



Sustained dynamic transience in a Lotka–Volterra competition model system for grassland species[☆]

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ABSTRACT

Theoretical approaches, such as the Lotka–Volterra framework, enable predictions about long term species coexistence based on stability criteria, but generally assume temporal constancy of system equations and parameters. In real world systems, temporal variability may interfere with the attainment of stable states. Managed grassland ecosystems in Northwestern Europe experience structural periodic fluctuations in environmental conditions: the seasons. In addition, periodic disturbances such as cutting are very common. Here we show, using a Lotka–Volterra system applied to grassland species with empirically derived parameters, that seasonal variability can result in a time dependent equilibrium and redirection of displacement processes.

Parameter estimates differed between species and – in most cases – between the seasons. As a result, five of the fifteen tested species combinations had different outcomes of species interactions between seasons. This indicates that systems remain in dynamic transience over the year as the equilibrium changes and the species composition of the system follows the equilibrium without ever attaining it. The non-attainment of the steady state enables coexistence of species even if there is competitive exclusion in one of the seasons. For three of the fifteen species combinations, cutting frequency affected the long-term coexistence patterns. Cutting resets the biomass of competing species and favours during regrowth those species that have a high growth rate, which can alter species coexistence in comparison to a Lotka–Volterra model without cutting. The Lotka–Volterra framework with seasonally changing empirical parameters predicts coexistence as a possible outcome of systems that in component seasons are characterised by exclusion, and vice versa.

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1. Introduction

Grasslands provide multiple functions, including forage production (Silvertown, 1980; Frame, 1990), biodiversity in agro-environmental schemes (Vickery et al., 2001; Barnett et al., 2004) and protection and conservation of specific species in conservation schemes (Berendse et al., 1992; Muller et al., 1998). Species coexistence patterns in grasslands can be affected by disturbances and temporal dynamics of environmental factors. For instance, disturbances like fire and cutting reduce the biomass of vegetation, which can lead to faster plant growth (Parsons et al., 2001) and changes

in the relative abundances of competing species (Huston, 1979; Pacala and Tilman, 2002). Seasonality has been shown to influence species specific growth in mixtures (Connolly et al., 1990), biomass accumulation (Turkington and Harper, 1979a; Fowler and Antonovics, 1981) and inter-specific interactions (Turkington and Harper, 1979b; Thórhallsdóttir, 1990). Therefore, disturbances and seasonal trends in species characteristics can potentially affect the long-term dynamics and coexistence of species.

A range of theoretical approaches have been developed to address plant competition and species coexistence, ranging from relatively simple analytical models such as the classic Lotka–Volterra framework (Begon et al., 1996) to comprehensive, process-based simulation models (Connolly and Wachendorf, 2001). Lotka–Volterra equations predict trends in paired species coexistence patterns, resulting in competitive exclusion of one of the species or coexistence. The strengths of the Lotka–Volterra framework are its simplicity, transparency, and the straightforward ecological interpretation of parameters (Begon et al., 1996). However, an important simplification in the classic Lotka–Volterra theory is the assumption of homogeneity in environmental

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conditions in space and time, which does not hold for real plant populations (Hutchinson, 1961; Chesson, 2000). Indeed, incorporating seasonality of resource availability in the parameters of the Lotka–Volterra equations shows that the competitive ranking of species can be reversed (Boyce, 1979). Chesson and Huntly (1989) reviewed several models on the potential for short term instabilities to long term coexistence, and concluded that the dependence of short term population dynamics on environmental variability is likely to be a very important factor.

The effect of forced fluctuations in environmental conditions has been investigated in multiple modelling studies, such as Grace (2001) who focused on the impact of seasonal variability of environmental conditions on community biomass and species richness. Schulte et al. (2003) suggested that seasonal environmental fluctuations, as well as “disturbances” such as cutting, can potentially lead to increased species coexistence in mixed swards. However, as these studies were not based on empirically derived parameters of the population dynamics the applicability of these studies to real world phenomena is unclear. Connolly and Wachendorf (2001) developed a comprehensive multi-site grassland model with a firm empirical base which was used to predict the development of clover/ryegrass communities in winter, spring, summer and autumn. Unfortunately, as a consequence of the model's complexity, the emerging patterns are difficult to interpret. Therefore, even though theory suggests that seasonality and disturbances can affect species coexistence, this has not yet been explored using empirically realistic parameters in a transparent model.

If temporal variability in environmental conditions can prevent a population from attaining the equilibrium point predicted by the Lotka–Volterra framework (Hutchinson, 1961; Koch, 1974; Huston, 1979), than the equilibrium point then becomes time dependent, where population dynamics follow but never attain the equilibrium due to growth rates and reaction time. Cushing (1976) provides mathematical proof that a Lotka–Volterra system with species that would exclude each other under constant conditions can co-exist in a limit cycle fashion when subjected to suitable periodic harvesting or removal rates. However, are real-world harvest rates (cutting or grazing) and environmental periodicities (seasons) suitable in the sense meant by Cushing (1976)? Answering this question requires empirical research, and parameter estimation of applicable models.

In this paper, we study how cutting and seasonally changing plant growth and competition parameters impact the within and across years population dynamics and coexistence of grassland species, using a model based on the Lotka–Volterra framework. The model is parameterized with empirically derived parameters which are reported here for the first time. In particular, we want to explore to which extent theoretical behaviours described by Cushing (1976) and Koch (1974) occur in real world in grassland communities.

2. Materials and methods

We first describe field experiments in which species' growth and competition parameters were determined. We then describe the classical Lotka–Volterra model, the estimation of model parameters from data, and finally the scenario studies for single versus multi-seasons simulations and cutting.

2.1. Field experiments and data collection

Species mixtures were sown at two sites in spring 2004. The sites were approximately 2 km apart at Teagasc farms at Johnstown Castle Environmental Research Centre, Co. Wexford, Ireland (52° 17' N, 06° 30' W). The soil of one site was moderately drained and the other site was poorly drained as defined by Schulte et al. (2005). At the moderately drained site, two fertilizer rates were used: 90 or 225 kg

N/ha, representing extensive or intensive farming practices, respectively. In line with agricultural practices in Ireland, only the lower fertilizer rate was applied at the wet site. The experiment thus included three treatments – well drained & heavily fertilized; well drained & moderately fertilized; and wet & moderately fertilized.

Twelve plant species were used to compose plant mixtures; six of which are production grasses: *Alopecurus pratensis* L., *Festuca pratensis* Huds., *Holcus lanatus* L., *Lolium perenne* L., *Phleum pratense* L., and *Poa pratensis* L.; and six other grassland species: *Agrostis stolonifera* L., *Centaurea jacea* L., *Plantago lanceolata* L., *Ranunculus repens* L., *Trifolium pratense* L., and *Trifolium repens* L. These species were sown singly or in mixtures of two or three species. Seed rate of a species in mixture was determined on the basis of the monoculture rate, which was 1000 germinable seeds (3 g) per m² for production grasses and 1.5 g m⁻² for the other plant species. A monoculture contained the first species at full seed rate, a two-species mixture contained the first and the second species both at half seed rate, and a three-species mixture was composed each species at one third of the usual seed rate. The first species could be any of the 12 selected included in the study; the second species was always *Lolium perenne*, since this is the largest component of most current seed mixtures; and the third species could be any of the following grassland species: *A. pratensis*, *F. pratensis*, *P. pratense*, *P. pratensis*, *A. stolonifera* or *T. repens*. In total 68 different seed mixtures were sown: 12 monocultures, 11 two-species mixtures of *L. perenne* and one of the other species and 45 three-species mixtures, i.e. each feasible mixture including *L. perenne* was sown. Each of the 68 seed mixtures treatments was sown in three replicates plots of 1.5 m × 1.5 m. Each set of seed mixture replicates was sown as a block, and within a block the layout of the seed mixtures was randomized. The whole of the experiment included 68 mixtures × 3 treatments × 3 blocks = 612 plots.

Measurements were taken in the second year (2005) of the experiment – one year after sowing – by which time the mixtures had established and most species were still present and competing for resources. Data was collected in three periods to capture seasonal growth differences among the plant species: spring (28 March–28 April), early summer (9 May–9 June) and late summer/autumn (2 August–1 September). For each plot, the accumulation of green plant area of each individual species, following a cut was monitored weekly, for five consecutive weeks in spring and four consecutive weeks in summer and autumn, using the method of inclined point quadrats (Wilson, 1963). This method allows making measurements without disturbing the vegetation, thereby enabling the monitoring of growth rates over time. All photosynthesizing parts of the plants (i.e. leaves and stems) were recorded. Twenty inclined point quadrats were taken in a 50 cm × 50 cm area in the center of each plot. This resulted in 68 (mixtures) × 3 (replicates) × 3 (treatments) × 3 (seasons) × 4–5 (consecutive weeks) × 20 (inclined point quadrats each time) = c. 150,000 inclined point quadrats to record the growth dynamics of individual species.

At the end of the last observation period, herbage was manually cut to ground level on four areas of 150 cm² within each plot. Biomass was subsequently dried and weighed to determine species-specific conversion factors of inclined point quadrats to dry matter weight.

2.2. Description of Lotka–Volterra model

The Lotka–Volterra system is commonly defined as:

$$\begin{cases} \frac{dY_1}{dt} = r_1 Y_1 \left(1 - \frac{Y_1 + \alpha_{12} Y_2}{K_1} \right) \\ \frac{dY_2}{dt} = r_2 Y_2 \left(1 - \frac{Y_2 + \alpha_{21} Y_1}{K_2} \right) \end{cases} \quad (1)$$

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