ORIGINAL PAPER

Reproductive biology of *Abies cephalonica* Loudon in Mount Aenos National Park, Cephalonia, Greece

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Abstract The reproductive biology of the endemic to Greece *Abies cephalonica* Loudon, including the phenology of the reproductive life cycle, cone production in relation to plant age and the required seed germination conditions, was studied. All individuals growing within 20 permanent plots of 100 m² each established in 11 different locations covering the entire strictly protected area of Mount Aenos National Park (Cephalonia) were monitored over a period of 4 years. The cones are formed on the upper part of the previous year's branches, mostly at the upper crown half of the reproductive individuals (over 53 years old). Female flowers are pollinated in spring and cone maturation lasts until the beginning of autumn, when seed dispersal occurs. The annual production of cones per individual varied significantly, revealing masting behavior for this tree. This behavior was also expressed in the number of trees producing cones, as well as the percentage of sound seeds per cone. A significant difference in the mass and the length of the cones between the years of low and high cone production was observed, being higher in the years of massive cone production. Similar germination percentages were observed in full darkness or under "canopy light" and "sun light", provided that the seeds were previously stratified for 6 weeks. It is concluded that *A. cephalonica* exhibits plasticity expressed in its reproductive behavior for alternating years of high to low cone production and in its seed germination for an array of habitat light conditions.

Introduction

The Mediterranean Basin hosts eight *Abies* taxa (Farjon and Rushforth 1989) and constitutes one of the genus distribution centres (Parducci 2000). Among those, the endemic to Greece *Abies cephalonica* Loudon (Greek fir) is the only Mediterranean taxon with island populations, in Euboea and Cephalonia, in the Aegean and the Ionian Sea, respectively. A decrease in Greek fir populations has been reported in Greece during the last five decades. This decrease has been attributed to various reasons such as drought-related extreme periods, infestation by mistletoe, pathogens or insects, as well as root damage (Kailidis and Georgevits 1968; Raftoyannis and Radoglou 2001; Tsopelas et al. 2001). Fire episodes spreading over high altitudes have been added recently to these risks, imposing an additional threat to this non-fire resilient species (Arianoutsou 2007; Arianoutsou et al. 2009).

Reproduction, seed dispersal, germination, and seedling establishment constitute the most critical stages in a plant's life cycle (Kavanagh and Carleton 1990). Aspects of the life cycles of *A. amabilis, A. balsamea, A. grandis, A. lasiocarpa* and *A. pinsapo* have been described in various levels of detail by many authors (see for example Owens and Molder 1977a, b; Powell 1970; Singh and Owens 1981, 1982; Arista and Talavera 1994b). *Abies* species require

Communicated by T. Grams.

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almost one and a half to 2 years for completing their reproductive cycle (Liu 1971; Singh and Owens 1981; Arista and Talavera 1994a; Edwards 2003; Messaud et al. 2007). Entry into the reproductive phase is an important milestone in the life of trees, as regards resource allocation. Assimilates previously reserved exclusively to vegetative growth are then allocated to generative processes too (Seifert and Müller-Starck 2009). High-altitude conifers mature reproductively around the age of 40–50 years (Burshel 1987).

Abies taxa are among the plants with masting behavior. Mast-fruiting or masting behavior has been interpreted mainly as the synchronous intermittent production of large seed crops in perennial plants (Kelly and Sork 2002) as well as the cumulative result of the reproductive patterns of individuals within a population (Koenig et al. 2003) in which there is a synchronization both in time and in size of crop. Most masting species are iteroparous, flowering and fruiting multiple times during their life span (Silvertown 1980). This phenomenon has been reported across a broad range of long-lived plants and in many forest ecosystems (Herrera et al. 1998; Koenig and Knops 2000; Kelly and Sork 2002; Schauber et al. 2002; Suzuki et al. 2005; Lázaro et al. 2006). The annual variability of cone production in populations of *A. cephalonica* has been reported following observations in northern Greece (Panetsos 1975; Dafis 1986), but little is known about the production of seeds, their dispersal and their germination.

Seedling emergence at the right place and time is important for a plant's life (Fenner and Thompson 2006). Sometimes, this requirement is satisfied by germination as soon as seeds are shed, but in most *Abies* species there is a delay of a few months. One important mechanism for achieving this delay is seed dormancy (Fenner and Thompson 2006). Most, if not all, fir species exhibit some degree of dormancy (Edwards 2003), the alleviation of which is succeeded by stratification (moist chilling) (Edwards 1982; Fady et al. 1991). Conditions of stratification are set to approximate the environments that autumn-ripening seeds might find themselves exposed to upon dissemination (Krugman et al. 1974). Stratification has been shown to improve the germination (in terms of capacity and/or speed) of several *Abies* species, which also proves that dormancy is relevant to these seeds (Edwards 1982). The presence of any form of obstacles on the ground (the presence of herbaceous plants, bryophytes, rocky outcrops and stones) creates a spatial pattern that may affect the distribution and survival of fir seedlings in the same way reported for other treeline conifers (Dobrowolska 1998; Germino et al. 2002; Politi et al. 2009).

Despite the importance of insular populations of *A. cephalonica* for the genetic integrity of the species and avoidance of its introgression in Greece and the Mediterranean Basin, practically no study has ever documented in detail the course of its reproductive biology, a step that is necessary in all management plans. Studies on the functional and population ecology of *A. cephalonica*, as well as simulation of population dynamics have been published only recently (Politi 2009; Politi et al. 2007, 2009; Fyllas et al. 2010). The aim of this work is to study the main aspects of *A. cephalonica*'s reproductive biology within the protected area of Mount Aenos National Park, Cephalonia Island, Greece, forming one of the two insular populations of the species. To achieve this, the phenology of *A. cephalonica*'s reproductive behavior was monitored in the field for a period of 4 years in permanently established plots distributed throughout the Park and covering the heterogeneity of the species' habitat (for details see Politi et al. 2009). Annual cone and seed production was also recorded over the same period in an effort to document its masting periodicity. Finally, the study was complemented with laboratory experimentation in order to test seed germination requirements in light regimes simulating various habitat conditions.

Methods

Study area

Mount Aenos National Park, designated as a Site of Community Importance (NATURA 2000 network), was established in 1962 with the purpose of preserving the forest ecosystem and protecting the endemic Greek fir, *Abies cephalonica*. The Park covers an area of 28.6 km², and runs almost 11 km from NW to SE (38°09′04″N, 20°38′38″E), from an elevation of 900 m to 1,628 m at the peak of Mount Aenos. *A. cephalonica* forms pure stands extending from the lowest to the highest point on the mountain, although a few scattered individuals occur at lower elevations. Forest coverage is about 94%, while several herbaceous endemic species flourish in the understorey (Politi 2009). Forest composition is constant along the elevation gradient and aspect.

According to Köppen's climate classification, the climate is characterized as Csb Mediterranean with wet winters and dry summers although occasional summer precipitation might occur. Temperature and rainfall might be different across the elevation gradient studied; however, this was not possible to be tackled as there are no weather stations established across this gradient. The temperature of the warmest month is below 22°C on average. The Adriatic Sea currents often bring fog that in the dry summer months may be critical for sustaining the growth of these large trees as it has been also found for other coastal coniferous

forests, e.g. Californian redwoods (Azevedo and Morgan 1974; Dawson 1998; Ewing et al. 2009).

Snow cover usually lasts from mid-December to mid-March. During the study period (2004–2007), annual precipitation varied between 600 and 1,500 mm, approximately. Higher precipitation was recorded for years 2005 and 2007 (857 mm and 1,515 mm respectively), in contrast to that recorded for 2004 and 2006 (584 and 654 mm, respectively). During the study period, mean air temperature reached the highest value during July 2007 (26.5°C) and the lowest (1.5°C) during January and February in most of the years of study.

The basement rock of the mountain is calcareous hard limestone, with a clay soil texture, while mineral soil depth is rather shallow (30–40 cm) with frequent rocky outcrops (for more details see Politi et al. 2009).

Monitoring of reproduction phenology

A network of 11 different locations covering the entire protected area of the National Park was used for monitoring the population of *A. cephalonica*. The locations extended over an altitudinal gradient ranging from 1,000 to 1,620 m and represented different topographic conditions (elevation, aspect and slope), as well as varying degrees of canopy closure and ground cover; canopy closure ranged from 0.07 to 0.37 in all study locations, where ground was more or less covered by rocks and logs (Politi et al. 2009). In each location, two permanent 100 m^2 plots were established, with the exception of two locations where only one plot could be established. All individuals occurring in the plots were assigned to a specific age class by correlating their morphometric characteristics to dendrochronological counts. A power function was applied for correlating *A. cephalonica*'s age and diameter at breast height (dbh) [($y = 14.771x^{0.4049}$), $R^2 = 0.59$], (Politi 2009). All mature trees occurring in the permanent plots were mapped—for a total of 150 trees—and each tree was monitored for its reproductive phenology over a 4-years period. The varying degree of canopy closure was similarly represented in all plots; hence the mean density of the mature standing trees was relatively homogeneous throughout the locations ranging from 600 to 700 individuals per hectare.

The process of cone maturation as well as the number of cones produced per tree was documented from the ground level using high optical quality binoculars (50 mm diameter and magnification 7×). This method has been broadly followed in a variety of conifer species (e.g. Shearer and Schmidt 1987; Goubitz et al. 2002; LaMontagne and Boutin 2007) and is also suggested by FAO (1985). Seed dispersal was monitored on daily visits to the permanent sites.

Cone collection, seed extraction and germination tests

Mature cones of *A. cephalonica* were collected manually in the last 3 years of the study, 2005, 2006 and 2007 with the use of a crane. For safety (and conservation) reasons, the crane vehicle remained strictly on the existing unpaved road network. Cones were collected randomly from the upper part of the crown of each tree covering as much as possible all aspects of the crown. An average number of forty (40) trees, different for each year, were cropped, all located outside the plots and covering the altitudinal gradient of the National Park. The cones were placed separately into paper boxes and transported to the laboratory. Their morphometric characteristics (length, width, and mass) were measured with the cone-scales unfolded. After being left to dry in well-ventilated rooms under cool shaded conditions (<10°C), the exfoliation process was completed and scales and seeds were separated from the central axis. Seed number and quality were estimated from a representative number of cones ($N = 5$, in total). Seed mass differentiation along the cone axis was estimated by measuring the mass of every seed starting from the bottom and ending at the upper edge of the cone. Seed mass was subsequently measured using an analytical balance (180 g $\pm$ 0.1 mg). All seeds collected were pooled in the seed lot of the respective year. Separator machines have been frequently used as a means of sorting empty and sound seeds in conifer species (see for example Messaud et al. 2007). However, in this study we performed a cutting test (using a razor blade) for a sample of 500 seeds in order to estimate the number of empty and sound seeds as well as the number of insect damaged seeds (containing the insect's larva).

For seed germination experiments, three categories were recognized based on seed morphology: (1) apparently sound seeds (medium to large round-shaped seeds); (2) apparently empty seeds (small flat seeds that had been aborted before pollination) and (3) insect damaged seeds (with an evident penetration hole on the seed coat). Empty and insect damaged seeds were discarded from the lot. All remaining seeds were stored in the dark, in sealed containers, at a temperature of 7 $\pm$ 2°C until their use for germination experiments.

Seed rain (no. of sound seeds/ha) was estimated for each year taking into account the mean number of adult trees per hectare, the mean number of cones that each tree produced as well as the number of sound seeds per cone.

Sound seeds selected for the germination experiments were carefully separated from their wing using pincers. Care was exercized at all stages of seed handling to avoid damage to seed coat, as bursting of resin vesicles might be a cause of reduced germinability of *Abies* species (Bouvarel and Lemoine 1958; Gunia and Simak 1970; Kitzmiller et al. 1975).

Seed germination experiments were performed in Petri dishes (11 cm diameter) lined with two filter paper discs

and moistened with 7 ml of de-ionized water. Constant temperature experiments (20°C) in darkness (simulating conditions of buried seeds) were performed in temperature-controlled growth chambers (model BK 5060 EL, W. C. Heraeus GmbH, Hanau, Germany). Germination experiments simulating "Spring-equinox" conditions were performed on a temperature—and light—programmable growth bench (model GB48, Conviron, Canada). Two different microsite conditions were simulated: (1) seeds found on the forest floor in canopy openings (alternating temperature of 20°C with white light for 12 h and 10°C in darkness for the remaining 12 h); and (2) seeds under the canopy of *Abies* trees (alternating temperature of 20°C with far red light for 12 h and 10°C in darkness for the remaining 12 h). Cold-moist stratification was achieved by maintaining imbibed seeds at a temperature of 1–3°C in the dark for 6 weeks. A seed was considered to have germinated when the radicle had emerged 2 mm from the seed coat. Measurements were taken twice a week and non-germinated seeds were removed from the Petri dishes. Germination tests were considered finished when no additional seeds were germinating.

Statistical analysis

The statistical significance of the years of low, high and medium cone production (2005, 2006 and 2007, respectively) on the morphometric characteristics of the cones was tested with the non parametric Mann–Whitney U test (Siegel 1956) using the Statsoft Inc. v.7 STATISTICA software. The same test was used for testing the statistical significance of differences observed among the various seed germination treatments.

Results

Phenology of reproduction

A. cephalonica is a monoecious species. Female strobili are erect, solitary or in groups of two (very rarely in groups of three), situated at the middle and upper portion of the crown, on the upper side of the previous year's branchlets. The female buds initiate during late spring and overwinter at this stage until the following spring when pollination occurs.

Buds burst at the beginning of May; cone elongation quickly follows. The female cone is light (or yellowish) green turning to brown at maturity. Wind pollination occurs by mid-May and fertilization takes place. Seeds mature during summer to early-autumn and dispersal usually begins in October, but it has also been recorded in late-September and early-November. At maturity, seeds separate from the scale, loosen and fall away from the central axis, which remains on the tree and may persist for several years. Dissemination is completed within 1 week starting from the lower elevations and continuing immediately to the highest. The dispersed seeds may be buried under the organic soil or snow forming a transient soil seed bank during winter. Seedling emergence starts in late-spring (Politi et al. 2009). No significant difference was observed in the initiation and enrolment of the major phenological events along the altitudinal gradient. The sequence of the phenological events and their related period are shown in Fig. 1.

During this study a small fluctuation in the seed dispersal period was observed. Dispersal was progressively moving earlier in autumn and also lasted for a shorter period. In 2004, seed dispersal began early in November and lasted for more than 10 days, while in 2007 seed dispersal began at the end of September and lasted for less than 1 week.

Cone and seed production

A. cephalonica in Mount Aenos National Park reaches its reproductive maturity at the age of 50 years approximately. Cone production lasts for many years after and reaches its maximum at the age of 100–140 years, when the reproductive potential of trees is reduced (Fig. 2). Measurements performed during the four consecutive years of the study revealed high interannual variability in the number of adult trees producing cones, as well as in cone and viable seed production, indicating masting behavior for the
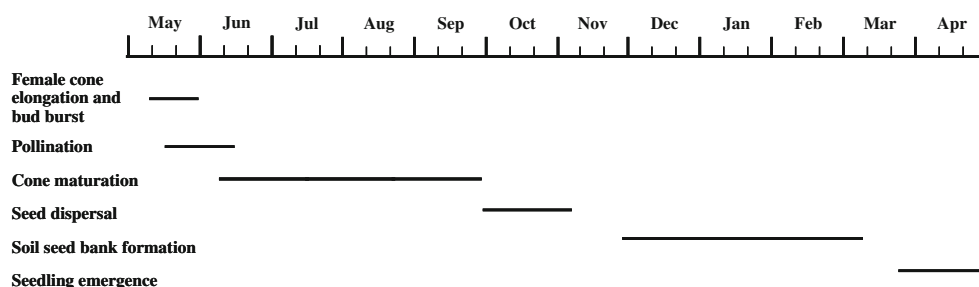

Fig. 1 Phenology of reproduction of *A. cephalonica* as recorded in Aenos National Park, Cephalonia (Greece)
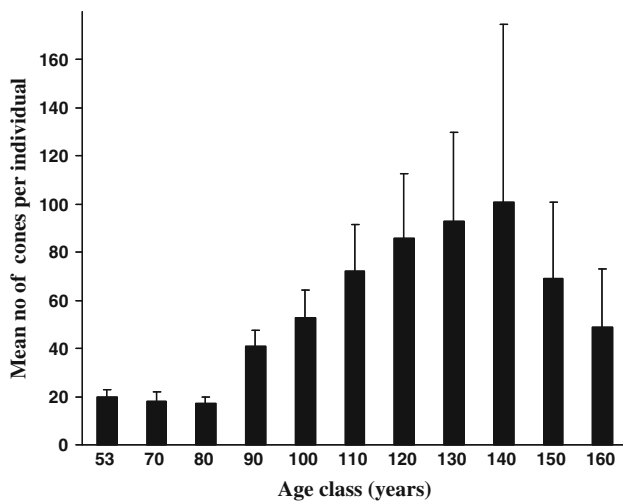
Fig. 2 Cone-production per individual of *A. cephalonica* in Mount Aenos National Park in relation to age classes. Values on the *x*-axis represent age-class midpoints

species (Fig. 3). An almost synchronous production of cones during the documented annual interval was recorded in the population. In the years 2004 and 2005, less than 30 mature individuals per hectare had invested in reproduction, while in the year 2006 about 500 trees per hectare (more than 60% of the population) had produced cones; a reduction was again recorded in the year 2007 with less
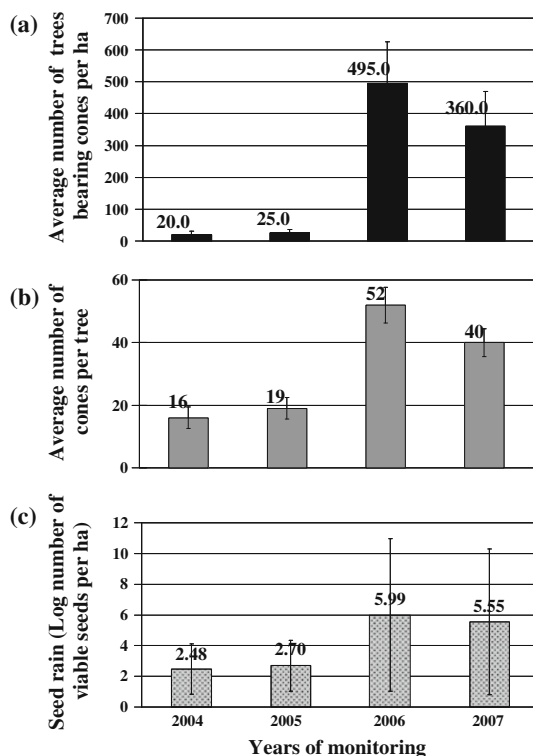
than 50% of population (360 individuals) in reproduction (Fig. 3a). A similar trend was recorded in the number of cones that were produced per tree (Fig. 3b). Overall, during the year of high production (2006) more than 60% of the mature individuals produced cones. This number was three times greater than the number produced by the same individual in the two previous consecutive years, 2004 and 2005, and 1.3 times greater than the production in the following year 2007.

The number of viable seeds produced per cone was one for the years 2004 and 2005, increasing to 38 for the year 2006 and 25 for the year 2007. The average number of viable seeds dispersed as seed rain per hectare was 300 and 500 during the years of low production, 2004 and 2005 respectively, significantly increasing to 988,000 in the year of the highest production (2006), dropping to 356,000 in the following year (2007), as shown in Fig. 3c. The proportion of sound seeds in relation to those infected by insects and empty ones presented high annual variability (Fig. 4). The highest percentage of sound seeds was recorded in the year of full masting (2006). It appears that the species follows a reproductive strategy namely, a 4-years masting cycle (minimum periodicity), with 2 years of poor crop (2004 and 2005) followed by a year of massive (2006) and a year of average (2007) cone production, accompanied by analogous sound seed production as well.

Cone morphometric characteristics and seed germination

The morphometric characteristics of the cones are presented in Table 1. The length of the cones was between 14 and 19.2 cm, while for nearly 40% of them it was 15–16 cm. A statistically significant difference was observed between the years 2005 and 2006 only ($p = 0.038$). The diameter of the

Fig. 3 Variability of trees bearing cones (**a**), cone production per tree (**b**) and seed rain (**c**) in *A. cephalonica* in Mount Aenos National Park for the period of study, ($N = 150$ trees)
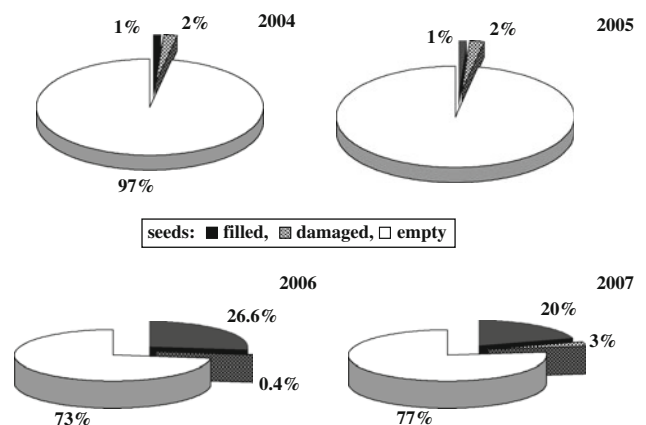

Fig. 4 Percentage of sound, insect-damaged and empty seeds over a representative seedlot of 500 seeds. Cones harvested in the years 2004–2007

Table 1 Morphometric characteristics of *A. cephalonica* cones per harvest year

Year of sampling	Sample number	Mean length cm ± SE (min–max)	Mean diameter cm ± SE (min–max)	Mean mass g ± SE (min–max)
2005	24	16.0 ± 0.3[a] (14.0–19.1)	4.6 ± 0.1[a] (3.5–5.4)	65.3 ± 3.4[a] (45.1–86.2)
2006	14	16.9 ± 0.4[b] (15.1–19.2)	4.8 ± 0.2[a] (3.6–5.6)	74.0 ± 3.7[b] (58.3–88.2)
2007	8	16.3 ± 0.7[a,b] (14.6–18.7)	4.7 ± 0.4[a] (3.4–5.7)	71.3 ± 2.6[a,b] (61.4–80.2)

Different characters beside means in each column symbolize statistically significant differences ($p < 0.05$)

SE standard error

cones varied between 3.4 and 5.7 cm, while for almost 40% of the cones it was 4.5–5 cm. Higher variability was recorded for the values of cone mass, which varied between 45.1 and 88.2 g. Statistical significance was also noted between the years 2005 and 2006 ($p = 0.046$). The spatial distribution pattern of seeds along the cone axis revealed that the heavier (sound) seeds are located mostly in the middle of the cone (Fig. 5).

The Mann–Whitney *U* test applied proved that there is a statistically significant difference in the mass ($p = 0.0465$) and the length ($p = 0.038$) of the cones between the years of low and high cone production (2005 and 2006, respectively) (Table 1). No significant difference was observed when comparing the year of average reproductive effort (2007) to that of maximum or minimum (2006 and 2005, respectively) effort.

Seeds are released from dormancy after a period of 4–6 weeks of cold stratification. The longer the duration of cold stratification the higher the final germination percentage was (data not shown). Data on final germination percentages for *A. cephalonica* seeds under different temperature and light conditions, after 6 weeks of cold stratification, are presented in Table 2. *A. cephalonica* seed germination presented statistically not significant similar patterns both in conditions simulating buried seeds or seeds found on the surface of the forest floor. Furthermore, for those seeds remaining on the forest floor, germination was similar in conditions simulating plant canopy (far red light) and those of open space (white light). Moreover, it appears that seed storage for 1 year leads to a 20% decrease in seed germinability, which was shown to be statistically significant ($p = 0.048$).

Discussion

Phenology of reproduction

All *Abies* species require almost 18 months in order to complete their reproductive cycle (e.g. Liu 1971; Arista

Fig. 5 Cones of *A. cephalonica* before and after seed dispersal (**a**), graphic representation of the distribution of the mean mass of seeds (mg) every six scales along the cone axis (**b**) and distribution of the different sizes of seeds and scales along the cone axis (**c**)
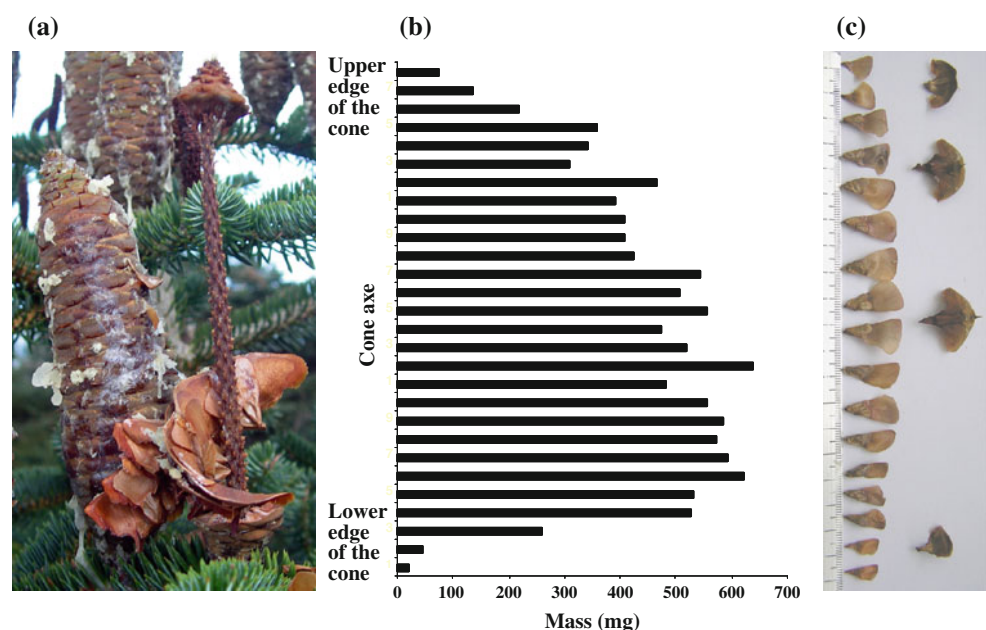
Table 2 Final germination percentages of *A. cephalonica* seeds, under different light and temperature conditions, after 6 weeks of cold stratification

	Temperature conditions (°C)	Light conditions	Germination (%)
Freshly harvested	20	Dark	59.60 ± 8.6
Stored (1 year)	20	Dark	39.46 ± 4.3
Stored (1 year)	20/10	White light/dark	42.11 ± 3.6
Stored (1 year)	20/10	Far red light/dark	45.61 ± 4.5

Untreated seeds germinated less than 5%

and Talavera 1994a; Edwards 2003). Almost a year after the formation of the differentiated buds (both male and female), the female cone elongates; pollination and fertilization follow, while the embryos in the cones develop until mid-autumn when seed dispersal takes place. *A. cephalonica* presented a similar reproductive cycle. The elongation of the female cone occurs in mid-spring, being among the earliest to burst. Wind pollination occurs by mid-May and lasts for almost a month. Duration of pollination may vary widely among the *Abies* species, from 18 days in *A. homolepis* (Itoo 1975) to a month in *A. pinsapo* (Arista and Talavera 1994b). Cone development and seed maturation last throughout summer, while cone ripening and seed dispersal take place within a few weeks in the beginning of autumn. Similar phenological patterns have been reported for *A. grandis* in Canada (Owens 1984) and for *A. pinsapo* in Spain (Arista and Talavera 1994b); see Table 3 for a comparative display of available similar studies.

Climatic conditions have proven to affect many of the vital activities of plants (Kohmann and Johnsen 1994; Stephenson 1998; Rehfeldt et al. 2002; Stephenson and van Mantgem 2005; Keeley and van Mantgem 2008; Levanič et al. 2009). Besides periods of drought, cold weather is also a factor that should be taken into account while evaluating the possible changes in conditions affecting firs (Aussenac 2002).

Firs are affected by spring frosts when buds are in the burst phase, and when air temperature is lower than or equal to 0°C (Aussenac 1980). *A. cephalonica* belongs to a group of species within the genus *Abies* that presents the earliest bud burst (Debazac 1965) and the shortest elongation period (Fady et al. 1991). These two characteristics give the species a disadvantage and an advantage at the same time. Very early bud burst increases the risk of late frost damage, while the completion of reproduction processes before the onset of dry period provides *A. cephalonica* with a remarkably high capacity to respond to large water deficiencies (Aussenac 1980; Bouachrine 1985; Fady 1993).

Several studies have documented the strong effect of climate on various phenological events of conifers, such as cone initiation, flowering, pollination, seed development and germination success (Pigott and Huntley 1981; Owens and Blake 1985; Fady 1993; Sirois 2000; Wenhui et al. 2006; Messaud et al. 2007). In this study we investigated the relationship between the dispersal period and annual variation in seed crop, with respect to temperature and precipitation, both for the bud burst period and the maturation period of male and female strobili (May, June, July and August, September, October, respectively). The results did not reveal any substantial variation as regards either the mean monthly or the range of lower and higher values of temperature recorded during the years of the study and for all slope aspects along the elevation gradient. Moreover, no late frosts occurred during bud burst throughout the study period, with no negative consequences on the reproduction processes. The progressive shift in the timing of cone maturation and seed dispersal period recorded during the 4 years of study was not accompanied by an analogous variation either in the mean monthly temperature of that period or in the respective autumn months during which male and female strobili mature. The mean temperature recorded for August, September and October in all four years of monitoring was similar (19 ± 0.5, 16 ± 0.4 and 13 ± 0.4, respectively) and summer drought did not differ from the usual. Similarly, the highest temperature values recorded in August, September and October presented a similar pattern showing practically no difference among the years of the study (22.5, 21.5, 21.5 and 24.5 in August, 20.5, 19.5, 19.5 and 19.5 in September and 17.5, 15.5, 15.5 and 16.5 in October for 2004, 2005, 2006 and 2007, respectively). All recorded values are within the range of respective values reported for the species. In particular, Fady et al. (1991) have found that sites occupied by *A. cephalonica* can be characterized by a sharp summer drought (3 months long on average) and a humid bioclimate (approximately 1,000 mm of rainfall per year), with the temperature ranging from extremely cold (average minimum of the coldest month: m < −7°C), to cool (0 < m < 3°C), which is a wide range for a Mediterranean fir. Furthermore, Aussenac (2002) has reported that *A. cephalonica* grows equally well in a relatively large mean annual temperature range, varying from 8 to 17°C across its natural distribution range.

Strobili production in many *Abies* species occurs in alternate years (Powell 1977; Arista and Talavera 1995; Messaud et al. 2007). This has been attributed to an endogenous rhythm not related to environmental factors (Greenbank 1963). In many trees growing at high altitudes of temperate and boreal zones, particularly high seed output follows a warm-dry summer (e.g. Houle 1999; Selås et al. 2002; Greene and Johnson 2004 and references therein), while a cool, moist summer in the year before seed maturation and a warm, dry summer in the year of

Table 3 Comparative display of major reproductive events reported for the life cycle of several *Abies* species

Species	Reproductive age (years)	Time of bud burst (month/season)	Time of cone ripening (month)	Seed dormancy (stratification period)	Average masting periodicity	Source
Mediterranean						
A. alba	60[1]	Late-May[2]	No data	No data	3–4 years[3]	[1]Grassi et al. (2004)
						[2]Aussenac (2002)
						[3]Skrzyszewska and Chłanda (2009)
A. bornmuelleriana	No data	Late-May	No data	No data	No data	Aussenac (2002)
A. cephalonica	53	Early-May	Late-September–early-November	Yes (6 weeks)	4 years	Present study
A. cilicica	No data	Early-May	No data	No data	No data	Aussenac (2002)
A. nordmanniana	No data	Late-May[1]	No data	Yes (6 weeks)[2]	No data	[1]Aussenac (2002)
						[2]Gosling et al. (1999)
A. nebrodensis	No data					
A. numidica	No data	Mid-May	No data	No data	No data	Aussenac (2002)
A. pinsapo	50	Mid-spring	October–November	No data	No data	Arista and Talavera (1994b)
North American						
A. amabilis	20[1]	Mid-May[1]	No data	Yes (4 weeks)[2]	2–3 years[3]	[1]Owens and Molder (1977a)
						[2]Davidson et al. (1996)
						[3]Fowells (1965)
A. balsamea	No data	No data	Fall	No data	2 years	Messaud et al. (2007)
A. lasiocarpa	No data	Mid-May	No data	No data	2–3 years	Singh and Owens (1981)

Indicators refer to the corresponding source of data for each species

seed maturation might also act as a stimulus (Eis 1973). Our results indicate that during the 4-years study period, *A. cephalonica* did not follow the above pattern as massive cone production followed the year with the highest levels of summer precipitation (roughly 5% of the annual), while cone differentiation occurred in a year with the lowest summer precipitation (less than 1% of the annual). Nevertheless, there appears to be a relationship between the climatic conditions and the dispersal period, since the date of seed-fall was starting later at higher elevations. This is in accordance with observations on the *A. alba* population in Italy (Giami 1970).

Cone and seed production

For many *Abies* species, years of low production alternate with years of high production; moreover, a phenomenon of synchronized mass flowering and cone production, at irregular intervals, has also been recorded (Liu 1971; Powell 1970; McDonald 1992; Arista and Talavera 1995). This phenomenon has been reported for many tree and shrub species and a variety of ecosystems (Herrera et al. 1998; Koenig and Knops 2000; Schauber et al. 2002; Suzuki et al. 2005; Lázaro et al. 2006; Poncet et al. 2009). Many studies have shown that masting is caused by an interaction between abiotic and biotic factors (Mduma et al. 2007). The rhythm of this fluctuation is not stable;

however, an average periodicity, characteristic of each species, does exist (Silvertown 1980).

It is evident that for such a long living species as *A. cephalonica*, long term monitoring is required in order to arrive at solid conclusions on its masting periodicity. Despite this, during the 4 years of study we were able to record two consecutive years of very low cone production (years 2004 and 2005) which were followed by 1 year of high production (year 2006) and 1 year of average to low production (2007). Thus, 4-years masting behavior is at least plausible. A similar pattern has been reported for the other Mediterranean fir *A. alba* (Aussenac 2002; Grassi et al. 2004; Skrzyszewska and Chłanda 2009), while a shorter period has been documented for the North American fir species *A. amabilis*, *A. balsamea* and *A. lasiocarpa* (Fowells 1965; Owens and Molder 1977a; Singh and Owens 1981; Davidson et al. 1996; Messaud et al. 2007, see Table 3).

Several hypotheses have been proposed with regard to the selective advantages of masting (Waller 1979; Smith et al. 1990; Lalonde and Roitberg 1992). Initially Norton and Kelly (1988) and shortly after that Kelly (1994), categorized these hypotheses into two types: (1) "resource matching," in which plants vary their reproductive effort in response to fluctuations in available resources; and (2) "economy of scale," in which a larger reproductive effort is more efficient, favouring an occasional large effort rather

than a regular, smaller one. However, there are still few studies with sufficient quantitative data to test these hypotheses for masting species. The annual variability of cone production in populations of *A. cephalonica* from other parts of Greece has also been reported describing a periodicity of 2–4 years (Panetsos 1975; Dafis 1986; Stamatopoulos 1995). However, no information is available regarding the annual yield of cones or the relative amount and quality of seed production for the species. Our data indicate high interannual variation in cones and in respective viable seed production. A similar trend has been recorded by Houle (1999) for *A. balsamea* in a cold temperate forest of North America.

The year of highest cone production (masting year) was also characterized by the impressively high number of mature individuals producing cones (over 60%), as well as by the highest viable seed production. The mean annual production of viable seeds was 336,000 ± 269,000 per ha. Generally speaking, the seed output is low in the genus *Abies* (Fady 1992; Owens 1995; Takaso and Owens 1994). The high percentage of "non sound" seeds (damaged and empty) recorded seems to be a characteristic of many *Abies* species (Khutortsov 1987; Arista and Talavera 1995; Owens and Morris 1998; Wenhui et al. 2006). The low number of sound seeds may be attributed to many causes. Fir pollen is relatively heavy, which means that pollination distances greater than 60 m may be another limiting factor for viable seed production in firs (Edwards 2003). Self-pollination reduces seed yield, although seed germination is not affected (Sorensen et al. 1976). Late frosts may cause total abortion of female strobili in several species (Fowells and Schubert 1956; Franklin and Ritchie 1970). As mentioned above, *A. cephalonica* runs a high risk of late frost damage, since bud bursting occurs early in spring when snow might still prevail. It is generally accepted that isolated populations may experience lower genetic diversity which may be responsible for the lower species performance (Gitzendanner and Soltis 2000; Godt and Hamrick 2001). However, no data supporting either isolation or low genetic diversity is available for *A. cephalonica* in Mt Aenos National Park, despite its insularity. Terpene composition and height growth characteristics of *A. cephalonica* in the island of Cephalonia are not significantly different from those of other continental provenances and can indicate at least occasional pollen transport from the mainland (Fady 1990; Fady et al. 1992; Fady and Conkle 1993).

The proportion of germinable seeds is often reduced by frequent infestations of insects that damage both cones and seeds (Owens and Morris 1998; Petrakis 2004).

The cones were collected from a representative number of trees covering all the main age classes as well as the altitudinal gradient of the National Park. *A. cephalonica*

reaches maturity at the age of 53 years (Politi 2009). Similar ages of sexual maturation have been documented for *A. pinsapo* in Spain, with a minimum age of 50 years (Arista and Talavera 1994b, see Table 3), for *Picea abies* Karst. in Norway and *A. alba* Miller from the Italian Alps, with the minimum age for cone production being 60 years (Grassi et al. 2004) and for *A. alba* in Southern Poland (Skrzyszewska and Chłanda 2009). However, *A. amabilis* seems to become reproductively mature much earlier, as reported by Fowells (1965); Owens and Molder (1977a); Davidson et al. (1996) —see Table 3 for comparisons.

Cone production in *A. cephalonica* increased with age and therefore with tree size. However, it seems to diminish after a certain age (>140 years old) indicating the beginning of senescence. Seki (1994) found that cone production in *A. mariesii* in Japan increased as an exponential function of trunk diameter. Dodd and Silvertown (2000), however, correlated fecundity with tree age and DBH in *A. balsamea* in New York State and found that age was a non significant variable in all cases studied.

Cone morphometric characteristics and seed germination

A. cephalonica cones have been described in the past as "cylindrical tapering to a short-pointed nipple-like apex" (Liu 1971), 10–22 cm long and 3–5 cm in diameter (Bassiotis 1956; Debazac 1965; Panetsos 1975). The number and size of a cone is related to its position on the crown (Powell 1977; Wenhui et al. 2006), the average temperature and humidity of the environment during maturation (Okada 1983; Owens and Blake 1985), the age and size of the parent tree as well as its position in the stand (Arena 1960; Haq 1992; Arya et al. 1994). The results obtained from the measurements of the cones' morphometric characteristics are similar to those reported by Bassiotis (1956); Debazac (1965) and Panetsos (1975) for *A. cephalonica*. The relatively high variation in cone mass is probably due to the varying participation of sound seeds per cone in each year. The statistically significant difference in the mass as well as in the length of the cones in the years 2005 and 2006 indicates that the maximum reproductive effort (as recorded for the masting year 2006) was accompanied by heavier and longer cones. This annual fluctuation in the morphometric characteristics of the cones can again be attributed to the masting behavior of the species. The year with the highest reproductive output was accompanied by a larger cone size as well as a higher percentage of sound seeds.

Fir seeds ripen in two distinctive phases, the first being the accumulation of organic substances and the second involving metabolic changes within the seeds, so that germination capacity continuously increases up to (or

almost up to) seed dispersal (Edwards 1969, 1982; Yanagisawa 1965; Franklin 1974). It has been documented (Giami 1970; Houle and Payette 1991; Krajňáková et al. 2008) that seed germinability of many *Abies* species is improved when seeds are collected as close as possible to seed fall, i.e., when the embryo reaches its complete form. Incompletely ripened fir seeds are stored poorly, with serious losses in germination potential. The period of cone storage is governed by the natural disintegration of the cones; once they have fallen apart they can be regarded as fully mature (Edwards 1969, 1982; Muller 1971). *A. cephalonica* seeds were collected immediately after the first signs of cone ripening in order to avoid losses in germination ability due to immaturity (earlier collection) of seeds.

Seed dormancy in firs is quite variable (Edwards 2003) and it may be both physical and physiological, but it apparently does not reside in the embryo, because embryos excised from non-stratified *A. procera* seeds grow just as well as those from stratified seeds (Edwards 1969). Reasons for fir seed dormancy may be poor oxygen exchange or an inhibitor, because chipping the seed coat to expose and remove a sliver of mega-gametophyte was as effective as (or more than) stratification in stimulating germination of seeds of *A. procera*, *A. amabilis*, and *A. grandis* (Edwards 1969) and the European silver fir (Gogala and Vardjan 1989). Stratification also probably overcomes dormancy by reducing the mechanical restraint of the tissues surrounding the embryo (Edwards 1969; Jones et al. 1991). Although stratification is routinely prescribed for *A. alba* and *A. fraserii*, it has been reported (Zentsch and Jahnel 1960; Speers 1967) that some seedlots of both species show little or no dormancy.

The ISTA handbook of seed technology (ISTA 2003) suggests a three-week stratification period for breaking the dormancy of *A. cephalonica* seeds. However, our results show that a longer period of cold stratification leads to higher germination. These results are in accordance with experiments on *A. nordmanniana* [(Steven) Spach]; where 6 weeks of stratification, followed by germination at 20°C, produced the highest germination (Gosling et al. 1999), see Table 3 for comparison. A substantial difference was recorded in the number of seeds that remained non-germinated at the end of the test with over 90% of the seeds remaining non-germinated when not stratified, compared to just over 40% for stratified seeds. An additional finding was that the ISTA (2003) prescribed incubation temperature (20°C/30°C) was unfavorable for *A. cephalonica* seeds, which germinated better at 20°C. This could be probably explained by the prevalence of fungi, which infected emerging radicles at higher temperatures (Davidson et al. 1984). Moulds were observed in every germination box, without exception, by the fifth week of the

germination test, as is common for similar germination experiments undertaken for other *Abies* species (Kitzmiller et al. 1975; Edwards 1982; Davidson et al. 1996). Fungal growth was similar in stratified as in non-stratified seeds. The highest mean germination percentage was 60% in seeds that were not stored and dropped to 40% in seeds stored for 1 year. The highest mean germination percentage for *A. cephalonica* seeds was relatively high compared to the percentages recorded by other experiments on *A. cephalonica* seeds from various Greek areas performed earlier by Fady (1992). Low germination percentages may be due to a degradation process during storage, or to the accumulation of lethal or sub-lethal recessive homozygous genes (Fady 1992), or even to an ineffective break of dormancy or to an excessive sensitivity to the germination conditions (Gosling 1988; Gosling et al. 1999). However, it has been previously noted that total germination in *Abies* taxa rarely exceeds 50% (Arena 1960; Franklin 1974; Giannini and Tascione 1978; Fady 1992; Rawat et al. 2008; Skrzyszewska and Chłanda 2009). Duration of cold stratification was positively related to the final germination percentages; longer stratification periods led to higher germination percentages in all experiments performed. The inability of cold stratification to induce full germination in *A. cephalonica* could be explained by reduced seed viability caused by the environmental conditions prevailing during the period of embryo development as it has been documented by García et al. (2000) for junipers.

The lower germination percentages recorded for seeds that had been stored for 1 year may be due to unsuitable storage conditions (possibly higher temperature or moisture than the ones required). Most experts, however, agree that seeds lose viability quickly unless special precautions are taken, possibly because of the high oil and resin contents that may become toxic to the embryo when oxidized (Bouvarel and Lemoine 1958). Patterns of seed germination were similar for seeds either buried or remaining on the forest floor. For the latter, the application of conditions simulating plant canopy (far red light) or open space (white light) also produced similar patterns of final germination. Similar germination percentages observed in darkness or under simulated shading conditions (far red light) and white light could be related to shade tolerance of the species which is common for the genus *Abies* (e.g. *A. balsamea*, Rowland and White 2010 and *A. sachalinensis*, Iijima et al. 2009).

The pattern of fir regeneration under its own canopy has been a controversial issue (Gürth 1988; Ammer 1996). Existing literature supports that fir regeneration is better under a heterogeneous forest canopy as opposed to that created by pure fir stands. This has been attributed to the quantity of the scattered light reaching the forest floor and the spectral properties of the solar radiation reaching the

understory (usually greater transmission of blue and red energy bands—see Messier and Bellefleur 1988). It is generally believed that *Abies* spp. regeneration is more prolific with a certain degree of shade, usually provided by the thick canopy cover (Cochard 1992; Aussenac 2002). Nevertheless, these conditions have not been directly linked to the light regime required for *Abies* seed germination. Politi et al. (2009) have shown that *A. cephalonica* seedling emergence in the field is higher in the years of higher seed production and is primarily determined by ground obstacles/shelters and site elevation; fir canopy openness (hence quantity and quality of light passing through) was not a principal significant factor in the classification of seedling microhabitats as regards emergence. After the first period with the highest seedling mortality rate, seedling microhabitats were primarily classified according to their soil organic matter and secondarily according to their canopy openness in terms of seedling survival, with mean seedling survival density being relatively higher in closed or partially closed canopy as opposed to open canopy (fully or partially exposed ground). It appears that although seed germination can equally occur in any light regime found in the forest (as shown by seed germination tests and verified by recording seedlings in the field), seedling establishment and survival in time is better accomplished in the protective shade offered by elder plants. It is therefore reasonable to assume that for a masting species, the ability of its seeds to germinate almost equally in all light regimes, after their dispersal, gives the species an advantage in terms of space and time.

Conclusions

Although the endemic to Greece *A. cephalonica* species faces serious threats e.g. hybridization with *Abies alba* in its continental northern distribution range (Fady 1995) or climate change inducing drought and altered fire regime (Arianoutsou 2007), only a few forest areas occupied by the species are protected by specific legislation. Even in the cases where stands of *A. cephalonica* are thought to be protected, no special measures have been taken for rational management. The capacity to conserve, sustainably use and restore forests rests on our understanding and interpretation of pattern and process at several scales, the recognition of thresholds, and the ability to translate knowledge into appropriate management actions in an adaptive manner (Frelich and Reich 1998; Gauthier et al. 2009). Several ecological principles have been proposed by Thompson et al. (2009) in the latest technical report of the Secretariat of the Convention on Biological Diversity, among which maintenance of genetic diversity, stand and landscape

structural complexity are critical. This study contributes to the overall aim of preserving the integrity of pure *A. cephalonica* forests, which are areas of European Community Interest, such as the Mount Aenos National Park, by providing the basic ecological information about its reproductive patterns. Our data indicate that *A. cephalonica* is a species exhibiting plasticity in its reproductive behavior, both by being a masting species with periodical high yields in cone and seed production—with a minimum 4-years period—and by being relatively independent of light regimes for fulfilling its germination in the field. Given that gap regeneration is a strategy known to be followed by many conifer trees (see for example Spies and Franklin 1989; Yamamoto 1993; McCarthy 2001; Dobrowolska and Veblen 2008), and that emerging seedlings survive better in the relative protection of elder plants (Politi et al. 2009), the ability of fir seeds to germinate regardless of prevailing light conditions is a remarkably important adaptation. As stated by Politi et al. (2009), the Mount Aenos National Park could be the most important protected area for this endemic fir as regards the preservation of its integrity and the application of pre-emptive management schemes in the light of current and future threats. The knowledge obtained from this study may greatly contribute in that respect.

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