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Seed germination traits can contribute better to plant community ecology

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ABSTRACT

Analyses of functional traits have become fundamental tools for understanding patterns and processes in plant community ecology. In this context, regenerative seed traits play an important, yet overlooked role, because they largely determine the ability of plants to disperse and re-establish. A survey of recent publications in community ecology suggests that seed germination traits in particular are neglected at the expense of other relevant but overused traits based only on seed morphology. As a response to this bias, we discuss the functional significance of seed germination traits in comparison with morphological and biophysical seed traits, and advocate for their use in vegetation science. We also demonstrate how research in community assembly, climate change and restoration ecology can benefit from the inclusion of germination traits, encompassing functions that cannot be explained solely by adult plant traits. Seed germination experiments conducted in the laboratory or field to quantify these traits provide ecologically meaningful and relatively easy-to-obtain information about the functional properties of plant communities. We argue that bridging the gap between seed physiologists and community ecologists will improve the prediction of plant assemblages, and propose further perspectives for including seed traits into the research agenda of functional community ecologists.

KEYWORDS

Community assembly; Climate change; Dispersal, Plant functional traits; Regeneration niche, Restoration ecology; Seed germination; Seed morphology; Seed traits

Introduction

In the last few decades, an increasing number of studies have explored the role of functional traits to explain community patterns and processes (Díaz et al. 2004, McGill et al. 2006). Recent initiatives have aimed to standardize nomenclature (Violle et al. 2007), define measurement protocols (Pérez-Harguindeguy et al. 2013) and store trait information in databases on a global scale (Kattge et al. 2011). After an era of data compilation and pattern evaluation, there is an increasing need to select those traits that better respond to specific research questions for improving our predictions of species relative abundance (Laughlin 2014).

The number of plant traits to be used is enormous and measuring them for individual species can be time-consuming. In practice, only a few traits have been systematically employed in community ecology, particularly those reflecting the CSR (competitive/stress tolerant/ruderal) or LHS (leaf area/height of mature canopy/seed mass) plant strategy concepts (Weiher et al. 1999; Grime 2001). However, studies aiming to investigate the role of traits in community ecology have identified numerous functional dimensions (Westoby et al. 2002) and it is now clear that assessing species' responses to the environment is hardly possible without simultaneously considering clearly different traits (Kleyer & Minden 2015).

Grubb (1977) highlighted the ecological role of seed germination and seedling establishment in plant communities by defining the *regeneration niche* as “an expression of the requirements for a high chance of success in the replacement of one mature individual by a new mature individual of the next generation”. Indeed, seed germination and post-germination adaptation are currently recognized as crucial phases of the plant's life which are strongly dependent on environmental filters (Donohue et al. 2010). Surprisingly, germination traits are generally relegated to a secondary role or strongly underrepresented in compilations and reviews

on plant traits (Kleyer et al. 2008; Kattge et al. 2011; Pérez-Harguindeguy et al. 2013), which could reflect the underuse of seed germination traits in community ecology. Here we address the extent of this bias, demonstrating the functional significance of seed traits and the potential contribution of seed germination to plant community ecology.

Functional significance of seed traits in plant communities

Seed traits are often unrelated to leaf and whole-plant traits (Pierce et al. 2014), suggesting that their inclusion in community ecology adds a significant contribution to the understanding of the functional multidimensional space of plant traits (Laughlin 2014). Since recent studies have reviewed the general role of commonly-used seed traits in shaping plant communities (e.g. Poschlod et al. 2013; Saatkamp et al. 2014) we refer to these papers for detailed information about the general integration of seeds in vegetation ecology. However, we note a lack of comprehensive compilations of seed traits, or when existing (e.g. Poschlod et al. 2003) they are generally inserted in broader definitions of other plant traits. To fill this gap, and for a better understanding of the functional significance of seed biology in vegetation science, we compiled a non-exhaustive list of seed traits, and classify them into three practical groups: morphological, biophysical and germination traits (Table 1).

Morphological traits can be easily determined upon an external or internal inspection of the seed. They are functionally related to dispersal processes (e.g. seed surface structure, related to the "morphology of dispersal unit" in Kleyer et al. 2008) but also reflect other properties such as persistence in the soil and response to fire or water (Fenner & Thompson 2005). Correlations have been established between seed mass and seed shape, dispersal potential, persistence in soil seed banks, seed production, initial seedling size and germination (Grime et al. 1981; Westoby et al. 2002). Morphological traits are also associated with plant responses to disturbance, soil

resources and competition (Pérez-Harguindeguy et al. 2013). In addition to external morphological traits, embryo morphology varies widely and is correlated with dormancy (Baskin & Baskin 2007).

Biophysical traits reflect the physical-chemical properties of the seed coat, the endosperm or the embryo, and they have to be measured in the laboratory. These traits are mainly linked to the regulation of seed-water relations that occur during seed development and germination. They are also important to determine the ability of seeds to disperse by wind (e.g. terminal velocity, Tackenberg et al. 2003) or water (e.g. seed buoyancy, van Den Broek et al. 2005). Biophysical properties such as desiccation tolerance, oil content and water content can be also correlated with each other (Hamilton et al. 2013); some of them being habitat-dependent and closely correlated to latitudinal gradients (Tweddle et al. 2003). In addition, biophysical traits are linked to physical dormancy since particular conditions (e.g. high temperatures, fire) render the seed/fruit coat permeable to water.

Germination traits are those related to the time and conditions required by a seed to germinate, reflecting essential physiological processes controlled by the environment (Lambers et al. 2008). Germination traits must be evaluated in experimental studies in the laboratory or in the field, and preferably in both (Baskin et al. 2006). Germination temperature and the loss of physiological dormancy are assumed to be closely related to climate in the plant's habitat. Both these traits are driven by genetic adaptation, and the level of dormancy may also be affected by climate through maternal effects (Gutterman 2000; Rosbakh & Poschlod 2015). Response to diurnally fluctuating temperatures may be related to soil depth (Saatkamp et al. 2011), gap detection (Pearson et al. 2003) and drought (Brock & Casanova 1997). Germination traits can be used for evaluating ecological responses to extreme conditions such as salinity (Guja et al. 2010),

flooding (Mollard & Insausti 2011) or smoke (Nelson et al. 2012). Some germination traits are mutually dependent; for example, the response to light is related to the ability of seeds to persist in the soil, and the patterns of dormancy are linked to the temperature and precipitation regimes experienced by the seed following dispersal and until dormancy is broken (Saatkamp et al. 2011).

Which seed traits are used by vegetation scientists?

From a total of 226 community ecology studies published between 1990 and 2014 which contained keywords related to seed traits or regeneration traits (Fig. 1), we found the vast majority (>75%) used morphological traits to study plant communities. Almost half of these publications used seed mass and a quarter used seed dispersal mode. In fact, seed mass has been regularly used in plant community studies since 1990, but from 2008 onwards the number of studies doubled, probably due to the availability of global databases (e.g. LEDA Traitbase, www.leda-traitbase.org; TRY Plant Trait Database, www.try-db.org). Germination traits were listed in only 20% of the publications, in which germination rates and seed longevity were the most commonly used (3.5% and 3.2% respectively). Very few publications used biophysical traits such as oil content, reserve type, and buoyancy. Other germination traits, such as optimal temperature and salt tolerance, and morphological traits including embryo type and seed coat thickness were less commonly used, showing that these traits are under-represented in plant community studies.

The potential contribution of seed germination traits to plant community ecology

Community assembly

The main idea underpinning the regeneration niche hypothesis (Grubb 1977) is differential requirements, tolerance and resource use of different plant life stages. Thus, it is not

surprising that germination traits were considered first by Grime et al. (1981) and later by Keddy (1992) as key to understanding community assembly. In general, seeds respond to environmental changes and tend to germinate during conditions that are favourable for establishment. Because germination is an irreversible process and establishment is the most vulnerable stage of plant life cycle, regeneration from seeds is often more sensitive to variation in temperature, moisture, oxygen and salt than adult plant growth and survival. Indeed, recent studies suggest that environmental filtering plays a crucial role in early life-stage transitions (germination, seedling survival and seedling growth) by determining the distribution of adult stages in plant communities (Fraaije et al. 2015; Mondoni et al. 2015). Species cannot be part of the community if environmental conditions are only suitable for plant growth and survival, but not for seed germination, and variation in adult plant traits is not always enough to explain plant coexistence in natural communities (Poschlod et al. 2013). Therefore, plant community ecologists should consider the disjunction between traits related to seed germination, seedling establishment and reproduction of adults to better infer assembly rules (see reviews by Leck et al. 2008; Donohue et al. 2010).

Germination traits, together with dispersal-related traits, are expected to play an important role in the processes that filter regional species pools into local communities (Fig. 2). Available evidence suggests that divergence in germination traits of sympatric and closely related species helps explaining trait-environmental associations, variation in micro-environmental conditions, species coexistence, ecological breadth and geographic ranges (Daws et al. 2002; Donohue et al. 2010; Marques et al. 2014). It seems that investigating traits without a clear physiological response, such as seed size or dispersal mode, can only tell part of the story on community assembly and dynamics. An example is seed resistance to pathogens, a major

force driving persistence in soil seed banks which requires careful study under lab conditions (Gallery et al. 2014). In addition, new evidence is coming to light that germination traits may be better predictors of seed persistence, which influences plant community dynamics, than morphological traits (Saatkamp et al. 2011). Also, dormancy and germination responses to temperature may be good predictors for germination niches (Kahmen et al. 2002, Merritt et al. 2007, Rosbakh & Poschlod 2015), which can be used, alone or in combination with establishment traits, to evaluate environmental filtering in plant communities.

Climate change

Predicting the responses of plant communities to climate change will require a better understanding of the influence of temperature and moisture on seed germination (Walck et al. 2011). Indeed, a combination of functional traits for adults and seeds will probably result in better prediction of climate-driven responses, assuming both plant life stages may have different requirements and respond differently (Donohue et al. 2010; Mondoni et al. 2015). Changing temperature regimes, moisture availability and fire frequency in natural habitats may alter dormancy loss, germination timing and seed persistence, resulting in changes in population dynamics and community composition (Walck et al. 2011; Ooi 2012). For example, changing temperatures are known to influence the timing of *in-situ* seed germination in alpine communities (Mondoni et al. 2012; Jaganathan et al. 2015; Rosbakh & Poschlod 2015), fire-prone ecosystems (Hudson et al. 2015) and hot deserts (Kimball et al. 2010).

The effect of climate on seed regeneration traits has been mostly demonstrated at the species level and more studies are needed to explore the response of dormancy and germination to altitudinal and latitudinal gradients at the community level (Jaganathan et al. 2015). Indeed, there is evidence of variation in patterns of germination and dormancy that suggests

environmental filtering by climate across world biomes (Baskin & Baskin 2014). At both global and local scales, major vegetation types show clear differences in the germination traits of their constituent species (Grime et al. 1981, Poschlod et al. 2013), and some studies suggest the existence of functional germination groups along environmental gradients in relatively similar vegetation types (Fernández-Pascual et al. 2013). These relationships support the effect of global and local climate on seed germination traits that filter the regional species pool into local communities (Fig. 2). Like in other functional traits, intra-specific variation should be also considered, and dormancy status seems to be more influenced by aridity, elevation and latitude than seed mass or germination rate (Cochrane et al. 2014).

Restoration ecology

Ecological restoration aims to help an ecosystem recover after it has been damaged (SERI Science & Policy Working Group 2004). Seeds are a key component in ecosystem recovery as a source of propagules for restoration, so a better understanding of germination requirements will improve restoration outcomes. While some restoration practices rely on natural dispersal of seeds, or recruitment from the existing soil seed bank to assist in ecosystem recovery (Bakker et al. 1996), others use topsoil containing the seed bank which has been removed, stored and replaced, seeds contained within plant mulch or hay, applied seed and/or planted seedlings (Rokich & Dixon 2007). Hence, in highly degraded landscapes, where dispersal processes have been disrupted or habitats are too isolated, germination traits may be of greater importance than dispersal traits to re-assembly of plant communities. Even species reintroduction, translocation or assisted migration programs which rely on planted seedlings or cuttings will need to consider germination traits, as their offspring will need to be able to germinate to ensure the recruitment of subsequent generations.

Knowledge of germination traits such as seed dormancy (Merritt & Dixon 2011) and the ability to germinate under water stress (Bochet et al. 2007) may improve restoration outcomes from sown seed. As recruitment from soil seed banks is influenced by seed persistence (Bakker et al. 1996; Long et al. 2015), elucidating germination traits correlated with persistence and gap detection mechanisms (which include germination rate, light requirement and response to fluctuating temperatures, see Saatkamp et al. 2011) may improve restoration outcomes from existing or replaced soil seed banks. Given that restoration ecology can be also used to test ecological theory (Bradshaw 1983), experiments exploring the influence of these germination traits, may not only be of benefit to restoration ecology, but may also be of great use to integrate other fields of research such as community re-assembly (Temperton et al. 2004).

Conclusions and further perspectives

Despite regeneration traits having always been considered as a fundamental aspect of plant community ecology (Grubb 1977; Keddy 1992), seed traits have been largely ignored for explaining species occurrence and abundance (Poschlod et al. 2013). In this paper we have shown that there is clear evidence of the role of germination patterns in structuring plant communities. Nevertheless, germination-related traits are still rarely integrated into studies at the community level. There are several reasons for explaining the bias towards morphological traits related to dispersal (mass, shape) to the detriment of germination traits. Firstly, a lack of knowledge of the functional significance of the latter traits may have led to their underuse in community ecology studies. Seed germination has been traditionally approached by plant ecophysiologicalists in laboratory experiments, while community ecologists have been mainly interested in field data (either descriptive or experimental). Physiologists and ecologists have different views on seed traits such as dormancy, which can lead to poor communication and a

lack of understanding between the two disciplines (Vleeshowers et al. 1995), and in many cases they publish in different journals within plant sciences. Another reason for explaining the underuse of germination traits in community ecology could be simply that this information is not available, and measurements may be thought to be a difficult task. However, the latter is only partly true; although measurements on seed germination may be time-consuming, time may be not an argument to neglect them for a better understanding on community structure and dynamics.

The current development of integrative approaches by considering taxonomic, functional and phylogenetic diversity provides a favourable context to reduce this misconception. Still, germination traits are largely ignored in measurement protocols of plant functional traits (e.g. Pérez-Harguindeguy et al. 2013) and even in large databases like TRY (www.try-db.org) where less than 1% of all entries correspond to germination traits (Kattge et al. 2011). In response to the current trend of neglecting germination traits, we suggest community ecologists pay attention to the vast information generated by seed eco-physiological studies over the last few decades. Much of this information has been compiled in Baskin & Baskin (2014) by classifying germination studies in global habitats and vegetation types with a biogeographic and evolutionary perspective. In parallel, several on-line databases are continuously updating seed traits with a special focus on germination traits (e.g. The Seed Information Database, <http://data.kew.org/sid/>). Nonetheless, more effort is needed to generate new data covering seed trait strategies at the community level, and new approaches are still necessary to implement relevant traits in vegetation ecology. For example, the potential of seed dormancy could be effective when this trait will be used in a quantitative dimension and integrated with phylogenetic data (Willis et al. 2014).

Because germination traits rarely overlap or correlate with CSR and LHS plant-strategy traits, we advocate for the inclusion of germination experiments in vegetation ecology. Germination trials are relatively easy to perform and they can be developed either in the field or the laboratory, providing valuable ecological information when they are conducted properly (see Baskin et al. 2006). Sampling fresh seeds is essential to conduct this research, and sampling size must also be adequate to consider general factors influencing wild populations such as inbreeding, population size, etc. In this regard, the protocols for maximizing genetic diversity of seed collections can be assimilated from ad hoc manuals (e.g. the ENSCONET seed collection manual, available in <http://ensconet.maich.gr/>). We also note that, as in any other study based on plant traits, germination experiments should be based on specific questions about the expected response of plant communities to a given environmental factor. Depending on the study system, some traits will be relevant, while others will not be relevant. For example, in ecosystems in which fire does not occur, smoke responsiveness may not be relevant, while in fire-adapted ecosystems it may be a major driver for plant recruitment from seeds. In addition, in ecosystems where there is no possibility for dispersal by water, then whether or not seeds are buoyant is not relevant, in contrast with riparian and coastal ecosystems where buoyancy is critical to explain dispersal. Resolving functional-based questions is probably the next phase in the development of trait-based studies to understand processes affecting plant communities, and many aspects of functional properties and multidimensionality of traits must still be approached (Laughlin 2014). Detailed protocols for sampling communities and for developing germination experiments and meaningful variables are therefore urgently needed in the plant-trait agenda of functional ecologists. Thereby, the integration of germination traits together with other vegetative or regeneration traits will help the further development of plant community ecology.

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Table 1. Main seed traits with potential to improve predictability in vegetation ecology and examples of their functional significance across different ecosystems. Classification in morphological, biophysical and germination traits is based on their biological properties as well as in their requirements for measurement (see details in the text). Note that many traits may be correlated with each other. The term “seed” can refer to the whole dispersal unit, i.e. the seed together with attached fruit structures.

Seed trait	Units	Functional significance
<i>Morphological traits</i>		
Seed surface structure	Categorical	Colonization capacity, dispersal mode, plant-animal interactions
Embryo type	Categorical	Position and structure of the embryo in the seed (linked to dormancy)
Embryo:seed ratio	Ratio	Size of the embryo relative to the seed (linked to dormancy)
Seed coat thickness	Ratio	Fire-tolerance, persistence in soil, resistance to pathogens and predators
Seed mass	mg	Dispersal distance, persistence in soil, predation likelihood
Seed shape	Quantitative but dimensionless	Burial and persistence in soil
Seed size	mm	Dispersal potential, reproductive output
<i>Biophysical traits</i>		
Buoyancy	Time or rates	Floating capacity, dispersal ability by water (linked to seed structure)

Coat chemical content	Categorical	Defence against pathogens
Coat water permeability	Percentage	Fire-tolerance, defence against predators. Linked to physical dormancy
Desiccation tolerance	Categorical	Persistence and ageing in different climates and habitats (e.g. aquatic, terrestrial; grasslands, forests)
Oil content	Percentage	Energy provision for seedlings, water relations with the environment
Reserve type	Categorical	Nutritional value, persistence in soil
Terminal velocity	m/s	Dispersal distance, dispersal potential
Water content	Percentage	Desiccation tolerance, longevity in soil

Germination traits

After-ripening	Weeks, months; percentage	Climate adaptation, seasonal germination niche (linked to dormancy)
Dormancy	Categorical, quantitative	Delay of germination until embryo is completely developed (morphological, MD) or a given environmental factor affects the embryo growth potential (physiological, PD) or specialised structures in the seed coat (Physical, PY), or combinations of the above (MPD, PD+PY), or no delay in germination – non-dormant (ND) (linked to other traits)
Germinability	Percentage	Colonization capacity, seed vigour and viability. (generally the result of the influence of other traits)
Germination rate (speed)	Days, t_{50}	Competitive ability, ability to germinate under dry conditions, time for recruitment
Germination synchrony	Quantitative but dimensionless	Gap detection in natural habitats

Germination temperature (min, max or optimal)	Degrees, percentage	Climate adaptation, detection of season, niche breadth
Fluctuating temperatures	Range, ΔG_{DFT}	Gap detection in natural habitats, adaptation to day-night temperature regimes
Heat (shock) requirement	Percentage	Response to fire, ability to germinate after heat shock (linked to seed coat thickness and physical dormancy)
Light requirement	Percentage, ΔG_{light}	Persistence in soil, soil depth signalling, gap detection, recruitment after disturbance
Nitrate	Percentage	Gap detection, nutrient availability
Oxygen requirement	Percentage	Ability to germinate under anaerobic conditions
Red:far red ratio	Proportion	Gap detection, ability to germinate under shaded conditions
Salt tolerance	max/dS/m	Ability to germinate under saline conditions
Seed longevity	Months, years	The lifespan of a seed after maturity/dispersal
Smoke requirement	Percentage	Fire adaptation, ability to germinate after smoke application
Stratification	Weeks, months; percentage	Climate adaptation, seasonal germination niche (linked to dormancy)
Water potential	Percentage, MPa	Ability to germinate in dry/wet conditions

ΔG_{DFT} : relative germination rates for fluctuating temperatures ΔG_{light} : relative germination rates for light;
 t_{50} : time to germination of 50% of seeds; MD: morphological dormancy; PD: physiological dormancy;
 PY: physical dormancy.

Figure 1. Number of published papers per year (1990 – 2014) in community ecology using seed and germination traits. The survey was conducted in the ISI Web of Knowledge (searched in March 2015) by searching for papers containing the terms "seed traits" and "community", and also individual traits (see Table 1) and "community". The studies were grouped according to whether they utilised morphological, germination or biophysical traits as described in Table 1. Only studies that were related to description of plant communities or research on community assembly are considered.

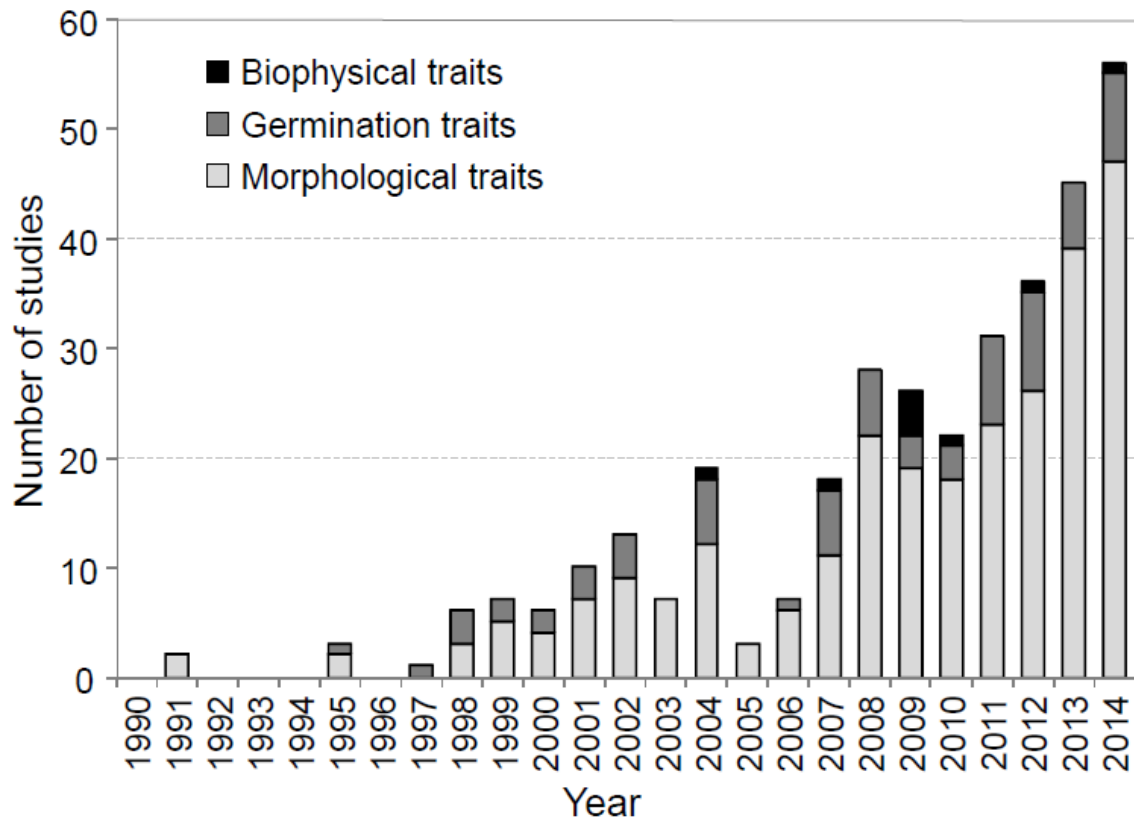


Figure 2. Expected relationships between selected seed traits and the main processes involved in the filtering of regional species pools into local plant communities (capital letters refer to different species).

