



## Trait variability in diaspores and fruits of *Zelkova abelicea* (Ulmaceae) across its distribution range

Laurence Fazan<sup>a,\*</sup>, Daniele Certini<sup>b</sup>, Salvatore Pasta<sup>c</sup>, Ilektra Remoundou<sup>d</sup>, Dany Ghosn<sup>d</sup>, Giuseppe Garfi<sup>c</sup>, Gregor Kozlowski<sup>a,e,f</sup>

<sup>a</sup> Department of Biology and Botanical Garden, University of Fribourg, Chemin du Musée 10, 1700, Fribourg, Switzerland

<sup>b</sup> School of Engineering, Institute of Energy Systems, University of Edinburgh, Sanderson Building, Robert Stevenson Road, Edinburgh, EH9 3FB, United Kingdom

<sup>c</sup> Institute of Biosciences and BioResources, National Research Council, Corso Calatafimi 414, 90129, Palermo, Italy

<sup>d</sup> Department of Geoinformation in Environmental Management, CIHEAM Mediterranean Agronomic Institute of Chania, Alysilio Agrokepiou, 73100, Chania, Greece

<sup>e</sup> Natural History Museum Fribourg, Chemin du Musée 6, 1700, Fribourg, Switzerland

<sup>f</sup> Eastern China Conservation Centre for Wild Endangered Plant Resources, Shanghai Chenshan Botanical Garden, 3888 Chenhua Road, Songjiang, 201602, Shanghai, China

### ARTICLE INFO

#### Keywords:

Seed soundness  
Pre-dispersal embryo abortion  
Mast seeding  
Crete Greece  
Environmental gradient  
Relict tree species  
Mediterranean islands

### ABSTRACT

In the tree genus *Zelkova* (Ulmaceae), diaspores show a unique morphology amongst woody angiosperms. Shoots with leaves and fruits detach and act as flying dispersal units. Surprisingly little attention has been given to these structures, and it is unknown whether the characteristics of these diaspores vary amongst species or within the range of a single species. The endemic Cretan *Z. abelicea* (Lam.) Boiss. is one of two *Zelkova* species occurring at the western end of the distribution range of the genus. This relict species grows in a typical Mediterranean climate, in conditions completely different from the warm and moist climate that occurred during the apogee of the genus in the Paleogene, or that are still found for the three East Asiatic species of the genus. Here we studied for the first time the characteristics of diaspores, including fruit traits, of *Z. abelicea* across the whole range of the species. We showed that most traits are very variable amongst individual trees but less so between mountain ranges and that only diaspore stem length and proportion of sound seeds per diaspore and per tree vary significantly amongst mountain ranges. We showed that trees from central and eastern Crete produce extremely low to null proportions of sound seeds and that those trees oftentimes are smaller and have shorter diaspores with less leaves and fruits. Furthermore, we found that diaspores that were severely affected by a gall midge species (Cecidomyiidae) produced less fruits, but that seed soundness was not significantly impacted by the presence or absence of the galls. The very low proportion of sound seeds found in central and eastern Crete raises concern about the long-term persistency and regeneration of the species in those areas.

### 1. Introduction

The seed dispersal units (hereafter called diaspores) of the species within the genus *Zelkova* are unique among angiosperms (Certini et al., 2020; Hoshino, 1990). The diaspore is an annually produced shoot specialised in flowering and dispersal and is morphologically different from the non-flowering, perennial shoots (see Hoshino, 1990 for details). On this unit, leaves and flowers (male, female, hermaphrodite) and subsequently fruits are produced (Fig. 1A). Fruits are generally found in the axil of the alternate leaves (usually one fruit per axil) and closer to the top of the unit due to a clear zonation of flower sex on the

shoots with clusters of caducous male flowers being proximal, usually solitary hermaphrodite flowers being intermediate and solitary female flowers being distal. In autumn, the shoot abscises at the base and falls off with dried leaves and fruits, i.e., the so-called diaspore (Fig. 1B). In the genus *Zelkova*, dispersal is mainly through wind (anemochory) and gravity (barochory) (L. Fazan, pers. obs.; Egli, 1997; Hoshino, 1990; Oyama et al., 2018), but zoochory has also been reported for the East Asiatic *Z. serrata* as macaques eat fresh fruits (Nakagawa, 1990; Tsuji and Takatsuki, 2004). For *Z. abelicea* (Lam.) Boiss., secondary dispersal (diplochory) has been observed through ants transporting fallen fruits to their nests (L. Fazan, G. Garfi & S. Pasta, pers. obs.; Egli 1997). The genus

\* Corresponding author. Department of Biology and Botanic Garden, University of Fribourg, Chemin du Musée 10, 1700, Fribourg, Switzerland.

E-mail addresses: [laurence.fazan@unifr.ch](mailto:laurence.fazan@unifr.ch) (L. Fazan), [d.certini@ed.ac.uk](mailto:d.certini@ed.ac.uk) (D. Certini), [salvatore.pasta@ibbr.cnr.it](mailto:salvatore.pasta@ibbr.cnr.it) (S. Pasta), [hlektra@maich.gr](mailto:hlektra@maich.gr) (I. Remoundou), [dghosn@maich.gr](mailto:dghosn@maich.gr) (D. Ghosn), [giuseppe.garfi@ibbr.cnr.it](mailto:giuseppe.garfi@ibbr.cnr.it) (G. Garfi), [gregor.kozlowski@unifr.ch](mailto:gregor.kozlowski@unifr.ch) (G. Kozlowski).

<https://doi.org/10.1016/j.actao.2023.103896>

Received 9 December 2021; Received in revised form 27 January 2023; Accepted 31 January 2023

Available online 6 February 2023

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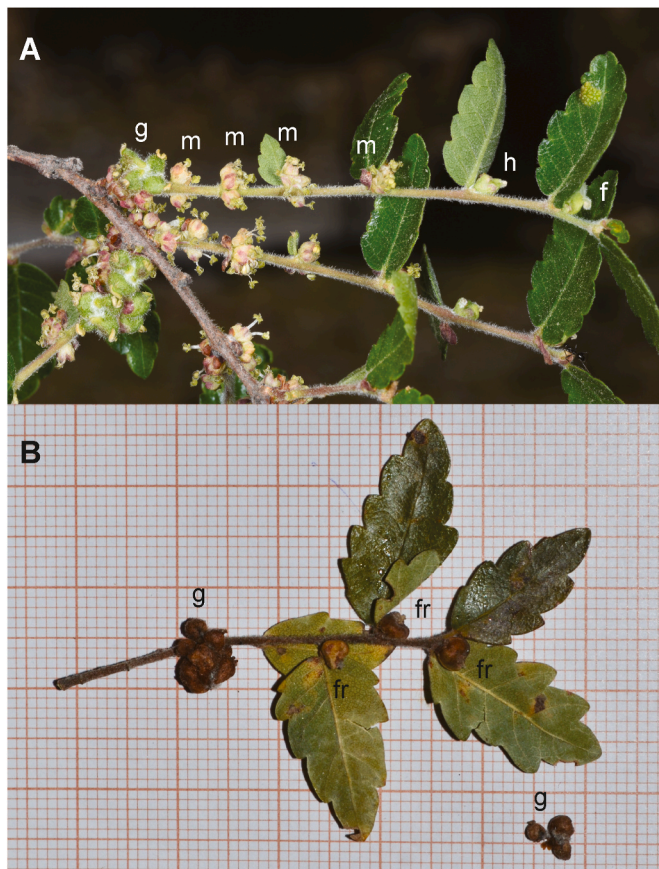


Fig. 1. A. Flowering shoots of *Z. abelicea* with leaves, proximal male flowers with (g) or without galls (m), intermediate hermaphrodite flower (h) and distal female flower (f). B. diaspore of *Z. abelicea* with leaves, galls (g) and fruits (fr). Pictures: E. Kozłowski (A), S. Pasta (B).

is characterised by a bimodal dispersal scheme. Fruits disperse either attached to the diaspore or as single fruit that detach and fall off (Certini et al., 2020; Oyama et al., 2018).

The genus *Zelkova* is a climate relict with a north Pacific (Burnham, 1986) or north-eastern Chinese (Zhang et al., 2017) origin that thrived under warm and humid climatic conditions. The genus was widespread throughout the Northern Hemisphere during most of the Paleogene. Due to the dramatic climatic changes during the late Miocene and early Quaternary, the distribution range of the genus drastically shrunk so that it is now found and restricted to two disjunct refugial areas and includes six extant species (Kozłowski and Gratzfeld, 2013). Three are located in south-eastern Asia, namely *Z. serrata* (Thun.) Makino, *Z. schneideriana* Hand.-Mazz. and *Z. sinica* C.K. Schneid., where they thrive under temperate and humid climates with no summer drought (Garfi et al., 2021). The remaining three species are found in southwestern Eurasia. *Z. carpinifolia* (Pall.) K. Koch grows in the Transcaucasian and Middle East regions under almost constant moist conditions with a very short dry summer season (Garfi et al., 2021; Kvavadze and Connor, 2005). The two remaining species are restricted to the Mediterranean area. *Z. sicula* Di Pasq., Garfi & Quézel is endemic to the Italian island of Sicily and *Z. abelicea* is endemic to the Greek island of Crete. The two Mediterranean *Zelkova* species occur in areas with climatic conditions distinct from the other extant *Zelkova* species, characterised by three to four months of pronounced summer drought.

Little is known about diaspore and fruit traits within the *Zelkova* genus. Although being mainly descriptive, such trait studies are of high importance as they may yield essential knowledge about the dispersal capacities, seed soundness and regeneration potential of the studied species. They provide basic information on traits that may play a key

role in future comparative studies and are important to detect potential intraspecific changes in species located in areas subject to rapidly changing environmental conditions, which is the case for the two Mediterranean *Zelkova* species (Cos et al., 2022; Giorgi and Lionello 2008; Lionello et al., 2014). In addition, studying trait variation across the range of the species may put into light unseen or hidden trends or patterns that may be of importance for both the survival and the conservation of a species (Westerband et al., 2021). Moreover, several *Zelkova* species have been recorded as having low to null natural regeneration. This fact has important conservation implications, leading to the classification of all but one species of the genus as threatened on the IUCN Red List of Threatened Species (Bétrisey et al., 2018a, 2018b, 2018c; Garfi et al., 2017; Kozłowski et al., 2012; Song et al., 2018).

Characteristics of diaspores of *Z. abelicea* have only been partially described by Jasińska et al. (2015, 2021) who studied leaf morphology of the three westernmost species, while Certini et al. (2020) investigated the flight behaviour of *Z. abelicea* diaspores. Seed soundness of the latter species, despite being crucial for plant propagation actions within conservation projects, has only been described from a low number of trees and mainly from a small portion of the range of the species (Egli, 1997; Fournaraki and Thanos, 2006; Søndergaard and Egli, 2007).

The response of plant species in constraining environments can involve significant failure or ineffectiveness of sexual regeneration or propagation, as is the case with species living at the edge of the distribution range of their genus (Garfi et al., 2021). Therefore, in this paper, we describe and study for the first time several traits of the diaspores and of the fruits of *Z. abelicea* across its entire distribution range in order to 1) evaluate the characteristics of different traits of the diaspores and of the fruits and any possible variation across the range of the species, 2) assess seed soundness at a species, mountain and tree level, and 3) check for possible explanations of the spatial variability of the investigated traits. The results of our study are of high importance to improve knowledge about the dispersal and sexual reproductive performance of this threatened relict tree species in view of future implementation of conservation efforts.

## 2. Material and methods

### 2.1. The species

*Zelkova abelicea* is a monoecious, broadleaved tree. The species grows in all mountainous areas of Crete between 800 and 1800 m a.s.l. in woodland communities in supra- and oro-Mediterranean climatic conditions with mean annual temperatures of ca. 9.3–12.7 °C, and up to 1100–1600 mm of precipitation in the rainiest areas (Fazan et al., 2017; Ghosn et al., 2010). The species has been assessed as Endangered (EN) on the IUCN Red List of Threatened Species (Kozłowski et al., 2012) and is threatened throughout its range mainly with intense and localized caprine and ovine pastoralism, causing overbrowsing, trampling and associated soil erosion and environmental degradation (Egli, 1995, 1997; Fazan et al., 2012; Fournaraki and Thanos, 2006; Kozłowski et al., 2018; Søndergaard and Egli, 2007). Overbrowsing by goats hinders tree growth and keeps individuals in a stunted dwarf-like form (Fazan et al., 2012). Dwarfs cannot produce fruits and are only able to propagate asexually via root suckers, which the species does profusely, especially when disturbance occurs (Egli, 1997; Fazan et al., 2012; Kozłowski et al., 2018). Only trees that have grown tall enough to escape browsing produce fruits. Fruiting trees are estimated to make up only ca. 5% of all *Z. abelicea* individuals (Kozłowski et al., 2014). Fruit production follows a masting behaviour with massive and widespread fruit production every two to three years (L. Fazan, pers. obs.; Egli, 1997; Fournaraki and Thanos, 2006; Søndergaard and Egli, 2007). The proportion of fruits with sound seeds is highly fluctuant, and has been reported to be ranging from 0% to 56% depending on the sampled tree, locality, and year of collection (Egli, 1997; Fournaraki and Thanos, 2006; Søndergaard and Egli, 2007), but has not been systematically studied throughout the

range of the species. Pre-dispersal seed predation has never been reported up to the present. However, trees in several localities were noticed to have galls made by gall midges (family: Cecidomyiidae, class: Diptera) on the male flowers (L. Fazan, *pers. obs.*) and it is unknown whether this may influence fruit quantities, seed soundness or other diaspore traits. Seedling survival in the wild is low at best, supposedly due to adverse conditions (e.g. browsing, summer drought). However, hundreds of seedlings have been propagated in forest nurseries over the past few years in the scope of local conservation projects (Abelitsia, 2021; Zelkova, 2021).

## 2.2. Plant material collection and preparation

Thirty-seven fruiting trees were randomly sampled throughout the distribution range of *Z. abelicea* (Fig. 2) in October 2017, i.e. during a masting year when numerous *Z. abelicea* trees bore fruits. This was not the case in the preceding and subsequent years in which only a few trees were found to bear fruits (L. Fazan, *pers. obs.*). Twenty-four trees were sampled in the Levka Ori, three trees on Mt. Psiloritis and ten trees on Mt. Dikti, reflecting the natural distribution of *Z. abelicea* populations throughout its range (Kozłowski et al., 2014). The easternmost mountain, namely Thripti, was not sampled because it does not host at present any flowering trees and Mt. Kedros was not visited. The geographic position and altitude of each tree are found in Table S1 in the Supplementary Material.

Fifteen diaspores (Fig. 1B) were randomly handpicked from the sampled trees, except for one tree for which only 14 diaspores were sampled and one tree for which no diaspores were collected. The diaspores were then stored individually, as flat as possible, in paper envelopes and left to dry for 4 months at room conditions (20 °C, 40–50% relative humidity). Each diaspore was then processed individually, and the following traits were measured or counted: number of leaves per diaspore, leaf length, leaf width, leaf area, leaf weight, diaspore stem length, number of fruits per diaspore and number of galls per diaspore. Leaf mass per area (LMA) was calculated as dry leaf mass divided by leaf surface and was computed for each leaf. Leaves were weighed on a Mettler Toledo AG204 analytical balance (Mettler, 2021). All other leaf measurements were done using Fiji of ImageJ2 (Rueden et al., 2017; Schindelin et al., 2012). The single-seeded fruits (Fournaraki and Thanos, 2006) found on the diaspores were opened to assess visually seed soundness and the proportion of sound seeds per diaspore (i.e. number

of sound seeds compared to the total number of seeds of a given diaspore). Galls triggered by the presence of a previously unknown gall midge (family: Cecidomyiidae, class: Diptera; L. Fazan, *pers. obs.*) occur on male flower parts, on the otherwise caducous stamens that grow abnormally and become enlarged and persistent (Fig. 1). During spring, these galls host the insect larvae which then exit the galls before the onset of the summer season. Due to the persistency of galled flowers, galls are also found on, and dispersed with, diaspores in autumn (L. Fazan, *pers. obs.*; Planchon, 1873).

To have a more statistically robust estimation of seed soundness per tree (especially for trees in which seed soundness was extremely low), fruits were additionally collected for each tree using the method described in Proto and Zimbalatti (2015) and Sola-Guirado et al. (2014) for manual olive collection. The trees were beaten using a wooden stick and all fallen material was gathered on large collecting nets that had been placed under the trees. The collected material was then sorted and the fruits were separated from the remaining material (leaves, twigs, galls) by sieves (mesh sizes between 2 mm and 6.3 mm) and by using a column blower CB-1 (Agriculex 2018).

From the outside, fruits with sound or unsound seeds are indistinguishable. Fournaraki and Thanos (2002) have shown that fruits with sound seeds of *Z. abelicea* can be separated due to their heavier mass from the lighter fruits with unsound seeds in which the embryo has not developed. Therefore, to assess the proportion of sound seeds per tree, fruits were sorted according to their weight, separately for each tree, using a column blower following the methodology used by Fournaraki and Thanos (2006). From all the sorted fruits, an average of 37 sound (range: 2–93) and 43 unsound (range: 10–126) fruits per tree were weighed on a Mettler Toledo AG204 analytical balance (Mettler, 2021). To assess the accuracy of the column blower method, fruits were cut open to test for seed soundness (the exact number of weighed fruits per tree is presented in Table S1 in the Supplementary Material). All fruits were opened for trees with less than 40 (sound) fruits. The number of misplaced fruits (i.e., unsound within sound and vice-versa) amongst the opened fruits was used to give a rough estimate of the accuracy of this method. When opened, sound seeds had a developed, white, fleshy embryo beneath the seed coat, filling most of the fruit cavity. On the contrary, aborted, unsound seeds had an undeveloped shrunken seed or vestigial ovule that does not grow and most of the space within the fruit was empty (Fig. 3).

In addition, to see if tree size could influence diaspore and fruit traits,

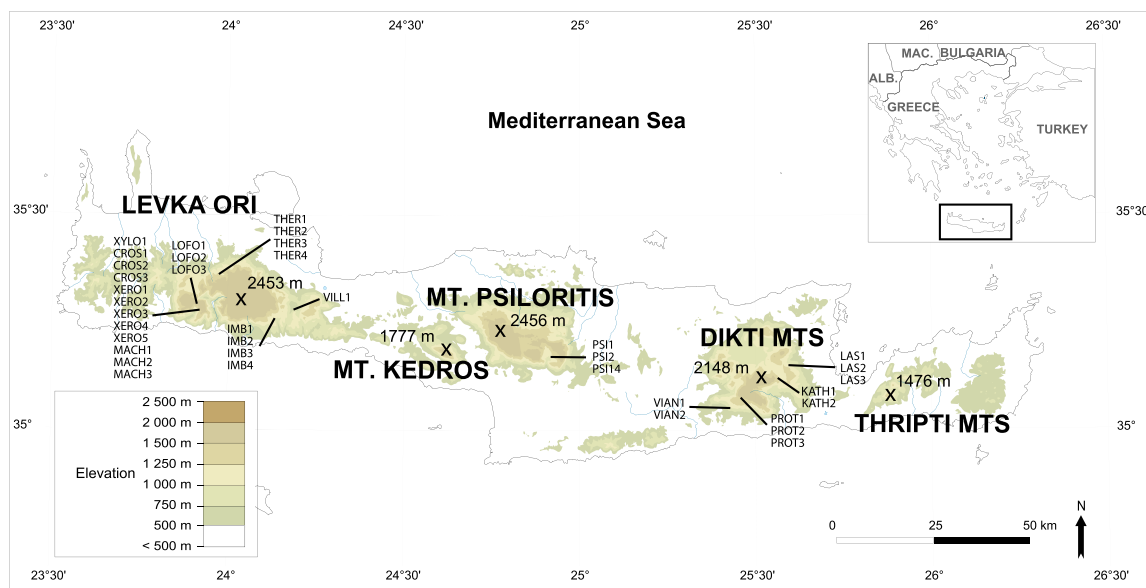


Fig. 2. Location of the 37 sampled trees in the five mountain ranges (Levka Ori, Mt. Kedros, Mt. Psiloritis, Dikti Mts. and Thripti Mts.) of Crete.



**Fig. 3.** Left: section of a fruit with a sound seed with a fleshy white viable embryo beneath the seed coat that occupies most of the available space. Right: section of a fruit with a small undeveloped and withered seed containing a non-viable or aborted embryo that does not fill up the fruit cavity.

trunk circumference at breast height was measured on each tree using a measuring tape, tree height was calculated using a clinometer and a measuring tape (“tangent method” described by Larjavaara and Muller-Landau, 2013), and canopy extension was estimated (i.e., the

sum of canopy radii in 4 directions: north, east, south, west).

**Table 1**

Diaspore traits averaged for the 37 studied trees. # Lf: number of leaves, # Fr: number of fruits, Prop sfr: proportion of fruits with sound seeds, # Gl: number of galls, SL: stem length, LfL: leaf length, LfW: leaf width, LMA: leaf mass per area. NA: missing value. The overall median, mean, standard deviation (SD), minimum and maximum were computed directly over the raw unaveraged measurements.

Mt	Tree-ID	# Lf	# Fr	Prop sfr	# Gl	SL (mm)	LfL (mm)	LfW (mm)	LMA (mg/mm <sup>2</sup> )
Levka Ori	XYLO1	4.7	2.7	0.13	0	31.50	18.42	10.58	0.12
	CROS1	4.0	0.4	0.67	3.60	20.85	12.46	8.04	NA
	CROS2	5.5	1.1	0.13	1.00	23.73	15.16	9.61	NA
	CROS3	5.7	2.1	0.28	0.20	42.87	17.70	10.84	NA
	XERO1	4.4	2.9	0.55	0.20	30.10	19.26	10.91	0.10
	XERO2	5.7	1.6	0.29	0.07	24.27	13.69	7.93	0.06
	XERO3	5.3	1.6	0.42	0	23.43	12.29	6.91	0.07
	XERO4	4.3	2.7	0.58	0	21.77	12.46	7.76	0.08
	XERO5	5.3	2.2	0.42	0.33	29.70	13.00	8.07	0.09
	MACH1	4.3	3.1	0.43	0.07	25.60	14.15	8.73	0.10
	MACH2	4.6	1.7	0.42	2.87	35.70	16.13	10.45	0.08
	MACH3	6.5	2.3	0.40	0.13	35.47	23.42	10.18	0.09
	LOFO1	4.1	1.3	0.26	1.13	20.47	15.83	9.41	0.06
	LOFO2	5.0	0.9	0.14	1.27	19.33	11.24	6.36	0.06
	LOFO3	3.2	1.0	0.20	0.73	18.73	12.69	8.38	0.06
	THER1	5.2	1.3	0.15	1.40	32.22	17.20	9.92	0.07
	THER2	3.6	0.5	0.38	2.47	26.46	16.92	9.48	0.07
	THER3	4.7	1.7	0.28	1.27	25.16	15.33	7.97	0.09
	THER4	4.1	1.4	0.38	4.13	23.64	12.88	7.64	0.09
	IMB1	2.9	2.5	0	0	28.27	17.99	9.22	0.08
IMB2	4.3	1.9	0.03	0	29.50	18.09	9.59	0.06	
IMB3	NA	NA	NA	NA	NA	NA	NA	NA	
IMB4	4.7	2.5	0	0	31.66	17.10	8.83	0.10	
Psiloritis	VILL1	4.4	1.5	0	0	19.06	18.98	10.32	0.09
	PSI1	4.6	1.7	0	0	14.93	15.48	9.37	0.08
	PSI2	4.5	2.3	0	0	18.63	17.51	10.44	0.09
	PSI14	4.2	1.8	0	0	10.59	15.14	9.27	0.08
Dikti	PROT1	5.7	3.1	0	0	23.03	12.61	8.35	0.09
	PROT2	4.3	2.5	0	0	19.29	16.18	10.03	0.10
	PROT3	5.5	3.4	0	0	25.26	13.13	8.88	0.08
	VIAN1	3.9	1.5	0	0	19.39	17.49	11.38	0.11
	VIAN2	4.1	1.3	0	0	27.18	17.37	10.52	0.10
	LAS1	3.7	1.2	0	0	12.97	11.84	7.01	0.08
	LAS2	3.7	1.1	0	0	14.14	13.39	8.04	0.08
	LAS3	4.5	1.2	0	0.57	20.50	18.01	10.99	0.08
	KATH1	4.9	1.4	0.14	0.40	21.06	13.72	7.37	0.09
	KATH2	4.5	1.1	0	6.47	25.50	14.57	8.90	0.12
Overall	Median	5.00	2.00	0.00	0.00	23.00	15.00	9.00	0.08
	Mean	4.57	1.79	0.18	0.79	24.26	15.56	9.10	0.08
	SD	1.26	1.00	0.33	1.85	8.60	4.78	2.67	0.02
	Minimum	1	0	0	0	6.00	3.00	2.00	0.01
	Maximum	8	6	1	13	65.00	36.00	19.00	0.18

### 2.3. Statistical analyses

All statistical analyses were done using R (version 4.0.2) (R Core Team, 2021). Kruskal-Wallis rank sum tests using function `kruskal.test` in package `stats` (R Core Team, 2021) were carried out to check for significant differences between trees and between mountain ranges of diaspore traits, as well as seed soundness, weight and size of individual trees. This test was also carried out to see if significant differences exist in the weight of fruits containing sound or unsound seeds. For traits that showed significant differences between mountains, pairwise Wilcoxon rank sum tests using function `pairwise.wilcox.test` of package `stats` (R Core Team, 2021) were carried out to assess more precisely which mountain ranges were significantly different.

Linear and generalised linear models with tree identity nested in mountain identity were used to partition the variation in diaspore traits, seed soundness and weight between trees and mountains. Function `lmer` of package `lme4` (Bates et al., 2015) was used for continuous variables (leaf width, leaf length, LMA, stem length, fruit weight), while function `glmer` was used for count variables (family: Poisson, nb. of leaves, nb. of fruits and nb. of galls) and proportions of fruits with sound seeds per diaspore (family: binomial). Tree identity and mountain identity were used as random effects, specifying that tree identity was nested within mountain identity.

Spearman's rank correlation coefficients (Hollander and Wolfe, 1973) among diaspore traits as well as for the proportion of fruits with sound seeds per tree and fruit weight were computed using function `cor` in package `stats` (R Core Team, 2021) to assess relationships and the direction of the relationship between variables.

## 3. Results

### 3.1. Diaspore traits

Per tree summaries are presented in Table 1 and Supplementary Material Fig. S1, and trends per mountain are shown in the Supplementary Material Fig. S2. 58% of the investigated trees had sound seeds but only 18% of all the seeds attached to the diaspores were sound. The proportion of fruits with sound seeds per diaspore varied between 0 (only unsound seeds) and 1 (only sound seeds), but the average for diaspores with fruits containing sound seeds was 0.67. Significant variations were found in diaspore stem lengths (range: 6–65 mm, average: 24.26 mm), leaf lengths (range: 3–36 mm, average: 15.56) and leaf widths (range: 2–19 mm, average: 9.10 mm). LMA varied between 0.01 and 0.18 mg/mm<sup>2</sup> with an average of 0.08 mg/mm<sup>2</sup>. Diaspores had between one and eight leaves, but five leaves on average. Fruits per diaspore varied between zero to six fruits with an average of two fruits per diaspore. Galls were found on 53% of the trees, namely on most of the sampled trees from Levka Ori (70%), several from Dikti (30%) but none from Psiloritis (0%). The number of galls varied between 0 and 13, but the average for galled diaspores was three galls per diaspore.

### 3.2. Variation among trees and mountains of diaspore traits

All of the diaspore traits showed significant ( $p < 0.05$ ) variation amongst trees. In contrast, between mountain ranges, significant variation was found only for diaspore stem length and proportion of fruits with sound seeds per diaspore (Table 2). Diaspores from trees in the Levka Ori had in general higher sound seed proportions and longer diaspore stem lengths than trees from Psiloritis or Dikti, while the latter two had similar values (Table 3). The nested linear models confirmed these findings (Table 4). Indeed, for all diaspore variables except for proportion of fruits with sound seeds per diaspore and diaspore stem length, most of the observed variation found within the variables was imputable to differences amongst trees and not to differences between mountain ranges. Indeed, for most traits the variance for mountain ranges was very low or close to zero. Only diaspore stem length showed

**Table 2**

Results of the Kruskal-Wallis rank sum test to test for significance of differences between different trees or mountain ranges for each diaspore trait, fruit weight, proportion of fruits with sound seeds and tree size. Significant ( $p < 0.05$ ) values are given in bold. Degrees of freedom for trees is 35 (except for weight of sound fruits, df: 23) and for mountains is 2 (except for weight of sound fruits, df: 1). NA values are given for variables for which only one value is measured per tree.

Trait	Trees		Mountains	
	X <sup>2</sup>	p-value	X <sup>2</sup>	p-value
Nb. fruits	300.7	<0.0001	0.67	0.72
Nb. leaves	184.15	<0.0001	0.62	0.73
Leaf length	294.27	<0.0001	0.89	0.64
Leaf width	251.07	<0.0001	0.88	0.64
LMA	1075.7	<0.0001	3.11	0.21
Stem length	323.14	<0.0001	11.88	<b>0.003</b>
Nb. galls	363.21	<0.0001	5.98	0.05
Prop. sound fr. per diaspore	224.32	<0.0001	18.02	<b>0.0001</b>
Weight sound fruits	494.53	<0.0001	2.14	0.14
Weight unsound fruits	1029.9	<0.0001	4.01	0.13
Prop. sound fr. per tree	NA	NA	20.78	<0.0001
Tree height	NA	NA	10.31	<b>0.006</b>
Trunk circumference	NA	NA	1.26	0.53
Canopy extension	NA	NA	5.06	0.08

**Table 3**

P-values of pairwise comparisons between mountain ranges using Wilcoxon rank sum test with continuity correction for proportion of fruits with sound seeds per diaspore and per tree as well as diaspore stem length. Significant ( $p < 0.05$ ) values are in bold.

		Psiloritis	Dikti
Prop. sound fruits per diaspore	Levka Ori	<b>0.03</b>	<b>0.0005</b>
	Psiloritis	–	0.72
Stem length	Levka Ori	<b>0.002</b>	<b>0.04</b>
	Psiloritis	–	0.08
Prop. sound fruits per tree	Levka Ori	<b>0.02</b>	<b>0.0002</b>
	Psiloritis	–	0.50
Tree height	Lekva Ori	<b>0.02</b>	<b>0.04</b>
	Psiloritis	–	0.11

slightly higher variation amongst mountain ranges than amongst trees whereas proportion of fruits with sound seeds per diaspore showed over 3.5 times more variation amongst mountain ranges than amongst trees (Table 4).

### 3.3. Seed soundness per tree

26% of all collected fruits were estimated to have sound seeds. However, seed soundness per tree strongly varied amongst trees, with 32% of investigated trees having 0% of fruits with sound seeds and the remaining 68% of trees having values ranging from 0.15% to 56% of sound seeds (average 23%, Table 5 & Supplementary Material Fig. S3). Seed soundness proportion per tree and proportion of trees with sound seeds strongly varied between regions. In western Crete in the Levka Ori, average seed soundness per tree was 23.59%, and all but one of the sampled trees had fruits with sound seeds. None of the sampled trees of central Crete (Psiloritis) had fruits with sound seeds. In eastern Crete on Mt. Dikti, average seed soundness per tree was 0.64% and only two trees had fruits with sound seeds. Variations in the proportion of seed soundness were significantly different between the three investigated mountain ranges (Table 2), and the Levka Ori had significantly higher sound seed proportions than Psiloritis and Dikti. At the same time, the latter two showed no significant differences (Table 3).

### 3.4. Fruit weight

Fruit weight was on average  $15.45 \pm 2.87$  mg (range: 11.06–22.17 mg) for sound fruits and  $9.12 \pm 1.34$  mg (range: 5.91–12.95 mg) for

**Table 4**

Summary of the nested linear models. Two ecological scales were used: trees and mountains. Trees were considered as being nested amongst mountains. The evaluated variables were: leaf width, leaf length, leaf mass per area, diaspore stem length, number of leaves, number of fruits, number of galls, the proportion of fruits with sound seeds per diaspore and fruit weight. Degrees of freedom of trees: 36 (except for sound fruit weight: 24), mountains: 3 (except for sound fruit weight: 2). Variance, standard deviation (Std. dev.) and the number of observations (N) are given.

		Variance	Std. dev.	N
Leaf width	Tree	1.60	1.23	2170
	Mountain	0.00	0.00	
	Residual	5.51	2.35	
Leaf length	Tree	6.95	2.64	2225
	Mountain	0.00	0.00	
	Residual	12.40	3.92	
Leaf mass per area	Tree	0.0002	0.02	2037
	Mountain	0.00003	0.01	
	Residual	0.0002	0.02	
Stem length	Tree	30.39	5.51	534
	Mountain	30.67	5.54	
	Residual	30.39	5.51	
Nb leaves	Tree	0.01	0.11	539
	Mountain	0.00	0.00	
	Residual	1.00	1.00	
Nb fruits	Tree	0.15	0.38	539
	Mountain	0.00	0.00	
	Residual	1.00	1.00	
Nb galls	Tree	7.27	2.70	539
	Mountain	1.24	1.11	
	Residual	1.00	1.00	
Prop. sound fr. per diaspore	Tree	1.81	1.35	501
	Mountain	6.48	2.55	
	Residual	1.00	1.00	
Weight sound fruits	Tree	11.57	3.40	924
	Mountain	1.67	1.29	
	Residual	11.69	3.42	
Weight unsound fruits	Tree	3.59	1.89	1591
	Mountain	0.21	0.46	
	Residual	2.37	1.54	

unsound fruits (Table 5 and Supplementary Material Fig. S4). Wilcoxon signed rank test (on the 24 trees for which there are both sound and unsound fruit weight data) showed that the weight of sound and unsound fruits in a given tree was significantly ( $p$ -value  $<0.001$ ) different. Fruit weight (both sound and unsound) was not found to be significantly different ( $p$ -values  $>0.05$ ) between mountain ranges (Table 2), although sound fruits from Dikti (12.51 mg) were on average lighter than those of Levka Ori (15.71) and the unsound fruits from Psiloritis were on average lighter (7.09 mg) than those of Levka Ori (9.40 mg) and Dikti (9.04 mg), respectively (Table 5). Indeed, fruit weight showed higher variability between trees than amongst mountain ranges (Table 4).

### 3.5. Tree size

Tree height, trunk circumference at breast height and canopy extension for every sampled tree are shown in Table 6 and per mountain range in Supplementary Material Fig. S5. Tree height varied significantly between mountain ranges (Table 2) and was significantly higher in the Levka Ori compared to both Psiloritis and Dikti (Table 3). Psiloritis had the smallest sampled trees, but no statistically significant difference was found with trees from Dikti. Trunk circumference was rather homogenous between mountain ranges and no significant differences were found (Table 2). Although no significant differences were detected between mountain ranges for canopy extension (Table 2), several trees in the Levka Ori had larger canopies than trees anywhere else (Table 6 and Supplementary Material Fig. S5).

### 3.6. Correlation between variables

Spearman's correlation coefficients between diaspore traits, fruit weight, seed soundness and tree size are presented in Fig. 4. The number of fruits per diaspore is significantly positively correlated with LMA and sound fruit weight and is negatively correlated with number of galls per diaspore. In addition, trees that have heavier fruits also tend to have significantly more fruits and leaves per diaspore, bigger leaves, and longer diaspore stems. Fruit weight is not significantly correlated with the proportion of fruits containing sound seeds per diaspore but is positively correlated with the proportion of fruits containing sound seeds per tree. There is no significant correlation between the number of galls and the proportion of fruits with sound seeds. However, a significant negative correlation exists between the number of galls per diaspore and sound fruit weight. In general, the number of galls per diaspore is (significantly or not) negatively correlated with most other variables. In addition, both tree height and canopy extension are significantly and positively correlated with diaspore stem length and proportion of fruits with sound seeds per tree.

## 4. Discussion

### 4.1. Architecture and effectiveness of the diaspores

Several traits of the diaspores of *Z. abelicea* were analysed for the first time within this study. To our knowledge, only Certini et al. (2020) and Jasińska et al. (2021) mentioned some characteristics of *Z. abelicea* diaspores. Certini et al. (2020) reported (albeit from a single cultivated *Z. abelicea* specimen growing in Switzerland) on average 3.88 leaves (range: 3–6) and 2.00 fruits (range: 1–3) per diaspore. In our study, we found an average of 4.57 leaves (range 1–8) and 1.79 fruits (range 0–6) per diaspore. Since only a single (cultivated) tree was sampled by Certini et al. (2020), we cannot assess if the differences in fruit and leaf number compared to the present study are due to tree specificities or can be imputed to differences in environmental conditions. Jasińska et al. (2021) found averages of 19.80 mm in length and 12.20 mm in width of leaves from fructifying shoots (i.e., diaspores) of *Z. abelicea*. In our study, the average leaf length was 15.56 mm and width 9.10 mm. The slight differences in leaf size found by these authors compared to the values of the current study are probably imputable to differences in sampling strategy, sampling sites and trees as well as sample size. Jasińska et al. (2015, 2021) further studied leaf length and width on fructifying shoots of *Z. carpinifolia* (average 34.3 and 18.2 mm, respectively) and *Z. sicula* (23.9 and 14.0 mm, respectively). These results show that diaspores of *Z. abelicea* have smaller leaves than both other species, measuring half the size of those of *Z. carpinifolia* and about two-thirds the size of the leaves of its Sicilian relative. Moreover, Hoshino (1990) investigated the number of leaves, the number of fruits and the stem length of diaspores of *Z. serrata* individuals from Japan. He found the following average values: 4.10 leaves and 2.70 fruits per diaspore, with an average length of 47.8 mm. Diaspores of *Z. abelicea* have on average more leaves, but fewer fruits and measure ca. half of the length of those of *Z. serrata*.

The short diaspores and small sized leaves of *Z. abelicea* are probably evolutionary adaptations to local conditions and a consequence of the long isolation of the species within its current refugial area, as previously hypothesised by Christe et al. (2014), Garfi et al. (2021) and Jasińska et al. (2021). Indeed, thermo-hydric stress is known to reduce growth in trees (Bréda et al., 2006; Fotelli et al., 2000; Garfi et al., 2021), and plants growing in xeric environments are known to have small leaves that are better adapted to withstand drought than larger ones (Farooq et al., 2009). Wang et al. (2001) state that the small-sized leaves of both Mediterranean *Zelkova* species can be explained by the high levels of evapotranspiration experienced by these species in their habitat during summer.

*Z. abelicea* has more leaves per diaspore while having shorter stem lengths than *Z. serrata* which implies that the leaves are more densely

**Table 5**

Total collected fruit counts, number of fruits with sound and unsound seeds, estimated proportion of fruits with sound seeds over the entire seed lot (Est. sound fr. prop) and average weight for sound and unsound fruits. For sound and unsound fruits, the percentage of misplaced fruits (i.e. unsound in sound and vice-versa) is given in parenthesis. Standard deviations of fruit weight per tree are also provided. \* shows trees for which the percentage of misplaced fruits was not calculated when there was less than 50 sound fruits.

Mountain	Tree ID	Fruit number			Est. sound fr. prop. (%)	Av. fruit weight (Mg)	
		Total	Sound	Unsound		Sound	Unsound
Levka Ori	XYLO1	1312	297 (2%)	1015 (3%)	22.64	21.77 ± 4.04	12.95 ± 2.23
	CROS1	250	49*	201 (2%)	19.60	11.06 ± 2.94	5.91 ± 1.07
	CROS2	2619	499 (9%)	2120 (0%)	19.05	14.60 ± 1.95	7.35 ± 1.00
	CROS3	3057	634 (0%)	2423 (3%)	20.74	20.52 ± 4.10	12.24 ± 2.47
	XERO1	1175	400 (0%)	775 (4%)	34.04	18.36 ± 3.24	9.34 ± 1.56
	XERO2	5796	2669 (21%)	3127 (9%)	46.05	16.20 ± 2.59	10.39 ± 1.74
	XERO3	923	514 (10%)	409 (3%)	55.69	14.10 ± 2.06	8.90 ± 1.07
	XERO4	12287	6912 (1%)	5375 (13%)	56.25	13.41 ± 2.55	9.72 ± 1.30
	XERO5	5440	2909 (10%)	2531 (0%)	53.47	17.85 ± 6.31	11.08 ± 3.05
	MACH1	2007	637 (0%)	1370 (0%)	31.74	22.17 ± 3.74	10.44 ± 1.84
	MACH2	2055	857 (0%)	1198 (0%)	41.70	19.44 ± 3.22	11.22 ± 1.17
	MACH3	2056	1003 (10%)	1053 (6%)	48.78	20.45 ± 2.85	12.24 ± 1.61
	LOFO1	873	132 (3%)	741 (10%)	15.12	15.28 ± 3.02	10.05 ± 1.46
	LOFO2	840	177 (3%)	663 (6%)	21.07	13.78 ± 2.88	8.78 ± 1.62
	LOFO3	1347	186 (8%)	1161 (2%)	13.81	13.74 ± 2.33	8.13 ± 1.36
	THER1	1470	231 (2%)	1239 (0%)	15.71	17.43 ± 3.14	11.49 ± 1.54
	THER2	388	76 (3%)	312 (13%)	19.59	12.70 ± 2.97	8.93 ± 1.76
	THER3	2368	285 (17%)	2083 (3%)	12.04	11.88 ± 2.05	6.21 ± 1.14
	THER4	1062	197 (2%)	865 (7%)	18.55	11.23 ± 1.47	6.63 ± 0.82
	IMB1	1340	4*	1336 (0%)	0.30	13.75 ± 3.18	8.63 ± 0.79
	IMB2	1317	2*	1315 (0%)	0.15	NA	6.52 ± 0.81
	IMB3	2221	30*	2191 (0%)	1.35	11.71 ± 1.34	7.42 ± 0.88
	IMB4	1403	15*	1388 (0%)	1.07	14.28 ± 2.62	9.56 ± 0.96
	Psiloritis	VILL1	429	0	429 (0%)	0.00	-
PSI1		49	0	49 (0%)	0.00	-	7.60 ± 0.94
PSI2		34	0	34 (0%)	0.00	-	6.56 ± 1.40
Dikti	PSI14	78	0	78 (0%)	0.00	-	7.12 ± 1.10
	PROT1	4426	0	4426 (0%)	0.00	-	8.82 ± 1.04
	PROT2	3063	0	3063 (0%)	0.00	-	9.62 ± 1.22
	PROT3	5696	0	5696 (0%)	0.00	-	9.57 ± 1.10
	VIAN1	623	0	623 (0%)	0.00	-	8.00 ± 1.11
	VIAN2	1467	0	1467 (0%)	0.00	-	8.06 ± 1.32
	LAS1	951	0	951 (0%)	0.00	-	9.37 ± 1.17
	LAS2	786	0	786 (0%)	0.00	-	9.93 ± 0.95
	LAS3	935	0	935 (0%)	0.00	-	12.69 ± 1.81
	KATH1	721	13*	708 (0%)	1.80	13.26 ± 2.27	7.41 ± 0.94
KATH2	153	7*	146 (0%)	4.58	11.77 ± 2.11	6.94 ± 0.86	
	Total	73017	18735 (6%)	54282 (3%)	15.54	15.45 ± 2.87	9.12 ± 1.34
	Levka Ori (N = 24)	54035	18715	35320	23.69	15.71 ± 2.94	9.40 ± 1.44
	Psiloritis (N = 3)	161	0	161	0	-	7.09 ± 1.15
	Dikti (N = 10)	18821	20	18801	0.64	12.51 ± 2.19	9.04 ± 1.15

arranged on the diaspore. Despite these structural differences, [Certini et al. \(2020\)](#) pointed out that flight mechanisms and velocity of diaspores were similar in both species, suggesting a remarkable evolutionary conservation of the traits responsible for dispersal. We hypothesise that leaf blade size reduction – most likely an adaptive trait related to more xeric environmental conditions as discussed above – is compensated by an increase in the number of leaves to preserve flight and dispersal effectiveness. However, this topic, as well as the fact that *Z. abelicea* has fewer fruits per diaspore compared to its Asian relative, need yet to be further investigated.

#### 4.2. Fruit weight

Until the present study, the only published records concerning fruit weight in *Z. abelicea* were those reported by [Fournaraki and Thanos \(2002\)](#) and [Certini et al. \(2020\)](#). The former reported an average weight of  $15.22 \pm 0.22$  mg for 120 sound fruits collected from a single location (unknown number of trees) in the Omalos region in the Levka Ori mountains in western Crete. [Fournaraki and Thanos \(2002\)](#) also stated that fruits with unsound seeds usually weigh less than 10 mg but did not give more details, nor how many fruits they weighed. [Certini et al. \(2020\)](#) sampled a single cultivated tree growing in Switzerland, which

had only fruits with unsound seeds and gave an average weight of 10.6 mg (27 fruits, range 8–13 mg). With the present study, we analysed the fruit weight of 2519 fruits (1591 unsound, 928 sound) from throughout the distribution range of *Z. abelicea*. The among-tree average of 15.45 mg for sound fruits is similar, albeit slightly higher than the above-mentioned value found by [Fournaraki and Thanos \(2002\)](#). For unsound fruits, we found lower values than those given by [Certini et al. \(2020\)](#). Moreover, in our study, we noticed that fruit weight is highly fluctuant amongst trees ([Table 5](#)) and that no significant differences were found between mountain ranges. Indeed, trees taken in the same area as [Fournaraki and Thanos \(2002\)](#) and less than 4 km apart from one another hold the average maximum (22.17 mg, MACH1) and minimum (11.06 mg, CROS1) fruit weight for sound fruits and also maximum (12.95 mg, XYLO1) and minimum (5.91 mg, CROS1) fruit weight for unsound fruits. Nevertheless, sound fruits of trees from the Levka Ori are on average heavier than those from Dikti (but the very small sound fruit sample size of Dikti may have biased the results), whereas unsound fruits from Psiloritis are lighter than those of the two other mountain ranges.

**Table 6**

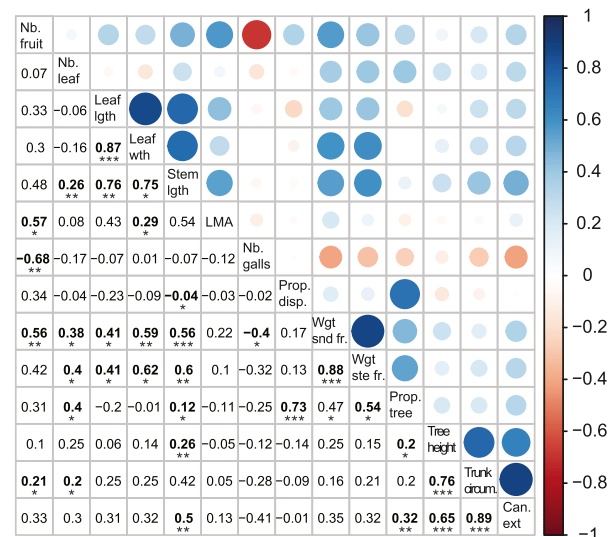
Tree size variables: tree height, trunk circumference (circum) at breast height and canopy extension (can. ext.) for each sampled tree with mountain-wise averages.

Mountain	Tree ID	Height (m)	Circum (m)	Can. ext. (m)	
Levka Ori	XYLO1	10.93	1.44	20.70	
	CROS1	8.27	0.63	12.00	
	CROS2	11.85	0.55	9.50	
	CROS3	5.36	0.66	12.10	
	XERO1	7.30	0.70	16.50	
	XERO2	12.61	2.75	21.00	
	XERO3	11.58	1.76	25.20	
	XERO4	7.09	0.83	11.80	
	XERO5	9.09	0.84	17.20	
	MACH1	9.35	0.82	11.40	
	MACH2	14.04	2.21	20.40	
	MACH3	9.64	1.44	19.80	
	LOFO1	6.13	0.60	9.90	
	LOFO2	8.77	0.41	5.40	
	LOFO3	9.89	0.94	15.80	
	THER1	8.41	0.70	12.60	
	THER2	8.23	1.06	13.90	
	THER3	11.41	1.15	13.10	
	THER4	7.01	0.90	13.10	
IMB1	10.52	1.25	17.80		
IMB2	14.28	1.20	17.90		
IMB3	11.29	1.27	20.10		
IMB4	8.10	1.37	19.60		
VILL1	3.50	0.40	4.65		
Mountain average		9.36	1.08	15.06	
Psiloritis	PSI1	4.81	1.40	11.80	
	PSI2	3.55	0.80	11.70	
	PSI14	6.01	0.95	12.80	
	Mountain average		4.79	1.05	12.10
Dikti	PROT1	8.34	2.30	16.40	
	PROT2	8.31	0.86	NA	
	PROT3	8.73	1.90	9.70	
	VIAN1	6.51	0.75	13.10	
	VIAN2	8.01	0.82	12.80	
	LAS1	5.54	0.50	7.60	
	LAS2	3.91	0.36	6.20	
	LAS3	5.45	0.68	12.00	
	KATH1	5.94	0.50	10.40	
	KATH2	10.16	0.94	12.70	
	Mountain average		7.09	0.96	11.21

#### 4.3. Seed soundness within diaspores and trees: a longitude-dependent fitness pattern

Twenty-five out of the thirty-seven sampled trees (i.e., 68%) had fruits with sound seeds, with a vast soundness variation ranging from 0.15% to 56.25%. These values are in line with the few and geographically restricted previous studies (Egli, 1997; Fournaraki and Thanos, 2006; Søndergaard and Egli, 2007). The positive correlation between seed soundness rates of trees and diaspores shows that in general, trees that have higher proportions of sound fruits also have higher ratios of sound fruits per diaspore.

A highly interesting finding is the striking geographical difference in seed soundness. Indeed, all but one sampled tree from Levka Ori had fruits with sound seeds, whereas soundness reached only 20% in Dikti and was null for all sampled trees from Psiloritis. This means that based on our study, for a majority of trees growing in the populations located outside of the westernmost mountains (Levka Ori), the production of sound seeds is relatively poor. These results suggest that seed soundness is most probably strongly influenced by a factor following a longitudinal gradient in Crete. Such an assumption goes in the same direction as the findings of Fazan et al. (2022a) who found that shoots of *Z. abelicea* trees in western Crete grow more than shoots of trees in eastern Crete due to a west-to-east gradient of seasonal precipitation. It is most probable that this climatic gradient also strongly impacts the reproductive biology of the species. At present it is not possible to test this assumption further due to the need for precise enough weather data for



**Fig. 4.** Spearman's rank correlation results between diaspore traits, fruit weight, proportion of fruits with sound seeds per tree and tree size. Leaf lgth: leaf length, leaf wth: leaf width, stem lgth: diaspore stem length, LMA: leaf mass per area, prop. disp.: proportion of fruits with sound seeds per diaspore, wgt snd fr.: weight sound fruits, wgt ste fr.: weight unsound fruits, prop. tree: proportion of fruits with sound seeds per tree, trunk circum: trunk circumference, can. ext.: canopy extension. Significant rho estimates are given in bold with significance levels (\* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ ). Red circles indicate negative correlations while blue circles indicate positive correlations.

interpolating weather patterns occurring in the Cretan mountains (see Fazan et al., 2022a for a discussion on the subject). Further research should be carried out to understand why embryos do not develop in some seeds, and if this could be due to a pollination failure, or if embryos started developing and then halted due to, e.g., embryo development limiting environmental conditions.

In addition, we lack a multi-year perspective to see if our results could differ depending on yearly precipitation amounts and/or in relation to masting events. Other authors have shown that fruit weight tends to be stable for a given tree species between years (Augspurger et al., 2016). Water stress, however, has been found to explain higher levels of seed abortion in other Mediterranean tree species (e.g., Espelta et al., 2008; García et al., 2000; Pérez-Ramos et al., 2010). The fact that the proportion of sound seeds is deficient in central and eastern Crete, coupled with less favourable growth conditions, could explain the absence of *Z. abelicea* seedlings already recorded by Fazan et al. (2021) in those areas. The fact that all sampled trees in Psiloritis had unsound seeds, while at the same time having the lowest fruit weight is pre-occupying. These results may be biased by the small sample size in that location, but could also mirror more adverse conditions, inhibiting normal seed and fruit development. Indeed, Fazan et al. (2022b) also showed poorer site conditions in Psiloritis than other sites hosting *Z. abelicea* trees. Nevertheless, since Christe et al. (2014) found strong genetic differences in *Z. abelicea* populations growing on each mountain range, we cannot rule out a possible genetic control that would be mirroring the longitudinal gradient found in terms of diaspore stem length and proportion of fruits with sound seeds.

#### 4.4. The importance of intraspecific trait variations

Most of the investigated traits showed stronger between-tree variation than between-mountain variation. This result supports the highly conservative aspect of the investigated traits within the species, despite a history of mountainwise isolation and drift (Christe et al., 2014).



Moreover, this also suggests the absence of a significant influence of environmental factors on many traits. High intraspecific variation in traits linked with dispersal is not uncommon in tree species (e.g. Augspurger et al., 2016; Sipe and Linnerooth, 1995; Song et al., 2020; Wyse et al., 2019) and may result from high heritability (Wyse et al., 2019). However, it could also be a kind of bet-hedging strategy (Song et al., 2020; Wyse et al., 2019), to maximise the species chances of effective dispersal and may have important evolutionary and ecological implications (Sipe and Linnerooth 1995). In addition, in a context of rapidly changing climatic conditions, high intraspecific variation may also benefit to the species (Chevin et al., 2010; Forsman, 2013).

#### 4.5. Influence of tree size and galls on seed soundness

Our results showed a positive relationship between larger tree size, higher proportion of sound seeds per tree, heavier fruit weight and longer diaspores with more fruits and leaves. Sampled trees from Levka Ori were also bigger, although not significantly, than those from Psiloritis and Dikti. These findings, in addition to the mountain-wise difference in proportion of fruits with sound seeds tend to point towards a general reduction trend outside of the Levka Ori, both in terms of number and size of diaspore traits but also tree size. Reduction patterns and small size are considered an adaptive response to thermo-hydric stress (Abeli et al., 2014; Garfi et al., 2002, 2021). These assumptions are supported by the strong climatic gradients found on Crete, with a sharp decrease in precipitation occurring from west to east (Agou et al., 2019; Goedecke and Bergmeier, 2018; Varouchakis et al., 2018). In addition, an increase in LMA is visible eastwards (Supplementary Material, Fig. S2E), although differences between mountain ranges are not significant. LMA has been reported to be negatively correlated with soil water content and availability as it increases with water stress (de la Riva et al., 2016; Poorter et al., 2009), therefore clearly demonstrating that trees in central and eastern Crete suffer more from water depletion than trees in western Crete.

A biotic agent was also found to affect fruit production and negatively correlate with most tree traits. Galls were found on 53% of the sampled trees. However, this result strongly depended on the sampling design, and numbers may have been entirely different if other trees had been sampled. The number of galls per diaspore does not seem to follow a geographical pattern on the island but varies according to the sampled tree. Galls were present or absent from some trees both in western and eastern Crete, although none of the investigated trees in Psiloritis contained galls, suggesting unsuitable conditions for the development of the Cecidomyiidae larvae or an absence of colonisation by the insect in this area. No strong and significant relationship between seed soundness and gall presence or quantities were found, which reinforces the idea that seed soundness is mainly driven by environmental gradients. Nevertheless, we found a clear trend showing that diaspores with higher number of galls tended to have fewer and lighter fruits, and galls were overly negatively correlated, albeit often not significantly, with most other variables. Although further investigations should be carried out, this could imply a negative effect of gall abundance and presence on flowering or fruit production. This could be explained by the fact that the larvae cause abnormal development and functioning of stamens, therefore, preventing pollination, or that plants invest energy to produce galls, thus inducing a shortage of resources to be allocated to viable embryo development (Collins and Drummond, 2019; Koprudova et al., 2015).

#### 4.6. Implications for conservation

Our findings suggest that morphological traits of diaspores are ultimately not significantly affecting the functioning of dispersal mechanisms of *Z. abelicea* at an inter-population level. This is not the case for recruitment through seed, which is relatively successful in the westernmost populations but is entirely ineffective in those from central and

eastern Crete. In these latter areas, *Z. abelicea* trees produce lower to null sound fruit proportions, are smaller and their diaspores and fruit weight show features typical of trees suffering (more) from suboptimal growth conditions compared to those of western Crete. This fact is alarming for the long-term persistency of *Z. abelicea*, at least outside of the Levka Ori mountain range. Although *Z. abelicea* is known to sucker profusely, especially after disturbance events (Egli, 1997; Fazan et al., 2012; Kozłowski et al., 2018), the absence of sexual reproduction and/or efficient recruitment will ultimately lead to the reduction or even to the disappearance of the most marginal populations (García et al., 2000; Hampe, 2005; Hampe and Arroyo, 2002). The fact that no fruiting trees were observed in the easternmost population of Thripti may already point towards this ongoing process. The lack of sexual reproduction and the shrinkage or extinction of *Z. abelicea* populations on a local scale will impoverish the high genetic diversity still detected within the species (Christe et al., 2014) and thus impact the evolutionary and adaptation potential to climate change of the remnant populations (Hampe and Petit, 2005).

## 5. Conclusions

Diaspore traits, fruit weight and seed soundness of *Z. abelicea* were studied for the first time over the whole species distribution range. We found substantial variability between trees but less so between mountain ranges. However, the few variables that varied depending on the mountain range all point towards trees thriving better in western Crete. Seed soundness showed a clear longitudinal pattern, probably following a gradient in environmental factors, the most probable being longitudinal precipitation gradients. Trees in central and eastern Crete seem to suffer more from water-limiting climatic conditions than trees in western Crete. These findings are preoccupying for the long-term persistency of *Z. abelicea* in the most marginal parts of its natural distribution range.

### Author contributions

**Laurence Fazan:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data Curation, Writing – Original Draft, Visualization, Project administration, **Daniele Certini:** Writing – Review & Editing, **Salvatore Pasta:** Conceptualization, Methodology, Investigation, Resources, Data Curation, Writing – Review & Editing, **Ilektra Remoundou:** Writing – Review & Editing, **Dany Ghosn:** Writing – Review & Editing, **Giuseppe Garfi:** Conceptualization, Methodology, Investigation, Writing – Review & Editing, Supervision, **Gregor Kozłowski:** Writing – Review & Editing, Supervision, Project administration, Funding acquisition.

### Funding

This work was supported by the Fondation Franklinia. Permits to study, collect, and export plant material was granted from the Greek Ministry of Environment, and the regional CITES Management Authority of Crete under permits n°155924/1184, n°160737/2258 and n°2522.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data availability

Data will be made available on request.

## Acknowledgements

We thank Polymnia Sklavaki from the Forest Directorate of Chania, Hara Kargiolaki from the Forest Directorate of Rethymno, Emmanouil Flouris from the Forest Directorate of Iraklio, Emmanouil Siligardos from the Forest Directorate of Lassithi for their support during the implementation of in the project, Panagiota Gotsiou, Christini Fournaraki, Adamantia Kokkinaki and Eleni Markaki from the Mediterranean Plant Conservation Unit of the Mediterranean Agronomic Institute of Chania for their technical support, Prof. Costas Thanos from the National and Kapodistrian University of Athens for sharing his knowledge and his suggestions, Dimos Dimitriou from the Forest Directorate of Chania and Eirini Koukoulou for their support during fieldwork, Maria Litto from the University of Fribourg for tips using ImageJ, François Rion for his support and Evelyne Kozłowski for permission to use her picture. We thank the anonymous reviewers who read and commented on a previous version of the manuscript.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.actao.2023.103896>.

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