

The GenTree Leaf Collection: Inter- and intraspecific leaf variation in seven forest tree species in Europe

Raquel Benavides¹  | Bárbara Carvalho¹  | Cristina C. Bastias^{1,2}  | David López-Quiroga¹ | Antonio Mas¹ | Stephen Cavers³ | Alan Gray³ | Audrey Albet⁴ | Ricardo Alía⁵ | Olivier Ambrosio⁶ | Filippos Aravanopoulos⁷ | Francisco Auñón⁵ | Camilla Avanzi⁸ | Evangelia V. Avramidou⁷  | Francesca Bagnoli⁸ | Eduardo Ballesteros⁵ | Evangelos Barbas⁷ | Catherine Bastien⁹ | Frédéric Bernier⁴ | Henry Bignalet⁴ | Damien Bouic⁴ | William Brunetto⁶ | Jurata Buchovska¹⁰ | Ana M. Cabanillas-Saldaña¹¹ | Nicolas Cheval⁴ | José M. Climent⁵ | Marianne Correard¹² | Eva Cremer¹³ | Darius Danusevičius¹⁰ | Benjamin Dauphin¹⁴  | Fernando Del Caño⁵ | Jean-Luc Denou⁴ | Bernard Dokhelar⁴ | Rémi Dourthe⁴ | Anna-Maria Farsakoglou⁷ | Andreas Fera¹⁵ | Patrick Fonti¹⁴  | Ioannis Ganopoulos^{7,16} | José M. García del Barrio⁵ | Olivier Gilg¹² | Santiago C. González-Martínez¹⁷ | René Graf¹⁴ | Delphine Grivet⁵ | Felix Gugerli¹⁴  | Christoph Hartleitner¹⁸ | Katrin Heer¹⁹ | Enja Hollenbach¹⁹ | Agathe Hurel¹⁷ | Bernard Issehuth⁴ | Florence Jean⁶ | Veronique Jorge⁹ | Arnaud Jouineau⁶ | Jan-Philipp Kappner¹⁹ | Katri Kärkkäinen²⁰ | Robert Kesälahti²¹ | Florian Knutzen¹³ | Sonja T. Kujala²⁰ | Timo Kumpula²¹ | Mariaceleste Labriola⁸ | Celine Lalanne¹⁷ | Johannes Lambertz¹⁹ | Martin Lascoux²² | Gregoire Le Provost¹⁷ | Mirko Liesebach²³  | Ermioni Malliarou⁷ | Jérémy Marchon¹⁴ | Nicolas Mariotte⁶ | Elisabet Martínez-Sancho¹⁴  | Silvia Matesanz²⁴  | Helge Meischner¹⁹ | Célia Michotey²⁵ | Pascal Milesi²² | Sandro Morganti¹⁴ | Tor Myking²⁶ | Anne E. Nilsen²⁶ | Eduardo Notivol²⁷  | Lars Opgenoorth^{14,19}  | Geir Østreg²⁶ | Birte Pakull²³ | Andrea Piotti⁸  | Christophe Plomion¹⁷ | Nicolas Poinot⁴ | Mehdi Pringarbe¹² | Luc Puzos⁴ | Tanja Pyhäjärvi²¹  | Annie Raffin⁴ | José A. Ramírez-Valiente⁵ | Christian Rellstab¹⁴  | Sebastian Richter¹⁹ | Juan J. Robledo-Arnuncio⁵ | Sergio San Segundo⁵ | Outi Savolainen²⁰ | Volker Schneck²⁸ | Silvio Schueler¹⁵  | Ivan Scotti⁶ | Vladimir Semerikov²⁹ | Jørn Henrik Sønstebo²⁶ | Ilaria Spanu⁸ | Jean Thevenet¹² | Mari Mette Tollefsrud²⁶ | Norbert Turion¹² | Giovanni Giuseppe Vendramin⁸ | Marc Villar⁹ | Johan Westin³⁰ | Bruno Fady⁶ | Fernando Valladares^{1,24}

¹LINCglobal, Department of Biogeography and Global Change, Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain

²UMR 5175 CEFE, Univ Montpellier, CNRS, EPHE, IRD, Univ Paul Valéry, Montpellier, France

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2020 The Authors. Global Ecology and Biogeography published by John Wiley & Sons Ltd

³UK Centre for Ecology and Hydrology, Penicuik, United Kingdom

⁴INRAE, UEFP, Cestas, France

⁵Department of Forest Ecology and Genetics, Forest Research Centre, Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, INIA-CIFOR, Madrid, Spain

⁶INRAE, URFM, Avignon, France

⁷Laboratory of Forest Genetics and Tree Breeding, School of Forestry and Natural Environment, Aristotle University of Thessaloniki, Thessaloniki, Greece

⁸Institute of Biosciences and BioResources, National Research Council (CNR), Sesto Fiorentino, Italy

⁹INRAE, ONF, BioForA, Orléans, France

¹⁰Vytautas Magnus University, Akademija, Lithuania

¹¹Departamento de Agricultura, Ganadería y Medio Ambiente, Gobierno de Aragón, Spain

¹²INRAE, UEFM, Avignon, France

¹³Bavarian Office for Forest Seeding and Planting – ASP, Teisendorf, Germany

¹⁴Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

¹⁵Department of Forest Growth and Silviculture, Austrian Research Centre for Forests BFW, Vienna, Austria

¹⁶Institute of Plant Breeding and Genetic Resources, Hellenic Agricultural Organization DEMETER (ex NAGREF), Themi, Greece

¹⁷INRAE, Univ. Bordeaux, BIOGECO, Cestas, France

¹⁸LIECO, Kalwang, Austria

¹⁹Department of Biology, Philipps-Universität Marburg, Marburg, Germany

²⁰Natural Resources Institute Finland, University of Oulu, Oulu, Finland

²¹University of Oulu, Oulu, Finland

²²Department of Ecology and Genetics, Evolutionary Biology Center, Science for Life Laboratory, Uppsala University, Uppsala, Sweden

²³Thünen Institute of Forest Genetics, Grosshansdorf, Germany

²⁴Área de Biodiversidad y Conservación, Universidad Rey Juan Carlos, Móstoles, Spain

²⁵INRAE, URGI, Route de Saint-Cyr, Versailles, France

²⁶Division of Forestry and Forest Resources, Norwegian Institute of Bioeconomy Research (NIBIO), Norway

²⁷Centro de Investigación y Tecnología Agroalimentaria de Aragón - Unidad de Recursos Forestales (CITA), Zaragoza, Spain

²⁸Thünen Institute of Forest Genetics, Waldsiedersdorf, Germany

²⁹Institute of Plant and Animal Ecology, Ural Branch of RAS, Ekaterinburg, Russia

³⁰Skogforsk, Sweden

Correspondence

Raquel Benavides, LINCGlobal, Department of Biogeography and Global Change, Museo Nacional de Ciencias Naturales, CSIC, C/ Serrano 115 dpdo, 28006, Madrid, Spain. Email: rbenavidescalvo@gmail.com

Funding information

Horizon 2020, Grant/Award Number: 676876, 4540-143AP, 6 and 0032; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - CAPES (Brazil)

Editor: Zhiheng Wang

Abstract

Motivation: Trait variation within species can reveal plastic and/or genetic responses to environmental gradients, and may indicate where local adaptation has occurred. Here, we present a dataset of rangewide variation in leaf traits from seven of the most ecologically and economically important tree species in Europe. Sample collection and trait assessment are embedded in the GenTree project (EU-Horizon 2020), which aims at characterizing the genetic and phenotypic variability of forest tree species to optimize the management and sustainable use of forest genetic resources. Our dataset captures substantial intra- and interspecific leaf phenotypic variability, and provides valuable information for studying the relationship between ecosystem functioning and trait variability of individuals, and the response and resilience of species to environmental changes.

Main types of variable contained: We chose morphological and chemical characters linked to trade-offs between acquisition and conservation of resources and water use, namely specific leaf area, leaf size, carbon and nitrogen content and their ratio, and the isotopic signature of stable isotope ¹³C and ¹⁵N in leaves.

Spatial location and grain: We surveyed between 18 and 22 populations per species, 141 in total, across Europe.

Time period: Leaf sampling took place between 2016 and 2017.

Major taxa and level of measurement: We sampled at least 25 individuals in each population, 3,569 trees in total, and measured traits in 35,755 leaves from seven European tree species, i.e. the conifers *Picea abies*, *Pinus pinaster* and *Pinus sylvestris*, and the broadleaves *Betula pendula*, *Fagus sylvatica*, *Populus nigra* and *Quercus petraea*.
Software format: The data files are in ASCII text, tab delimited, not compressed.

KEYWORDS

European forests, intraspecific variability, leaf economics spectrum, leaf functional traits, phenotypic variation, tree species

1 | INTRODUCTION

Leaves are the primary site for photosynthesis in terrestrial ecosystems, generating resources and underpinning ecosystem functions. Nitrogen uptake and carbon assimilation by plants are the basis of trophic interactions and, together with leaf decomposability, drive the terrestrial biogeochemical cycling. These essential roles imply the simultaneous performance of multiple functions, for example light interception, water and nutrient transport, gas exchange and heat dissipation, in addition to deploying defence mechanisms against herbivores and pathogens and physical damage. Trade-offs among these functions exist such that under different environmental pressures, shape, anatomy and chemical composition of leaves exhibit great diversity arising from phylogenetic and adaptive processes over evolutionary time (Ackerly & Reich, 1999; Nicotra et al., 2011). Wright et al. (2004) examined 2,548 plant species and found a comprehensive global pattern, suggesting that the trade-offs span a leaf economics spectrum (LES). This spectrum shows a strong relationship among leaf traits related to the growth potential versus construction costs, going from plants with low photosynthetic rates and slow return on investment of leaf dry matter and nutrients (long life span), to plants with high rates and a rapid return (short life span). The LES concept led to the adoption of leaf trait syndromes being widely used to define species strategies, as they describe how species manage resources (Garnier et al., 2016) from a whole-plant perspective (Poorter et al., 2014).

Traits are measured at the individual plant level and can thus reflect the individual resource use and plant–plant interactions beyond the species averages (McGill et al., 2006). It has been shown that 25% of the estimated trait variation in plant communities occurs at the intraspecific level (Siefert et al., 2015), highlighting the importance of this component of variation for ecosystem functioning (Crutsinger et al., 2006; Pérez-Ramos et al., 2019; Siefert et al., 2012) and warning us against neglecting it. In fact, datasets such as LEDA (Kleyer et al., 2008), TRY (Kattge et al., 2011) and BROT (Tavsanoglu & Pausas, 2018), amongst others, that compile functional traits from different species, biomes and traits incorporate data at the individual level. This variation arises from phenotypic plasticity, genetic diversity and their interaction, driven by adaptation to different local environments (Leimu & Fischer, 2008) and to environmental

gradients at different scales (Messier et al., 2010). Nevertheless, a large effort is required to quantify and collate trait variation within species, and accordingly it is frequently under-represented with data from a limited number of individuals per species.

Here, we present a dataset of inter- and intraspecific variation in leaf traits from seven ecologically and economically important tree species, evaluated from materials collected in populations across Europe. These data were collected as part of the European research project GenTree (<http://www.gentree-h2020.eu>), which aims to characterize phenotypes (see also Martínez-Sancho et al., 2020) and genetic variation in a set of European tree species. The final dataset will be of interest to study the relationships between ecosystem functioning and trait variability, to evaluate the relative extents to which genetic variation and plasticity contribute to intraspecific phenotypic variation, to assess the association between genetic and phenotypic variation, and ultimately to estimate the adaptive potential and resilience of species to environmental changes.

2 | METHODS

2.1 | Data source

We study leaf traits in seven European tree species in populations across their distributions. The species list comprised the conifers Norway spruce (*Picea abies* (L.) Karst), maritime pine (*Pinus pinaster* Aiton) and Scots pine (*Pinus sylvestris* L.), and the broadleaves silver birch (*Betula pendula* Roth), European beech (*Fagus sylvatica* L.), European black poplar (*Populus nigra* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.).

Between 18 and 22 populations per species (141 populations in total) were selected in pairs across Europe (Table 1, Supporting Information Table S1; Figure 1) to represent the range of environmental variation experienced by the species but excluding stands disturbed by intense or very recent natural or anthropogenic actions. Locally, population pairs were sampled along an environmental gradient (such as elevation, water availability or day length), but they were close enough to be connected by gene flow. A paired design offers increased statistical power to detect signatures of selection, whilst minimizing the confounding effect of population genetic

TABLE 1 Geographical and altitudinal ranges across sampled species, and sample sizes for leaf trait estimation. For each species, the table gives the number of study populations (Npop), surveyed trees (Ntrees), subsampled trees for chemical leaf trait assessment (Ntree_{ch}) and leaves measured to assess morphological leaf traits (Nleaf_{morp})

| Species | Latitudinal range (° N) | Longitudinal range (° E) | Elevational range (m a.s.l.) | Npop | Ntrees | Ntree _{ch} | Nleaf _{morp} |
|-------------------------|-------------------------|--------------------------|------------------------------|------|--------|---------------------|-----------------------|
| <i>Betula pendula</i> | 41.9689–66.3663 | –3.6645–29.2824 | 14.6–1,552.1 | 20 | 505 | 280 | 5,053 |
| <i>Fagus sylvatica</i> | 40.5484–59.3843 | –1.0280–23.7195 | 75.4–1,626.2 | 22 | 558 | 308 | 5,574 |
| <i>Populus nigra</i> | 40.1605–51.1556 | –4.4065–22.8203 | 5.2–764.9 | 18 | 471 | 279 | 4,709 |
| <i>Quercus petraea</i> | 38.1406–58.4150 | –3.0298–23.7577 | 10.0–1,619.9 | 20 | 500 | 280 | 4,999 |
| <i>Picea abies</i> | 41.4808–66.4354 | 6.4809–58.8777 | 81.8–2,029.1 | 20 | 499 | 272 | 5,060 |
| <i>Pinus pinaster</i> | 36.8246–44.9702 | –5.1238–11.3479 | 10.7–1,084.3 | 20 | 500 | 280 | 5,000 |
| <i>Pinus sylvestris</i> | 40.1907–66.4371 | –5.3659–29.3002 | 18.7–1,857.4 | 21 | 536 | 298 | 5,360 |

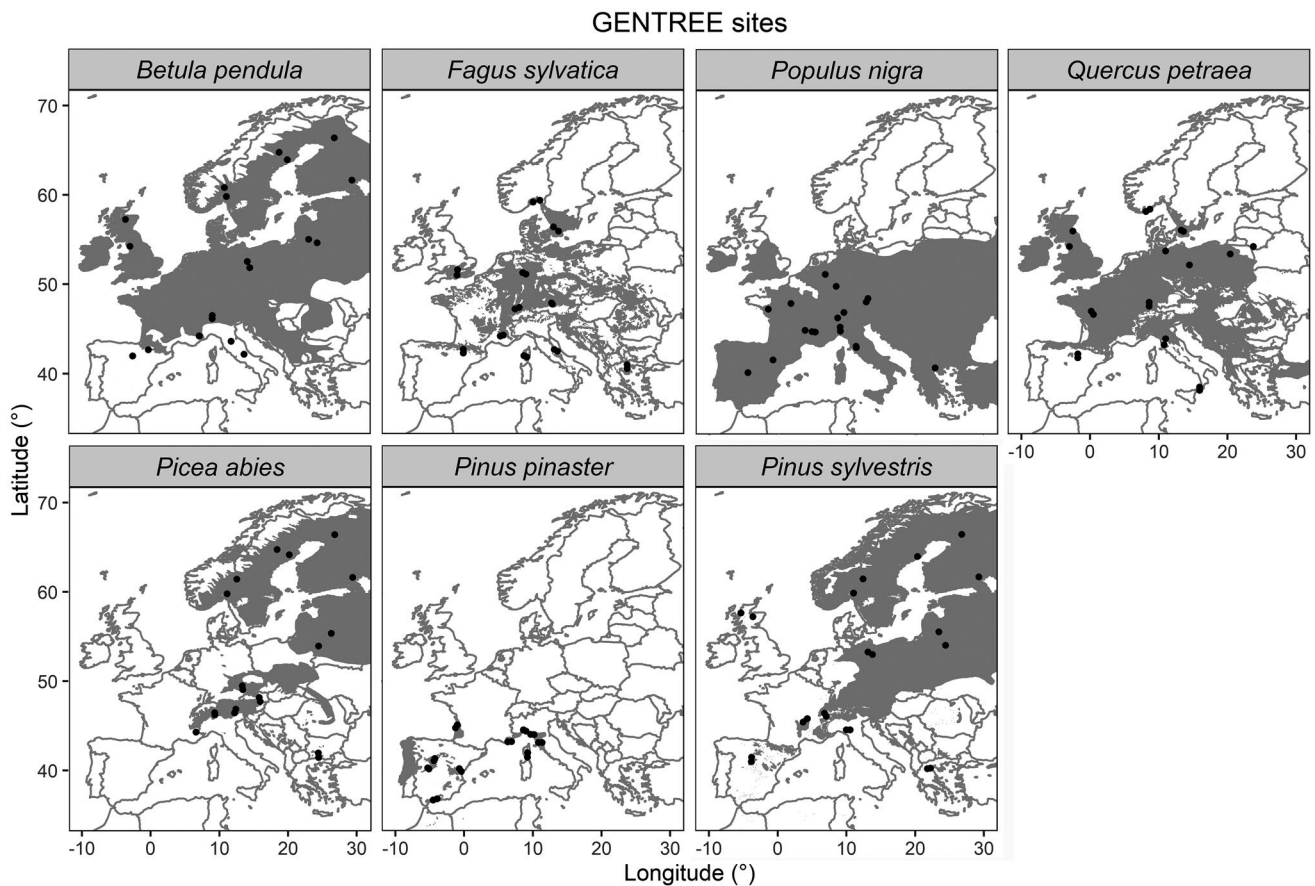


FIGURE 1 Distribution maps and site locations of the seven study tree species. Distribution information was downloaded from European Forest Genetic Resources Programme (<http://www.euforgen.org>)

structure (Lotterhos & Whitlock, 2015). In the north, where it is mostly flat and the gradient was often day length, distance within a pair was sometimes large. Nevertheless, site selection was done considering genetic estimates of gene flow and differentiation of

the species there, which showed that distances under c. 100 km do not prevent gene flow and are not sufficient to yield significant differentiation among populations (Robledo-Arnuncio et al., 2004; Rusanen et al., 2003; Tollesfrud et al., 2009). Further details about

the selection of populations can be found at <https://ec.europa.eu/research/participants/documents/downloadPublic?documentId s=080166e5b2f16f3e&appId=PPGMS>

2.2 | Variables

The specific leaf area (SLA, the area of an individual fresh leaf divided by its dry mass; mm²/mg) is one of the most frequently used traits in functional ecology. This is partly due to its ease of measurement, but also because it can be used to estimate the position of a species along the acquisition–conservation continuum on the leaf economics spectrum (Garnier et al., 2016). Very sensitive to variation in resource availability, high SLA is common in nutrient rich or shady environments (i.e. acquisitive value) and low SLA in nutrient poor and exposed environments (i.e. conservative value) (Pérez-Harguindeguy et al., 2013). The area of a leaf (LA; mm²) is linked to the energy balance and water-use during photosynthesis. Small leaves can easily maintain favourable temperature and photosynthetic water-use efficiency under stressful conditions such as low water availability and high solar radiation compared to large leaves (Parkhurst & Loucks, 1972). LA varies at the interspecific and intraspecific levels, and it is influenced by different factors at different scales including phylogeny, climate, geology, altitude, latitude and allometry (Ackerly et al., 2002).

Leaf nitrogen and carbon contents (LNC, LCC; %) are indicative of variation in resource acquisition (nitrogen and carbon assimilation). Leaf N constitutes the proteins involved in the photosynthesis, especially RuBisCO, which fixes CO₂ inside the leaf (Lambers et al., 2008). Thus, photosynthetic capacity (A_{\max} , the photosynthetic rate per unit leaf mass) correlates linearly with LNC (Field & Mooney, 1986). Nutrient rich environments favour the allocation of an important fraction of leaf N to the photosynthetic machinery, instead of to defensive compounds or supporting tissue, which is more typical in poor environments (Berendsen et al., 2007). LCC is the structural basis and constitutes a rather stable 50% of plant dry mass, and its usefulness lies in its relationship with other nutrients (leaf stoichiometry) that can be indicative of life history strategies, such as responses to stress (Zhang et al., 2017). For instance, an increase in the C : N ratio in plant tissues can reflect a shift from photosynthetic to structural tissue allocation under harsher conditions (Ågren, 2008).

The estimation of stable isotope abundance in leaves can provide information about the physical, chemical and metabolic processes (Griffiths, 1991; and references therein). Plant photosynthesis discriminates against the stable ¹³C isotope (Faquhar et al., 1989) until stomata close and intercellular CO₂ concentration drops. Consequently, the isotopic signature $\delta^{13}\text{C}$ (‰; Equation 1) is linked to plant's water use efficiency (WUE), with higher levels of $\delta^{13}\text{C}$ achieved under prompt stomatal closure. In this way, higher $\delta^{13}\text{C}$ is observed in drier sites and during drier years (Marshall et al., 2007).

$$\delta\text{isotope} = \left(\frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \right) \times 1,000, \quad (1)$$

where R is the ratio between the amount of the heavy isotope of an element to the amount of the light isotope in a sample, in reference to a ratio of a given standard material.

The isotopic signature of stable isotope ¹⁵N in leaves ($\delta^{15}\text{N}$; ‰; Equation (1)) varies among species, ecosystems and climatic gradients, and thus it can reveal spatial and temporal patterns of N cycling (Craine et al., 2009, and references therein). For example, at large scales and under cool and wet conditions, there is a trend towards increasing losses of the heavier ¹⁵N in soils resulting in ¹⁵N-depleted forms of NO₃, N₂O and other N-containing compounds, and hence lower $\delta^{15}\text{N}$ in plants (Amundson et al., 2003). Contrastingly, rain events after dry periods cause a larger proportional loss of ¹⁴N and increased $\delta^{15}\text{N}$ in N compounds in ecosystems (Ogaya & Peñuelas, 2008). Hence, $\delta^{15}\text{N}$ can reflect time-integrated measures of N storage and terrestrial N cycling (Amundson et al., 2003).

2.3 | Data collection and trait estimation

We selected at least 25 healthy adult individuals within each population, totalling 3,569 trees. Ten young but fully expanded leaves were taken from a fully exposed branch – from the top of the crown – without visible herbivory or other damage. They were scanned within 48 hr and LA of each leaf was assessed using WinFOLIA (Regent Instruments Inc., Canada). All samples were then oven-dried at 60 °C for 72 hr and each leaf weighed for dry mass with an electronic balance to the nearest 0.1 mg (Kern ALS 120-4N, Balingen, Germany) to assess SLA. Leaf collection, storage, processing and morphological trait measurement followed Pérez-Harguindeguy et al. (2013). This resulted in 35,755 leaves being used for leaf morphological trait assessment (Supporting Information Table S2, Figures S1, S2).

For a subset of 14 trees out of 25 alternatively selected in each population, together with the whole set from two populations (see below for details), a sample composed of several leaves was oven-dried and ground. Then, 3–3.5 mg of the ground material was weighed and sealed in tin foil capsules. These samples from 1,997 trees were shipped to the UC Davis Stable Isotope Facility, where the chemical analyses were carried out with an elemental analyser interfaced to a continuous flow isotope ratio mass spectrometer (IRMS; see the website for details <https://stableisotopefacility.ucdavis.edu/>). The final δ isotope values are expressed relative to international standards Vienna Pee Dee Belemnite (VPDB) and Air for carbon and nitrogen, respectively (Supporting Information Table S2, Figures S3, S4, S5, S6, S7).

2.4 | Technical validation

The assessment of morphological leaf traits is relatively simple but sample processing needs to be transparent and repeatable to avoid mistakes. Hence, we generated a sampling protocol followed by all project partners to ensure that samples of each surveyed tree could be tracked (<https://ec.europa.eu/research/participants/docum>

ents/downloadPublic?documentIds=080166e5b2f16f3e&appId=PPGMS).

Morphological trait assessment and sample preparation for chemical analyses were conducted entirely at the Museo Nacional de Ciencias Naturales (Consejo Superior de Investigaciones Científicas, Madrid). After recording weights and leaf area values, we examined the outliers within each population and checked their credibility by examining the samples and images. We kept these values as long as they were not identified as typos or mixed-up samples. This process was repeated after the estimation of SLA.

The validation technique used for the chemical analysis can be found on the UC Davis Stable Isotope Facility website (<https://stabileisotopefacility.ucdavis.edu/>).

3 | DATA STRUCTURE

3.1 | Data tables

The dataset comprises three files. The first file (*morpho_leaf_traits.csv*) provides the morphological traits (i.e. SLA and LA) at leaf level, meaning a dataset with 35,755 observations. The second file (*chemical_leaf_traits.csv*) contains the chemical composition (LNC, LCC, and isotope signatures) in a subset of 14 trees of each population and the whole batch from two populations of *Populus nigra* (FR_PO_04 and FR_PO_06), totalling 1,997 observations. In both files, each population has its own code, composed of two letters indicating the country, another two letters indicating the species and a two-digit number (from 01 to 22) to indicate the population. For example, ES_FS_01 is the code of a population located in Spain (ES) of *Fagus sylvatica* (FS), numbered 01. Moreover, each sampled tree has a unique identifier, which includes the population code with an additional two-digit number indicating the order of survey (from 01 to 25). Country acronyms are: AT: Austria, CH: Switzerland, DE: Germany, ES: Spain, FI: Finland, FR: France, IT: Italy, GB: Great Britain, GR: Greece, LT: Lithuania, NO: Norway, PL: Poland, RU: Russia, SE: Sweden. Species acronyms are: BP: *Betula pendula*, FS: *Fagus sylvatica*, PA: *Picea abies*, PO: *Populus nigra*, PP: *Pinus pinaster*, PS: *Pinus sylvestris*, QP: *Quercus petraea*.

A third file (*sites_leaves.csv*) contains information about sites (target species, population code, site name, country, geographical coordinates and elevation).

3.2 | Format type

Each data file is in ASCII text, semicolon delimited, not compressed.

3.3 | Header information

Header information includes the population code (population), the tree identifier (treeID), the leaf identifier (leafID) in the file with data at the

leaf level, and the acronyms of the variables: specific leaf area (SLA), leaf size (LA), leaf carbon content (LCC), leaf nitrogen content (LNC), ratio between carbon and nitrogen (C:N), isotopic signature of stable ^{13}C isotope ($\delta^{13}\text{C}$), isotopic signature of stable ^{15}N isotope ($\delta^{15}\text{N}$).

3.4 | Row information

Each row represents a single measurement.

3.5 | Variable definition

All variables measured in the seven species are detailed in the Methods section.

ACKNOWLEDGMENTS

The authors thank Giorgia Beffa, Guillaume Bodineau, Dieter Boedecker, Sabine Brodbeck, Jean-Paul Charpentier, Nicolas di Gerardi, Patricia Faivre Rampant, Marina Fonti, Vanina Guerin, Kevin Kleeb, Vincent Lejeune, Benjamin Meier, Pekka Närhi, Daniel Nievergelt, Francis Gouvrit, Hans Nyeggen, Gilbert Pichetlt, Patrick Poursat, Antoine Poursat, Frederick Reinig, Vincent Segura, Arne Steffenrem, Jussi Tiainen, Mattias Wellern and also other members of INRAE, UE0570, UEFP (<https://doi.org/10.15454/1.5483264699193726E12>) and INRAE, UE0995, GBFOR (<https://doi.org/10.15454/1.5572308287502317E12>) for their support in the field and laboratory; and especially those involved in the leaf weighing and grinding: Aurora Castro Aguilar, Reyes Martín-Toral, Pablo Castro and Pablo Tabarés. We are also grateful to all the forest owners and national administrations for providing sampling permissions.

All authors acknowledge support from the European Union's Horizon 2020 Research and Innovation Programme under grant agreement no. 676876 (Project GenTree). Laboratory work was also supported by other projects: COMEDIAS (CGL2017-83170-R, Spanish Ministry of Science, Innovation and Universities), REMEDINAL IV (TE-CM S2018/EMT-4338, Project of the Autonomous Community of Madrid, Spain), SPONFOREST (BIODIVERSA-3, PCIN-2016-055), and International Laboratory of Global Change (LINCGlobal 4540-143AP). The Swiss contribution was supported by the Swiss Secretariat for Education, Research and Innovation (SERI) under contract no. 6.0032. BC was funded by a Scholarship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - CAPES (Brazil).

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

RB, BF, FV, BC and CCB wrote the leaf sampling protocol, coordinated the leaf sampling, received, and stored all images and samples collected by the different groups.

RB, BC, CCB, DLQ and AM measured morphological leaf traits and prepared samples for the chemical analyses.

RB checked the data quality, wrote the manuscript and prepared the data files.

All the authors contributed to the field sampling, leaf scanning and commented on earlier versions of the manuscript and approved the current version.

DATA AVAILABILITY STATEMENT

We stored the dataset in a repository (Benavides et al., 2020) and it can be freely downloaded at <https://doi.org/10.6084/m9.figshare.12044370>.

ORCID

- Raquel Benavides  <https://orcid.org/0000-0003-2328-5371>
 Bárbara Carvalho  <https://orcid.org/0000-0002-4129-2746>
 Cristina C. Bastias  <https://orcid.org/0000-0002-2479-2001>
 Evangelia V. Avramidou  <https://orcid.org/0000-0002-5932-1189>
 Benjamin Dauphin  <https://orcid.org/0000-0003-0982-4252>
 Patrick Fonti  <https://orcid.org/0000-0002-7070-3292>
 Felix Gugerli  <https://orcid.org/0000-0003-3878-1845>
 Mirko Liesebach  <https://orcid.org/0000-0001-8840-5026>
 Elisabet Martínez-Sancho  <https://orcid.org/0000-0003-4413-6818>
 Silvia Matesanz  <https://orcid.org/0000-0003-0060-6136>
 Eduardo Notivol  <https://orcid.org/0000-0003-4272-4536>
 Lars Opgenoorth  <https://orcid.org/0000-0003-0737-047X>
 Andrea Piotti  <https://orcid.org/0000-0002-3324-5325>
 Tanja Pyhäjärvi  <https://orcid.org/0000-0001-6958-5172>
 Christian Rellstab  <https://orcid.org/0000-0002-0221-5975>
 Silvio Schueler  <https://orcid.org/0000-0003-0155-5692>

REFERENCES

- Ackerly, D. D., Knight, C. A., Weiss, S. B., Barton, K., & Starmer, K. P. (2002). Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: Contrasting patterns in species level and community level analyses. *Oecologia*, *130*, 449–457.
- Ackerly, D. D., & Reich, P. B. (1999). Convergence and correlations among leaf size and function in seed plants: A comparative test using independent contrasts. *American Journal of Botany*, *86*, 1272–1281.
- Ågren, G. I. (2008). Stoichiometry and nutrition of plant growth in natural communities. *The Annual Review of Ecology, Evolution, and Systematics*, *39*, 153–170.
- Amundson, R., Austin, A. T., Schuur, E. A. G., Yoo, K., Matzek, V., Kendall, C., & Baisden, W. T. (2003). Global patterns of the isotopic composition of soil and plant nitrogen. *Global Biogeochemical Cycles*, *17*, 1031.
- Benavides, R., Carvalho, B., Bastias, C. C., López-Quiroga, D., Mas, A., Cavers, S., ... Valladares, F. (2020). The GenTree Leaf Collection: Inter- and intraspecific variation of leaf traits in seven forest tree species across Europe. *Figshare*, <https://doi.org/10.6084/m9.figshare.12044370>
- Berendsen, F., de Kroon, H., & Braakhekke, W. G. (2007). Acquisition, use and loss of nutrients. In F. I. Pugnaire, & F. Valladares (Eds.), *Functional plant ecology* (2nd ed., pp. 259–283). CRC Press/Taylor & Francis Group.
- Craine, J. M., Elmore, A. J., Aida, M. P. M., Amundson, R. G., Bustamante, M., Coetsee, C., & Wright, I. J. (2009). Nitrogen isotopes in leaves index global patterns of nitrogen availability. *Global Change Biology*, *18*, 980–992.
- Crutsinger, M., Collins, M. D., & Fordyce, J. A. (2006). Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science*, *313*, 966–968.
- Farquhar, G. D., Ehleringer, J. R., & Hubick, K. T. (1989). Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology*, *40*, 503–537.
- Field, C. B., & Mooney, H. A. (1986). The photosynthesis-nitrogen relationship in wild plants. In T. J. Givnish (Ed.), *On the economy of plant form and function* (pp. 25–55). Cambridge University Press.
- Garnier, E., Navas, M. L., & Grigulis, K. (2016). Plant functional diversity. *Organism traits, community structure, and ecosystem properties*. Oxford University Press.
- Griffiths, H. (1991). Applications of stable isotope technology in physiological ecology. *Functional Ecology*, *5*, 254–269. <https://doi.org/10.2307/2389263>
- Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönsch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J., Cornelissen, J. H. C., Violle, C., Harrison, S. P., Van Bodegom, P. M., Reichstein, M., Enquist, B. J., Soudzilovskaia, N. A., Ackerly, D. D., Anand, M., ... Wirth, C. (2011). TRY – A global database of plant traits. *Global Change Biology*, *17*, 2905–2935. <https://doi.org/10.1111/j.1365-2486.2011.02451.x>
- Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., Poschlod, P., van Groenendael, J. M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G. M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., ... Peco, B. (2008). The LEDA Traitbase: A database of life-history traits of the Northwest European flora. *Journal of Ecology*, *96*, 1266–1274. <https://doi.org/10.1111/j.1365-2745.2008.01430.x>
- Lambers, H., Chapin, F. S., & Pons, T. L. (2008). *Plant physiological ecology* (2nd ed.). Springer.
- Leimu, R., & Fischer, M. (2008). A meta-analysis of local adaptation in plants. *PLoS ONE*, *3*, e4010. <https://doi.org/10.1371/journal.pone.0004010>
- Lotterhos, K. E., & Whitlock, M. C. (2015). The relative power of genome scans to detect local adaptation depends on sampling design and statistical method. *Molecular Ecology*, *24*, 1031–1046. <https://doi.org/10.1111/mec.13100>
- Marshall, J. D., Brooks, J. R., & Lajtha, K. (2007). Sources of variation in the stable isotopic composition of plants. In K. Lajtha, & R. Michener (Eds.), *Stable isotopes in ecology and environmental science* (2nd ed., pp. 22–60). Blackwell Scientific Publications.
- Martínez-Sancho, E., Slámová, L., Morganti, S., Grefen, C., Carvalho, B., Dauphin, B., Rellstab, C., Gugerli, F., Opgenoorth, L., Heer, K., ... Fonti, P. (2020). The GenTree Dendroecological Collection, tree-ring and wood density data from seven tree species across Europe. *Scientific Data*, *7*, 1.
- McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, *21*, 178–185. <https://doi.org/10.1016/j.tree.2006.02.002>
- Messier, J., McGill, B. J., & Lechowicz, M. J. (2010). How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters*, *13*, 838–848. <https://doi.org/10.1111/j.1461-0248.2010.01476.x>
- Nicotra, A. B., Leigh, A., Boyce, C. K., Jones, C. S., Niklas, K. J., Royer, D. L., & Tsukaya, H. (2011). The evolution and functional significance of leaf shape in the angiosperms. *Functional Plant Biology*, *38*, 535–552. <https://doi.org/10.1071/FP11057>
- Ogaya, R., & Peñuelas, J. (2008). Changes in leaf $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for three Mediterranean tree species in relation to soil water availability. *Acta Oecologica*, *34*, 331–338. <https://doi.org/10.1016/j.actao.2008.06.005>

- Parkhurst, D., & Loucks, O. (1972). Optimal leaf size in relation to environment. *Journal of Ecology*, *60*, 505–537. <https://doi.org/10.2307/2258359>
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., ... Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*, 167–234. <https://doi.org/10.1071/BT12225>
- Pérez-Ramos, I., Matías, L., Gómez-Aparicio, L., & Godoy, O. (2019). Functional traits and phenotypic plasticity modulate species coexistence across contrasting climatic conditions. *Nature Communications*, *10*, 2555. <https://doi.org/10.1038/s41467-019-10453-0>
- Poorter, H., Lambers, H., & Evans, J. R. (2014). Trait correlation networks: A whole-plant perspective on the recently criticized leaf economic spectrum. *New Phytologist*, *201*, 378–382. <https://doi.org/10.1111/nph.12547>
- Robledo-Arnuncio, J. J., Smouse, P. E., Gil, L., & Alía, R. (2004). Pollen movement under alternative silvicultural practices in native populations of Scots pine (*Pinus sylvestris* L) in central Spain. *Forest Ecology and Management*, *197*, 245–255. <https://doi.org/10.1016/j.foreco.2004.05.016>
- Rusanen, M., Vakkari, P., & Blom, A. (2003). Genetic structure of *Acer platanoides* and *Betula pendula* in northern Europe. *Canadian Journal of Forest Research*, *33*, 1110–1115.
- Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., & Wardle, D. A. (2012). Incorporating intraspecific variation in tests of trait-based community assembly. *Oecologia*, *170*, 767–775. <https://doi.org/10.1007/s00442-012-2351-7>
- Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W., Baraloto, C., Carlucci, M. B., Cianciaruso, M. V., de Dantas, V. L., de Bello, F., Duarte, L. D. S., Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., ... Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, *18*, 1406–1419. <https://doi.org/10.1111/ele.12508>
- Tavsanoglu, Ç., & Pausas, J. G. (2018). A functional trait database for Mediterranean Basin plants. *Scientific Data*, *5*, 180135.
- Tollefsrud, M. M., Sønsteby, J. H., Brochmann, C., Johnsen, Ø., Skrøppa, T., & Vendramin, G. G. (2009). Combined analysis of nuclear and mitochondrial markers provide new insight into the genetic structure of North European *Picea abies*. *Heredity*, *102*, 549–562. <https://doi.org/10.1038/hdy.2009.16>
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., ... Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*, 821–827. <https://doi.org/10.1038/nature02403>
- Zhang, H., Yang, X., Wang, J., Wang, G. G., Yu, M., & Wu, T. (2017). Leaf N and P stoichiometry in relation to leaf shape and plant size for *Quercus acutissima* provenances across China. *Scientific Reports*, *7*, 46133. <https://doi.org/10.1038/srep46133>

BIOSKETCH

Raquel Benavides is a forest ecologist working at the Museo Nacional de Ciencias Naturales-CSIC (Madrid). Her main interests lie in the functional diversity of forests and tree species' responses (performance and traits) to global change. She held a Marie Curie Fellowship at the University of Freiburg (project DIVERFOR) where she started to analyse the role of the intraspecific component of functional diversity in ecosystem functioning.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

How to cite this article: Benavides R, Carvalho B, Bastias CC, et al. The GenTree Leaf Collection: Inter- and intraspecific leaf variation in seven forest tree species in Europe. *Global Ecol Biogeogr.* 2021;30:590–597. <https://doi.org/10.1111/geb.13239>