A Two-Year Life History Cycle Model for Autumn and Spring Seedling Coexistence in an Annual Plant - an Example of Intraspecific Niche Differentiation

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Abstract:

Intraspecific variation plays an important role in species coexistence and community assembly. In this paper, we propose a model for the coexistence of autumn and spring seedlings within one species of annual plants—intraspecific niche complementarity of a two-year life history cycle. There is an unsynchronized germination behavior in some species exhibiting a two-year life history cycle in which one population produces coexisting autumn and spring seedlings. Our soil seed bank coexistence model predicts that the optimal autumn germination fraction must maximize the harmonic mean of the number of seeds that germinate in two different seasons. Moreover, we extended classic annual soil seed bank dynamic models using evolutionary stability and density dependent theory. Our model can be applied not only to winter or spring annuals but also to autumn- and spring-seedling plants coexisting in one population. Under an evolutionarily stable coexistence of autumn- and spring-seedling plants within one population, our model suggests that the greater the ratio of seeds produced by a plant germinated in spring relative to the seeds germinated in autumn, the greater is the germination fraction in autumn. The germination behaviors of plants with unsynchronized two-year life history cycles are a new example of intraspecific niche differentiation in annuals.

Keywords: seed germination; **evolutionary stable** coexistence; life history cycle, germination fraction; Reciprocal Yield Law

1. INTRODUCTION

Competition and coexistence of species within communities is a fundamental and current topic of ecological research. Recently, ecologists reconsidered the importance of intraspecific trait variability (Violle et al. 2012), which is important as interspecific trait variability and has significant effects on community assembly. Currently, most research explores intraspecific niche differentiation mainly by individual species with functional trait differences (Bagousse-Pinguet 2014, Albert 2014). However, the role of individual differences caused by unsynchronized life history cycles in intraspecific niche differentiation remains largely unknown.

Life history can be considered a comprehensive reaction to environmental stress. Seed germination timing is a key feature of the plant life cycle because it affects the survival of seedlings (Baskin, 1985), individual fitness, and life history (Masuda and Washitani 1992). Life history differences within individual species can also promote species coexistence (Violle et al, 2012).

We note that most of the population of an annual plant germinates in autumn in one year and in spring in the next. However, in a given year, the same population is composed of autumn-germinating and spring-germinating individuals. In this study, in the two-year life history cycle of annual plants, the change in seed germination time follows a cycle of two years: seeds produced by a spring-germinating plant in the first year germinate largely in autumn of the first year, and seeds produced by an autumn-germinating plant in the first year germinate largely in spring of the second year largely, for a cycle interval of two years. This cycle is different from the classic one-year life history cycle, in which germination time does not change over years (Baskin, 1985) (see Figure 1).

Annual plants are an important part of the vegetation in arid and semiarid areas (Ludwig et al, 1988) and, subsequently, have an important impact on the stability and biodiversity of desert ecosystems. Annuals are an ideal system for examining variable response to precipitation and their impact on population and community dynamics (Angert et al, 2009). There are **two types of annual plants: 1) the winter annuals, including species that germinate during autumn and reproduce during early summer**

and2) the summer annuals, including species that germinate during early spring and complete their life-cycles during summer.

At present, there is substantial evolutionary ecology research focusing on winter annuals because of special function in community (Montesinos-Navarro et al 2012, Huxman et al 2013, Gremer and Venable 2014). There are also many theoretical models that describe and predict germination fractions and differences in germination timing (Andrea and Eva 2002, Jessica and Pete 2009, Kimball et al 2011, Linkies and Leubner-Metzger 2012, Bessho and Iwasa 2012, Gremer and Venable 2014). However, winter annuals include two groups, obligate winter annuals and facultative winter annuals (Baskin and Baskin 2014). Seeds of obligate winter annuals only germinate during autumn (Cici and Van 2009). Most seeds of facultative winter annuals germinate during autumn; however, some germinate during spring, which results in the coexistence of autumn and spring seedlings. This type of coexistence is widespread in regions such as the cold deserts and high altitude regions. However, a soil seed bank dynamic model for populations in which autumn and spring seedlings coexist has not yet been formulated.

In this paper, we used an evolutionary perspective (see (i) and (ii) of Box 1) to show that a two-year life history cycle allow improves autumn and spring seedling coexistence in populations. To further understand the mechanism of evolutionarily stable coexistence and to predict the proportion of seeds with autumn germination, we developed a new soil seed bank dynamic coexistence model using evolutionary stability theory and density dependent theory.

2. Two Years Life History Cycle for Autumn and Spring Seedling Coexistence within-species

There are annual species show variable germination time, one of most notable example is *Bromus tectorum* in Western US (Mack and Pyle 1983). The seeds of some annuals can germinate not only in spring but also in autumn so that there is autumn and spring seedling coexistence in one population (Zhang et al 2007). Also, there are some the species we surveyed in Appendix 1. The site is located in the southern Junggar Basin and in the southern Gurbantunggut Desert, N44°23'52"–N45°31'57" and E84°54'37"–E88°50'03". The altitude is 255–699 m. The climate is temperate arid. Annual evaporation is between 2000 and 2800 mm, and annual precipitation is between 50 and 160 mm. Average snow depth in winter is 10–30 cm (Zhang and Chen 2002). For the region, with specific reference to the past 50 years, recent climate change research showed that autumn was the season when the temperature increased most dramatically, and winter and autumn were the seasons when the precipitation increased most dramatically (Xu et al 2014). In an ecological context, knowledge of intraspecific variation during dormancy and germination is necessary for both practical and theoretical reasons (Violle et al. 2012). In the present study, we elucidated the theoretical reasons for variable germination times.

Please insert Figure 1 about here

There is life history cycle diversity for annuals. Some species is life cycle of type 1 (Fig.1 A), and some species is life cycle of type 2 (Fig.1 B). For a large number of spring and autumn germinating seedlings co-existence appearing in spring, there are life cycle of type 3 and type 4 (Fig.1 C and D). For life cycle of type 4 (Fig.1 D), there are two separate life history patterns within a species, and both of them are one-year life history cycles (Baskin and Baskin 1989). We believe life cycle of type 3 (Fig.1 C) which is one life history patterns with a two-year life history circle is possible because of the evolution of phenotypic plasticity and a long-term niche differentiation. Accordingly, the life history cycle of species cannot be synchronized at the population level such that a fraction of the seeds germinate in autumn (an autumn germination fraction) in one year and two phenotypes subpopulations of seeds are produced in spring that germinate in either spring or autumn. What is the optimal relationship between the two phenotypes subpopulations, or in other words, what is the optimal autumn germination fraction? Accordingly, we examined the coexistence of autumn and spring seedlings using evolutionary stability theory and density dependent theory.

3 The stable coexistence of autumn- and spring-seedlings.

We present a soil seed bank model for populations of annuals in which autumn and spring seedling coexist in cold desert. The germination fraction of seed is g . Seed germination in autumn have different fates in winter. Because the seedlings must grow enough before winter to survive over winter, the seed germinated in autumn was divided into two types: winter-successful and winter-dying types. Only winter-successful seedlings will participate in competition the following spring. The fraction of winter-successful autumn germination is g_f . The fraction of winter-dying autumn germination is g_d , which is determined by species and winter temperature but not by density dependence. So $g_f + g_d$ is not

affected by spring precipitation. Because there is no mortality from cold temperatures, seeds germinating in spring have only one fate. The fraction of spring germination is g_s which is affected by spring precipitation. So we have the following relationship: $g_s + g_f + g_d = g$.

Variable germination times are important not only for avoiding the crowds but also making life cycle evolution from one to another in unstable weather conditions in cold desert regions. There are many species that can germinate in autumn, not only for some winter annuals but also some spring annuals, but have not been eliminated by natural selection in cold desert. With fluctuating climate, we speculate that the boundaries between winter and spring annual species are not clear, mainly because $g_d > 0$. But Karlsson and Milberg discovered that germination in autumn occurs but plants survive winters poorly for spring annuals and that strong dormancy restricts the portion of each seed batch that germinates each autumn and thus reduces the risk of winter mortality (Karlsson and Milberg 2008). Here, there are some seeds that germinate with bad timing, e.g., before the first snow, so by the definition of g_d , $g_d > 0$, and we expect that g_d is constant for a given species.

Please insert Box 1 about here

Cohen analysis of seed banks is a classical theoretical study (Cohen 1966). Ellner improved Cohen's model using a yield-density law (Ellner 1985) that is the "Reciprocal Yield Law" (RYL) first proposed by Shinozaki and Kira (Shinozaki and Kira 1956). The model taking into account density dependence is summarized in the dynamic seed bank model developed (Bulmer 1984, Ellner 1985) and achieved Eq. (1):

$$S(t+1) = S(t)gf(x)H + S(t)(1-g)(1-d)(1)$$

Where $S(t)$ is the number of seed bank in the t^{th} season. H is the average yield of each plant in the t^{th} season. g is the total germination ratio (germination fraction). d is the death rate of seed dormancy. $f(x) = Q/(Q+x)$ (RYL) represents the function of density dependence, and $x = gS(t)$ denotes the surviving seeds after germination competition, where Q is the carrying capacity of the system (Bulmer 1984, Ellner 1985), i.e., the maximum density of adult plants supported by the environment.

In order to investigate the coexistence of autumn- and spring-germinating seedlings from the evolutionary point of view, we will present a model describing soil seed bank dynamics of coexisting autumn- and spring-seedling plants based on the requirements of density dependent evolutionary stability.

After the seedling stage, how is the difference reflected in density dependence? Considering the coexistence of spring and autumn seedlings, the first part of the left-hand side of Eq. (1) must be expanded, and the second part may remain unchanged.

Density-dependence in every phenotype subpopulation follows the Reciprocal Yield Law. When seeds are dispersed, the resources and ecological niche utilized by the seed bank are already occupied; therefore, autumn- and spring-germinating seedlings during spring have their own carrying capacity and density restrictions.

Using the Reciprocal Yield Law, we let $y_f(t) = Q_f g_f S(t) / (Q_f + g_f S(t))$ and $y_s(t) = Q_s g_s S(t) / (Q_s + g_s S(t))$, where $y_f(t)$ (or $y_s(t)$) is the number of plants growing from autumn (spring)-germinating seeds without interference from the spring (autumn)-germinating seedlings, and $Q_f / (Q_f + g_f S(t))$ (or $Q_s / (Q_s + g_s S(t))$) consider only intraspecific competition in autumn (spring)-germinating seedlings. Q_f (or Q_s) is the number of the autumn (spring)-germinating seedlings of environment permitting.

$F_s(y_s(t), y_f(t))$ (or $F_f(y_s(t), y_f(t))$) as a competition limitation provides the biomass of the spring (autumn) cohort under resource competition between two cohorts, only considering interspecific competition. $Y_s(t) = g_s S(t) \left(\frac{Q_s}{Q_s + g_s S(t)} \right) F_s(y_s(t), y_f(t))$ $H_s = y_s(t) F_s(y_s(t), y_f(t))$ or $(Y_f(t) = g_f S(t) \left(\frac{Q_f}{Q_f + g_f S(t)} \right) F_f(y_s(t), y_f(t))$ $H_f = y_f(t) F_f(y_s(t), y_f(t))$ is the seed production of the spring (autumn) cohort lastly, where $Q_s / (Q_s + g_s S(t))$ can be seen as resource competition within the spring cohort, and $F_s(y_s(t), y_f(t))$ (or $F_f(y_s(t), y_f(t))$) represents resource competition between two cohorts.

Please insert Figure 2 about here

We have a new model from Figure 2 and Box 1:

$$S(t+1) = \frac{y_s(t)y_f(t)}{y_s(t) + Ay_f(t)} H_f + \frac{y_f(t)y_s(t)}{y_f(t) + ay_s(t)} H_s + S(t)(1-d)(1-g)(2)$$

Where $S(t)$ is the number of seed bank in the t^{th} season; g is the total germination fraction; d is the death rate of dormant seeds; H_f (or H_s) is the number of seeds produced by one autumn (spring)-germinated plant. Where A , is constant, which also is relation between autumn-germinating and spring-germinating seedlings.

4 Results

For life cycle of type 3 (Fig. 1 C), it is need to define one important requirement of the optimal autumn germination fraction for a two-year life history cycle permitting the evolutionary coexistence of a population whose individuals germinate in autumn and spring simultaneously in the same year. $Y_s(t) = y_s(t)F_s(y_s(t), y_f(t))H_s$ (or $Y_f(t) = y_f(t)F_f(y_s(t), y_f(t))H_f$) is seed production of the spring (autumn) cohort lastly. The coexistence of the two phenotypes subpopulations reaches evolutionary stability in long time (see Fig. 3) as $S(t) = S(t+1)$, $Y_f(t) = Y_f(t+1)$ and $Y_s(t) = Y_s(t+1)$. When $S(t+1) = S(t)$, as far as possible to avoid the extinction risk from environmental fluctuation, maximizing the number of dormant seeds with no seed deaths $S(t)(1-g)(1-d) = S(t) - (Y_f(t) + Y_s(t))$ (determined by g_s, g_f, g_d and d (g_d and d were constant in the present paper)) is required, which is equivalent to maximizing $1/(Y_f(t) + Y_s(t))$. Solving for maximizing the internal stability strength of the two-year life history cycles according to evolutionary stability is equivalent to maximizing $Y_s(t)Y_f(t+1)$ and $Y_f(t)Y_s(t+1)$ (see Fig. 2), which is equivalent to maximizing $Y_s(t)Y_f(t)$. Therefore, the two subpopulations reaching evolutionary stability over a long time must maximize $Y_s(t)Y_f(t)/(Y_s(t) + Y_f(t))$.

Please insert Figure 3 about here

When $Y_s(t) + Y_f(t)$ is unchanged in the ideal case of evolutionary stability for a seed bank, $Y_s(t)Y_f(t)$ is maximized when $Y_s(t) = Y_f(t)$, but the optimal relationship between the two phenotypes subpopulations cannot be solely determined from this information describing soil seed bank dynamics and trends in the germination fraction. So the descriptions of these new soil seed bank dynamics of autumn- and spring-seedling plants coexisting in one species need use evolutionary stability and the density dependent theory.

For a two-year life history cycle to result in coexistence between autumn- and spring-germinating seedlings, and for an evolutionary stable selection of germination timing, the condition is $Y_s(t) = Y_f(t)$. Therefore, when coexisting populations reach evolutionary stability, we have $A = 1/a = H_f/H_s$.

Combining the above information, we have

$$S(t+1) = Y_z(t) + S(t)(1-d)(1-g)(3)$$

Where $Y_z(t)$ is the number of seeds produced by all seedlings,

$$Y_z = 2y_s(t)y_f(t)H_sH_f/(y_s(t)H_s + y_f(t)H_f)$$

It is reasonable that RYL is selected as a density-dependence law in Eq. (1) from economical points of view (Han et al 2014).

Eq. (3) also can be rewritten as

$$S(t+1) = \frac{Q_z}{Q_z + (g-g_d)S(t)}(g-g_d)S(t)H_z + S(t)(1-d)(1-g) \quad (4)$$

$$\text{Where } Q_z = \left(\frac{2H_sH_fQ_sQ_f}{H_sQ_s + H_fQ_f} \right) / \left(\frac{2H_fH_s(g-g_f-g_d)g_f}{(H_s(g-g_f-g_d) + g_fH_f)(g-g_d)} \right), H_z = \frac{2H_fH_s(g-g_f-g_d)g_f/(g-g_d)^2}{H_s(g-g_f-g_d)/(g-g_d) + g_fH_f/(g-g_d)}$$

Q_z is the carrying capacity of the system. H_z is the number of seeds produced by spring and autumn germinating adult plants.

For Eq.(3), when the total carrying capacity Q is determined by the position and size occupied by seeds in soil and autumn and spring -germinating seedlings in spring. Approximatively, in the case $Q_s = Qg_s/(g-g_d)$, $Q_f = Qg_f/(g-g_d)$, so $Q_z = Q$ (from definition of Q_z). In this case, when H_z is maximum, Y_z is maximum. Thus, for Eq.(3) deriving g_f is maximizing H_z , we have

$$\frac{g_f + g_d}{g - g_d} = \frac{\sqrt{v}}{\sqrt{v} + 1} + \frac{g_d}{g - g_d} \quad (5)$$

217 Where $v = H_s/H_f$. Without loss of generality, let $g_d = 0$, we have Fig.4.

218
219 Please insert Figure 4 about here
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221 From Fig.4, we can see that the strategy of autumn species in population level is “the greater the
222 fitness advantages of spring seedling, the larger the proportion of autumn germination.” In other words,
223 the greater the ratio of seeds produced by a plant germinated in autumn relative to the seeds germinated
224 in spring, the smaller is the germination fraction in autumn.

225 Equation 2 can be applied not only to autumn-germinating and spring-germinating plants
226 coexisting in one species for life-cycle of type 3 (Fig. 1C) but also other life-cycles.

227 (i) when $A = 0, a = +\infty$, we have $S(t+1) = Q_f g_f S(t) / (Q_f + g_f S(t)) + S(t)(1-d)(1-g)$, and $g_f \approx g$
228 should be best in this case. The species is almost entirely autumn-germinating; namely, a winter annual
229 species (Fig. 1 A).

230 (ii) Or when $A = +\infty, a = 0$, we have $S(t+1) = Q_s g_s S(t) / (Q_s + g_s S(t)) + S(t)(1-d)(1-g)$, $g_s \approx g$
231 should be best in this case, the species is almost entirely spring-germinating; namely, a spring annual
232 species (Fig. 1 B).

233 For both (i) and (ii) there are many studies (Venable 2007, Childs 2010, Gremer and Venable
234 2014). Here we do not discuss further (see Fig. 1 A and B).

235 (iii) $A=0$ and $a=0$, there is no relationship between two cohorts of autumn-germinating and
236 spring-germinating plants. From Eq. (2) we have

237
$$S(t+1) = Q_s g_s S(t) H_s / (Q_s + g_s S(t)) + Q_f g_f S(t) H_f / (Q_f + g_f S(t)) + S(t)(1-d)(1-g) \quad (6)$$

238 In this case, autumn-germinated plants and spring-germinated plants germinated almost
239 independently of each other. If the growing season of autumn-germinated plants and spring-germinated
240 plants were staggered, or seeds germinated in autumn stayed together, and seeds germinated in spring
241 stayed together, so that autumn and spring-germinating seedlings in the spring do not interact in
242 resource competition. For example, when spring arrives, autumn-germinating seedlings are taller and
243 have deeper roots than spring-germinating seedlings. Thus, the two subpopulations occupy different
244 ecological niches, and their competition with each other can be ignored. Further, when
245 autumn-germinating seedlings mature, their competition with each other can be ignored such that there
246 is always no competition between the two subpopulations. From Equation 6, it is evident that “the
247 greater the fitness advantage of the spring seedlings, the larger the proportion of spring germination.” In
248 this case, the two genotype subpopulations can be considered to be two cases of the classic one year life-
249 history cycles or two separate populations (see Fig. 1D) as the evolution of phenotypic plasticity.

250 5 Discussions

251
252 Please insert Figure 5 about here
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254 Equation 3–5 examines competition only within genotypes and between two phenotype
255 populations for life-cycle 3 (Fig. 1C). Equation 5 is deduced based on Equation 4 for the autumn
256 germination fraction in evolutionary stability. Equation 4 shows that when the life-cycle of type 3
257 reached evolutionary stability, its soil seed bank dynamics model was consistent to the models of
258 classic life-cycle 1 and 2 in form. Life-cycle of type 1, 2 (classic (see Fig. 1A, B)), 3 (Eq. 3, 4 (see
259 Fig. 1C)), and 4 (Eq. 6 (see Fig. 1D)) can be observed from Figure 5.

260 We believe that germination within the life-cycle of certain annuals was simple; for example, certain
261 species always germinate during autumn or spring, whereas others may have a mixed life-history with
262 varying focus. Nevertheless, Equation 2 can be used to describe them (see Fig. 5). There are several
263 studies regarding the life-cycle of type 1, 2 (Bulmer 1984, Ellner 1985, Gremer and Venable 2014), and
264 here, we focus on the life-cycle of type 3 and 4, particularly the life-cycle of type 3. From Figure 4, it is
265 evident that the strategy of choice for life-history phenotypic differentiation at a population level which
266 is “the greater the fitness advantages of spring seedling, the larger the proportion of autumn
267 germination.”

268 As an early life-history trait, germination phenology can be critical in determining the fate of the
269 organism because plasticity can synchronize the most vulnerable life-history stages with favorable
270 environmental windows (Forrest 2010, Montesinos-Navarro et al 2012) and is influenced by strong
271 natural selection (Donohue et al. 2005). There is a rich differentiation between species and within
272 species (Barua 2012, Montesinos-Navarro et al 2012, Basin et al. 2014), even among
273 populations (Fernández-Pascual et al 2013). Various factors affect seed germination and dormancy,
274 including species genetics, the seed maturation process, and environment experience, particularly the
275 maternal environment affects the genetic basis of seed dormancy (Postma and Agren 2015).

From our observations, the phenology of autumn germinating plants are earlier than spring germinating plants, such that two cohorts experience significantly different temperatures, photoperiod, and moisture during seed maturation and development, which strongly influence primary dormancy induction (and breakage), secondary dormancy induction (and breakage), and the conditions that permit the germination of non-dormant seeds (Donohue 2009). Seeds matured under long, warm days exhibited greater germination than those matured under short, warm days (Barua et al. 2012). The spring germinating plants experienced longer warm days than autumn germinating plants, whose seeds can germinate during autumn when germination conditions were satisfied. The maternal environment during seed maturation affects seed dormancy and consequently seed longevity. With downy brome, for example, if the seed maturation period is prolonged the seed dormancy period increases (Allen and Meyer 2002). Similarly, for cleavers, Mennan and Ngouajio (2006) reported that seeds from fall-emerging cohorts germinated more quickly than seeds from spring-emerging cohorts.

Meanwhile, the seed coat (testa) can be a physical constraint on dormancy and germination because of mediating seed water permeability and/or oxygen uptake and the light environment experienced by the embryo. Plants were from autumn germinating seedlings, and experienced autumn, winter, and spring with a long growing season and more available resources; therefore, they produced more seeds during summer (Appendix 1, Table 2), and most of the seeds had full, thick testa than spring germinating seedlings. Although germination conditions were met during autumn, most of these seeds did not easily germinate and germinated the following spring. However, the autumn-germinating plants had a larger biomass and more than twice the seed yield of spring-germinating plants in the present study. There is a negative correlation between the number of offspring produced and germination rate (Tielbörger and Petru 2010). Therefore, the dormancy of seeds produced by spring annuals is generally less than that of seeds produced by winter annuals when undergoing suitable temperature and moisture conditions. For the above and other reasons, the life-cycle of type 3 (two-year life-history cycle) was inevitable emergence.

Seed germination is often controlled by the existence of dormancy cycles and occurs at the right time of the season to provide the best chance for plant development, particularly in arid and semiarid climates. Hence, the formation of the seed dormancy cycle is because of the combined action between seed annual dormancy induction (and breakage) and post-germination traits (Baskin et al. 1993, Donohue et al. 2010, Cao et al. 2013, Montesinos-Navarro et al. 2012). The post-germination traits regulate interspecific interactions, intraspecific density dependence, and inorganic environment stress and react to germination time (Tielbörger and Valleriani 2005, Gremer and Venable 2014). Selection could favor divergence of the seasonal cue level that triggers a life-cycle transition, resulting in stable coexistence of phenological polymorphisms within a population or the potential for multiple phenological responses associated with a single genotype (Metcalf et al. 2015). In the present study, life-history 3 and life-history 4 were evident, which have obvious advantages for stable coexistence within a population. Possession of life-history 3 and life-history 4 mainly varies with the species, population, and local environment. A two-year life-history cycle is advantageous for post-germination traits and should exist under natural conditions.

In recent years, there has been a rapid increase in the number of published reports of intraspecific variability in plant ecology (Albert 2014). Our theory regarding germination behavior within a two-year life history cycle in one population provides a new example of intraspecific niche differentiation in plants. A two-year life history cycle provides more niche space than a one-year life history cycle because the seed germination times of winter and spring annuals are not synchronized in one population. Life history strategy is one of the most important sources of intraspecific niche differentiation caused by individual differences (Zupping-Dingley et al. 2014) and should therefore receive more attention in plant community ecology theory. Therefore, we can expect that intraspecific niche differentiation produced by life history cycles to have significant effects on community assembly and coexistence.

It is difficult to describe the interaction between two populations in coexistence theory. The interaction between the two phenology subpopulations is unchanged whether they are achieved evolutionary stable coexistence or not, so with the requirements of the evolutionary stability, we can get more information about the interaction between the two populations. For understanding the effect of two-year life history on evolution, we extended previous annual soil seed bank dynamics models (Bulmer 1984, Gremer and Venable 2014) based on requirements of evolutionary stability and density-dependence. Our model can be applied not only to winter or spring annuals but also to autumn-seedling and spring-seedling plants coexisting in one population. Our model quantified the evolution of autumn germination, which to our knowledge has never been done in the previous literature.

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A: Winter annuals
Seeds germinate in autumn and plants reproduce in the spring, which is a one-year life history cycle. Seedlings need to survive in winter.

B: Spring annuals
Seeds germinate in spring and plants reproduce in the summer, which is a one-year life history cycle.

C: Coexistence with two years life history cycle
There is one life history patterns with a two-year life history circle. Different seed germination times result in the autumn and spring seedling coexistence.

D: Coexistence by mixing with two life history patterns
There are two separate life history patterns within a species, and both of them are one-year life history cycles such that there is autumn and spring plants coexistence in one population.

Plant stage

Seed stage

Fig.1. the different life history cycles of annuals and the different niche characteristics permitting coexistence within one population in long time.

Fig.2. Different germination timing produces different fate and life history variation in annuals. Where $S(t)$ is the number of seed bank in the t^{th} season; g is the total germination ratio (germination fraction); d is the death rate of dormant seeds; The fraction of winter-successful autumn germination is g_f . The fraction of winter-dying autumn germination is g_d , which is determined by species and winter temperature but not by density dependence; the fraction of spring germination is g_s affected by spring precipitation. $y_f(t)$ is the number of plants from autumn-germinating seeds without interference from the spring-germinating seedlings. $y_s(t)$ is the number of plants from spring-germinating seeds without interference from the autumn-germinated seedlings; $Y_e(t)$ is the number of seeds produced by all germinating seed in the comprehensive case (the seeds produced by both spring and autumn germinating plants).

Fig. 3. The two years life history cycle in one population of annuals

Fig.4. The relationship of the proportion of autumn germination in total germination (germination fraction) g_f/g and the ratio between plants produced during spring and autumn germination $v = H_s/H_f$.

$Y_z(t) = \frac{y_s(t)y_f(t)H_f}{y_s(t) + Ay_f(t)} + \frac{y_f(t)y_s(t)H_s}{y_f(t) + ay_s(t)}$	<pre> graph LR subgraph Seedlings S[Spring seedlings] A[Autumn seedlings] end subgraph Seeds S1[Seeds reproduced by spring seedling] A1[Seeds reproduced by autumn seedling] end S --> S1 S --> A1 A --> S1 A --> A1 </pre>
$a \rightarrow +\infty, A \rightarrow 0, Y_z(t) = \frac{Q_f g_f S(t)}{Q_f + g_f S(t)} H_f$	<pre> graph LR subgraph Seedlings A[Autumn seedlings] end subgraph Seeds A1[Seeds reproduced by autumn seedling] end A --> A1 </pre>
$a \rightarrow 0, A \rightarrow +\infty, Y_z(t) = \frac{Q_s g_s S(t)}{Q_s + g_s S(t)} H_s$	<pre> graph LR subgraph Seedlings S[Spring seedlings] end subgraph Seeds S1[Seeds reproduced by spring seedling] end S --> S1 </pre>
$a \rightarrow 0, A \rightarrow 0, Y_z(t) = \frac{Q_s g_s S(t)}{Q_s + g_s S(t)} H_s + \frac{Q_f g_f S(t)}{Q_f + g_f S(t)} H_f$	<pre> graph LR subgraph Seedlings S[Spring seedlings] A[Autumn seedlings] end subgraph Seeds S1[Seed reproduced by spring seedling] A1[Seeds reproduced by autumn seedling] end S --> S1 A --> A1 </pre>
$A = 1/a = \frac{H_f}{H_s}, Y_z = \frac{2y_s(t)y_f(t)}{y_s(t) + y_f(t)} H_f H_s$	<pre> graph LR subgraph Seedlings S[Spring seedling] A[Autumn seedlings] end subgraph Seeds S1[Seeds reproduced by spring seedling] A1[Seeds reproduced by autumn seedling] end S --> S1 S --> A1 A --> S1 A --> A1 </pre>

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517 Fig.5. There are different life history cycles in annuals and different soil dynamic models because $Y_z(t)$
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Box.1 the stable coexistence of the two cohorts

We generally consider a mixed coexistence region over a long period. There are autumn and spring cohorts competition within and among each other. In this paper, $y_f(t)$ (or $y_s(t)$), simply written as y_f (or y_s) in this box, is the number of plants from autumn (spring)-germinating seedlings without interference from the spring (autumn)-germinating seedlings, which are following "Reciprocal Yield Law". $y_f(t) = Q_f g_f S(t) / (Q_f + g_f S(t))$ and $y_s(t) = Q_s g_s S(t) / (Q_s + g_s S(t))$, g_f is the fraction of winter-successful autumn germination, g_s is the fraction of spring germination, Q_f (or Q_s) is the number of the autumn (spring)-germinating seedlings of environment permitting.

There are competitions between autumn and spring cohorts of plants. Let $F_s(y_s(t), y_f(t))$ and $F_f(y_s(t), y_f(t))$ be competitive limitation of autumn and spring cohorts competition among them. We hypothesize that if there is a slight increase in total precipitation in spring, each germination ways is simultaneously increased by k times (with k not very large), the total revenue must also increase k times. Thus, we have $F_s(ky_s, ky_f)ky_s = F_s(y_s, y_f)ky_s$ and $F_f(ky_s, ky_f) = F_f(y_s, y_f)ky_f$. When the number of one type of seedlings is very small because of some occasional interference, the restriction of that cohort of seedlings by the other type will be small because of their own ecological niche. Thus, we have $F_s(1, y_f) \approx 1$ (when $1 \ll y_f$) and $F_f(y_s, 1) \approx 1$ (when $1 \ll y_s$), $\lim_{y_f \rightarrow 0} F_f(y_s, y_f) = 1$, $\lim_{y_s \rightarrow 0} F_s(y_s, y_f) = 1$.

(ii) Generally we can let $F_f(y_s, y_f) = y_s / (y_s + A_1 y_f + \alpha_1(y_s, y_f))$ and $F_s(y_s, y_f) = y_f / (a_1 y_s + y_f + \alpha_2(y_s, y_f))$, where a_1 and A_1 are constant. We hope to know what is $\alpha_i(y_s, y_f)$, $i = s, f$. Because $\lim_{y_f \rightarrow 0} F_f(y_s, y_f) = \lim_{y_s \rightarrow 0} F_s(y_s, y_f) = 1$, $F_i(ky_s, ky_f) = F_i(y_s, y_f)$, $\alpha_i(y_s, y_f) = \sum e_{i,j} y_s^{k_{1,j}} y_f^{1-k_{1,j}}$, ($i = s, f$). Because $F_s(1, y_f) \approx 1$ (when $1 \ll y_f$) and $F_f(y_s, 1) \approx 1$ when $(1 \ll y_s)$, $A_1 \ll y_s$, $\alpha_1(y_s, 1) = \sum e_{1,j} (y_s)^{k_{1,j}} \ll y_s$ so $e_{1,j} (y_s)^{k_{1,j}} \ll y_s$ when $(1 \ll y_s)$ and $a_1 \ll y_f$, $\alpha_2(1, y_f) = \sum e_{2,j} (y_f)^{1-k_{2,j}} \ll y_f$ so $e_{2,j} (y_f)^{1-k_{2,j}} \ll y_f$ when $(1 \ll y_f)$. So for $e_{1,j} (y_s)^{k_{1,j}}$, there are $e_{1,j} \approx 0$ or $k_{1,j} \approx 0$ so that $y_s^{k_{1,j}} y_f^{1-k_{1,j}} \approx y_f$ and $\sum e_{1,j} y_s^{k_{1,j}} y_f^{1-k_{1,j}} \approx c_1 y_f$ ($c_1 \ll y_s$ when $1 \ll y_s$), and for $e_{2,j} (y_f)^{1-k_{2,j}}$, $e_{2,j} \approx 0$ or $1 - k_{2,j} \approx 1$ so that $y_s^{k_{2,j}} y_f^{1-k_{2,j}} \approx y_s$ and $\sum e_{2,j} y_s^{k_{2,j}} y_f^{1-k_{2,j}} \approx c_2 y_s$ ($c_2 \ll y_f$ when $1 \ll y_f$).

So $A_1 y_f + \alpha_1(y_s, y_f) \approx A y_f$, $a_1 y_s + \alpha_2(y_s, y_f) \approx a y_s$, where A , a is constant, which also can be seen as relations between autumn-germinating and spring-germinating plants. And so $F_f(y_s, y_f) \approx y_s / (y_s + A y_f)$ and $F_s(y_s, y_f) \approx y_f / (a y_s + y_f)$. So

$$S(t+1) = \frac{y_s(t) y_f(t)}{y_s(t) + A y_f(t)} H_f + \frac{y_f(t) y_s(t)}{y_f(t) + a y_s(t)} H_s + S(t)(1-d)(1-g)$$

Where $S(t)$ is the number of seed bank in the t^{th} season; g is the total germination fraction; d is the death rate of dormant seeds; H_f (or H_s) is the number of seeds produced by one autumn (spring)-germinated plant.

Appendix 1 Field experiment

The site is located in the southern Junggar Basin and in the southern Gurbantunggut Desert, N44°23'52"–N45°31'57" and E84°54'37"–E88°50'03". The altitude is 255–699 m. The climate is temperate arid. Annual evaporation is between 2000 and 2800 mm, and annual precipitation is between 50 and 160 mm. Average snow depth in winter is 10–30 cm (Zhang and Chen 2002). In early November 2009, two typical plots representing the growth environment and distribution features were sampled in areas where the six species were distributed, one a dune and the other a plain. In the dune plots, 10 small quadrats (10 × 10 m) at right angles to the dune were established by the method of continuous sampling. In the plain, two horizontal transects 1 km apart were laid out and along the transect eight quadrats (10 × 10 m) were established at 1-km intervals.

Six annual species were chosen for the study: *Erodium oxycarrhynchum*, *Trigonella arcuata*, *Malcolmia scorpioides*, *Tetracera recurvata*, *Lappula semiglabra*, and *Plantago minuta*. These species were selected because they are among the most abundant species and are widely distributed in the Gurbantunggut Desert. Furthermore, experimental studies have indicated the importance of generalized competition for seedling survival of these six species.

Before snow in early November 2009, the germinating plants in every quadrat were marked. The surviving autumn-germinating together with the spring-germinating plants in the quadrats were counted in early April 2010. At the beginning of June, the numbers of spring- and autumn-germinating plants with fruits, the proportion of autumn and spring germination, and the death rates of spring and autumn seedlings in spring were determined. To measure the yield of mature plants, 20 plants germinating in spring and autumn were sampled at the mature stage. The numbers of deciduous seeds were determined on the basis of residual fruits.

In early April, when the plant is in the seedling stage, the morphology of autumn seedlings is larger than that of spring seedlings. The survival advantage of resistant autumn seedlings is greater (Table 1). The seed production (Table 2) and the death rate for spring and autumn germination (Table 3) and of the six species were substituted in the model to calculate the autumn-to-spring ratio of seed germination.

The survey revealed that (i) in spring, the biomass of autumn-germination plants was significantly greater than that of spring-germination plants (Table 1), indicating a large difference between the autumn- and spring-germination plants with respect to environmental capacity (the maximum density of adult plants supported by the environment); (ii) the seed yield of

autumn-germinating plants was two times that of spring-germinating plants (Table 2); and (iii) thus, when autumn- and spring-germination plants coexist in one community, there are different density dependences (Table 3), meaning that there should be different RYL. The seed yield of autumn-germinating plants was two times that of spring-germinating plants, and, surprisingly, the seed yield of autumn germination for *T. arcuata* and *P. minutaw* was five times that of spring germination (Table 2).

Table 1. Biomass differences between spring and autumn seeding in early spring (kg)

Species	Biomass		<i>f</i>	<i>P</i> value
	Germinated in spring	Germinated in autumn		
<i>Erodiumoxyrhynchum</i>	0.005 ± 0.001	0.082 ± 0.008	101.79	0.000
<i>Trigonellaarcuata</i>	0.013 ± 0.002	0.033 ± 0.004	19.63	0.000
<i>Malcolmiascorpioides</i>	0.006 ± 0.001	0.056 ± 0.007	49.13	0.000
<i>Tetracmerecurvata</i>	0.031 ± 0.001	0.027 ± 0.005	19.85	0.000
<i>Lappulasemiglabra</i>	0.010 ± 0.002	0.060 ± 0.010	23.76	0.000
<i>Plantagominuta</i>	0.011 ± 0.002	0.057 ± 0.007	41.06	0.000

Table 2. Numbers of seeds produced by plants germinated in autumn (H_s) and spring (H_f) (Mean ± SE)

Species	H_s	H_f	<i>f</i>	<i>P</i> value
<i>Erodiumoxyrhynchum</i>	86.00 ± 13.44	291 ± 25.43	50.91	0
<i>Trigonellaarcuata</i>	3.75 ± 1.20	22.75 ± 3.83	22.42	0
<i>Malcolmiascorpioides</i>	1428.75 ± 242.19	3150.75 ± 286.13	21.59	0
<i>Tetracmerecurvata</i>	948.00 ± 153.56	3483.00 ± 579.28	17.89	0
<i>Lappulasemiglabra</i>	36.80 ± 4.43	101.45 ± 17.77	12.46	0.001
<i>Plantagominuta</i>	51.75 ± 7.66	276.30 ± 21.94	93.4	0

Table 3. The mortality rate of autumn seedling (K_s) and spring seedling (K_f) (% ± SE)

Species	K_s	K_f	<i>f</i>	<i>P</i> value
<i>Erodiumoxyrhynchum</i>	41.89 ± 11.96	9.29 ± 3.51 (In spring 3.20 ± 1.71)	6.86	0.040
<i>Trigonellaarcuata</i>	56.34 ± 21.19	35.45 ± 9.62 (In spring 24.97 ± 7.75)	0.81	0.420
<i>Malcolmiascorpioides</i>	26.61 ± 3.89	25.17 ± 2.74 (In spring 8.28 ± 0.88)	0.56	0.496
<i>Tetracmerecurvata</i>	62.53 ± 4.90	25.00 ± 5.50 (In spring 9.63 ± 5.00)	24.97	0.001
<i>Lappulasemiglabra</i>	20.01 ± 2.80	24.70 ± 8.68 (In spring 6.66 ± 2.03)	0.26	0.634
<i>Plantagominuta</i>	15.47 ± 5.39	29.23 ± 3.66 (In spring 9.05 ± 1.74)	4.46	0.102