Papaver* spp. | $-1.63+0.312t$ | 0.26 | 30 | 0.56 | 0.49 |
| *Poa annua* | $-3.54+0.4397t$ | 0.22 | 35 | 1.13 | 0.86* |
| *Poa trivialis* | $-1.06-0.003t$ | 0.98 | 0 | 0.70 | 0.52 |
| *Ranunculus arvensis* | $-0.48-0.091t$ | 0.54 | 10 | 0.56 | 0.78 |
| *Tripleurospermum inordorum* | $0.27-0.213t$ | 0.19 | 39 | 0.56 | 0.89* |
| *Vicia sativa* | $-1.44+0.030t$ | 0.91 | 39 | 1.01 | 0.30 |

The models are of the form $\ln[c/(1-c)] = a+bt$, where $a$ and $b$ are fitted parameters, $t$ = time in years, coding 1962 as year 1; and $c=(n+1)/85$ where $n$ is the cover value out of a maximum of 85 (see text for details). Three measures of fit are indicated; $P$, the significance level of the model; $r^2$ and the standard error of the sampled mean $s$. The linear correlation $r$ of the cover values with those on Section IA are also shown; asterisks indicate correlations significant at $P<0.05$ (two-tailed, 4 $df$)

**Table 3.** Summary of life-history data and analysis of the Broadbalk data

| Species | CSR | Life hist | Regen | Bank | %germ | $s$ | | | Sum of ranks |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | IA | IA($r$) | VB | |
| *Tussilago* | CR | P | (V), W | 1 | – | 2 | 2 | | 4 |
| *Equisetum* | CR | P | V, W | 1 | – | 4 | 4 | 1 | 5 |
| *Cirsium* | C | P | V, W, Bs | ?3 | – | 1 | 1 | 6 | 7 |
| *Ranunculus* | ?R | Aw | Bs | ?4 | 54 | 3 | 3 | 4.5 | 7.5 |
| *Alopecurus* | R/CR | Aw | S | 3 | 94 | 7 | 9 | 3 | 12 |
| *Medicago* | R/SR | A/P | Bs | 4 | 45 | 8 | 10 | 2 | 12 |
| *Tripleurospermum* | R | Aws | S, Bs | 3 | 70 | 6 | 8 | 4.5 | 12.5 |
| *Agrostis* | ?CR | P | V, Bs | 3 | – | 12 | 6 | 7 | 13 |
| *Poa trivialis* | CR/CSR | P | V, Bs | 3 | – | 10 | 5 | 8 | 13 |
| *Papaver* | R | Asw | Bs | 4 | 63 | 5 | 7 | 9.5 | 16.5 |
| *Vicia* | R/CSR | Aw | ?Bs | 4 | 48 | 11 | 11 | 9.5 | 20.5 |
| *Poa annua* | R | A/P | V, S, Bs | 3 | – | 9 | 9 | 11 | 20 |

For each species, the strategy class is given (CSR: C, competitor; S, stress-tolerator; R, ruderal, and intermediate combinations); the life-history classification (Life hist; Aw, winter annual; As, summer annual; Aws, either winter or summer annual; P, polycarpic perennial); the regeneration strategy (Regen; Bs persistent bank of seeds or spores; S, seasonal regeneration by seed; V, lateral clonal spread; (V) between V and seasonal regeneration from vegetative means; and W, regeneration with numerous widely dispersed seeds or spores: if several are indicated, the first listed is the most prevalent) and the properties of the seed bank (Bank; 1, most seeds germinate shortly after being shed; 3, concentrations of seeds are high just after being shed, but some persist; and 4, a large bank of persistent seeds throughout the year) [terminology from Grime et al. (1988); data from Grime et al. (1988) except for *Ranunculus arvensis* and *Alopecurus myosuroids*, and values for *Papaver rhoeas* are used for *Papaver* spp.]. The percentage of seedlings which emerged in the first year after sowing are also given for some species (% germ; Thurston 1969). The rank order of $s$ are given from Tables 1 and 2, along with those including the revised models shown in Table 1. The ranks of the $s$ values from Sections VB and IA (using the alternative models) data are then added to give the sum of rank values, except for *Tussilago*, where only one value is available, this is doubled. See Tables 1 and 2 for details and full species names. The species are listed in order of the sum of ranks

habitats, ruderals in disturbed habitats and stress-tolerators in predictably poor habitats. Intermediate strategies are also identified. Species are classified to particular strategies according to growth and life-history patterns. Unlike $r$-$K$ theory, there are no explicit links to the population dynamics of the species.

Is it possible that the differences in short-term variability observed at Broadbalk can be related to the C-S-R classification of the species involved? The species in this study differ in strategy according to Grime et al. (1988) from the competitive *Cirsium* to the ruderals *Poa annua*, *Papaver* and *Tripleurospermum* (Table 3), and one can interpret the strategies along a continuum from C to CR and CR/CSR, to R/other and finally to R. If the species are ranked by C-S-R class (C = 1; CR, CR/CSR = 2; R/other = 3; R = 4) and are correlated with the variability rankings (Table 3), the chances of there being no relationship are less than 10% [using the combined $s$ ranks, Spearman rank correlation $r_s = 0.52$, $n = 12$, $P$(2-tailed) $< 0.10$; using only the longer Section IA data, $r_s = 0.55$, $n = 12$, $P$(2-tailed) $< 0.10$]. This represents weak evidence of a relationship between strategy and short-term variability; the more ruderal the species, the greater the short-term variability.

A comparison of life histories and regenerative strategies is more revealing than a simple consideration of the C-S-R classification. In particular, there is a weak correlation between seed bank behaviour as classified by Grime et al. (1988) (Table 3) and the ranked $s$ values [Spearman rank correlation, regarding both variables as already ranked, $r_s = 0.62$, $n = 12$, $P$(2-tailed) $< 0.05$ for the combined rank values, $r_s = 0.50$, $n = 12$, $P$(2-tailed) $< 0.10$ for Section IA only]. This result suggests that those species with persistent seed banks with high carry-over from the first year (data from Thurston 1969, Table 3) were more variable over the short term than those displaying a perennial life history and having little or no long term seed bank (Table 3).

The degree of synchrony between the two parts of the experiment can offer some insights into these issues. *Equisetum* and *Cirsium* both show synchronous behaviour, consistent with long-term responses to management [interpreted by Thurston (1969) as responses to the herbicide regime]. *Medicago* behaved quite differently on the two sections, suggesting that it was acting as two separate populations, or that the combined data for each section were disguising substantial variation between plots. Thurston's (1969) observations agree: she stated that *Medicago* was characteristic of no- or low-N plots, a local factor. According to Thurston (1969), *Tripleurospermum* fared better after dry summers – a factor common to the whole experiment, but not one which would have resulted in an overall long-term trend; indeed, this species was highly synchronous, but no significant long-term trend was observed. Different species responded to different sources of environmental variation.

Environmental variation also helps explain the more variable behaviour of those species with persistent seed banks. Several of the population changes were interpreted by Thurston (1969) in terms of seedling emergence time and the behaviour of the seed bank, notably the time of peak emergence compared with the time of cultivation. In general terms, the seed banks of arable seeds decline exponentially (e.g. Roberts and Feast 1973), but temperature and water availability can influence emergence rates (e.g. Forcella 1992), and the consistency of timing of emergence can vary between species (e.g. Roberts 1986). Environmental variation therefore can induce substantial fluctuations in recruitment and survival for some species with persistent seed banks – indeed, the very existence of a persistent seed bank is interpreted as an evolutionary response to fluctuating environments (Venable and Brown 1988). While seed banks dampen short-term variation within a species (Pacala 1986; Thrall et al. 1988), that does not imply that species with seed banks display less short-term variation than those without them.

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