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EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

EARLY EMERGENCE ENHANCES PLANT FITNESS: A PHYLOGENETICALLY CONTROLLED META-ANALYSIS

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Abstract. The time at which a seedling emerges can determine its future success as a plant. Despite the large number of studies that have examined the effect of emergence time on different components of plant fitness (survival, growth, and/or fecundity), the potential evolutionary response to selection on seedling emergence date is still poorly known. In this study, we review 55 of those studies by a random-effects meta-analysis, considering the phylogenetic relatedness among taxa. We test the following hypotheses: (1) early emergence increases seedling survival, growth, and fecundity, (2) early emergence is more advantageous to large-seeded species than to small-seeded ones, as the former can compensate for the lower number of seeds by increasing seedling survival, (3) perennial plants benefit more than annuals from early emergence, as the iteroparity of the former allows them to risk seedling emergence to the best conditions each year, whereas the semelparity of the latter forces them to spread the risk of emergence over time, and (4) the effect of emergence time may depend upon the experimental conditions (field vs. controlled experiments in a greenhouse or laboratory). Our results show that early emergence differentially affects components of plant fitness, with no effect on seedling survival but large benefits to seedling growth and fecundity. Such effects vary depending upon intrinsic factors like seed size or life-form, and also upon methodology (census time and experimental conditions). Large-seeded species gain from emerging early by growing more during their first growing seasons, although they survive and reproduce similarly to small-seeded species. The survival benefit of early emergence is greater in perennial than in annual species, thus supporting hypothesis 3. The relationship between emergence time and seedling growth appears to be stronger under controlled conditions than in the field, probably as a result of the unlimited nutrient and water resources of the former. In field conditions, in contrast, limited resources probably decelerate the growth of early seedlings, precluding the detection of differences between these and late seedlings.

Key words: comparative method; life-form; meta-analysis; phylogenetic signal; seed size; seedling emergence.

INTRODUCTION

Seedling emergence constitutes one of the crucial events in the life cycle of plants, because the time at which this process occurs often determines subsequent plant performance and success (Harper 1977, Weiner 1988). Very short delays in the seedling emergence time (i.e., in the number of days elapsed from the start of the germination season until the seedling emerges from the ground) can be magnified into large differences in final biomass and reproduction, especially un-

der competitive situations (e.g., Ross and Harper 1972, Venable and Brown 1988, Streng et al. 1989, Rice 1990, Kelly and Levin 1997, Dyer et al. 2000). Early emergence and establishment may be of critical importance, for instance, when interspecific competition for light is intense as seedling density increases (Miller et al. 1994). In mediterranean and arid environments, it may also be particularly important for perennial species that must grow sufficiently during spring to survive summer drought. However, early-emerged seedlings may also have a higher risk of mortality due to seasonal hazards (pathogens, predation, desiccation) (e.g., Marks and Prince 1981, Jones and Sharitz 1989, Rice 1990), and thus emergence time is probably influenced by a com-

bination of different abiotic (e.g., soil temperature, soil moisture) and biotic factors (e.g., competitive neighborhood, herbivore pressure).

Even within a population, there is often considerable variation in the time of seedling emergence, which can be spread over several weeks or even moths. Although some studies (Howell 1981, Stanton 1985, Narita 1998) have found clear directional selection for earlier emergence (earlier emergents surviving better and reproducing more than later ones), others have found opposite results (Baskin and Baskin 1972, Lacey 1982). Still, other studies have found some trade-offs, for instance, that early seedlings have a lower probability of survival but a greater fecundity than late seedlings (e.g., Venable et al. 1987, González-Astorga and Núñez-Farfán 2000). For most species examined to date, we have little knowledge of the potential evolutionary response to selection on seedling emergence date (Kelly and Levin 1997 and references therein). However, a recent review of inheritance and natural selection on functional traits has shown that early emergence is a heritable trait subject to strong selection pressure mediated by competitive interactions (Geber and Griffen 2003).

Emergence time is often related to seed mass, although this relationship may vary among natural environments (e.g., Kalisz 1989, Gross and Smith 1991, Seiwa 2000, but see Howell 1981, Jones et al. 1997). Westoby et al. (2002) hypothesized that the maximization of seedling survival is the main strategy of large-seeded species, whereas maximizing of seed production is the strategy of the small-seeded species. If this is true, then the seedling survival benefit of early emergence should increase with seed size.

Temporal variation in environmental conditions represents a strong selective force favoring a mechanism that spreads the risk of reproduction through time (i.e., seed dormancy) (Venable and Brown 1998). Extending the emergence period may be a suboptimal strategy in good years, but protects parent fitness from extremely bad years (Mathias and Kisdi 2001). While annuals are expected to evolve risk-spreading strategies because reproduction occurs only once, perennials are buffered from temporal environmental variations due to their iteroparous reproduction (Rees 1996, Mathias and Kisdi 2001). According to this pattern, theoretical models predict that increases in adult longevity select against seed dormancy (Rees 1994), and comparative tests support this hypothesis (Rees 1996).

In addition to life history traits, phylogenetic relatedness of species may explain a significant proportion of the variance in emergence time. For example, Figueroa and Armesto (2001) found that 12% of the emergence time variance of 44 temperate rain forest species was explained by phylogeny, followed by dispersal period (7%), biogeographical origin (6%), dispersal syndrome (5%), life-form (4%), and seed mass (2%). It is clear that for any cross-species comparison,

we need to take into account phylogenetic relatedness of the species in order to avoid pseudoreplication derived from common ancestry (Harvey and Pagel 1991, Verdú and Traveset 2004).

Another source of variation in comparative studies is the experimental condition under which the study was performed (Traveset and Verdú 2002). Such conditions are known to influence seed germination and seedling emergence success, and contrasting results are often found when comparing the same species in controlled vs. field experiments (e.g., Bustamante et al. 1993, Figueiredo and Perin 1995, Traveset et al. 2001). Most reported information comes from studies carried out under controlled (favorable) circumstances, usually in the laboratory (Traveset and Verdú 2002 and references therein), yet this may often obscure significant differences between treatments (Herrera 2000, Traveset et al. 2001).

Differences in the effect of emergence time have been found among species within a community, and at a spatial and temporal level within a species (e.g., Miller 1987, Battaglia 1996, Kelly and Levin 1997, Dyer et al. 2000). In this study, we review a large subset of those studies using a statistically powerful approach, meta-analysis, which combines the different results found in such studies and controls for sampling effects. We also employ the comparative method to consider the phylogenetic relatedness among taxa, something rarely performed in other meta-analyses (but see Møller and Thornhill 1998, Verdú and Traveset 2004). The hypotheses we want to test with such analysis and with the available data are the following:

1) Early emergence increases fitness components of plant seedlings (survival, growth and fecundity).

2) Early emergence is more advantageous to large-seeded species than to small-seeded ones, as the former can compensate for the lower number of seeds by increasing seedling survival (Westoby et al. 2002).

3) Perennials benefit more from early emergence than do annuals because the iteroparity of the former allows them to risk the emergence of all their seedlings to the best conditions each year, whereas the semelparity of the latter forces them to spread the risk of emergence over time.

4) The effect of emergence time may depend upon the conditions under which the experiment is carried out (field vs. controlled conditions in a greenhouse or laboratory).

METHODS

Studies dealing with the effect of emergence time in any of the fitness components (survival, growth, or fecundity) were searched in an electronic database (ISI Web of Science 1945–2003 [*available online*])[4] by using a combination of ''emergence,'' ''germination,'' and ''tim*'' keywords. (tim* allows the search engine

[4] ⟨http://go5.isiknowledge.com/⟩

to look for time and timing.) More studies were found within the reference lists of the gathered papers. Finally, we asked for unpublished data by directly contacting colleagues working on this field. After discarding 42 studies due to lack of essential information (mainly standard errors and sample sizes), we ended up with a database consisting of 55 studies (49 published and 6 unpublished; see Appendix A). Such studies contained 127 effect sizes for survival, 61 for growth, and 25 for fecundity that corresponded to 72, 29, and 12 species, respectively (see Appendix B).

Seedlings usually emerge synchronously in groups, named cohorts (Kelly and Levin 1997). We used the same cohorts defined by the authors for the emergence time effect size calculations. The chronological order in which the cohorts emerged is the relevant parameter to test the hypotheses addressed here of fitness benefits associated with early emergence. Thus, for each experiment we numbered cohorts from 1 (the most precocious) to n (the latest).

The effect size selected for the meta-analyses was the Fisher's z transformation of the Pearson's product-moment correlation coefficient r. Pearson's r measuring the association between emergence time and survival was calculated for each experiment by constructing a $2 \times n$ contingency table crossing the n cohorts with the survival outcome (dead/alive). The chi-square value of the contingency table was transformed to r. The association between emergence time and seedling growth was estimated by calculating r from the mean, standard deviation, and sample size of seedling height/ biomass in each cohort. In many cases, r was calculated from other statistical tests (usually ANOVAs). Effects of emergence time on fecundity were estimated as described for seedling growth. The number of flowers or fruits per plant was the output variable for the fecundity analysis. Statistical transformations to obtain r were performed with the help of meta-analysis calculators (Rosenberg et al. 2000, L. C. Lyons [*available online*]).[5] Data from graphs were obtained by scanning them and using the Datathief II software (B. Tummers [*available online*]).[6] The predictors included in the analysis were mean seed size (log-transformed), census time (number of months spent since the first emergence recorded until the quantification of survival, growth, or fecundity), experimental conditions (field vs. laboratory, greenhouse, or nursery conditions), and lifeform (annual vs. perennial).

The effect size of each experiment was calculated in the MetaWin 2.0 statistical program (Rosenberg et al. 2000). After checking the existence of heterogeneity among studies, we discarded fixed-effects models and fitted random-effect models. Random-effects models assume that studies differ not only by sampling error (as fixed-effects models do), but also by a random component in effect sizes between studies, which is named ''pooled study variance'' (Rosenberg et al. 2000). A random-effects meta-regression estimated via the method of moments was used to test for the effect of predictors on the survival, growth, and fecundity effect sizes (Thompson and Higgins 2002). Categorical variables were dummy coded before entering into the meta-regression, which was fitted with the help of the MetaReg macro for SPSS (D. B. Wilson, *unpublished program*).

The effect of publication bias (i.e., significant findings have a greater chance to be published than nonsignificant ones [Palmer 1999]) was tested by calculating Rosenthal's fail-safe number, that is, the number of studies with an effect size of zero that would be necessary to add to the meta-analysis to nullify its overall effect size. If the fail-safe number is larger than five times the sample size plus 10, it is safe to conclude that results are robust regarding publication bias (Rosenthal 1979).

Two sources of pseudoreplication were considered (see Traveset and Verdú 2002); the first one is that derived from the fact that the same species could be involved in several experiments; the second one refers to the phylogenetic relatedness among the species. In the first case, the meta-analyses were rerun after calculating a single (cumulative) effect size per species as the weighted average of effect sizes, the weight being the inverse of the variance (Rosenberg et al. 2000). In the second case, we first tested for the presence of a phylogenetic signal in the effect sizes by means of the phylogenetically independent contrasts procedure outlined by Garland et al. (1993) in the PDAP software manual (T. Garland, Jr., P. E. Midford, J. A. Jones, A. W. Dickerman, and R. Diaz-Uriarte, *unpublished manuscript*). The variance of the effect size contrasts was compared with a simulated distribution obtained by a randomization procedure in which the effect sizes are shuffled across the tips of the phylogenetic tree. One thousand permutations were run to construct the distribution. If a phylogenetic signal exists, the variance for the real data is expected to be significantly lower than the variance of randomly permuted data. Then, if the variance of the real data is smaller than at least 95% of the variances of the randomized values, there is evidence of a phylogenetic signal. After this, phylogenetic information was implemented in the meta-analyses models by means of the lm.phylog function in the PHYLOGR package for R written by R. Díaz-Uriarte and T. Garland for the Comprehensive R Archive Network (*available online*).[7] This function allowed us to perform weighted least squares in which the phylogenetic information is included as a variance–covariance matrix. The inverse of the effect size variance was incorporated as the vector of weights, as meta-analyses do. Significance tests were obtained by

[5] ⟨http://www.lyonsmorris.com/MetaA/⟩

[6] ⟨http://www.nikhef.nl/~keeshu/datathief/⟩

[7] ⟨http://cran.r-project.org/⟩

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TABLE 1. (A) Survival benefits of early emergence depend on census time and plant life-form in the non-phylogenetically informed analysis, but (B) these predictors are marginally significant or nonsignificant when considering phylogenetic relatedness.

A) Non-phylogenetically informed meta-regression

Parameter	B	SE	Z	P
Constant	−0.0069	0.0457	−0.1502	0.8806
Seed size	0.0186	0.0247	0.7518	0.4522
Census time	0.0058	0.0023	2.5416	0.0110
Life-form	−0.1811	0.0498	−3.6368	0.0003
Experimental conditions	0.0407	0.0672	0.6060	0.5445

B) Phylogenetically informed meta-regression

Parameter	Coefficient	F†	P
Intercept	0.152		
Seed size	0.032	0.594	0.58
Census time	0.003	0.657	0.52
Life-form	−0.317	20.897	0.06
Experimental conditions	−0.094	1.059	0.51

Notes: The meta-regression models test the effect of seed size (log-transformed), census time, life-form, and experimental conditions (field vs. non-field conditions) on the survival effect size, i.e., the relationship between early emergence and seedling survival. Census time is the number of months elapsed from seedling emergence to the evaluation of survival, and life-form is annual vs. perennial.

† We tested the significance of the F statistic by contrasting the observed values against simulated distributions after 1000 permutations, rather than a known Gaussian distribution, so df values are not applicable.

contrasting the observed values against simulated distributions after 1000 permutations run in the PDSIMUL module of the PDAP program (Garland et al. 1993).

The phylogenetic trees used to statistically ''inform'' the comparative analyses (see Appendix C) were constructed by pruning the Soltis et al. (2000) tree to the family level and subsequently grafting the species under the family level following Doyle et al. (1997) for Fabaceae, Eriksson et al. (2003) and R. Evans (*unpublished phylogeny*) for Rosaceae, and Chaw et al. (1997) for gymnosperms. Thus, we obtained phylogenetic trees with a very good resolution (just 1–2 polytomies per tree) in which unit branch lengths were assumed (see Verdú [2002] for a similar procedure).

RESULTS

Survival

A heterogeneity test of fixed-effect models was highly significant (Qt = 14 262; df = 126; P < 0.00001, where Qt indicates the total heterogeneity of a sample), and therefore random-effect models were fitted hereafter. The overall test indicated that the effect of emergence time on survival was low (Zr = −0.0443) and nonsignificantly different from 0 because the 95% bias-corrected bootstrap confidence limits (−0.0870, 0.0044) did not exclude zero. Zr is the effect size; ''Z'' comes from Fisher's z transformation and ''r'' comes from the Pearson's product-moment correlation, *r*. Z is a function that transforms r. However, some effects could be envisaged after including predictors in the model (Table 1A). For example, survival benefits of early emergence were significantly greater for perennials (Zr = −0.097; [−0.143, −0.050]) than for annuals (Zr = 0.035; [−0.0433, 0.1250]). Confidence intervals showed that mean effect size was significantly different from zero in perennials but not in annuals. The weighted histogram (Fig. 1) of survival effect sizes showed that perennials tended to concentrate in the left tail (i.e., early emergents surviving more), whereas annuals spread along the whole distribution, with some species benefiting from early emergence, but others from late emergence.

The other significant predictor in the model was census time (Table 1A), indicating that the probability of survival of early relative to late emergents decreased with time elapsed from the first emergence to the date survival was recorded. Neither seed size nor experimental conditions significantly explained any of the variance found among survival effect sizes (Table 1A).

Results were consistent after accounting for pseudoreplication at the species level; there was a small, nonsignificant overall effect size (Zr = −0.0507; [−0.1099, 0.0054]), and life-form and census time were the two significant predictors of the meta-regression (−0.15 ± 0.07 and 0.007 ± 0.003; B ± SE for the two predictors, respectively, where B is the coefficient of regression).

Once the phylogenetic relationship at the species level was taken into account, there was no evidence of a phylogenetic signal in the survival effect sizes, because the observed variance of the effect size contrasts (0.03847) did not significantly differ from the variances of permuted data (P = 0.17). Results obtained after accounting for phylogeny were thus rather similar to those that did not consider it (Table 1B): life-form was marginally significant (i.e., survival benefits of early emergence tended to be greater for perennials than for annuals), but the slight effect of census time was no longer significant.

FIG. 1. Greater survival of early emergents is more frequent in perennials than annuals, as shown in the weighted histogram of survival effect sizes (Zr for survival). Negative effect sizes indicate that early emergents survive more than later ones, whereas positive effect sizes indicate the opposite.
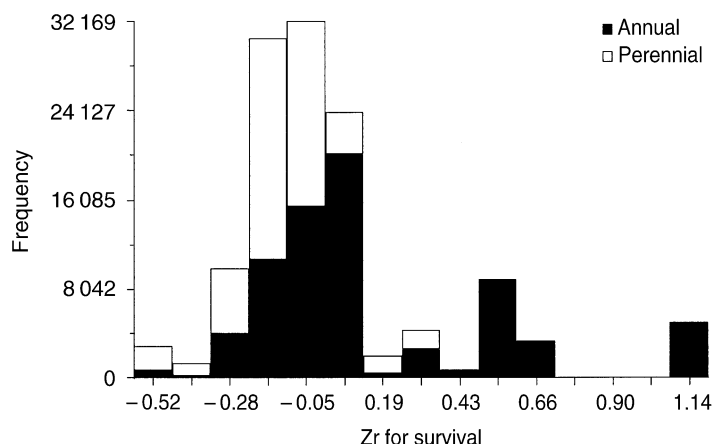
Growth

A significant heterogeneity among studies was evidenced (Qt = 5237; df = 60; P < 0.00001), and the random-effects model revealed that the effect size of emergence time on growth was negative (i.e., early seedlings grow more than later ones) and significantly different from zero (Zr = −0.2665; [−0.4131, −0.1517]). Only one predictor (experimental conditions) explained a significant portion of the variability in effect sizes (Table 2A); the growth benefit of early emergence was much greater under controlled conditions (Zr = −0.4582) than in the field (Zr = −0.1766). This finding might actually result from the extremely strong effect sizes found in a few studies performed under controlled conditions (Fig. 2). To exclude the effect of pseudoreplication, we repeated the analyses with one effect size per species, and found that none of the results had changed (not shown).

We detected a phylogenetic signal in the effect of emergence time on seedling growth, as the observed variance of the effect size contrasts (0.0964) was small-er than 100% of the simulated values. Controlling for phylogeny, similar results were obtained (Table 2B); growth benefits of early emergence were marginally greater under controlled conditions than in the field. However, in this case, seed size became marginally significant in the model, indicating that large seeds benefit more than small ones from an early emergence.

Fecundity

Heterogeneity across studies was again highly significant (Qt = 5943; df = 24; P < 0.00001). As in the case of seedling growth, the effect of emergence time on fecundity was negative, i.e., early seedlings were more fecund than later ones, and significantly different from zero (Zr = −0.2680; [−0.4672, −0.1513]), and this was consistent across studies (Fig. 3). Because of the low sample size and the lack of variability in predictors' values (most are annuals in which fecundity was measured in field conditions within a few months after seedling emergence), only seed size was included in the model. However, we found no significant cor-

TABLE 2. Growth benefits of early emergence depend only on experimental conditions in the non-phylogenetically informed analysis (A). This predictor, as well as seed size, becomes marginally significant once phylogenetic relatedness is taken into account (B).

A) Non-phylogenetically informed meta-regression

Parameter	B	SE	Z	P
Constant	−0.0611	0.1949	−0.3135	0.7539
Seed size	−0.2680	0.1900	−1.4106	0.1584
Census time	−0.0087	0.0142	−0.6153	0.5384
Life-form	−0.0471	0.3089	−0.1525	0.8788
Experimental conditions	−0.9399	0.3765	−2.4964	0.0125

B) Phylogenetically informed meta-regression

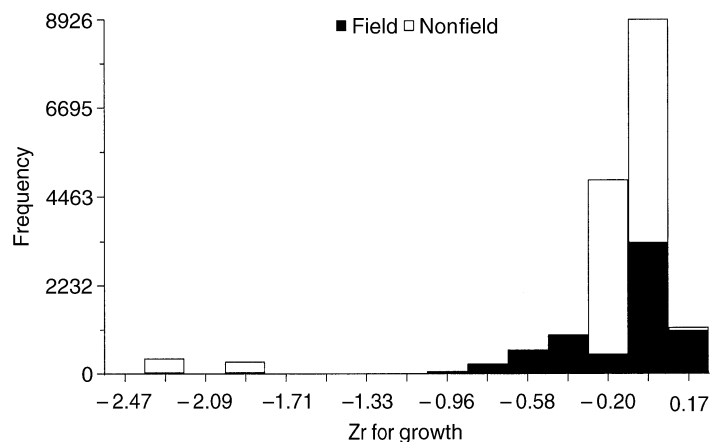| Parameter	Coefficient	F	P
Intercept	0.002		
Seed size	−0.614	6.709	0.06
Census time	−0.018	0.362	0.42
Life-form	0.462	0.712	0.40
Experimental conditions	−1.392	4.545	0.07

Note: See Table 1 for explanation of the models.

FIG. 2. The growth benefit of early emergence is greater under non-field (greenhouse, nursery, or laboratory) conditions than in the field, as shown in the weighted histogram of growth effect sizes. Negative effect sizes indicate that early emergents grow more than later ones, whereas positive effect sizes indicate the opposite. Frequency is a weighted frequency (weights = 1/variance) rather than a true frequency. Therefore, the weighted histogram shows the relative contribution of the data to each effect class rather than the sample size for that effect class.

relation between seed size and effect size ($B \pm 1$ SE = -0.004 ± 0.109; $P = 0.97$). Identical results (not shown) were obtained in a separate analysis at the species level.

The observed variance of effect size contrasts (0.1939) did not significantly differ from the variances of permuted data ($P = 0.37$), and therefore there is no evidence of a phylogenetic signal. However, the non-significant result may also be a consequence of the low power of the test, with rather low sample sizes ($n < 20$). The results obtained after accounting for phylogeny did not change because seed size remained non-significant (coefficient = -0.12; $F = 0.86$; $P = 0.76$).

Publication bias

The fact that the overall survival effect size did not differ from zero implied that publication bias does not exist regarding survival, and thus the calculation of a fail-safe number is not necessary. Regarding seedling growth, Rosenthal's fail-safe number was 243 studies, which is lower than 5 times the sample size plus 10: [$243 < (5 \times 60) + 10$]. Thus we cannot safely conclude that results are robust regarding publication bias. For fecundity, the fail-safe number obtained (13 315) was

much greater than expected ($130 = [(5 \times 24) + 10]$) without publication bias, which supports the robustness of our results.

Discussion

Our analyses show that an early emergence does influence plant fitness, although the effect varies among the different fitness components. While early emergence appears to have large benefits on seedling growth and fecundity, it has no effect on seedling survival. Emergence time explained ~7% of the variance in both seedling growth and fecundity, but only 0.2% of the variance in seedling survival (computed after back-transformation of the Zr effect size into Pearson's r). In ecological and evolutionary meta-analyses, the explained variance ranges from 2.5 to 5.4% (reviewed in Møller and Jennions 2002); thus, we can argue that early emergence has a strong positive effect on plant fitness. After accounting for publication bias, we can state that our results are robust, except in the case of seedling growth, for which the fail-safe number was slightly smaller than expected. We also need to consider the possibility of another bias produced because a large fraction of the studies reviewed here are from temperate
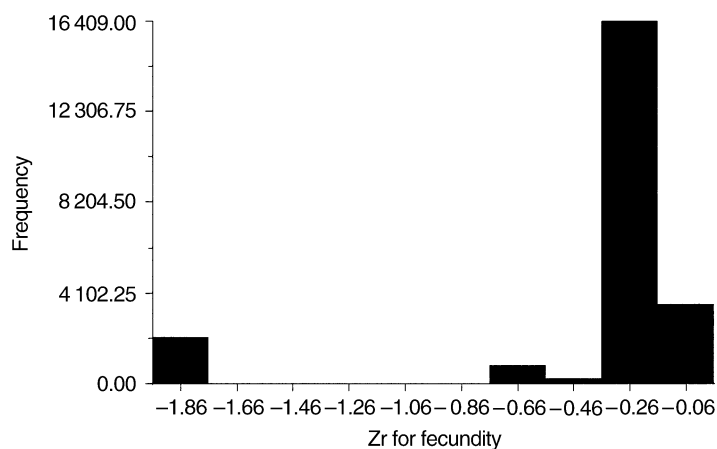

FIG. 3. Early emergents reproduce more than later ones, as shown in the weighted histogram of fecundity effect sizes (Zr for fecundity). The more negative the effect size, the higher is the benefit of early emergence on fecundity.

systems. Studies from the tropics are much fewer, either because they have been less frequently performed there, or because electronic databases from developing countries, mostly found in the tropics, are not available (Zielinski 1995). Consequently, further research in tropical ecosystems is needed to determine the generality of the patterns obtained in this study.

Our results reveal that the effect of emergence time on plant fitness varies depending upon intrinsic factors such as life-form or seed size, and also upon the methodology employed (like census time and experimental conditions). Indeed, the effect that emergence time has on plant fitness components is clearly context dependent, reflecting the contingent nature of evolution of life history traits. These contingencies can be viewed as statistical interactions between the trait (emergence time) and other traits and/or the physical environment (de Queiroz 2002).

Large-seeded species have been hypothesized to compensate for low seed production by increasing seedling survival (Westoby et al. 2002). After accounting for phylogeny, we have found a compensation mechanism of large-seeded species, although only for seedling growth, not survival or fecundity. This implies that large-seeded species take advantage of emerging early by growing more, although they finally survive and reproduce similarly to small-seeded species. Moles and Westoby (2004) found that, under experimentally imposed hazards, the seedling survival advantage of large vs. small-seeded species disappeared once seed reserves were deployed. Because all the studies we included in the meta-analysis recorded seedling survival once seed reserves had been depleted (mean, minimum, and maximum census times are 11, 2, and 36 months, respectively), the early benefits associated with seed size (greater growth) had probably disappeared without enhancing either future survival or fecundity. It follows from our results that it is important to account for the time elapsed from emergence until survival is recorded. We found that the greater the age of the seedlings studied, the weaker was the survival benefit of early emergence, which suggests that later events (i.e., summer droughts, competition, etc.) may reset the survival to similar values among cohorts. Moreover, the extent to which census time is important to estimate the relationship between seed size and fitness-related traits, such as fecundity, has recently been revealed by Moles et al. (2004), who have found that the relationship across species between seed size and fecundity disappears when the whole lifetime of the individual is considered.

It is worth noticing that the growth benefit of large-seeded species was only detected once phylogenetic relatedness among species was considered. Although the effect of emergence time on plant fitness components largely depends on its local ecological history, it is difficult to estimate to what extent this ecological history may override the phylogenetic effects derived from common ancestry (Bolmgren et al. 2003). The rapid development of the comparative method techniques helps to detect a phylogenetic signal in ecological-driven processes that are subjected to strong environmental effects, like plant survival, growth, and fecundity. In general, the phylogenetic signal is near omnipresent in cross-species datasets, including those containing traits that are expected to be subjected to nongenetic environmental effects (Bolmgren et al. 2003). Here, we detected a phylogenetic signal only in the relationship between emergence time and seedling growth. (The low sample size in the case of fecundity probably precluded finding such a signal.) This indicates that the growth, but not the survival, advantage of early emergence is similar between closely related species. Such a phylogenetic signal reinforces the importance of the implementation of phylogenetically based statistical methods for analyses of comparative datasets. However, the lack of phylogenetic signal does not imply that comparative methods do not need to be adopted (Bolmgren et al. 2003). This is ratified here with the different results found in the phylogenetically informed and the non-phylogenetically informed analyses in both data sets with and without phylogenetic signal (growth and survival, respectively) (Tables 1 and 2).

Two factors that behaved similarly in both phylogenetically and non-phylogenetically informed analyses were life-form and experimental conditions of the study. Plants with different life-form had different relationships between emergence time and fitness components. Among perennials, early emergents survived and grew more than later ones (few studies are available for fecundity), while among annuals, precocious emergents survived like later ones, but grew and reproduced more. When comparing both life-forms, the survival benefit of early emergence was greater in perennial than in annual species. This supports our hypothesis that perennials benefit more from early emergence because they can bet that all their seedlings will emerge in the best conditions each year, whereas annuals need to spread the emergence risk temporally to avoid a complete reproductive failure in bad years (Rees 1994, 1996, Mathias and Kisdi 2001). Some annual species can indeed benefit from late emergence, although an early emergence does enhance the future fecundity of annuals (e.g., Venable et al. 1997, González-Astorga and Núñez-Farfán 2000). This kind of trade-off between current and future fitness components is incorporated into the life history of an organism generating delayed life history effects with large demographic and evolutionary consequences (Beckerman et al. 2002, 2003).

The experimental conditions did not affect the relationship between emergence time and seedling survival. However, the observed benefit of early emergence on growth was greater under controlled conditions than in the field. This is not a surprising result,

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as controlled conditions are usually favorable, with no nutrient or water limitation. In natural conditions, in contrast, other factors (mainly abiotic, but also biotic) probably decelerate the growth of early seedlings, precluding the detection of differences between these and late seedlings (e.g., Traveset et al. 2001). Several examples of different experimental conditions leading to different responses in seedling emergence and growth are known, although the direction of the differences is not consistent. A first group of studies shows that differences in seedling emergence or growth between treatments are usually magnified under harsh (field) conditions. For example, Herrera (2000) only detected seedling emergence differences between seeds from two pollination regimes when planted in the field, but not in the greenhouse. Similarly, Traveset et al. (2001) only found a positive effect of seed ingestion by birds on seedling emergence in outdoor conditions, and not in a growth chamber or a greenhouse. A second group of studies shows the opposite direction, with a greater effect in laboratory compared to field experiments (Bustamante et al. 1992, 1993, Figueiredo and Perin 1995, Yagihashi et al. 1999). And finally, a third group of studies finds similar results between the two conditions (Figueiredo and Perin 1995, Figueiredo and Longatti 1997). In a recent study, comparing seedling emergence responses of a dozen species to seed treatment in the frugivores' guts, significant differences for most species have been observed between field and controlled conditions in a common garden in the two directions (Rodriguez-Pérez et al., *in press*). The causes of such heterogeneity in responses by the different species to the two conditions remain unknown. In our database, no single study tested the effect of emergence time under field and non-field conditions, but the meta-analytical approach across studies has allowed us to recognize the importance of the experimental conditions to understand the processes determining seedling growth.

In summary, given that emergence time is a heritable trait under selective pressure (Geber and Griffen 2003), we can conclude that early emergence can enhance the fitness of plants due to immediate (survival and growth) and/or delayed (fecundity) effects. At the same time, we argue that selection on emergence time may vary on time and space and across life history episodes, which may slow the rate of evolutionary change, maintain the population genetic diversity, and select for plasticity (Geber and Griffen 2003).

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APPENDIX A

A reference list of the published studies included in the meta-analysis of the effect of emergence time on plant fitness components is available in ESA's Electronic Data Archive: *Ecological Archives* E086-075-A1.

APPENDIX B

A database used in the meta-analysis of the emergence time effect on plant fitness components (survival, growth, and fecundity) is available in ESA's Electronic Data Archive: *Ecological Archives* E086-075-A2.

APPENDIX C

A figure showing the phylogenetic relationships of the species included in the data set in which the effects of emergence time on survival, growth, and fecundity have been studied is available in ESA's Electronic Data Archive: *Ecological Archives* E086-075-A3.

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