Medina et al. Annals of Forest Science (2024) 81:50
https://doi.org/10.1186/s13595-024-01267-2

INRAE

Annals of Forest Science

DATA PAPER

Open Access

Ex situ germination of European acorns: data from 93 batches of 12 Quercus species

María Medina[1], Marino P. Reyes-Martín[1], Laura Levy[1], Alba Lázaro-González[1,2], Enrique Andivia[3], Peter Annighöfer[4], Farhah Assaad[4], Jürgen Bauhus[5], Raquel Benavides[6], Henrik Böhlenius[7], Vito E. Cambria[8], María D. Carbonero[9], Jorge Castro[1], Akaki Chalatashvili[10], Donato Chiatante[11], Claudia Cocozza[12], Sofia Corticeiro[13], Dagnija Lazdina[14], Giovanbattista De Dato[15], Michele De Sanctis[8], Jovana Devetaković[16], Lars Drossler[17], Lenka Ehrenbergerová[18], Peter Ferus[19], Lorena Gómez-Aparicio[20], Arndt Hampe[2], Kjersti H. Hanssen[21], Berthold Heinze[22], Marcin Jakubowski[23], María N. Jiménez[24], Branko Kanjevac[16], Jan J. Keizer[25], Ivona Kerkez-Janković[16], Marcin Klisz[26], Wojciech Kowalkowski[23], Klaus Kremer[5], Johan Kroon[27], Dario La Montagna[8], Jelena Lazarević[28], Emanuele Lingua[29], Manuel E. Lucas-Borja[30], Adrian Łukowski[23], Magnus Löf[7], Paula Maia[31], Paola Mairota[32], Alberto Maltoni[12], Barbara Mariotti[12], Antonín Martiník[18], Raffaella Marzano[33], Luis Matías[34], Ryan W. Mcclory[35], Manuel Merino[36], Lucia Mondanelli[1,12], Antonio Montagnoli[11], Maria C. Monteverdi[15], Ricardo Moreno-Llorca[36], Francisco B. Navarro[37], Marina Nonić[16], Luís Nunes[38,39], Juan A. Oliet[40], Maria S. Patrício[38,39], Zoran Poduška[41], Vladan Popovic[41], Radosław Puchałka[42], José M. Rey-Benayas[43], Piotr Robakowski[23], Piotr Sewerniak[44], Marek Szczerba[45], Carmen Ureña-Lara[3], Viktorija Vendina[14], Pedro Villar-Salvador[43], Johanna Witzell[27] and Alexandro B. Leverkus[1,36,43*]

Abstract

Key message We provide data on seedlot germination potential—a key trait related to regeneration—of 12 oak species. Germination was tested at the University of Granada following international protocols with 8985 acorns from 93 batches and 16 countries across Europe. Data on germination probability, acorn origin, mass, and moisture content measured on another 4544 acorns are available at https://doi.org/10.30827/Digibug.87318. Associated metadata are available at https://metadata-afs.nancy.inra.fr/geonetwork/srv/fre/catalog.search#/metadata/a742c6d8-bc37-4ca2-8b81-2447c5a8858d.

Keywords Acorn, Germination test, Seedlot germination potential, Seed mass, Seed moisture, Seed viability

Handling editor: Véronique Lesage and Irène Gabriel.

*Correspondence:
Alexandro B. Leverkus
leverkus@ugr.es
Full list of author information is available at the end of the article

1 Background

Quercus L. is one of the most extended tree genera in the Northern Hemisphere. Oaks dominate forests, savannas, and shrublands and are also present as secondary species in many ecosystems (Madrigal-Gonzalez et al. 2017). Oak-dominated forests are widespread in Eurasia and North America, and they support high biodiversity and provide important ecosystem services (Johnson et al. 2019). Additionally, oak forests, due to their high resilience to disturbance and environmental stress, offer a promising alternative for inclusion into management plans to address increasingly common extreme weather events (Harvey et al. 2020). In Europe, there are about 22 species of oaks, which include some widely distributed shrubs and trees that contribute to ecosystem structure, composition, and function (Campos et al. 2013) and ultimately to the provision of a plethora of ecosystem services. The success of natural and assisted regeneration of oaks hinges upon the probability of transition among plant life stages (Pulido and Díaz 2005), including the germination of acorns. The germination in oak species is influenced by environmental conditions, as acorns are highly susceptible to desiccation (Xia et al. 2012) and predation (Birkedal et al. 2009). Some studies, both under controlled and field conditions, indicate that germination varies among oak species (Reyes and Casal 2006; Urbieta et al. 2008) and depends on acorn characteristics such as size, morphology, and composition. Many field studies provide data on seedling emergence from seeded acorns (e.g., (Urbieta et al. 2008; Lázaro-González et al. 2023)), yet comparable data on germination potential under controlled conditions remain scarce and dispersed.

As part of a European-scale, collaborative experiment to assess the effectiveness of seeding and planting with European oaks (Leverkus et al. 2021), we conducted a germination test of 93 seed batches from 12 species from different sites across Europe. The acorn batches were sent from 16 countries across Europe to the University of Granada (Spain), where different acorn subsets were weighed or monitored for germination in growth chambers.

This publication aims to provide data that allows to:

1) Assess the germination success of different *Quercus* species from across Europe; and
2) Estimate the variability among populations within a given species in germination success, acorn size, and moisture content.

2 Methods

2.1 Acorn collection sites

We collected acorns at multiple European locations as part of a collaborative experiment on assisted regeneration. Initially, the members of the PEN-CAFoRR COST Action (http://www.pen-caforr.org/) were invited to collaborate, yet the invitation to participate was later extended to researchers from across Europe following the publication of a study protocol that established the conditions for participation (Leverkus et al. 2021). The protocol describes an experiment in which participants would establish a field site near their home institution to monitor the success of revegetation with one or more local oak species. Whereas that experiment is not the target of the present dataset, its protocol established that the collection of acorns would be made "as close as possible" to the field site. The 93 acorn batches resulting from this procedure were collected at 76 sites in 16 countries (Fig. 1). They belonged to 12 native or naturalized oak species (Table 1). Hereafter, we refer to the collaborators who joined the study by collecting and sending acorn batches as "participants" and to the members of the group at the University of Granada who conducted the germination tests as the "coordinating team."

2.2 Acorn collection procedure

The protocol for acorn collection required participants to identify a source population of native or naturalized, locally growing oak species. A minimum of 500 mature, healthy-looking acorns were collected from the branches preferably, including a similar number of acorns from each of at least 10 mother trees to avoid overrepresentation of individual trees in the acorn batch. Local acorn collection was not possible at some sites due to low amounts or absence of acorn crops; in these cases, the geographical origin of the acorn batch is indicated in the database. Most acorn batches were collected in 2021 and a few only in 2022. In some cases, they were collected over these two consecutive years, resulting in two batches from the same location and species but different years. The collected acorns were stored and subjected to a selection procedure (see below).

2.3 Acorn selection

The first selection was made in the field, where the acorns were inspected for signs of injury. Only mature and healthy-looking acorns (i.e., without signs of insect or fungal damage) were collected. The second selection was through the flotation method (Gribko and Jones 1995), where the collected acorns are immersed in water and the floating acorns are sorted out, as these usually contain insect larvae feeding on the cotyledons or have dried out in the field. This produced the ultimate seed batches, from which a random subset of 150 acorns was sent to the University of Granada. In some cases (5/93 batches), fewer acorns were sent due to the inability to obtain more healthy acorns.

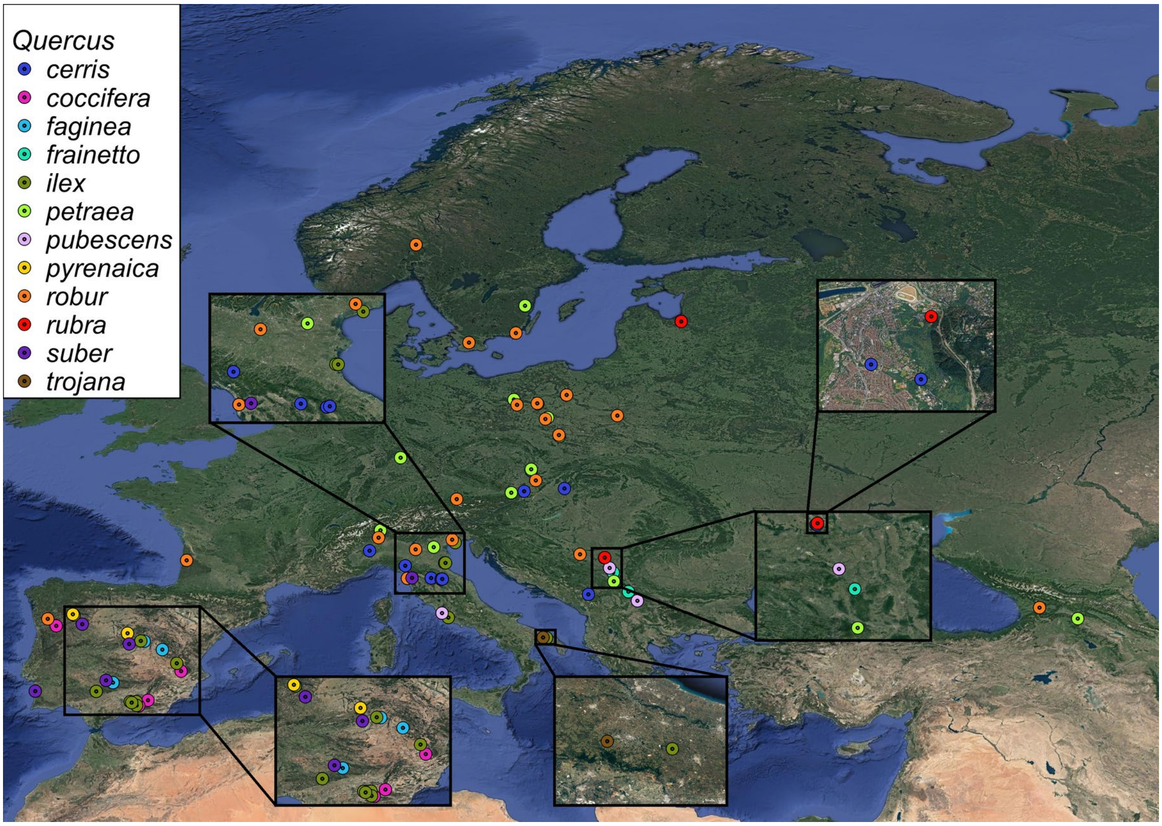

Fig. 1 Map with the sites of collection of the acorn batches and the species identified by colors. The coordinates and further characteristics are identified in the database (Map data ©2024 Google)

Table 1 Number of batches analyzed for germination in the dataset per species

Species	Batches	Countries
Q. cerris L	15	Austria, Czech Republic, Italy, Montenegro, Serbia, Slovakia
Q. coccifera L	6	Portugal, Spain
Q. faginea Lam	6	Spain
Q. frainetto Ten	2	Serbia
Q. ilex L	15	Italy, Portugal, Spain
Q. petraea (Matt.) Liebl	14	Austria, Bulgaria, Czech Republic, Georgia, Germany, Italy, Poland, Serbia, Sweden
Q. pubescens Willd	3	Italy, Serbia
Q. pyrenaica Willd	3	Portugal, Spain
Q. robur L	21	Czech Republic, Georgia, Germany, Italy, Latvia, Norway, Poland, Portugal, Serbia, Sweden
Q. rubra L	2	Latvia, Serbia
Q. suber L	5	Italy, Portugal, Spain
Q. trojana Webb	1	Italy

2.4 Acorn storage and shipping

Upon collection, the selected acorns were left to dry for 24 h at laboratory temperature. Then, they were stored in zip polyethylene plastic bags with a thickness of 50 μm and refrigerated between 1 and 4 °C. The bags were provided to all participants by the coordinating team. Acorns were inspected periodically during storage for early detection of possible rottenness, in which case affected acorns were discarded. If any acorn germinated, it was kept for the field or nursery, but not for shipment.

The bags were stored open and not stacked to facilitate gas exchange. As soon as possible, the acorn bags were posted to the University of Granada by express courier service. They were posted inside the aforementioned polyethylene zip bags and cushioned to avoid mechanical damage.

2.5 Acorn weighing

Upon reception at the University of Granada, the batches consisting of 150 acorns were visually inspected and refrigerated until the start of the germination testing. From each batch, 50 acorns were used to measure fresh and dry acorn weight. If fewer acorns had been sent, the germination test was prioritized. Before measuring fresh weight, the acorns were soaked in water for 24 h, externally dried with a paper towel, and weighed to obtain the fresh mass of the whole set of 50 acorns. Then, they were dried for a minimum of 3 days in a stove at 65 °C until constant weight, after which their dry weight was assessed. This allowed us to obtain, for each acorn batch, (a) the mean acorn fresh weight, (b) the mean acorn dry weight, (c) the standard deviation of acorn dry weight, and (d) the mean acorn moisture content.

2.6 Germination test

From each batch, 100 acorns were used for the germination test, for which we followed the recommendations from the International Seed Testing Association (ISTA 2010). First, the acorns were soaked in water for 48 h. Then, we covered trays (of 23.5×30×4 cm) in silica sand with an approximate depth of 2–3 cm and placed 50 acorns per sub-batch in each tray, with about 2/3 of each acorn buried sideways in the sand. The trays (hereafter referred to as sub-batches) were then placed in growth chambers at a constant temperature of 20 °C and monitored for 8 weeks (twice as long as recommended by the above-cited ISTA protocol). The sub-batches were randomly allocated to one of five growth chambers, yet the two sub-batches from each batch were always placed in different chambers. The specifications of the chambers are:

(1) Ing. Climas, model "GROW 600/HR," Barcelona (Spain)—two chambers (identified in the database as "SA" and "SB");
(2) Liebherr, model "FKS 5000" (adapted for heat), Bulle (Switzerland)—two chambers (identified as "M10" and "M11");
(3) Hedera helix, model "FN-70P-L-NI," Bizkaia (Spain)—one chamber (identified as "T").

The trays with sand and the acorns were initially soaked in water and thereafter irrigated with 250 mL of water three times per week. Every week, we registered the number of newly germinated acorns for each sub-batch and marked the corresponding acorns to avoid double-counting. An acorn was considered germinated when the radicle had emerged. If necessary, the acorns were manually rotated to check if they had germinated. Although acorns were posted prior to germination, some germinated during shipping. This was accounted for in 40 of the sub-batches (7 of which had germinated acorns, indicated in "week 0"), and in the other sub-batches, they are included in week 1.

3 Access to the data and metadata description

The database is organized at the sub-batch level. It consists of 186 rows, with two rows per acorn batch. The columns with data specific to each row, and therefore to the sub-batch, are as follows: Sub_batch_ID, Observations, Date_start, Chamber_id, and the germination data (Week_0 – W8, Total_germinated, Total_N_tested, Germination_percentage). The last 7 columns (N_weighed, Fresh_weight_g, Dry_weight_g, Mean_fresh_weight, Mean_dry_weight, SD_dry_weight, Moisture_content) are the data for the weighed acorns (i.e., a different subset from the batch than the one used for germination), so the information can only be found in the first row of each batch to avoid the repetition of data. All the remaining columns contain data collected at the level of the entire acorn batch and this information can be found in both rows, even if it is the same data, to facilitate analysis. This allows one to group numerical values based on different characteristics, such as the country of the acorns or the species.

"Sub_batch_id" and "Batch_id" identify each sub-batch and each batch, respectively. The subsequent 12 columns contain information about the batch, namely, the year of acorn collection ("Year"; either *2021* or *2022*), the code of the site from which they were sent ("Site_id"; identified with a number), the specific epithet of the species involved ("Species"; genus is *Quercus* in all cases), the subspecies if applicable ("Subspecies"), the country where the acorns were collected ("Country"), how the acorns were obtained ("Origin"; *Collected* if they were collected personally by a participant following the protocol, or *Obtained* if they were purchased or obtained from third parties), the location of the population from which the acorns were obtained ("Collection_location"), and the coordinates of acorn collection ("Coordinate_long" and "Coordinate_lat"). In cases where the acorns were obtained from third parties (29 batches), extra information includes the reason for non-collection by the participant ("Reason_non_collection") and the supplier of the acorns ("Supplier"). The name of the participant responsible for obtaining and posting each acorn batch is indicated in "Contact_person" and any deviation from protocol or relevant comment to the batch or sub-batch in "Observations.

The dates include that of acorn collection ("Date_collected"), shipping ("Date_shipment"), reception at the University of Granada ("Date_received"), and the beginning of the germination test ("Date_start").

The next columns are specific to the germination test, namely: the identification of the chamber where the test was performed ("Chamber_id"; *SA* and *SB* for Ing. Climas growth chambers, *M10* and *M11* for Liebherr growth chambers, and *T* for the Hedera helix growth chamber, respectively), 9 columns indicating the number of acorns that germinated in a given week ("Week_0" to "W8," where "Week_0" stands for those acorns germinated before starting the germination test, although this is not available for all the sub-batches), the cumulative number of acorns germinated after 8 weeks ("Total_germinated"), the number of acorns tested ("Total_N_tested"), and the percentage of germination ("Germination_percentage," which is calculated with the previous two columns).

Finally, the weight data is only found in the first row of each batch. This includes the number of acorns weighed ("N_weighed"), the fresh weight of those acorns in g ("Fresh_weight_g"), the dry weight of the acorns in g ("Dry_weight_g"), the acorn-level mean fresh weight ("Mean_fresh_weight"), the acorn-level mean dry weight ("Mean_dry_weight"), and the standard deviation of the dry weight ("SD_dry_weight"). In addition, we calculated moisture content in "Moisture_content" according to Bonner (1981) as $(("Mean\_fresh\_weight" - "Mean\_dry\_weight")/"Mean\_dry\_weight") \times 100$.

The database is available in csv format at Digibug digital repository (Sampere-Medina et al, 2024): https://doi.org/10.30827/Digibug.87318. The associated metadata is available at https://metadataafs.nancy.inra.fr/geonetwork/srv/fre/catalog.search#/metadata/a742c6d8-bc37-4ca2-8b81-2447c5a8858d.

4 Technical validation

As described before, we tested the germination potential of each acorn batch in two sub-batches, which were placed in different growth chambers to avoid potential bias related to the choice of the chamber. When using the germination data, the chamber ID can be used to account

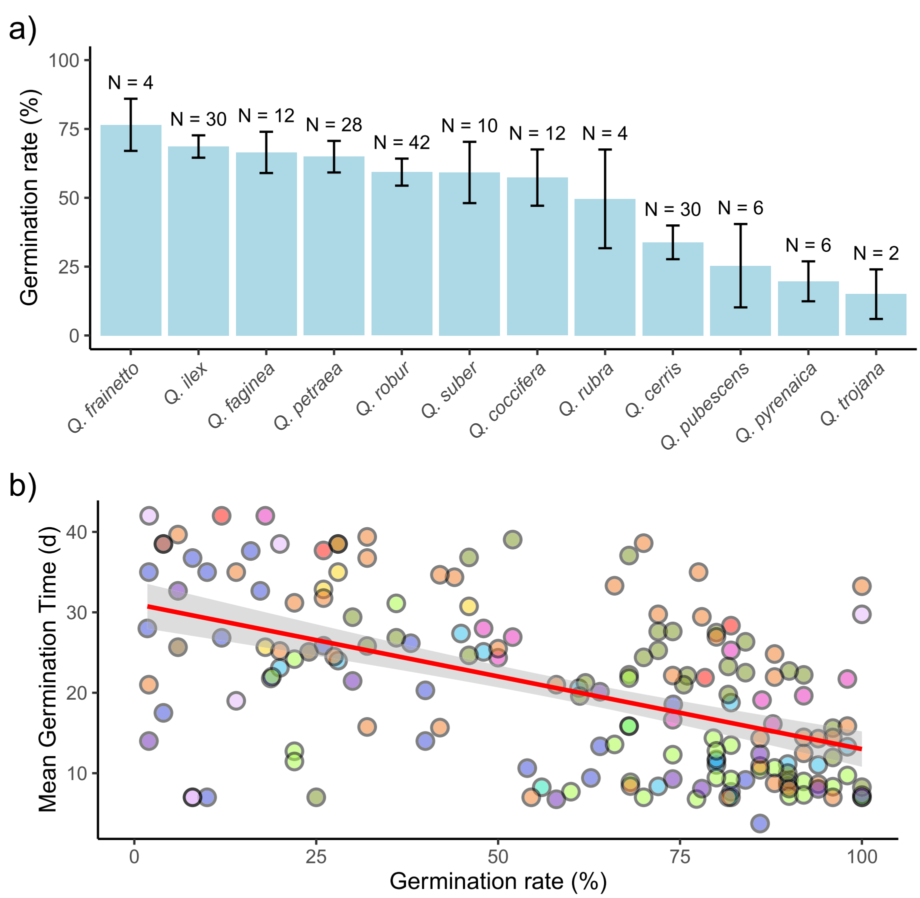

Fig. 2 **a** Germination rate (%) of the different oak species. The "N" corresponds to the number of sub-batches analyzed. **b** Correlation between mean germination time in days and the germination rate (%). The colors of the points indicate the different species, and they correspond with the colors of the map in Fig. 1. Each point is the data from one sub-batch

for potential effects of the chamber. Furthermore, within each chamber, we systematically rotated the sub-batches every week, bringing each tray one level down and the trays from the bottom to the top of the chamber (there were 3–5 levels in each chamber) to avoid potential bias related to the position of the tray within the chamber.

5 Reuse potential and limits

This database can be freely downloaded and used for any purpose, citing its source.

The database focuses on the ex situ germination success of *Quercus* spp., comprising data from 93 batches of acorns sourced across Europe. Germination—the transition from seed to seedling—constitutes a key demographic transition in the process of regeneration and reproduction (Reyes and Casal 2006). The original purpose of the database was to compare the results of seeding in the field with the intrinsic germination capacity of acorns from the same batches and, therefore, to assess the limitation on germination imposed by environmental factors in an ongoing experiment (Leverkus et al. 2021). However, this database may also prove valuable for other studies, for instance to analyze the differences in germination potential between species (Fig. 2a) or populations and the effects of acorn weight and moisture content on germination probability. It is also possible to calculate new variables from the data, such as the mean germination time (Fig. 2b), which is calculated as $\sum$(germination day x number of seeds germinated on that day)/total seeds germinated (Bewley et al. 2013). Additionally, for direct-seeding operations in the field or sowing in the nursery, data on germination potential may help estimate the quantity of acorns required to obtain a certain number of seedlings. The dataset may also aid in identifying acorn origin populations with higher germination potential, thereby supporting efforts to optimize seedling production in nurseries or other controlled settings. Also, it can help to develop predictive models for seedling production, based on correlations between germination success and seed traits such as weight and moisture content. The dataset may additionally be used in future meta-analyses (e.g., Maleki et al. 2024) or integrated in plant trait databases such as TRY (Kattge et al. 2020), thereby leveraging its reuse potential in future studies in biogeography, evolutionary ecology, community ecology, applied ecology, and functional ecology (Jiménez-Alfaro et al. 2016; Saatkamp et al. 2019).

One limitation of our dataset is that some of the seed batches were obtained from different suppliers due to the lack of local acorns in the years of the study, and we therefore lack some information about seed collection methods. Such situations are specified in the database, including the location of collection by the suppliers. Furthermore, one of the germination chambers had a technical failure at a given point and all the acorns that were inside were lost (11 sub-batches in total); for those acorn batches, we used replacement acorns, which were fortunately available in all cases, albeit in some batches only at small numbers. The number of acorns from which we estimated acorn weight and germination is always indicated in the database. Additionally, due to the need to post the acorn batches to conduct the germination tests under the same controlled conditions, the time spans between collection and the beginning of the test varied among batches. On average, the time between the acorn collection and the start of the germination test in Granada was 65.13 (± 38.57) days. To be able to account for such variability, we provide the dates of collection, shipment, reception, and the beginning of the germination tests. Despite these drawbacks, all the germination tests were carried out in the same place under the same conditions and the identified sources of variability are indicated in the database.

Acknowledgements

The authors thank Adela González Mejías for lending us laboratory equipment, and Cristina Rus, Pedro Solera-Álvarez, Ángel Gutiérrez-López, Marina Moreno-Molina, and Natalia Celaya-Rojas for their assistance in the germination tests. Paola Mairota acknowledges the collaboration of the Reparto Carabinieri Biodiversità Martina Franca (TA, Italy) in the persons of the Lieutenant colonel Giovanni Notarnicola, the Appuntato scelto Giuseppe Geronimo, and the civil servants Alessia Perrini, Doriana Ferri, and Luca Moschetti. Paula Maia and Sofia Corticeiro thank the financial support of the ERA Chair BESIDE project financed by the European Union's H2020 under grant agreement No 951389, DOI10.3030/951389 and Centre for Environmental and MarineStudies (CESAM) by FCT/MCTES (UIDP/50017/2020+UIDB/50017/2020+ LA/P/0094/2020), through national funds. Farhah Assaad thanks Andreas Ludwig at the Bayerische Staatsforsten (Germany) for sourcing acorns. Johan Kroon thanks Skogforsk, The Forestry Research Institute of Sweden.

Code availability

Not applicable.

Authors' contributions

MM created the database, coordinated with co-authors, and wrote the first draft. MPRM, LL, and ALG: collected local acorns, organized shipments, and carried out the germination tests. ABL designed the study, published the protocol, coordinated the project, and supervised the writing. All other co-authors (EA, PA, FA, JB, RB, HB, VEC, MDC, JC, AC, DC, CC, SC, DL, GDD, MDS, JD, LD, LE, PF, LGA, AH, KHH, BH, MJ, MNJ, BK, JJK, IKJ, MK, WK, KK, JK, DLM, JL, EL, MEL, AL, ML, PM, PM, AM, BM, AM, RM, LM, RWM, MM, LM, AM, MCM, RAM, FBN, MN, LN, JAO, MSP, ZP, VP, RP, JMRB, PR, PS, MS, CUL, VV, PVS, JW) collected and shipped acorns according to protocol, submitted data, and reviewed and approved the final manuscript.

Funding

This research was funded by grant TRANS-ECO (TED2021-130976B-100) from Ministry of Science and Innovation/NextGeneration, grant RESISTRES (C-EXP-267-UGR23) from University of Granada/Junta de Andalucía/FEDER, and grant RESTAURABIEN (RTI2018-096187-J-100) from the Spanish Ministry of Science, Innovation and Universities/FEDER, the PEN-CAFoRR (Pan-European Network for Climate Adaptive Forest Restoration and Reforestation) COST Action (European Cooperation in Science and Technology), and local funders for the fieldwork of each co-author.

Data availability

The dataset is available as open data via the University of Granada online data repository "Digibug": https://doi.org/10.30827/Digibug.87318.

Declarations

Ethics approval and consent to participate
The permits for acorn collection were obtained locally by participants where relevant. The shipments of acorns as biological material from outside the European Union were carried out with the corresponding customs procedures and seed import permits.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

Author details
[1]Department of Ecology, University of Granada, Granada 18071, Spain. [2]BIOGECO, INRAE, University of Bordeaux, Cestas 33610, France. [3]Department of Biodiversity, Ecology and Evolution, Faculty of Biological Sciences, Universidad Complutense de Madrid, Jose Antonio Novais 12, 28040 Madrid, Spain. [4]School of Life Sciences, Technical University of Munich, 85354 Freising, Germany. [5]Chair of Silviculture, Institute of Forest Sciences, University of Freiburg, Tennenbacherstraße, 79106 Freiburg, Germany. [6]Centro Para La Biodiversidad y Desarrollo Sostenible, Universidad Politécnica de Madrid (CBDS-UPM), C/José Antonio Novais 10, 28040 Madrid, Spain. [7]Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre, Sundsvägen, Sweden. [8]Department of Environmental Biology, Botanic Garden of Rome, Sapienza University for Rome, Piazzale Aldo Moro 5, 000185 Rome, Italy. [9]Andalusian Institute of Agrarian Fishing Food Investigation and Ecological Production Hinojosa del Duque Center, Hinojosa del Duque Center, Road El Viso Km 2, 14270 Hinojosa del Duque, Córdoba, Spain. [10]WWF Caucasus, 11 Merab Aleksidze Street, 0193 Tbilisi, Georgia. [11]Department of Biotechnology and Life Science, University of Insubria, Via Dunant, 3 - 21100 Varese, Italy. [12]Department of Agriculture, Food, Environment and Forestry (DAGRI), University of Florence, Via San Bonaventura 13, 50145 Florence, Italy. [13]Department of Environment and Planning and Centre for Environmental and Marine Studies, Universidade de Aveiro, Campus Universitario de Santiago, 3810-193 Aveiro, Portugal. [14]Latvian State Forest Research Institute Silava, Riga Street 111, Salaspils, Latvia. [15]CREA Research Centre for Forestry and Wood, Viale Santa Margherita 80, 52100 Arezzo, AR, Italy. [16]Faculty of Forestry, University of Belgrade, Kneza Višeslava 1, Belgrade, Serbia. [17]Ilia State University, Cholokhashvili Ave. 3/5, 0162 Tbilisi, Georgia. [18]Mendel University in Brno, Zemědělská 1, Brno 613 00, Czech Republic. [19]Department of Dendrobiology, Institute of Forest Ecology SAS, Vieska Nad Žitavou 178, Slepčany 95152, Slovakia. [20]Institute of Natural Resources and Agrobiology of Seville (IRNAS), CSIC, Avenida Reina Mercedes 10, 41012 Seville, Spain. [21]Norwegian Institute of Bioeconomy Research, P.O. Box 115, 1431 Ås, Norway. [22]BFW Austrian Research Centre for Forests, Seckendorff-Gudent Weg 8, 1130 Vienna, Austria. [23]Faculty of Forestry and Wood Technology, Poznań University of Life Sciences, Wojska Polskiego, Poznań, Poland. [24]Department of Botany, University of Granada, 18071 Granada, Spain. [25]Department of Environment and Planning, and GeoBioTec, University of Aveiro, Campus Universitário de Santiago, 3810-193 Aveiro, Portugal. [26]Department of Silviculture and Forest Tree Genetics, Forest Research Institute, Braci Lesnej 3, Sękocin Stary, 05-090 Raszyn, Poland. [27]Department of Forestry and Wood Technology, Linnaeus University, Georg Luckligs Väg 1, 35195 Växjö, Sweden. [28]Biotechnical Faculty, University of Montenegro, Mihaila Lalica 15, Podgorica, Montenegro. [29]Dept. TESAF, University of Padova, Viale Dell'Università, 16 I-35020 Legnaro, PD, Italy. [30]Castilla La Mancha University, Campus Universitario S/N, 02071 Albacete, Spain. [31]Department of Biology and Centre for Environmental and Marine Studies, Universidade de Aveiro, Campus Universitário de Santiago, 3810-193 Aveiro, Portugal. [32]Dipartimento Di Scienzedel, Della Pianta E Degli Alimenti - Di.S.S.P.A, Università Degli Studi Di Bari Aldo Moro, Via Amendola 165/A, 70126 Bari, Italy. [33]Department of Agricultural, Forest and Food Sciences (DISAFA), University of Torino, Largo Braccini 2, IT, 10095 Grugliasco, TO, Italy. [34]Facultad de Biología, Universidad de Sevilla, Av. Reina Mercedes SN, Seville, Spain. [35]School of Agriculture, Policy and Development, University of Reading, Whiteknights, PO Box 237, Reading RG6 6EU Reading, UK. [36]Laboratory of Ecology (iEcolab), Inter-University Institute for Earth System Research in Andalusia (IISTA), Granada, Spain. [37]Andalusian Institute of Agricultural Research and Training (IFAPA), Camino de Purchil S/N, 18004 Granada, Spain. [38]CIMO, LA SusTEC, Instituto Politécnico de Bragança, Campus de Santa Apolónia, 5300-253 Bragança, Portugal. [39]Laboratório Associado Para a Sustentabilidade E Tecnologia Em Regiões de Montanha (SusTEC), Instituto Politécnico de Bragança, Campus de Santa Apolónia, 5300-253 Bragança, Portugal. [40]Universidad Politécnica de Madrid, ETS Ingeniería de Monte, Forestal y del Medio Natural. José Antonio Novais 10, 28040 Madrid, Spain. [41]Institute of Forestry, Kneza Višeslava 3, Belgrade, Serbia. [42]Department of Ecology and Biogeography, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100 Toruń, Poland. [43]Forest Ecology and Restoration Group, Departamento de Ciencias de La Vida, Universidad de Alcalá, 28805 Alcalá de Henares, Madrid, Spain. [44]Department of Soil Science and Landscape Ecology, Nicolaus Copernicus University in Toruń, Lwowska 1, 87-100 Toruń, Poland. [45]Regionalna Dyrekcja Lasów Państwowych W Szczecinie Wydział Użytkowania Lasu, Ul. Juliusza Słowackiego 2, 71-434 Szczecin, Poland.

Received: 30 January 2024 Accepted: 4 November 2024
Published: 19 December 2024

References

Bewley JD, Bradford KJ, Hilhorst HWM, Nonogaki H (2013) Seeds: physiology of development, germination and dormancy. Springer, New York

Birkedal M, Fischer A, Karlsson M, Löf M, Madsen P (2009) Rodent impact on establishment of direct-seeded *Fagus sylvatica*, *Quercus robur* and *Quercus petraea* on forest land. Scand J for Res 24:298–307. https://doi.org/10.1080/02827580903055125

Bonner FT (1981) Measurement and management of tree seed moisture. US Dep Agric For Serv Res Pap 50–177, 10 p. South For Exp Stn New Orleans, La

Campos P, Huntsinger L, Oviedo JL, Starrs PF, Díaz M, Standiford RB, Montero G (2013) Mediterranean oak woodland working landscapes. Springer, New York

Gribko LS, Jones WE (1995) Test of the float method of assessing northern red oak acorn condition. Tree Planters' Notes 46:143–147

Harvey JE, Smiljanić M, Scharnweber T, Buras A, Cedro A, Cruz-García R, Drobyshev I, Janecka K, Jansons Ā, Kaczka R, Klisz M, Läänelaid A, Matisons R, Muffler L, Sohar K, Spyt B, Stolz J, van der Maaten E, van der Maaten-Theunissen M, Vitas A, Weigel R, Kreyling J, Wilmking M (2020) Tree growth influenced by warming winter climate and summer moisture availability in northern temperate forests. Glob Change Biol 26:2505–2518. https://doi.org/10.1111/gcb.14966

International Seed Testing Association (ISTA) (2010) International Seed Testing Association Rules Proposals for the International Rules for Seed Testing 2011 Edition. Bassersdorf, Switzerland

Jiménez-Alfaro B, Silveira FA, Fidelis A, Poschlod P, Commander LE (2016) Seed germination traits can contribute better to plant community ecology. J Veg Sci 27:637–645. https://doi.org/10.1111/jvs.12375

Johnson PS, Shifley SR, Rogers R, Dey DC, Kabrick JM (2019) The ecology and silviculture of oaks. CABI, UK

Kattge J et al (2020) TRY plant trait database – enhanced coverage and open access. Glob Chang Biol 26:119–188. https://doi.org/10.1111/gcb.14904

Lázaro-González A, Tamulaitytė G, Castro J, Uscola M, Leverkus AB (2023) Seedling establishment in a deciduous and an evergreen oak under simulated climate change. For Ecol Manage 550:378–1127. https://doi.org/10.1016/j.foreco.2023.121498

Leverkus AB, Levy L, Andivia E, Annighöfer P, De Cuyper B, Ivetic V, Lazdina D, Löf M, Villar-Salvador P (2021) Restoring oak forests through direct seeding or planting: Protocol for a continental-scale experiment. PLoS ONE 16(16):e0259552. https://doi.org/10.1371/journal.pone.0259552

Madrigal-Gonzalez J, Ruiz-Benito P, Ratcliffe Sophia and Rigling A, Wirth C, Zimmermann NE, Zweifel R, Zavala MA (2017) Competition drives oak species distribution and functioning in Europe: implications under global change. In: Gil-Pelegrín E, Peguero-Pina JJ, Sancho-Knapik D (eds) Oaks Physiological Ecology. Exploring the functional diversity of genus *Quercus* L. Springer International Publishing, Gewerbestrasse 11, Cham, CH-6330, Switzerland, pp 513–538. doi.org/https://doi.org/10.1007/978-3-319-69099-5

Maleki K, Soltani E, Seal CE, Colville L, Pritchard HW, Lamichhane JR (2024) The seed germination spectrum of 486 plant species: a global meta-regression and phylogenetic pattern in relation to temperature and water potential. Agric for Meteorol 346:109865. https://doi.org/10.1016/j.agrformet.2023.109865

Pulido FJ, Díaz M (2005) Regeneration of a Mediterranean oak: a whole-cycle approach. Ecoscience 12:92–102. https://doi.org/10.2980/i1195-6860-12-1-92.1

Reyes O, Casal M (2006) Seed germination of *Quercus robur*, *Q. pyrenaica* and *Q. ilex* and the effects of smoke, heat, ash and charcoal. Ann for Sci 63:205–212. https://doi.org/10.1051/forest:2005112

Saatkamp A, Cochrane A, Commander L, Guja LK, Jimenez-Alfaro B, Larson J, Nicotra A, Poschlod P, Silveira FAO, Cross AT, Dalziell EL, Dickie J, Erickson TE, Fidelis A, Fuchs A, Golos PJ, Hope M, Lewandrowski W, Merritt DJ, Miller BP, Miller RG, Offord CA, Ooi MKJ, Satyanti A, Sommerville KD, Tangney R, Tomlinson S, Turner S, Walck JL, Walck JL (2019) A research agenda for seed-trait functional ecology. New Phytol 221:1764–1775. https://doi.org/10.1111/nph.15502

Sampere-Medina M, Reyes M, Marino P, Levy L, Lázaro González A, Leverkus AB (2024) Germination of European acorns: Data from 93 batches of 12 Quercus species. [Dataset]. V1. Digibug. https://digibug.ugr.es/handle/10481/87318.Accessed 25 Jan 2024.

Urbieta IR, Pérez-Ramos IM, Zavala MA, Marañón T, Kobe RK (2008) Soil water content and emergence time control seedling establishment in three co-occurring Mediterranean oak species. Can J for Res 38:2382–2393. https://doi.org/10.1139/X08-089

Xia K, Daws MI, Hay FR, Chen WY, Zhou ZK, Pritchard HW (2012) A comparative study of desiccation responses of seeds of Asian Evergreen Oaks, *Quercus* subgenus *Cyclobalanopsis* and *Quercus* subgenus *Quercus*. S Afr J Bot 78:47–54. https://doi.org/10.1016/j.sajb.2011.05.001

Publisher's Note