An Analysis of Spatial and Temporal Variation in Seedling Survival of a Monocarpic Perennial, Conium maculatum
Author(s): Mark Tremlett, Jonathan W. Silvertown, Chris Tucker
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Demographic variability is a well documented phenomenon, but quantitative methods for analysing it are still needed. This paper illustrates such a method using data from a demographic study of *Conium maculatum* L. (Umbelliferae), in which substantial variation in seedling survival between quadrats and between cohorts-within-quadrats was found.

M. Tremlett, J. W. Silvertown and C. Tucker, Dept of Biology, Open Univ., Walton Hall, Milton Keynes, Bucks MK7 6AA, England.

Демографическая вариабельность - хорошо изученное явление, но количественные методы анализа пока нуждаются в разработке. Данная статья иллюстрирует такой метод с помощью данных демографических исследований *Conium maculatum* L., у которых установлены широкие различия выживаемости всходов в разных участках и в разных когортах в пределах одного участка.

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Introduction

The accumulating literature on plant population dynamics is beginning to reveal significant spatial and temporal variation in the demography of plants. Variability in the demography of certain species has been attributed to differences within and between patches in litter and vegetation cover (Holt 1972, Fenner 1978, Gross 1980, Silvertown and Wilkin 1983), soil topography (Harper et al. 1965), management practices (Bakker et al. 1980) and animal activity (Whelan and Main 1979, Thompson 1983). Phenotypic variability in life history within populations (Law et al. 1977) and temporal differences in the demographic characteristics of cohorts and individuals emerging at different dates (Black and Wilkinson 1963, Holt 1972) have also been studied. This paper illustrates a method for the quantitative analysis of demographic variation using data from a study of hemlock, *Conium maculatum* L., a monocarpic perennial umbellifer common in disturbed habitats in the British Isles.

Method

A study of the demography of *C. maculatum* was begun in Milton Keynes, UK in November 1981. Ten, 25 × 25 cm permanent quadrats were established in a 20 × 100 m area of riverbank, which had been severely disturbed by mowing in the autumn of 1981. The quadrats were chosen to include a range of litter and vegetation cover, between 0 and 95%, thus enabling an analysis of the effect of litter and vegetation cover on the demography of *C. maculatum* seedlings. Seedlings of *C. maculatum* germinate throughout the winter and early spring. Seedlings were first observed at this site on 26 November 1981 and all the quadrats were established by 4 December 1981. Emerging seedlings were marked with plastic rings. Visits were initially made at fortnightly intervals and subsequently at monthly intervals as the rate of emergence declined. All the seedlings recruited at one visit were identified by a new ring colour to distinguish cohorts. Survivors from existing cohorts were recorded at each visit. The amount of litter and vegetation cover within each of the 10 quadrats was recorded soon after establishment using photographs which were analysed using a Video Plan device. The proportion of each quadrat covered by litter and vegetation cover was obtained by tracing around the areas of visible bare soil (ignoring seedlings) in each photograph.

For each quadrat, percentage survival curves for each cohort were calculated, and the values obtained were transformed using the arcsine transformation (Sokal and Rohlf 1969). By applying confidence limits to the normalised survival data, comparisons between the survival curves were made.

Results

Spatial variation in seedling survival between quadrats

A total of 4645 seedlings were recorded emerging in the 10 quadrats in 9 cohorts between 4 December 1981 and 28 April 1982, after which no further germination was observed. Considerable variation in recruitment between quadrats was found. Recruitment and percentage cover (Tab. 1) within quadrats were negatively correlated (Spearman $r_s = 0.721$, $P < 0.05$, $N = 10$). The quadrats were ordered by percentage cover. The majority of seedlings (76%) were recruited to 3 cohorts (cohorts 1,4 and 5).

Survival curves for each of these cohorts (Figs 1c, 1b and 1a respectively) show considerable between quadrat variation in seedling survival. Quadrats 1, 5, 6 and 10 consistently fell outside the 95% confidence interval of the normalised suvival data. Recruits to all 3 cohorts had high survival in quadrat 5 and low survival in quadrat 4; recruits to 2 of the 3 cohorts had high survival in quadrat 1 (cohorts 1 and 5), and recruits to 2 of the 3 cohorts had low survival in quadrats 10 (cohorts 4 & 5), 6 (cohorts 1 & 4).

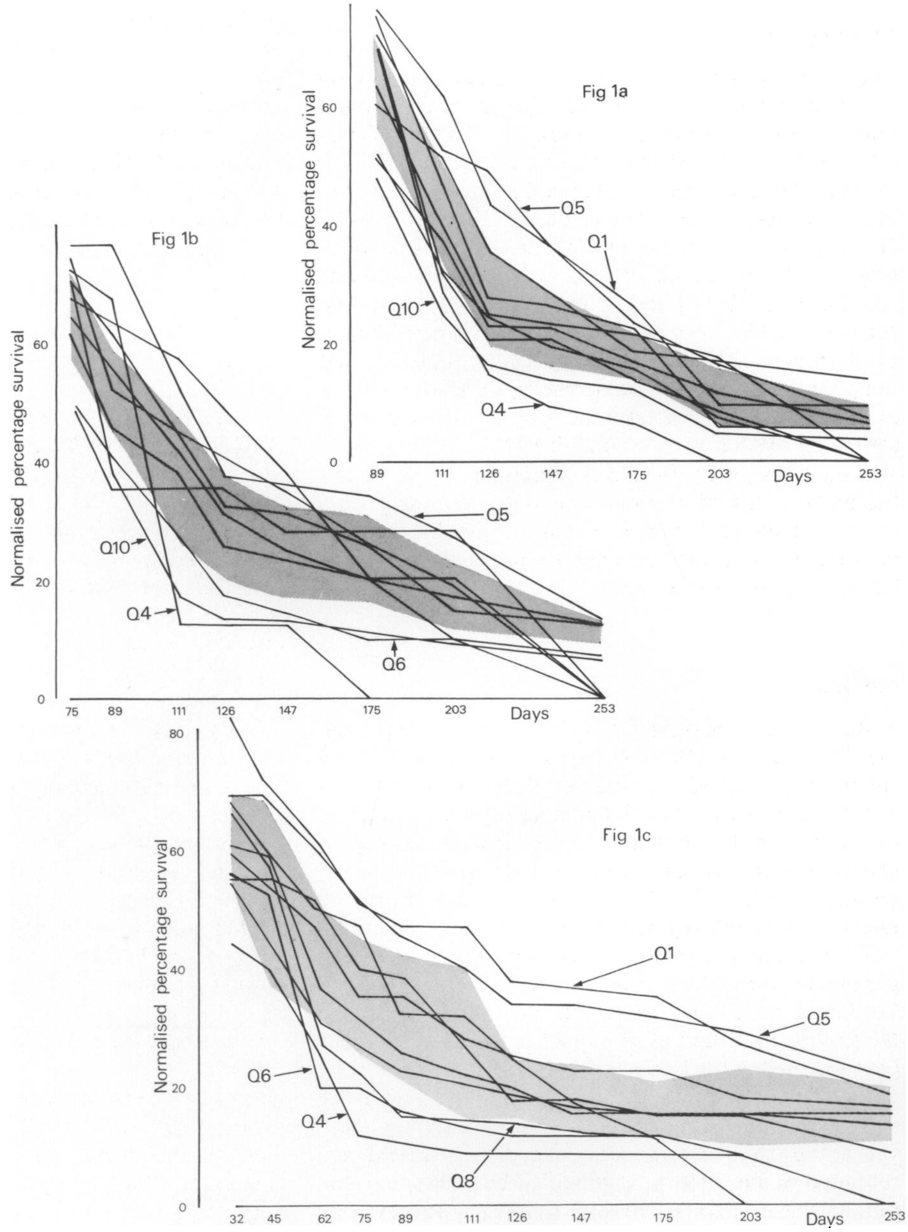
Temporal variation in seedling survival between cohorts

Normalised survival curves for all cohorts within four quadrats (quadrats 5, 8, 9 and 10) were adjusted to compare the proportions of each cohort surviving at 10 d intervals (Figs 2a–d respectively). In each of the 4 quadrats cohort 1 had consistently higher survival than all other cohorts, and in 3 of the 4 quadrats cohort 6 had lower survival. (Cohorts 7–9 had very low initial recruitment and the rapid extinction of these cohorts may have been partly due to the larger error associated with small sample sizes).

Tab. 1. Cumulative seedling emergence of *Conium maculatum* and percentage vegetation and litter cover in the ten quadrats established.

Quadrat number	1	2	3	4	5	6	7	8	9	10
Number of recruits	205	358	176	189	131	494	362	694	682	1323
Percentage cover (vegetation + litter)	93.9	87.4	79.1	72.0	45.9	38.2	17.1	13.8	8.6	7.4

Fig. 1. Survivorship curves for the three largest cohorts, showing variation between quadrats; (a) cohort 5, (b) cohort 4 and (c) cohort 1. 95% confidence limits are shown shaded. Quadrats falling outside these limits are identified (eg. Q1 = quadrat 1).



Discussion

Vegetation cover has been shown to decrease both recruitment and survival of emerging seedlings (Holt 1972, Gross and Werner 1982). The results of this study show that cover dependent recruitment occurs in *C. maculatum*. Quadrats with little vegetation cover show significantly higher recruitment than quadrats with high vegetation cover values; nonetheless the effect of vegetation cover on seedling survival is unclear from these results since seedling survival is low in quadrats with low (quadrat 10), intermediate (quadrat 6) and high (quadrat 4) vegetation cover values. Seedling survival was found to be greatest in quadrats 1 and 5 which had high and intermediate percentage vegetation cover values respectively. The survivorship curves for all cohorts of *C. maculatum* show high mortality at first, expectancy of further life increasing with age (Type III curves, Deevey 1947); these results are similar to another monocarpic perennial umbellifer, *Pastinaca sativa* L. (Baskin and Baskin 1979). Two recognised sources of error may influence our results. First, the frequency of visits may cause an underestimation of seedling recruitment and mortality, and secondly ringing seedlings may increase mortality. Greenhouse trials on the effect of ringing seedlings on their survival compared with unringed controls showed no significant effect of ringing (C. Tucker unpubl. data).

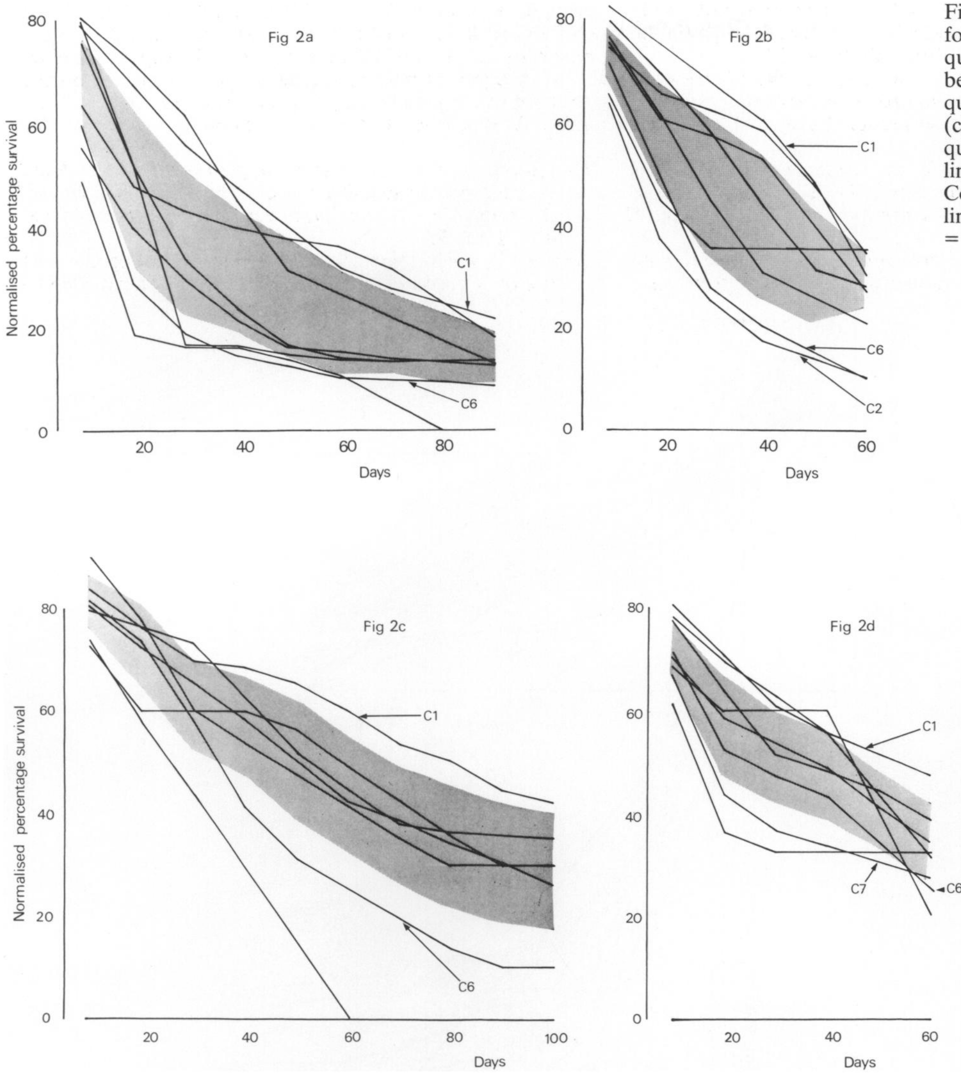


Fig. 2. Survivorship curves for four representative quadrats, showing variation between cohorts; (a) quadrat 10, (b) quadrat 8, (c) quadrat 5 and (d) quadrat 9. 95% confidence limits are shown shaded. Cohorts falling outside these limits are identified (eg. C1 = cohort 1).

Temporal variation in seedling survivorship was detectable in all quadrats despite significant variation in survival between quadrats. The possible sources of demographic variation are by no means exhausted by those demonstrated here. For example there is also likely to be demographic variation between years (Arthur et al. 1973). The data presented do demonstrate a simple method for analysing survival data, illustrating previously untested differences in survival, and seeking explanations for them.

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