

SylvanSeeds, a seed germination database for temperate deciduous forests

Author: Eduardo Fernández-Pascual **Institutional address:** Departamento de Biología de Organismos y Sistemas, Universidad de Oviedo, C/ Catedrático Rodrigo Uría, 33006 Oviedo/Uviéu, Spain **Email:** efernandezpascual@gmail.com **Telephone:** +34985104787

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Abstract

Seed traits have functional significance in all levels of plant biology, but there is a lack of germination databases of wide geographical scope. This report presents *SylvanSeeds* (<https://efernandezpascual.github.io/home/sylvanseeds.html>), a first global database of germination records for an ecologically coherent unit: Temperate Broadleaf and Mixed Forests. Data were gathered with a systematic literature search. A list of frequent taxa of the study area was created using 14,963 vegetation relevés from the sPlot database. The list was searched in the Web of Science. 6,791 references were screened, finding 555 articles from which data were extracted. *SylvanSeeds* includes 4,012 germination records of 334 species from 72 families (gymnosperms and angiosperms), collected in 46 countries between 1920-2017. It provides raw data for meta-analysis: proportions of seeds germinated in laboratory experiments of scarification, stratification, light-darkness, and constant-alternating temperatures. *SylvanSeeds* is freely distributed as a *.csv*. A shiny web app is also presented, to make data accessible to the public. *SylvanSeeds* advances functional seed ecology and brings two innovations to plant science. First, the data-gathering methodology can be extended to other biomes. Second, database and app can be a standard in further efforts to compile germination data.

Keywords: germination database, germination temperature, light and dark germination, nemoral, seed dormancy, seed traits, temperate broadleaf and mixed forests, temperate evergreen forests

Introduction

Seed traits have functional significance in all levels of plant ecology, from population dynamics (Huang et al. 2016) to community assembly (Larson & Funk 2016) and species distributions (Larson & Funk 2016). Recent discussions (Jiménez-Alfaro et al. 2016; Saatkamp et al. 2019) highlighted the lack of reliable germination databases of wide geographical scope as a major limitation to produce a global synthesis of the seed ecological spectrum. Seed germination is the first major developmental transition in the life of a plant, and it has profound effects on the plant's ecology (Donohue et al. 2010). As such, the timing of this transition is controlled by a combination of environmental signals. Amongst these are temperature (Fernández-Pascual et al. 2019), diurnal temperature alternation (Thompson et al. 1977), light (Carta et al. 2017) and seed

dormancy inductors and relievers (Finch-Savage & Leubner-Metzger 2006). All these signals interact to produce a coarse- and fine-scale regulation of germination timing, integrating inputs from both seasonal climatic cycles (Jurado & Flores 2005) and local environmental gradients (Fernández-Pascual et al. 2017). The practical consequence of this is that the response of seeds to, for example, light will depend on other conditions set by the experimenter. This makes it difficult to summarise germination “traits” into a single value in a way comparable to seed mass, specific leaf area or plant height (Pérez-Harguindeguy et al. 2013), and may explain the lack of global germination databases. Germination compilations with a biogeographical background, of which the prime example today is the cornerstone book of Baskin and Baskin (2014), only provide summary information, for instance the interpreted optimal germination temperature instead of the proportion of seeds germinated across a temperature gradient.

To fill this gap, this article presents *SylvanSeeds*, a first global database of raw germination data for an ecologically and biogeographically coherent unit: the temperate broadleaf and mixed forests biome (Olson et al. 2001) of the northern hemisphere (hereafter shortened to nemoral biome). Nemoral forests are dominant in temperate latitudes with mild to cold winters and relatively warm and wet summers, corresponding with the Cf climate in Köppen’s classification (mild temperate, fully humid) (Beck et al. 2018). Generally, these forests are characterized by some frost events during the winter while summers are moist and do not suffer drought for any relevant length of time, conditions that favour the dominance of broadleaf deciduous trees (Givnish 2002). In the northern hemisphere, they also form a coherent evolutionary and biogeographic unit, sharing a common Tertiary history until they became separated between North America, Asia and Europe (Milne & Abbott 2002). At the same time, a relatively high number of classic seed biology research groups have worked within the nemoral biome areas, e.g. in the USA (Baskin & Baskin 2014), the UK (Grime et al. 1981), Belgium (Van Assche & Vandeloock 2006) and Japan (Washitani 1988). To create *SylvanSeeds*, a systematic literature search (Koricheva et al. 2013) was applied to a list of frequent species representing the flora of the nemoral biome. This article makes the database accessible to the research community. Additionally, the *SylvanSeeds* shiny web app is presented to facilitate the exploration of the data.

Materials and Methods

Frequent species list

A systematic approach was followed to search for data, with the purpose of prioritising work and maximising its utility for vegetation science. In short, this approach consisted in (i) obtaining a representative number of vegetation plots for the biome from sPlot (<https://www.idiv.de/en/splot.html>); and (ii) using the plots to produce a list of frequent species (i.e. species that occur in at least 5% of the plots of a region).

A list of species for which to search germination data was created using vegetation relevés (i.e. records of plant species co-occurring in sampling plots) from *sPlot* (Bruehlheide et al. 2019). The terrestrial regionalization of the *World Wildlife Fund* (Olson et al. 2001) was used to select plots according to their coordinates. To ensure that plots were a representative sample of nemoral biome biodiversity, they were chosen from 17 ecoregions of the Temperate Broadleaf and Mixed Forests biome distributed throughout the northern hemisphere: (*Appalachian mixed mesophytic forests, Atlantic mixed forests, Cantabrian mixed forests, Caspian Hyrcanian mixed forests, Central Korean deciduous forests, Dinaric Mountains mixed forests, Euxine-Colchic broadleaf forests, Hokkaido deciduous forests, Manchurian mixed forests, Nihonkai evergreen forests, Nihonkai montane deciduous forests, Pindus Mountains mixed forests, Southeastern mixed forests, Taiheiyō evergreen forests, Taiheiyō montane deciduous forests, Western European broadleaf forests, Western Great Lakes forests*). Although temperate broadleaf and mixed forests also occur in a smaller area of the southern hemisphere, these southern forests form a separate evolutionary and biogeographical unit, not being related by a common history like the northern hemisphere ones (Milne & Abbott 2002). For this reason, they were not considered.

All chosen relevés had been classified as forest plots by *sPlot*, i.e. their plant cover was dominated by tree species. The taxa names were standardized to species level with *The Plant List* (2013) using the *Taxonstand* package (Cayuela et al. 2019) in *R* (R Core Team 2019). The final vegetation database contained 14,963 relevés and 7,133 standardized species names, considering only seed plants (gymnosperms and angiosperms), and encompassing all forest layers. To obtain the final list of species, only species that were present in at

least 5% of the relevés of an ecoregion were kept, rendering a list of 1,270 frequent species. There were two reasons to use this frequency threshold: (i) it made the search achievable with the resources available; and (ii) it filtered out rare species that may not be representative of the nemoral biome, and which could have been recorded for a variety of reasons (wrong taxonomical identifications, mistakes in plot coordinates, border areas, unnatural areas such as parks, etc.). The result is a list of plant species that occur with relatively high frequency in forest plots of the nemoral biome; this includes trees, shrubs and shade-tolerant forbs and grasses, as well as common semi-open species from forest margins, secondary forests, ruderalized forest plots, etc.

Web of Science literature search

The list of frequent species (plus the synonyms recorded in the relevés) was incorporated into a Boolean search string, together with the words “(seed OR seeds) AND (dormancy OR germination).” This string was searched in the *Thompson Reuters Web of Science* on 5 Mar 2019, returning 6,791 results. The processing of these results is described in a PRISMA flow diagram (**Appendix S1**). A first filter of the results by the relevance of the title retained 1,489 references. An effort was made to access the full text of all these references, using the following channels: (i) “Find Full Text” functionality in *EndNote X9*, (ii) online access to the journals using the institutional subscriptions of the University of Oviedo; (iii) request to the authors through *ResearchGate*; (iv) general search of *pdf* files in *Google* using the article details. Unfortunately, 236 references could not be accessed. Most of these belonged to smaller publishers not included in the subscriptions of the University of Oviedo, and to older journal issues which had not been digitalised. The resources of this project did not make it possible to further pursue these references, but they are included as a *BibTeX* file (**Appendix S2**) in case they can be processed in the future. The found texts were accessed to retrieve data for the database. At this stage, references were considered to be non-relevant if they (i) did not pertain to species in the original frequent species list; (ii) did not study germination in species monocultures (e.g. competition studies); (iii) did not report the minimal information needed (number of seeds sown, germination percentage and germination temperature). Records were also excluded when they pertained to special germination treatments that do not allow for general comparisons (i.e. use of germination promoters such as the plant hormone gibberellic acid; drought treatments, including polyethylene glycol solutions; application of heavy metals or other pollutants; smoke-related germination promoters such as karrikins). Of the accessed references, 698 were non-relevant (*BiBTeX* file in **Appendix S3**) and 555 provided relevant data (*BiBTeX* file in **Appendix S4**).

The systematic approach applied may fail to capture references on species belonging to the nemoral biome for three reasons: (1) the species is not recorded in the vegetation database; (2) the species has been recorded, but it is infrequent (see above the frequency criterion); or (3) the species is recorded and frequent and goes into the list, but the relevant germination references are not found by the web search because the species name is not mentioned in the title or the abstract. While points 1 and 2 are intentionally excluded by the applied methodology, point 3 would be a failure of the methodology (specifically, a failure of the search string to find a relevant paper). For this reason, a protocol was applied to detect the importance of point 3, using the book of Baskin and Baskin (2014) as a reference. After completing the database, species names in the frequent species list for which no relevant papers had been found were searched in the taxonomical index of the Baskin and Baskin book. There were 273 species with missing data and mentioned by Baskin and Baskin in their index. A random sample of 10% of these species were selected, and their references as mentioned in the book were searched. All of them were found to be either inaccessible (national journals or old conference proceedings not available online) or to have no relevant data (i.e. provided no primary germination data that could be retrieved). From this trial, it was concluded that the search string had found a reasonable amount of the available information, by comparing it to the best reference available, the review book of Baskin and Baskin.

Recording of the database

For each relevant reference, three blocks of information were recorded. The first block described the plant material, including the species, the populations that had been sampled, the year of sampling (or the year of publication if that information was missing), the country, the geographical coordinates (if not provided in the reference, the closest available toponyms were searched in *Google Maps*; in some cases the only

geographical information was the country, in these cases the coordinates of the capital city were recorded). The second block described the experimental conditions: experimental setting (greenhouse, incubator or room temperature), germination substrate and characteristics of the containers, seed storage, application of seed sterilization or nutrients, length of the germination incubations, use of stratification (none, cold [$< 15^{\circ}\text{C}$], warm [$\geq 15^{\circ}\text{C}$] or combinations of cold and warm), use of scarification, photoperiod, maximum germination temperature, minimum germination temperature, and weighted average germination temperature. The third block contained the final germination proportion: the reported final germination percentages (retrieved from the text, tables or figures) and the reported number of replicates and seeds per replicate were used to calculate a count of seeds sown and a count of seeds germinated.

Results

Summary of contents

The final database contains 4,012 records (germination proportions for a given seed lot of a species, recorded in a set of experimental conditions) from 555 references. The plant materials had been collected across the Temperate Broadleaf and Mixed Forest biome and surrounding areas (**Fig. 1**), in both hemispheres. Although the frequent species list was created using only relevés from the northern hemisphere, the web search of germination articles found studies of those species that had been performed in the southern hemisphere. These records are included in the database, and their geographical origin is reported. The oldest record was from 1920 and the top three contributing countries were the USA (780), the UK (543) and Japan (531). There were 334 species represented, from 72 seed plant families. The total estimate of seeds used in the experiments was 746,947. The range of germination temperatures (weighted average of the daily thermoperiod) went from -1 to 43°C , with 1,628 records of constant temperatures and 2,384 of alternating temperatures. Light was used in 2,524 records, darkness in 1,107 and 381 did not provide information on this parameter. The experiments were performed with unstratified seeds in 2,607 records, and of the rest, the majority (1,232) went through cold stratification. Scarification was applied to 248 records.

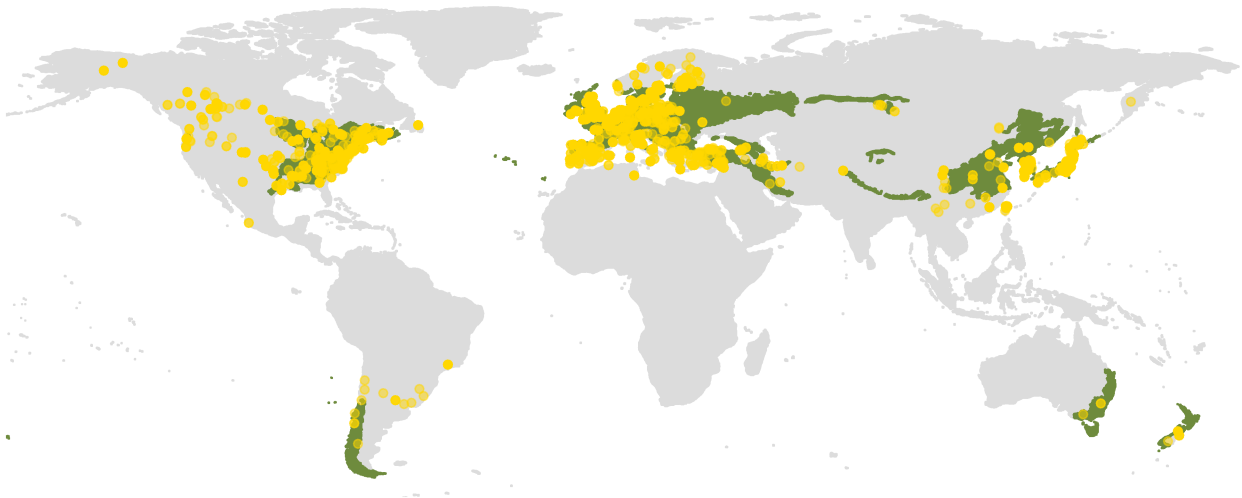


Figure 1: Geographical distribution of the germination records in the database. Each golden circle is a record. The green areas correspond to the extension of the Temperate Broadleaf and Mixed Forests biome according to the WWF.

Database file

The database is provided as a *csv* file, comma separated (**Appendix S5**). The first row of the file contains the header data, with the following variables: *Taxon* (the original species names, as used in the references),

TPLName (*The Plant List* species names), *Family* (the botanical family of the species), *Reference* (bibliographic source of the record), *Year* (year the seed lot was collected), *Country* (country where the seed lot was collected), *Population* (geographical information of the seed lot), *Latitude* (approximated latitude where the seed lot was collected, in decimal degrees), *Longitude* (approximated longitude where the seed lot was collected, in decimal degrees), *Dry_storage* (binary variable indicating whether the seed lot was kept at dry storage for more than a month between seed collection and start of the experiments), *Setting* (environs used to control germination temperature: either a greenhouse, a climatically-controlled incubator, or room temperature), *Sterilization* (note on surface sterilization treatments applied to the seed lot before the experiments), *Nutrients* (note on nutrient application to the germination substrate), *Substrate* (substrate used to hold the seeds during the germination incubation), *Container_type* (type of container used to hold the substrate and the seeds during the experiments), *Container_size* (dimensions of the germination containers), *Container_number* (number of germination containers used for the treatment), *Number_per_container* (number of seeds sown in each container), *Incubation_days* (number of days between the start of the experiment, not including stratification, and the last day when germinated seeds were counted), *Scarification* (binary variable indicating whether the seed lot was scarified before the test), *Stratification_days* (number of days the seed lot was exposed to any type of stratification, before the test), *Stratification_temperature* (temperature or temperatures used during the stratification treatment, in degrees Celsius), *Stratification_type* (type of stratification, which can be none, cold, warm or combinations of cold and warm), *Stratification* (binary variable indicating whether the seed lot was stratified or not before the test), *Light* (binary variable indicating whether the seed lot was germinated in light or in darkness), *Photoperiod* (number of hours of exposure to light in the daily photoperiod), *Alternating* (binary variable indicating whether the germination test was conducted under constant or alternating temperatures), *Tdif* (difference in degrees between the hottest and the coldest temperatures of the daily thermoperiod), *Tmax* (hottest temperature in the daily thermoperiod), *Tmin* (coldest temperature in the daily thermoperiod), *Tmean* (mean germination temperature, weighted by the length of each phase of the daily thermoperiod), *Temperature* (aggregation of the mean germination temperature in 5 °C intervals), *Germinated* (count of seeds that germinated during the experiment), *Number_seeds* (count of seeds used in the experiment). Each row below the header represents a record for a seed lot germinated in a given set of experimental conditions. Presenting the response variable as a proportion (i.e. number of successes *Germinated*, number of trials *Number_seeds*) has important benefits for meta-analysis of the database, as proportions can be analysed directly using a GLM, and a variance term does not need to be specified since it is incorporated as part of the analysis (Mengersen & Gurevitch 2013).

SylvanSeeds app

To facilitate the visualization of the database, the *SylvanSeeds* app was written using the *shiny* package (Chang et al. 2020). It is publicly accessible at <https://efernandezpascual.shinyapps.io/sylvanseeds/>. The app uses the *tidyverse* package (Wickham et al. 2019) to aggregate and show results for species and experimental treatments (i.e. aggregating all seed lots of the same species germinated in the same experimental conditions). To facilitate comparisons, germination temperatures are aggregated to 5 °C intervals. When there is only one seed lot per species and combination of experimental conditions, the binomial 95% confidence interval is calculated using the Wilson method in the *binom* package (Dorai-Raj 2014). When there is more than one seed lot per species and combination of experimental conditions, the aggregate proportion and binomial confidence intervals are calculated using binomial-normal meta-analysis models (Stijnen et al. 2010) as implemented in the package *metafor* (Viechtbauer 2010). By visiting the app, users can consult the available germination information for a species (**Fig. 2**), the origin of its seed lots, and the bibliographical references for the species.

Discussion

The database provided in this article, and the web app to visualize it, can have wide applicability in science and beyond. It can extend current trends in global analyses of plant traits at species (Díaz et al. 2016) and community levels (Bruehlheide et al. 2018) to seed germination. The ecological determinants of seed germination are also valuable information for species distribution models (Bykova et al. 2012). The visualization of the database with the *SylvanSeeds* app can help plant ecologists select experimental treatments that are adequate

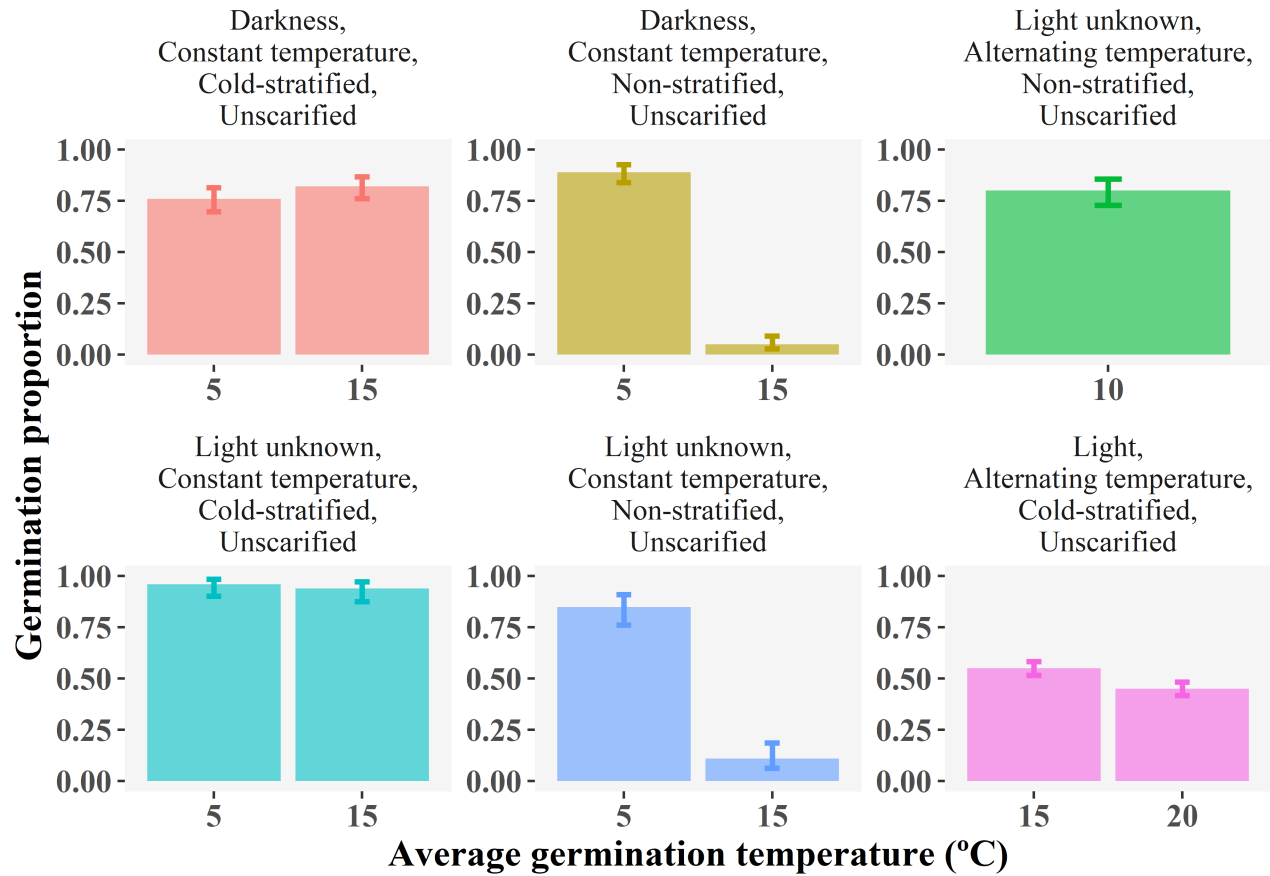


Figure 2: Example of the germination records as shown by the SylvanSeeds app. Records for one species, the European common beech, *Fagus sylvatica*. Each panel shows the results for a combination of experimental conditions, with the germination temperature varying within each panel. Bars represent the mean germination proportion and brackets the 95 per cent binomial confidence interval.

for their experiments (Baskin et al. 2006). Outside of academia, germination data are useful for seed industries (De Vitis et al. 2017), restoration practitioners (Ladouceur et al. 2018) and the implementation of regional schemes for seed-based landscape intervention (Jiménez-Alfaro et al. 2020). The app is accessible to citizens in general who are interested in germinating wild plants. Finally, apart from the database itself, this article can bring two innovations to the seed ecology community, helping to advance the agenda of functional seed ecology (Saatkamp et al. 2019). First, the meta-analysis-inspired methodology used to compile the database can be extended to other biomes and lists of species, contributing to the creation of a global database for ecologically and biogeographically coherent floras. Second, the database and the app can serve as a standard in further efforts to compile and standardize seed germination data. The version of the database presented here is a first building block that will be expanded by updating it with more records and integrating it with datasets from other biomes and regions. The website <https://efernandezpascual.github.io/home/sylvanseeds.html> will publish and describe updates. All people interested in contributing to the growth of this germination database are encouraged to contact the corresponding author.

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Supporting Information

Appendices S1-S4 PRISMA 2009 flow chart describing the process of reference screening and inclusion; bibliography in BibTeX format listing the not-found full texts, the non-relevant references and the relevant references included in the *SylvanSeeds* database. **Appendix S5** *SylvanSeeds* database in a single .csv file.

Data accessibility

All persons can use the database providing they cite this paper properly in any publications or in the metadata of any derived products that are produced using the database. The database is provided as **Appendix S5** of this manuscript, but please do visit <https://efernandezpascual.github.io/home/sylvanseeds.html> to check for updates. It can be visualized with the *SylvanSeeds* app at <https://efernandezpascual.shinyapps.io/sylvanseeds/>. The code to create this manuscript and the app is stored at <https://github.com/efernandezpascual/sylvanseeds>. A version of record of the repository can be found at <https://doi.org/10.5281/zenodo.4081377>.

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