



Variation in moisture duration as a driver of coexistence by the storage effect in desert annual plants



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ABSTRACT

Temporal environmental variation is a leading hypothesis for the coexistence of desert annual plants. Environmental variation is hypothesized to cause species-specific patterns of variation in germination, which then generates the storage effect coexistence mechanism. However, it has never been shown how sufficient species differences in germination patterns for multispecies coexistence can arise from a shared fluctuating environment. Here we show that nonlinear germination responses to a single fluctuating physical environmental factor can lead to sufficient differences between species in germination pattern for the storage effect to yield coexistence of multiple species. We derive these nonlinear germination responses from experimental data on the effects of varying soil moisture duration. Although these nonlinearities lead to strong species asymmetries in germination patterns, the relative nonlinearity coexistence mechanism is minor compared with the storage effect. However, these asymmetries mean that the storage effect can be negative for some species, which then only persist in the face of interspecific competition through average fitness advantages. This work shows how a low dimensional physical environment can nevertheless stabilize multispecies coexistence when the species have different nonlinear responses to common conditions, as supported by our experimental data.

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1. Introduction

Annual plant communities have figured prominently in both theoretical and empirical studies of the contribution of environmental variation to the maintenance of species diversity. Theoretical work illustrates how environmentally sensitive germination generates the storage effect coexistence mechanism in a temporally variable environment (Chesson, 1994, 2003; Chesson et al., 2004). This theory has primarily focused on the coexistence of species competing for resources (e.g. Chesson, 1994, 2003), although more recent work has extended these results to the storage effect acting through apparent competition (Kuang and Chesson, 2008; Chesson and Kuang, 2010). Several field studies have provided empirical support for the storage effect in annual plants arising from variable germination, variable growth, and competition between species (Facelli et al., 2005; Sears and Chesson, 2007; Angert et al., 2009a).

Theoretical models of coexistence in a temporally variable environment normally do not model the physical environment directly, but instead model fluctuations in population parameters, such as germination fraction, which are assumed to be driven

by fluctuations in the physical environment (Chesson et al., 2004; Kuang and Chesson, 2009). The probability distributions of fluctuations in these parameters (environmental responses) are the inputs to the models. These studies have provided general understanding of the ability of environmental fluctuations to promote coexistence in terms of the statistical properties of the environmentally dependent parameters (Chesson, 1994). In particular, the strength of the storage effect is determined by the variances and correlations of these fluctuating environmental responses (Chesson, 1994, 2003; Angert et al., 2009b). However, a key problem is determining what these variances and correlations are for input to the models.

Environmentally dependent germination rates provide the clearest example of fluctuating environmental responses in annual plants, although reproductive output also depends on environmental conditions during growth in ways that can promote the storage effect (Pake and Venable, 1995; Angert et al., 2009a). Although variances and correlations of germination fractions have been measured from field data (Angert et al., 2009a; Chesson et al., 2014) it is difficult to obtain long enough sequences of observations for much precision. In the absence of good estimates of species differences in these respects, the phenomenological germination fractions used in most theoretical studies assume a great deal of symmetry between species in the variances and correlations of germination fractions (Chesson et al., 2004; Kuang and Chesson, 2009). However, Angert et al. (2009a) provide good

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evidence for substantial asymmetries in these statistical properties for an annual plant community, in general agreement with findings for tropical forests (Wright et al., 2005). The strong symmetries imposed in theoretical models therefore may not provide accurate predictions for how the storage effect operates in nature.

Because fluctuations in germination fractions are driven by environmental fluctuations (Grubb, 1977; Adondakis and Venable, 2004; Facelli et al., 2005), one possible approach to a better understanding of the nature of germination fluctuations is to develop models of how fluctuations in physical environmental variables drive fluctuations in germination. This approach, which we explore here, potentially has great value for understanding coexistence in annual plants by better understanding the statistical structure (variances and covariances) of the responses of the different species in a community to the fluctuating environment. We are specifically concerned with arid systems where communities of annual plants form a major component of the flora (Venable et al., 1993; Facelli et al., 2005). In these systems, the soil surface, where most seeds can be found, is dry the majority of the time. Pulses of rain dampen the soil for different periods following rainfall (Kemp, 1983; Loik et al., 2004; Reynolds et al., 2004; Schwinning and Sala, 2004), and depending on associated environmental factors, can lead to germination pulses in the annual plant community (Beatley, 1974; Chesson et al., 2004).

Field and laboratory experiments have explored links between the environment and germination fraction, but in relatively limited ways. One principal finding is that variation in temperature at the time of rainfall drives variation in the germination fraction due to species-specific responses to temperature (Adondakis and Venable, 2004; Facelli et al., 2005; Chesson et al., 2014). It is also known that soil moisture level, dormancy cycles, and the history of environmental conditions that a seed has experienced can affect the germination response (Grubb, 1977; Baskin and Baskin, 1986; Baskin et al., 1993; Adondakis and Venable, 2004; Facelli and Chesson, 2008). However, these studies often restrict attention to total germination at a fixed time after wetting of the soil (Baskin et al., 1993; Adondakis and Venable, 2004). Natural rainfall patterns lead to a wide range of durations of soil moisture with potential major effects on the amount of germination overall and the relative germination fractions of different species. Therefore, these studies potentially miss much environmental variation of significance for the coexistence of annual plant species. Here we study this important but neglected aspect of environmental variation, the duration of sufficient moisture for germination in the soil surface. We use our findings to understand how species' responses to a given environmental driver of germination can structure the variances and correlations of germination fluctuations over time, and how the resulting asymmetric statistical properties affect species coexistence.

Seed germination is a biological process, and takes time as the seeds imbibe water and begin meristematic activity (Fenner, 1985; Bradbeer, 1988). As long as there is sufficient moisture, germination of a nondormant seed proceeds, but when the moisture is reduced to a sufficiently low level, germination stops (Fenner, 1985; Bradbeer, 1988). Seeds that have begun cell division are killed by the loss of moisture, while those that have not begun cell division dehydrate and rejoin the seed bank (Bradbeer, 1988; Baskin and Baskin, 1998). The germination fraction we consider here is the fraction of seeds that have begun cell division, as their germination is irreversible. The duration of soil moisture determines the duration of the germination process, and therefore the number of seeds that complete the process and germinate. The germination process is a clear biological link between the soil moisture duration and the resulting germination fractions.

To study how this link between soil moisture duration and germination affects coexistence, we first experimentally determine

how desert annual plant species differ from one another in their germination patterns as a function of time while sufficient soil moisture for germination is available. The patterns of germination variation are constrained by the one-dimensional nature of variation in soil moisture duration and the germination biology of the species. We develop a model of germination fraction as a function of soil moisture duration from the experimental results, and show how germination patterns generated by variation in the duration of soil moisture drive the storage effect. This analysis provides a powerful illustration of how a single, specific environmental variable has the potential to cause major variation in relative germination, stabilizing species coexistence. Even though the physical environmental variable is one-dimensional, different nonlinear responses to this variable allow multispecies coexistence.

2. Experiments

For temporal germination variation to affect coexistence, it must lead to variation in relative germination fractions either between years (Chesson et al., 2004) or within years (Mathias and Chesson, 2013). For variable soil moisture to generate this type of variation, it must lead to different communities of growing plants at different times after rainfall. We conducted growth chamber germination studies on plants from a well-studied annual plant community in the Chihuahuan Desert (Chesson et al., 2014). Details of the growth chamber study are provided in Appendix A, where the statistical tests demonstrating species-specific germination characteristics are given. Here we summarize the key results.

The cumulative germination fractions of seeds of different species as a function of time since the application of moisture are shown in Fig. 1. These curves show species-specific delays before appreciable germination occurs. Each curve then rises with species-specific steepness to a plateau, which is the species-specific final germination fraction. These shapes differ significantly between species within each temperature and moisture treatment, and these shapes change significantly between temperature and moisture treatments (Appendix A).

In nature, any rainfall event will be associated with a specific temperature, moisture level, and moisture duration. Although we did not experimentally vary moisture duration, the curves give cumulative germination as a function of time. Germination ceases following drying of the soil surface in the field, and so we interpret the cumulative germination up to a particular time as the total germination that would be observed had we dried the soil at that point. In nature the time of surface soil drying depends on many factors such as sunshine, wind, and repeat rains, as well as the total rain received and temperature. Our focus in the theoretical developments here is the effect of moisture duration as revealed in the cumulative germination curves as functions of time. The extent to which these curves lead to species-specific germination variation as a consequence of variation in moisture duration depends on how their shapes differ between species.

Fig. 2 illustrates species-specific temporal patterns in germination simulated from the experimental germination results. Although each species experiences the same soil moisture duration in each year, the species-specific nonlinearities in the germination curves lead to fluctuating relative germination rates. These germination patterns are not independent between species, as they are often assumed to be theoretically, because the germination for each species is monotonically dependent on the same underlying fluctuating environmental variable. This means that the degree of statistical dependence between species is quite high. Indeed, beyond the delay before appreciable germination occurs, each species' germination fraction can be predicted precisely from any other species' germination fraction from the knowledge of their germination curves.

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