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## SylvanSeeds, a seed germination database for temperate deciduous forests

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Author Contributions:

CUST\_AUTHOR\_CONTRIBUTIONS :No data available.

Author’s Data Availability Statement:

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 Supporting Information. It can be visualized with the \*SylvanSeeds\* app at <https://efernandezpascual.shinyapps.io/sylvanseeds/>. The code of the app is stored at (note: the GitHub repo is kept private until publication of the manuscript).

Author’s Conflict of Interest Statement:

CUST\_WILEY-NEW\_CONFLICT\_OF\_INTEREST-DETAILS :No data available.

# **SylvanSeeds, a seed germination database for temperate deciduous forests**

**Running title: SylvanSeeds, a forest germination database**

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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 article presents *SylvanSeeds*, a first global dataset 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 17,852 vegetation relevés from the sPlot database. The list was searched in the Web of Science. 6,791 references were screened, finding 614 articles from which data were extracted. *SylvanSeeds* includes 4,828 germination records of 364 species from 74 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. The shiny app *SylvanSeeds* (<https://efernandezpascual.shinyapps.io/sylvanseeds/>) 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

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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, seed dormancy, seed traits, temperate coniferous forests, 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 of 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 dataset of raw germination data for an ecologically and biogeographically coherent unit: the Temperate Broadleaf and Mixed Forests biome of the northern hemisphere (*TBMFNN*). Deciduous forests are dominant in temperate latitudes with mild to cold winters and relatively warm and wet summers. 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 *TBMFNN* areas, e.g. in the USA (Baskin 1995), 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 *TBMFNN*. 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

### *Species list*

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 *TBMFNN* biodiversity, they were chosen from 20 ecoregions distributed throughout the northern hemisphere: 17 ecoregions of the Temperate Broadleaf and Mixed Forests biome (*Appalachian mixed mesophytic forests*, *Atlantic mixed forests*, *Cantabrian mixed forests*,

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*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, Taiheiyo evergreen forests, Taiheiyo montane deciduous forests, Western European broadleaf forests, Western Great Lakes forests*), plus three neighbouring ecoregions of the Temperate Coniferous Forest biome (*Cascade Mountains leeward forests, Central and Southern Cascades forests, Eastern Cascades 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* version 3.6.2 (R Core Team 2019). The final vegetation database contained 17,852 relevés and 7,684 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 1,391 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 *TBMFNH*, 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 *TBMFNH*; 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.

## 109 **Web of Science literature search**

110 The list of frequent species (plus the synonyms recorded in the relevés) was  
111 incorporated into a Boolean search string, together with the words “(seed OR  
112 seeds) AND (dormancy OR germination)”. This string was searched in the  
113 *Thompson Reuters Web of Science* on 5 Mar 2019, returning 6,791 results. The  
114 processing of these results is described in a PRISMA flow diagram (**Supporting**  
115 **Information 1**). A first filter of the results by the relevance of the title retained  
116 1,489 references. An effort was made to access the full text of all these references,  
117 using the following channels: (i) “Find Full Text” functionality in *EndNote X9*, (ii)  
118 online access to the journals using the institutional subscriptions of the University  
119 of Oviedo; (iii) request to the authors through *ResearchGate*; (iv) general search of  
120 *pdf* files in *Google* using the article details. Unfortunately, 236 references could not  
121 be accessed. Most of these belonged to smaller publishers not included in the  
122 subscriptions of the University of Oviedo, and to older journal issues which had not  
123 been digitalised. The resources of this project did not make it possible to further  
124 pursue these references, but they are included as a *BibTeX* file (**Supporting**  
125 **Information 2**) in case they can be processed in the future. The found texts were  
126 accessed to retrieve data for the database. At this stage, references were  
127 considered to be non-relevant if they (i) did not pertain to species in the original  
128 frequent species list; (ii) did not study germination in species monocultures  
129 (e.g. competition studies); (iii) did not report the minimal information needed  
130 (number of seeds sown, germination percentage and germination temperature).  
131 Records were also excluded when they pertained to special germination  
132 treatments that do not allow for general comparisons (i.e. use of germination  
133 promoters such as the plant hormone gibberellic acid; drought treatments,  
134 including polyethylene glycol solutions; application of heavy metals or other  
135 pollutants; smoke-related germination promoters such as karrikins). Of the  
136 accessed references, 639 were non-relevant (*BibTeX* file in **Supporting**

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**Information 3)** and 614 provided relevant data (*BiBTeX* file in **Supporting Information 4**).

***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 4,828 records (germination proportions for a given seed lot of a species, recorded in a set of experimental conditions) from 614 references. The plant materials had been collected across the Temperate Broadleaf and Mixed Forest biome and surrounding areas (**Fig. 1**), in both hemispheres. The oldest record was from 1920 and the top three contributing



countries were the USA (1,357), the UK (591) and Japan (531). There were 364 species represented, from 74 seed plant families. The total estimate of seeds used in the experiments was 953,807. The range of germination temperatures (weighted average of the daily thermoperiod) went from -4 to 43 °C, with 2,107 records of constant temperatures and 2,721 of alternating temperatures. Light was used in 2,849 records, darkness in 1,227 and 752 did not provide information on this parameter. The experiments were performed with unstratified seeds in 3,227 records, and of the rest, the majority (1,421) went through cold stratification. Scarification was applied to 252 records.

### **Database file**

The database is provided as a csv file, comma separated, named **Supporting Information 5** (see online Supporting Information). 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),

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*Sown\_by\_container* (number of seeds sown in each container), *Incubation\_days* (number of days between the start of the experiment, not including stratification, and the 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), *Germinable* (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 *Germinable*) 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 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 dataset itself, this article can bring two innovations to the seed ecology community,

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helping to advance the agenda of functional seed ecology (Saatkamp et al. 2019). First, the meta-analysis-inspired methodology used to compile the dataset 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.

**Acknowledgements**

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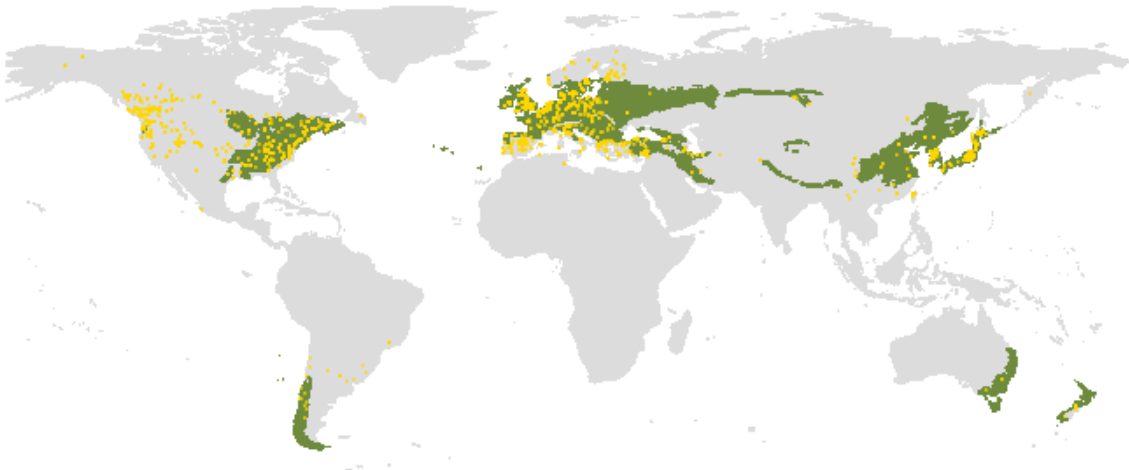
32 364 **Supporting Information**  
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35 365 **Supporting Information 1** PRISMA 2009 flow chart describing the process of  
36 366 reference screening and inclusion. **Supporting Information 2** BibTeX bibliography  
37 367 listing the not found full texts. **Supporting Information 3** BibTeX bibliography  
38 368 listing the non-relevant references. **Supporting Information 4** BibTeX bibliography  
39 369 listing relevant references included in the *SylvanSeeds* database. **Supporting**  
40 370 **Information 5** *SylvanSeeds* database in a single .csv file.  
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47 371 **Data accessibility**  
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50 372 All persons can use the database providing they cite this paper properly in any  
51 373 publications or in the metadata of any derived products that are produced using the  
52 374 database. The database is provided as Supporting Information. It can be visualized  
53 375 with the *SylvanSeeds* app at <https://efernandezpascual.shinyapps.io/sylvanseeds/>.  
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The code of the app is stored at (note: the GitHub repo is kept private until publication of the manuscript).

## Figures



*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.*

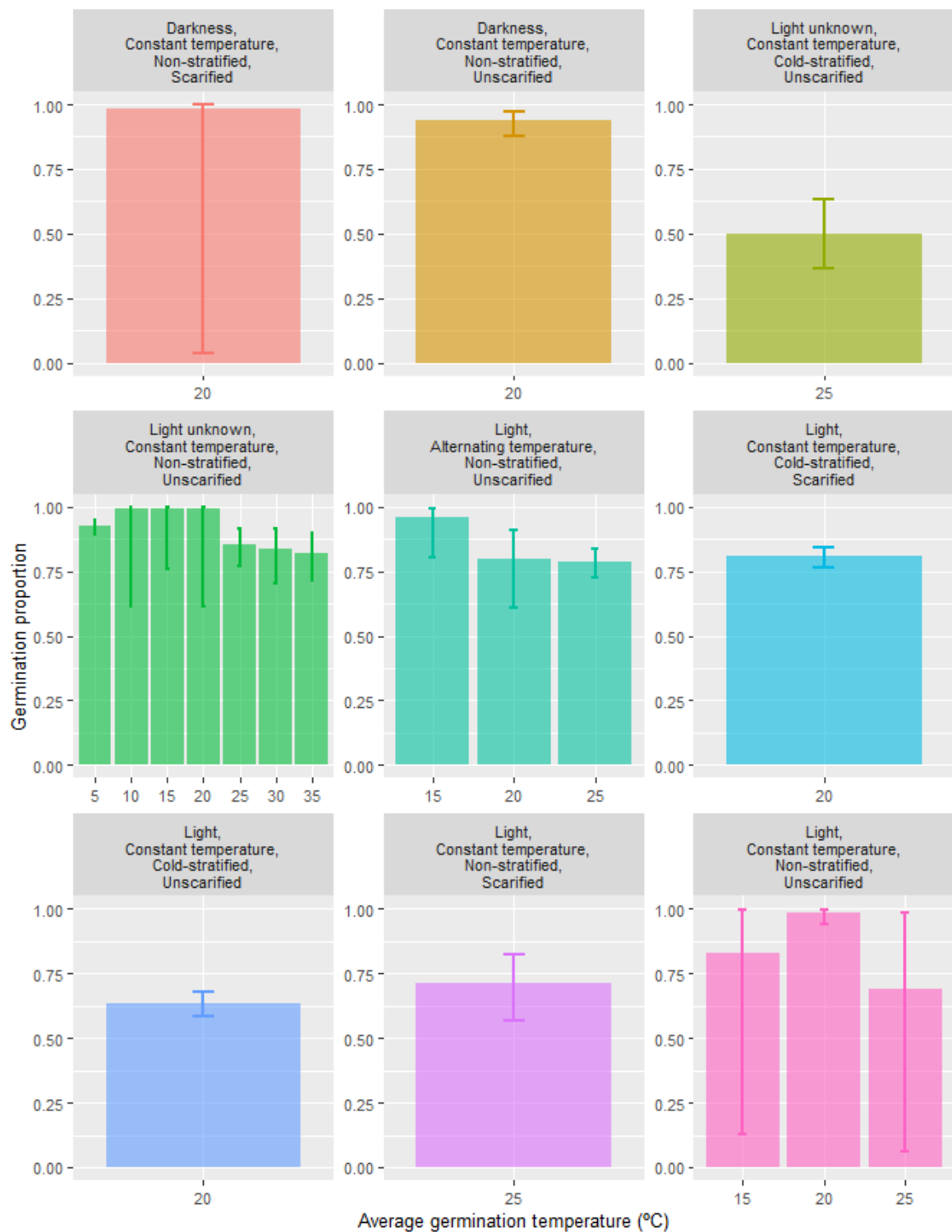


Figure 2: Example of the germination records as shown by the SylvanSeeds app. Records for one species, the European pedunculate oak, *Quercus robur*. Each

386 *panel shows the results for a combination of experimental conditions, with the*  
387 *germination temperature varying within each panel. Bars represent the mean*  
388 *germination proportion and brackets the 95% binomial confidence interval.*

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