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Patterns of *Abies cephalonica* seedling recruitment in Mount Aenos National Park, Cephalonia, Greece

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ABSTRACT

Patterns of *Abies cephalonica* Loudon seedling recruitment at its westernmost geographical limit (western Greece), were studied by monitoring their emergence, survival, and establishment for up to four years in the microhabitats to which seeds are dispersed. Seedlings were monitored on 200 permanent sampling plots established in 11 different locations covering the entire strictly protected Mount Aenos National Park (Cephalonia). Annual seedling mortality rate was estimated in relation to habitat characteristics as well as to their number of cotyledons. *A. cephalonica* presented the typical behaviour of a masting species in the number of seedlings produced over the four years of study. Of the habitat characteristics studied, ground cover, elevation, soil depth, slope and canopy openness were the main parameters that classified seedling habitat with respect to their emergence. Seedling survival was higher in years of low seedling production. Seedlings with higher cotyledon numbers exhibited higher survival. Our data indicate that *A. cephalonica* is characterized by remarkable reproductive plasticity, which is expressed in the number of seedlings produced each year and those surviving with respect to its habitat characteristics. Preserving the species implies preserving its habitat. In this sense, Mount Aenos National Park may be the most important protected area for the endemic fir in view of preserving its integrity through pre-emptive management, in the light of current and future threats.

1. Introduction

Eight *Abies* taxa occur in the Mediterranean Basin (Farjon and Rushforth, 1989), which is one of the distribution centres for the genus (Parducci, 2000). Of the Mediterranean fir taxa, *Abies nebrodensis* (Lojacono) and *Abies cephalonica* (Loudon) are the only two with island populations. *A. nebrodensis* is an extremely rare species with very limited distribution in the Madonie range of Sicily (Morandini et al., 1994; Parducci, 2000), while populations of the Greek endemic *A. cephalonica* (Greek fir) occur on two Greek islands, Euboea in the Aegean Sea and Cephalonia in the Ionian Sea. On the Greek mainland, a series of intermediate *Abies* forms occur, belonging to the putative hybrid species *Abies borisii-regis*. At the northern limit, the hybrid populations mostly resemble *Abies alba* and grow together with individuals of this species, while at the southern limit they mostly resemble *A. cephalonica* (Barbéro and Quézel, 1976; Mitsopoulos and Panetsos, 1987; Fady et al., 1991), which means that the Mount Aenos National Park on the island of Cephalonia is a crucial refuge for the genetic integrity of the species and avoidance of its introgression.

The isolated occurrence of *A. cephalonica* on the island of Cephalonia raises concerns about the impact of climate change on this species. In their landmark paper on the global biodiversity scenarios for 2100, Sala et al. (2000) concluded that the most critical factor in changing patterns of biodiversity are land-use changes followed by climate change. The same authors also suggest that the Mediterranean ecosystems are vulnerable to both these factors. For the Mediterranean Basin, a raise in temperature of up to 2–4 °C in the next century has been foreseen (Palutikof and Wigley, 1996), while rainfall is predicted to decrease in autumn (Déqué et al., 1998). An increase in temperature without an increase in rainfall, as predicted by the recent climate change scenarios of IPCC (IPCC, 2007) would generate a high risk for most of the fir species, including *A. cephalonica* (Aussenac, 2002). And this risk increases due to the susceptibility of the species to new fire episodes, which destroy large areas of this non-fire resilient species, as happened in the devastating fires of 2007 in Greece (Arianoutsou, 2007).

A decrease in Greek fir populations has been reported for Greece during the last five decades (Raftoyannis and Radoglou, 2001; Tsopelas et al., 2001). None of these studies have dealt with the population of the endemic *A. cephalonica* on Cephalonia, despite the considerable interest of many scientists in the genetics of this species (Fady, 1990; Fady et al., 1991; Guidi and Pelleri, 1990).

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Seed dispersal, germination, and seedling establishment are critical stages in any plant's life. The Greek fir is reported to posses a masting behaviour (Panetsos, 1975), thus being more vulnerable to environmental changes. Despite the importance of seedling recruitment in the life cycle of trees, practically no study, regarding *A. cephalonica*, has ever documented their dynamics in the isolated island population of Cephalonia or has investigated the relationships between dynamics and habitat characteristics.

Seedling establishment is a critical life history stage that determines whether or not a sexually reproductive species will be present in a given microsite. Evaluating the relative importance of spatial and temporal variability in recruitment requires data on the regeneration success of seedlings across environmental conditions and years (Beckage et al., 2005). The aim of the current work was to document the patterns of seedling recruitment for *A. cephalonica* within the protected area of Mount Aenos National Park, Cephalonia Island, Greece. A four-year monitoring study covering the entire area of the Park was undertaken on permanently established plots revealing the heterogeneity of the species' habitat.

2. Methods

2.1. Study area

Mount Aenos National Park, designated as a Community Important Site (NATURA 2000 network site), was established in 1962 with the purpose of preserving the forest ecosystem and protecting the endemic Greek fir, *Abies cephalonica*, from hybridization. The forest of *A. cephalonica* on Mount Aenos is highly esteemed for its floristic and ecological value (Phitos and Damboldt, 1985; Politi and Marcenò, 2001). In the past, the park has suffered from severe logging and fires at its periphery. There is historical evidence that the distribution of the fir population has been reduced to less than a quarter of the area occupied in the past (Samios, 1908).

The Park covers an area of 28.6 km^2, and runs almost 11 km from NW to SE (38°09′04″N, 20°38′38″E), from an elevation of 900–1628 m at the peak of Mount Aenos. *Abies cephalonica* extends from the lowest to the highest point on the mountain, although a few scattered individuals occur at lower elevations. According to Köppen's climate classification, the climate is characterized as temperate Mediterranean (Csa) with hot and dry summers, moderate temperatures and unpredictable, rainy weather due to the Adriatic Sea currents that often bring fog. Snow cover usually lasts from mid December to mid March. A fully equipped meteorological station was only recently (2007) established at high elevation (1000 m). Before that period meteorological data were available from a station situated in the western part of the island, almost at sea level. Annual precipitation in the last year of study (2007) reached 1500 mm. For the previous years, rainfall data from the lower elevation station showed variability during the study period. Higher precipitation was recorded for the years 2003 and 2005 (798 mm and 857 mm respectively), in contrast to that recorded for 2004 and 2006 (584 mm and 654 mm respectively). The basement rock of the mountain is calcareous hard limestone, soil texture is clay (3.5 ± 0.8% sand, 17.8 ± 1.6% silt, 78.8 ± 2.2% clay), while mineral soil depth is rather shallow (30–40 cm) with frequent rocky outcrops. Soil pH is alkaline ranging from 7.6 to 7.7 at all study sites. Soil water holding capacity ranged from 58 to 60%.

2.2. Study species

Abies cephalonica is the predominant woody species in the park, with 93.4% cover over the area of its occurrence (Forestry Department of Cephalonia, 1996), with a poor understory of

Table 1
Habitat characteristics of the sampling localities of Mount Aenos National Park.

Localities	1	2	3	4	5	6	7	8	9	10	11
Elevation (m)	1000	1010	1100	1200	1240	1350	1400	1500	1615	1620	1100
Aspect (°)	315–305	44–0	135–90	45–45	270–310	45	55–55	90–90	180	355–355	140–140
Slope (°)	10	3	10	45	20	35	30	5	5	40	0
Soil texture	Clay	Clay	Clay	Clay	Clay	Clay	Clay	Clay	Clay	Clay	Clay
Soil depth of organic horizon, (cm) (mean) ± s.e.[a]	40.25 ± 5.97	20.25 ± 1.91	21.75 ± 3.69	19.5 ± 3.82	31.0 ± 2.36	19.5 ± 0.41	26.75 ± 3.69	26.0 ± 5.50	23.75 ± 4.33	16.50 ± 2.86	15.75 ± 3.28
Canopy openness (CO)[b]	0.12–0.14	0.10–0.17	0.19–0.10	0.13–0.18	0.09–0.35	0.13	0.17–0.22	0.07–0.43	0.12	0.07–0.30	0.07–0.09

[a] 4 Samples form each locality were taken.
[b] Measured at the center of each locality

Table 2
Classes of habitat parameters measured and used in the statistical analyses.

Habitat parameters	Classes			
Elevation (m)	1000 (1000–1100)	1200 (1200–1300)	1400 (1350–1450)	1600 (1500–1620)
Aspect (°)	N (316–45)	E (46–135)	S (136–225)	W (226–315)
Slope (°)	10 (0–10)	20 (11–20)	30 (21–30)	40 (≥31)
Soil depth (cm)	1 (1–12)	2 (13–23)	3 (24–34)	4 (≥35)
CO	1 (shaded)	2 (partially shaded)	3 (partially open)	4 (open)
Grass cover	Open (<40% of the ground covered with herbs and/or bryophytes)		Closed (≥40% of the ground covered with herbs and/or bryophytes)	
Ground cover	Open (<40% of the ground covered with logs and/or rocks)		Closed (≥40% of the ground covered with logs and/or rocks)	

woody species in most of the area. Male flowers become noticeable by mid-winter (December–January). Pollen shed occurs at the beginning of May, mostly on the undersides of the lower branches, while erect female flowers (strobili) are found on the upper sides of the branchlets mostly in the upper portion of the crown. The majority of female flowers develop into cones. Cones complete their growth in early August, reach maturity in September and disperse their seeds in October (Panetsos, 1975). Dispersal of *A. cephalonica* seeds takes place between the end of September and the end of October (Politi et al., 2007), and seeds germinate in the following spring. No seed bank is created, either on the canopy of the tree or in the soil.

2.3. Experimental design—site selection and habitat characteristics

Seedling recruitment was monitored over a four-year period in a network of 11 different locations covering the entire protected area of the National Park. The locations extended over an altitudinal gradient ranging from 1000 to 1620 m and represented different topographic conditions (elevation, aspect and slope), as well as varying degrees of canopy closure and ground cover. In each of the localities, 20 permanent plots of 1 m^2 were established (with the exception of two localities where only 10 plots could be established) and regularly monitored for seedling emergence, survival and establishment over a four-year period.

Habitat characteristics for all localities are provided in Table 1. Elevation and aspect were determined using topographic maps, as well as a GPS MAP 60CSx GARMIN. Depth of the soil organic horizon was measured with the use of an iron ruler. Degree of canopy closure was estimated with the use of hemispherical photographs taken at the centre of each plot. Photographs were taken at a height of 1 m at dawn and before sunlight on July 2005 using a Nikon Coolpix 5400 camera with a fisheye adaptor (180° field of view). All photographs were oriented with magnetic north towards the top of the image. The hemispherical photographs were analysed by three researchers independently (see Fyllas et al., 2008) using the HemiView software program, version 2.1 (Delta-T Devices Ltd.). Site factors ranged from 1 (open sky) to 0 (complete obstruction). When multiplied by 100, this value expresses a measure of degree of canopy openness (CO) (Montgomery, 2004). Presence of herbaceous plants and bryophytes (hereafter called "Grass") and the evenness of ground cover (e.g. from a fallen log or from stones) (hereafter called "Ground") were visually quantified. In order to facilitate our analysis, habitat parameters were classified into groups of main classes as shown in Table 2.

2.4. Monitoring scheme for seedling recruitment

All seedlings emerging in the 200 permanent plots were monitored during the four years of study (2004–2007). Each individual seedling was tagged and its position in the plot was mapped. In spring 2004, 3503 seedlings were marked; their subsequent survival and establishment was monitored during each dry season until 2007 (well into the fourth growing season of the new individuals). The same procedure was followed for the seedling cohorts of 2005–2007. For each census, the status of each individual was recorded as either alive or dead and the number of cotyledons for each seedling was counted in its first growing season. All sound seeds dispersed in one year were germinating, leaving no seed bank on the ground. Seedling morphology was distinct and differed from that of the young sapling, which apart from the cotyledons had developed smaller needled leaves inside the star-like formation of the cotyledons.

2.5. Statistical analysis

The statistical significance of cotyledon number on seedling survival was tested with one way analysis of variance (STATISTICA software, Statsoft Inc.). The same type of analysis was used for the investigation of the effect of the habitat parameters on seedling emergence and survival. Normality of data were checked using the Shapiro–Wilks' test, while variance homogeneity by applying Levine's test. Independence of means–variance was also checked.

Further to these analyses patterns of seedling recruitment in the 200 permanent plots were examined in relation to their habitat characteristics. The data set for the 2004 seedling cohort was used for the analysis; this set was complete for all stages of recruitment (emergence, survival and establishment). The data were analyzed with respect to their habitat characteristics using classification trees (Breiman et al., 1984; Steinberg and Colla, 1995; De'ath and Fabricius, 2000) with STATISTICA software (Statsoft Inc.). Seedling emergence, survival and establishment were the response variables, and habitat parameters (ground, cover, elevation, canopy openness, slope) were the explanatory variables. The trees were constructed by binary recursive partitioning (CC & RT), which uses the most reliable pruning strategy for over-growing trees, ensuring that any important tree structure is not overlooked. The expected output was the hierarchical up-bottom classification of the data, revealing the statistically most important parameters for each of the stages of the response variable (seedling emergence, survival, and establishment).

3. Results

As expected for a species with masting behavior, seedling emergence varied between years. The number of emerged seedlings (3503) monitored during the first year of the study (spring 2004) was 76 and 389 times greater than that of the two subsequent years (46 seedlings in 2005 and only 9 seedlings in 2006; Table 3). Another massive seedling emergence occurred in spring 2007, with 1055 seedlings.

It is important to note that final seedling survival expressed as a percentage of the emerging seedlings is by far higher in years of low seedling production as compared to the years of massive seedling recruitment, reaching 39.13 and 77.78% for the former and only 16.04% for the latter, at the end of the first year (Table 3).

Table 3
Mean seedling density for all cohorts monitored at the time of their emergence and their subsequent survival.

Years of monitoring	Total number of emerging seedlings recorded per year of monitoring	Emerging seedlings density (individuals/m^2 ± s.e.)	Survived seedlings density (ind./m^2 ± s.e.) [% survival, 1st year]	Survived seedlings density (ind./m^2 ± s.e.) [% survival, 1st to 2nd year]	Survived seedlings density (ind./m^2 ± s.e.) [% survival, 2nd to 3rd year]	Total recorded survival (% of the initial appearance)
2004	3503	17.52 ± 1.07	2.81 ± 0.27 [16.04]	1.14 ± 0.13 [40.57]	0.59 ± 0.08 [51.75]	0.59 ± 0.08 (3.37)
2005	46	0.23 ± 0.05	0.14 ± 0.04 [60.87]	0.09 ± 0.03 [64.29]	n.r.	0.09 ± 0.03 (39.13)
2006	9	0.05 ± 0.02	0.035 ± 0.01 [77.78]	n.r.	n.r.	0.035 ± 0.01 (77.78)
2007	1055	5.28 ± 0.41	n.r.	n.r.	n.r.	n.r.

Total survival percentages are provided in parenthesis; n.r. stands for not recorded.

The overall number of seedlings finally recruited remained low regardless of the year or amount of seed production.

Patterns of seedling appearance, survival and establishment, differ between the three consecutive years of study (2004–2006), (Figs. 1–3). In order to check whether seedling emergence and survival vary significantly in relation to time, a repeated ANOVA test was used. Habitat parameters were entered in the analysis as independent variables. The results showed significant effect only for elevation ($p < 0.000,002$, repeated ANOVA test). Hence, those patterns are presented against elevation classes.

The 2004 seedling cohort with the highest number of individuals showed very high mortality rates (>80%) (Fig. 1) during the subsequent year, while this was not observed for the other two seedling cohorts of 2005 and 2006 (Figs. 2 and 3 respectively). Seedling mortality rate, after the end of their first year of life, was almost 40% for the 2005 cohort and 25% for that of 2006. This notably high self thinning of 1st year seedlings was not followed during the subsequent years of their lives (Fig. 1). Seedlings that had survived in the 1st year of life had a higher probability of entering the sapling stage, as their subsequent survival was always higher, in some cases reaching exceptionally high levels–(70–100%).

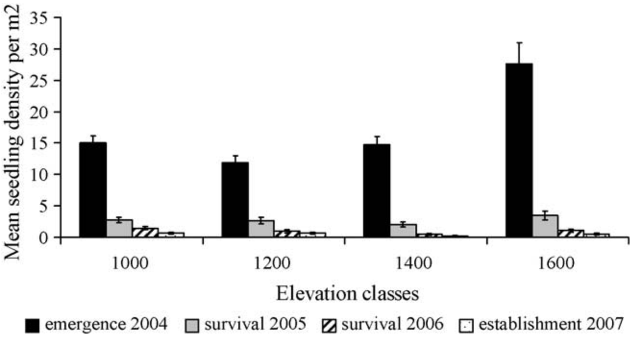

Fig. 1. Mean seedling density for the 2004 cohort (year of emergence) and their survival for the following three years of their life (2005–2007). Data distributed by elevation class.

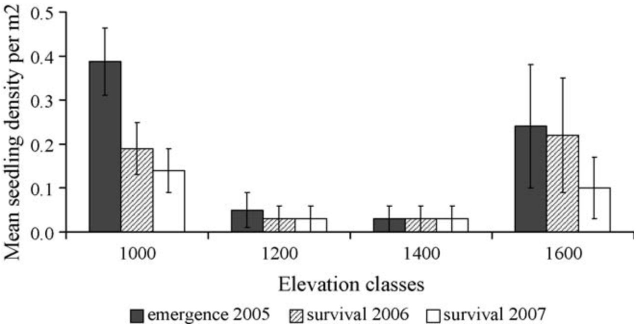

Fig. 2. Mean seedling density for the 2005 cohort (year of emergence) and their survival for the following two years of their life (2006 and 2007). Data distributed by elevation class.

Emerging seedlings typically exhibited 5, 6 or 7 cotyledons at all studied sites, with a variable range of 4–8 (Fig. 4). The number of cotyledons per seedling appeared to be constant in the four cohorts. The majority of emerged seedlings had 6 cotyledons at all study sites, while a slightly higher percentage of survival (7.2%) was recorded for 3-year old seedlings having 7 cotyledons compared to those having 5 (3.9%) and to those having 6 cotyledons (5.5%), (Fig. 4). The one-way ANOVA test applied proved that cotyledon number is a statistically significant variable affecting seedling establishment ($F = 6.46142$, $p = 0.002957$).

The classification tree models provide an insight into the way that permanent plots established for the study of seedling recruitment stages are classified in accordance to their habitat characteristics (Fig. 5a–d).

Ground is the explanatory variable which is the most decisive in classifying the plots as regards seedling emergence. Plots having a closed ground cover (e.g. from a fallen tree log or from a big stone) had the highest mean seedling emergence (24.69 versus 12.74 in the open). These plots (microsites) were subsequently classified by elevation and secondarily by soil depth, (left terminal node), while,

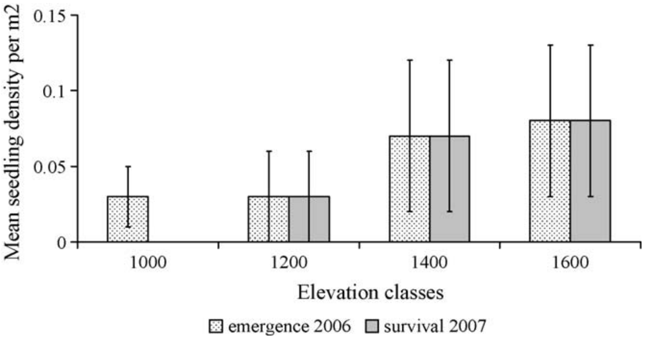

Fig. 3. Mean seedling density for the 2006 cohort (year of emergence) and their first year survival (2007). Data distributed by elevation class.

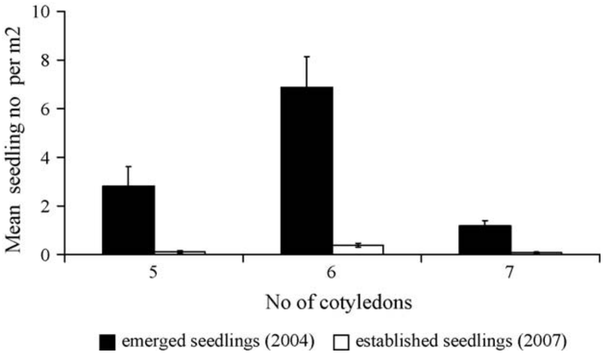

Fig. 4. Mean seedling density in relation to the number of cotyledons. Data refer to seedlings having emerged in 2004 and those established at the end of their 3rd year of life (2007). Individuals that had 4 cotyledons were included in the group of those having 5, and individuals that had 8 cotyledons in the group of those having 7.

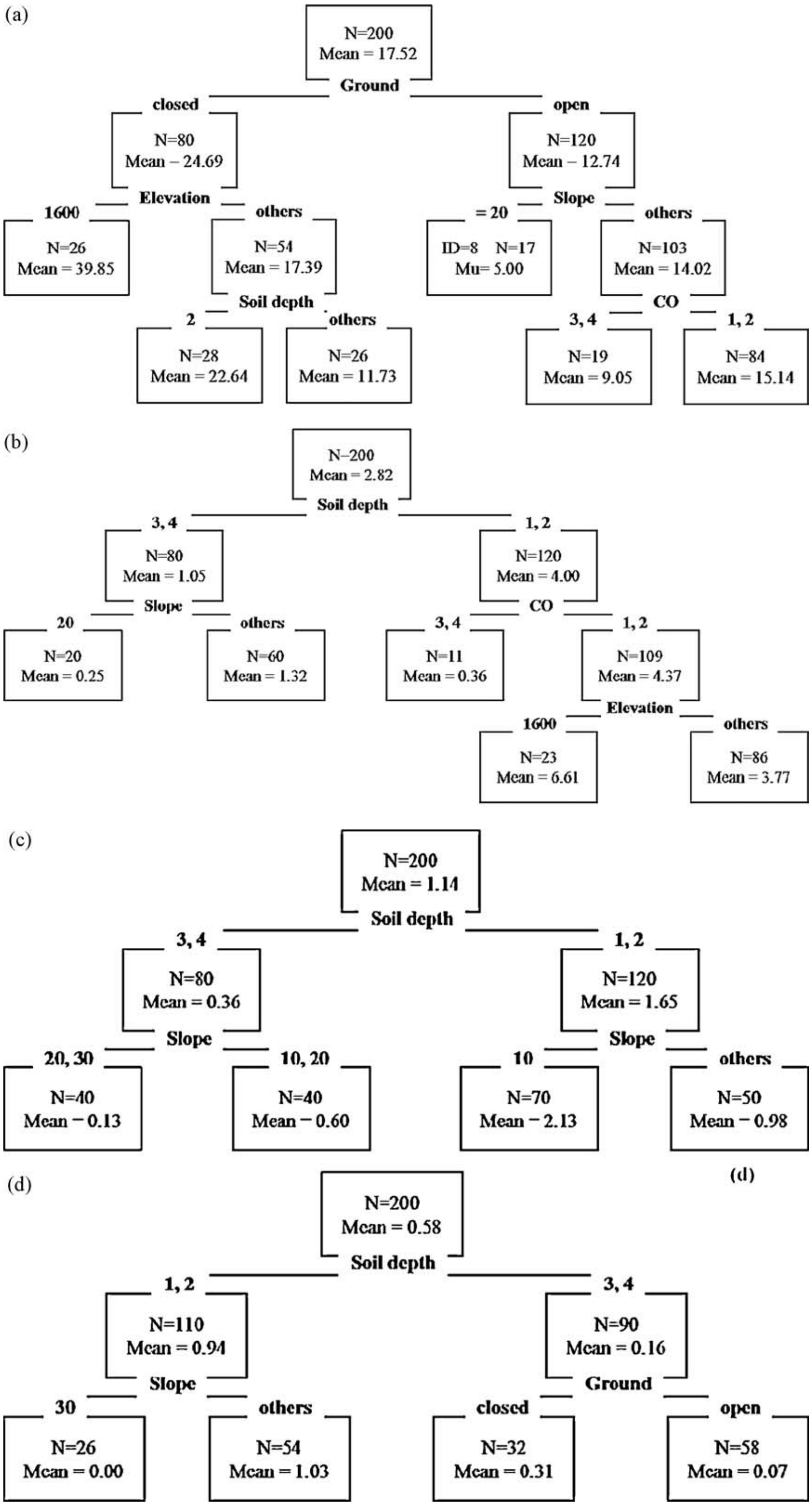

Fig. 5. Classification trees showing the effect of habitat characteristics on habitat classification with respect to seedling emergence (**a**) and subsequent survival over three years of monitoring (**b–d**). Explanatory variables used were: ground, which stands for percentage ground cover; open <40% of the ground covered with tree logs and/or rocks–closed ≥40% of the ground covered by tree logs and/or rocks, elevation, in classes of 1000, 1200, 1400 and 1600 meters, slope, in classes of 10, 20, 30 and 40°, soil organic horizon depth, organized in classes of 1, 2, 3 and 4 cm, canopy openness (CO), presented in the classes of 1, 2, 3 and 4 standing for shaded, partially shaded, partially open and open habitats respectively. N is number of plots, mean is mean seedling number.

at locations with no "obstacles", seedling emergence was primarily classified by the inclination of the site (slope) (Fig. 5a), and secondarily by canopy openness (CO). The elevation of 1600 meters being a terminal node, gathered the majority of emerged seedlings (39.85 mean seedling emergence versus 17.39 for all the other elevations together). The classification tree also revealed the way slope is interrelated with fir canopy openness (CO) as regards its effect on seedling emergence (Fig. 5a). Plots characterized as shaded (class **1**) and partially shaded (class **2**) microhabitats, were classified separately from those partially open (class **3**) and open (class **4**) microhabitats, showing higher mean seedling density (15.14 in the former versus 9.05 in the latter).

After the period with the highest mortality rate (survival 2005, Fig. 5b), plots were primarily classified by the depth of the organic soil layer (soil depth), and secondarily by the slope (slope) of the site (left branch) and canopy openness (CO) (right branch) in relation to seedling survival. Mean seedling survival density was higher on the 'others' slope (as in the case of emergence), being 1.32 as compared to 0.25 for category '20'. Plots characterized by closed or partially closed canopy openness (classes **1** and **2** respectively) had higher mean seedling survival (4.37) as opposed to open and partially open (classes **3** and **4** respectively). Elevation further prunes the right branch of canopy openness; as in case of emergence, seedling survival shows a higher mean of 6.61 at the elevation class **1600** versus 3.77 for the others.

When seedlings have reached their 3rd year of life (survival 2006, Fig. 5c) organic soil depth (Soil depth) is the habitat characteristic which continues to be a critical parameter for their survival, being the first to classify the plots. The classification tree is secondarily pruned by Slope for either of its branches.

In their 4th year of life (Fig. 5d) young established saplings continue to be primarily affected by organic soil depth (Soil depth), which is the explanatory variable first classifying the study plots. As in the previous tree, slope and ground condition (Ground) are the variables further pruning the classification tree.

4. Discussion

The forest regeneration process is one of the fundamental issues in forest ecology. Natural forest regeneration comprises seed production and dispersal and successful seedling germination and establishment. As expected for a masting species (Politi et al., 2007), the recruitment strategy of *A. cephalonica* varied from year to year. A year of high cone production leads to high seedling production as in other masting species of *Abies* e.g. *A. alba* Mill. (Dobrowolska, 1998); this high seedling production year was followed by two years of significantly lower seedling numbers, but also lower mortality when compared to that of the 1st year of massive seedling production. It appears that a compensation mechanism is set into motion as an adaptive strategy for this species. In a year of high seedling production, the species invests in numbers, and exhibits r-strategy characteristics whereas investing in survival of the few produced seedlings during the following years *A. cephalonica* displays K-strategy features (Grime, 1979).

Emergence, survival and final establishment of seedlings are stages of their recruitment which are greatly affected by habitat characteristics (Gray and Spies, 1996; Clark et al., 1999; Lee et al., 2004; Gómez-Aparicio et al., 2005; Frey et al., 2007). The presence of any form of obstacles on the ground (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). Besides, recruitment of tree seedlings on fallen tree logs is a common phenomenon in boreal and temperate forests (Harmon and Franklin, 1989). Our results indicate that herb and bryophyte cover (parameter "grass"–see Table 2) was not among the first explanatory variables to classify the study plots during any of the vital stages of seedlings. In contrast, ground cover (parameter "ground") was such a parameter both at the stages of emergence and of establishment. Studies on the development of conifer sapling roots suggest that *Abies* seedlings, germinating from large seeds, develop long tap roots. These allow them to be equally established on soil or fallen logs presenting a remarkable plasticity in their responses to microsites at least in their first years of life (Takahashi, 1997; Narukawa and Yamamoto, 2003).

Organic soil depth was found to be among the explanatory variables initially classifying the plots during the stage of seedling emergence. Stamatopoulos (1995) suggested that regeneration of *A. cephalonica* on Mount Parnitha (mainland Greece) reaches a maximum in areas with an organic horizon ranging between 1.5 and 2.5 cm in depth and becomes minimal in deeper soils. The rooting system of *A. cephalonica* is not very developed at the seedling stage, thus conferring an advantage to those seedlings that germinated on microsites with a thinner organic horizon, where roots reach the mineral soil, which is a most secure source of nutrients and water, easier and faster. Studies on the root growth of *A. cephalonica* have shown the relationship between fir decline symptoms (crown dieback, needle discoloration and loss) and root growth patterns (Raftoyannis et al., 2008). Although *A. cephalonica* can tolerate considerable drought in relation to other *Abies* species (Fady, 1992), their survival still requires that roots extend deeper, into the mineral soil to find sufficient water.

The effect of low slope angle ($<10^\circ$) has been postulated to be an obstacle for regeneration in coniferous boreal forests (Iovino and Menguzzato, 1993), but we found little evidence of this. Stamatopoulos (2005) has also found that regeneration of *A. cephalonica* on Mount Parnitha, was better on slopes up to 30%, without explaining whether this result had to do with seedling emergence and/or establishment. Our data suggest that slope is critical for classifying seedling habitats both at the stage of their emergence and that of establishment. Opinions about the role of elevation and aspect (both responsible for climatic gradients) on seedling recruitment, are conflicting. Consensus however exists on the way these environmental factors are known to control seedling dynamics (Clark et al., 1999, Stephenson and van Mantgem, 2005). In Mount Aenos National Park, elevation was a habitat parameter classifying seedling habitats at the stage of their emergence and 1600 m proved to be the most important class in this classification. A positive effect of elevation on seedling densities is consistent with other studies on *Abies* species (Borghetti and Vignali, 1988). The response of seedling densities to elevation may be mediated by a greater proportion of successfully germinated seeds. At higher elevations snow persists for a longer period of time, offering in this way a longer chilling period, which has been shown to be correlated with higher percentages of germination (unpublished data).

Many forests support dense understory that buffers the forest floor against canopy changes affecting light, moisture and nutrients (Beckage et al., 2000; Clinton et al., 1994; Harmon and Franklin, 1989; Nakashizuka, 1989), so that understory shrubs might neutralize recruitment opportunities for tree seedlings. Previous studies both in managed and unmanaged forest micro-environments have shown that residual overstory density is one of the key factors affecting emergence, survival and growth (Emmingham and Waring, 1973; Canham, 1988; Carter and Klinka, 1992; Gray and Spies, 1996; Aussenac, 2000; Myers et al., 2000; Beckage and Clark, 2003; Castro et al., 2004). The *Abies* forest of Mount Aenos National Park has practically no understory vegetation; a few scattered saplings of *A. cephalonica* can be observed which create different canopy micro-environments, depending principally on the age class of the individuals. The pattern of fir regeneration under its own canopy has been a controversial issue (Gürth, 1988; Ammer, 1996). Extensive literature exists relating better fir regeneration to conditions created under a mixed forest canopy as opposed to that of homogeneous fir canopy. This difference has been attributed to the quantity of scattered light reaching the forest floor as well as to the spectral properties of the solar radiation reaching the understory (usually greater transmission of blue and red energy bands; Messier and Bellefleur, 1988). It has been commonly believed that

Abies spp. regeneration is more abundant at a certain level of shade (usually provided by a thick canopy cover), where microclimatic conditions are thought to be more favourable (Caliskan, 1995; Cochard, 1992; Aussenac, 2002). However, these conditions have not been linked directly to either the light germination requirements of *Abies* spp. seeds or its light demand for subsequent growth. Despite the above, which is usually coupled by the argument whereby *A. cephalonica* seedlings are exclusively shade "demanding" until their sapling age, our data suggest that the microclimatic conditions created by shaded and partially shaded environments (CO classes 1 and 2) classified seedling habitats in the first two years of their life only. Germination experiments run in parallel with the current monitoring project have shown that, after 6 weeks of chilling, seeds were germinating at a final percentage of 50% in the dark, while a slightly less final germination was achieved in red or white light (Politi et al., in preparation). It is therefore reasonable to conclude that the degree of canopy openness is not as critical, at least for this stage of *A. cephalonica*'s life.

Patterns of seedling recruitment depend on a number of factors, particularly the availability of seed production, and germination conditions (Frey et al., 2007) as well as the support by embryonic structures such as cotyledons. Out of the 4613 fir seedlings tagged and monitored during the four years of study, the majority had 6 cotyledons. However, survival was higher for those individuals having 7 cotyledons, suggesting that the larger the number of cotyledons the higher the advantage of seedlings over their co-fellows with less cotyledons. Apart from being dependent on the storage compounds of their embryos, seedlings with a larger photosynthetic surface are more successfully equipped in their early critical life stage. Similar trends have been recorded for other coniferous species (Daskalakou, 1996). Most of the seedlings ($>$70%) lost their cotyledons after the third year of their life, when they can be considered as safely established.

In Greece, in general, forest areas occupied by *A. cephalonica* are not protected by specific legislation. But even in those cases which are under such protection, the species is endangered from either hybridization processes, by *A. alba*, or intense human impact. Protected areas are widely recognized for their value in the conservation of biodiversity (Brooks et al., 2004). Knowledge of processes and factors influencing natural regeneration is essential for successful management. To our knowledge, this is the first report on the occurrence and dynamics of young seedlings during their first few years of life in an area of European Community interest but also of wider ecological importance for its biodiversity. Our data indicate that *A. cephalonica* is a species showing remarkable reproductive plasticity expressed by the number of seedlings produced each year and those surviving with respect to its habitat characteristics. Preserving the species implies preserving the heterogeneity of its habitat. In this sense Mount Aenos National Park may be the most important protected area for this endemic fir as regards the preservation of its integrity and the adoption of pre-emptive management in the light of current and future threats.

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References

Ammer, C., 1996. Impacts of ungulates on structure and dynamics of natural regeneration of mixed mountain forests in the Bvarian Alps. Forest Ecology and Management 88, 43–53.

Arianoutsou, M., 2007. Resilience of Mediterranean Vegetation to Fire: Issues under the Global Change Scenarios, 2007. In: Rokich, D., Wardell-Johnson, G., Yates, C., Stevens, J., Dixon, K., R. McLellan, R., Moss, G. (Eds.), Proceedings of the MEDECOS XI 2007 Conference, Perth, Australia. Kings Park and Botanic Garden, Perth, Australia, pp. 5–7.

Aussenac, G., 2000. Interactions between forests stands and microclimate: ecophysiological aspects and consequences for silviculture. Annals of Forest Science 57, 287–301.

Aussenac, G., 2002. Ecology and ecophysiology of circum-Mediterranean firs in the context of climate change. Annals of Forest Science 59, 823–832.

Barbéro, M., Quézel, P., 1976. Les groupements forestieres de Grèce centro-meridionale. Ecologia Mediterranea 2, 3–86.

Beckage, B., Clark, J.S., Clinton, B.D., Haines, B.L., 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. Canadian Journal of Forest Research 30, 1617–1631.

Beckage, B., Clark, J.S., 2003. Seedling survival and growth of three forest tree species, the role of spatial heterogeneity. Ecology 84, 1849–1861.

Beckage, B., Lavine, M., Clark, J.S., 2005. Survival of tree seedlings across space and time: estimates from long-term count data. Journal of Ecology 93, 1177–1184.

Borghetti, M., Vignali, G., 1988. L' abete bianco nei boschi del Monte Nero. L' Italia Forestale e Montana 5, 312–328.

Breiman, L., Friedman, J., Olshen, R., Stone, C., 1984. Classification and regression trees. Wadsworth, Pacific Grove, CA.

Brooks, T.M., da Fonseca, G.A.B., Rodrigues, A.S.L., 2004. Protected areas and species. Conservation Biology 18, 616–618.

Caliskan, A., 1995. Growth patterns and silvicultural treatments in mixed Pinus sylvestris/Abies bornmulleriana/Fagus orientalis stands in the Buyukduz experimental forest, A42. Istanbul Universitesi Orman Fakultesi Dergisi Seri, pp. 183–210.

Canham, C.D., 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. Ecology 69, 786–795.

Carter, R.E., Klinka, K., 1992. Variation in shade tolerance of Douglas-fir, western hemlock, and western redcedar in coastal British Columbia. Forest Ecology and Management 55, 87–105.

Castro, J., Zamora, R., Hódar, J.A., Gómez, J.M., 2004. Seedling establishment of a boreal tree species (*Pinus sylvestris*) at its southernmost distribution limit: consequences of being in a marginal Mediterranean habitat. Journal of Ecology 92, 266–277.

Clark, J.S., Beckage, B., Camill, P., Cleveland, B., HilleRis-Lambers, J., Lichter, J., MacLachlan, J., Mohan, J., Wyckoff, P., 1999. Interpreting recruitment limitation in forests. American Journal of Botany 86, 1–16.

Clinton, B.D., Boring, L.R., Swank, W.T., 1994. Regeneration patterns in canopy gaps, mixed-oak forests of the southern Appalachians: influences of topographic position and evergreen understory. American Midland Naturalist 132, 308–319.

Cochard, H., 1992. Vulnerability of several conifers to air embolism. Tree Physiology 11, 73–83.

Daskalakou, E.N., 1996. Ecophysiology of the postfire regeneration in Aleppo pine (*Pinus halepensis*) forests (in Greek with an English summary). PhD Thesis, University of Athens, Athens, Greece.

De'ath, G., Fabricius, K.E., 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81, 3178–3192.

Déqué, M., Marquet, P., Jones, R., 1998. Simulation of climate change over Europe using a global variable resolution general circulation model. Climate Dynamics 14, 173–189.

Dobrowolska, D., 1998. Structure of silver fir (*Abies alba* Mill.) natural regeneration in the 'Jata' reserve in Poland. Forest Ecology and Management 110, 237–247.

Emmingham, W.H., Waring, R.H., 1973. Conifer growth under different light environments in the Siskiyou mountains of south-western Oregon. Northwest Science 47, 88–99.

Fady, B., 1990. Genetic variability of height growth components of the Greek fir (*Abies cephalonica*). Canadian Journal of Forest Research 20, 1453–1460.

Fady, B., 1992. Effect of osmotic stress on germination and radicle growth in five provenances of *Abies cephalonica* Loudon. Acta Oeologica 13, 67–69.

Fady, B., Arbez, M., Ferrandéz, P., 1991. Variability of juvenile Greek firs (*Abies cephalonica* Loud.) and stability of characteristics with age. Silvae Genetica 40, 91–100.

Farjon, A., Rushforth, K.D., 1989. A classification of *Abies* Miller (*Pinaceae*). Notes of the Royal Botanical Garden Edinburgh 46, 59–79.

Forestry Department of Cephalonia., 1996. General management plan of the National Park of Mount Aenos. Cephalonia, Greece (in Greek).

Frey, B.R., Ashton, M.S., McKenna, J.J., Ellum, D., Finkral, A., 2007. Topographic and temporal patterns in tree seedling establishment, growth, and survival among masting species of southern New England mixed-deciduous forests. Forest Ecology and Management 245, 54–63.

Fyllas, M.N., Dimitrakopoulos, P.G., Troumbis, A.Y., 2008. Regeneration dynamics of a mixed Mediterranean pine forest in the absence of fire. Forest Ecology and Management 256, 1552–1559.

Germino, M.J., Smith, W.K., Resor, A.C., 2002. Conifer seedling distribution and survival in an alpine-treeline ecotone. Plant Ecology 162, 157–168.

Gómez-Aparicio, L., Valladares, F., Zamora, R., Quero, J.L., 2005. Response of tree seedlings to the abiotic heterogeneity generated by nurse shrubs: an experimental approach at different scales. Ecography 28, 757–768.

Gray, A.N., Spies, Th.A., 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. The Journal of Ecology 84, 635–645.

Grime, J.P., 1979. Plant strategies and vegetation processes. John Wiley and Sons, Chichester.

Guidi, G., Pelleri, F., 1990. Prime osservazioni su due impianti sperimentali di abete Greco dell' appennino centro meridionale. Istituto Sperimentale per la Selvicoltura Arezzo 21, 109–134.

Gürth, P., 1988. Der Fruchtwechesel in Walde. Forst und Holz 10, 235–237.

Harmon, M.E., Franklin, J.F., 1989. Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. Ecology 70, 48–59.

Iovino F., Menguzzato G., 1993. L' abete bianco sull' appennino Lucano. Lavoro svolto nell' ambito della linea di ricerca Ecologia dell' abete bianco dell' I.E.I.F. (Istituto di Ecologia e Idrologia Forestale) del C.N.R. (Consiglio Nazionale delle Ricerche) di Cosenza, 7, 2–30.

IPCC, 2007. Climate Change 2007. Synthesis report. An Assessment of the Intergovernmental Panel on Climate Change.

Lee, C.S., Kimm, J.H., Yi, H., You, Y.H., 2004. Seedling establishment and regeneration of Korean red pine (*Pinus densiflora* S. et Z.) forests in Korea in relation to soil moisture. Forest Ecology and Management 199, 423–432.

Messier, C., Bellefleur, P., 1988. Light quantity and quality on the forest floor of pioneer and climax stages in a birch-beech-sugar maple stand. Canadian Journal of Forest Research 18, 615–622.

Mitsopoulos, D.J., Panetsos, C.P., 1987. Origin of variation in fir forests in Greece. Silvae Genetica 36, 1–15.

Montgomery, R.A., 2004. Effects of understory foliage on patterns of light attenuation near the forest floor. Biotropica 36, 33–39.

Morandini, R., Ducci, F., Menguzzato, G., 1994. *Abies nebrodensis* (Lojac) Mattei. Inventario 1992. Annali dell' Istituto Sperimentale Selvicoltura 22, 5–51.

Myers, G.P., Newton, A., Melgarejo, O., 2000. The influence of canopy gap size on natural regeneration of Brazil nut (*Bertholletia excelsa*) in Bolivia. Forest Ecology and Management 127, 119–128.

Nakashizuka, T., 1989. Role of uprooting in composition and dynamics of an old-growth forest in Japan. Ecology 70, 1273–1278.

Narukawa, Y., Yamamoto, S., 2003. Development of conifer seedlings roots on soil and fallen logs in boreal and subalpine coniferous forests of Japan. Forest Ecology and Management 175, 131–139.

Palutikof, J., Wigley, T., 1996. Developing climate change scenarios for the Mediterranean region. In: Jeftic, L., Keckes, S., Pernetta, J.C. (Eds.), Climate Change and the Mediterranean, Vol. 2. Arnold, London, pp. 27–56.

Panetsos, K.P., 1975. Monograph of *Abies cephalonica* Loudon. Annals of Forestry Zagreb 7, 1–22.

Parducci, L., 2000. Genetics and Evolution of the Mediterranean *Abies* Species. Doctoral Thesis. Swedish University of Agricultural Sciences.

Phitos, D.G., Damboldt, J., 1985. Chloris of Cephalonia. Botanika Chronika 5 (in Greek, with an English summary).

Politi, P.I., Marcenò, C., 2001. Lineamenti geobotanici di Monte Aenos (Cefalonia, Grecia). Università degli studi di Palermo Tesi di Laurea. (In Italian).

Politi, P.I., Arianoutsou, M., Georghiou, K., 2007. Aspects of the reproductive biology of the Greek fir (*Abies cephalonica* Loud.) in the Mt. Aenos National Park. In: Rokich, D., Wardell-Johnson, G., Yates, C., Stevens, J., Dixon, K., McLellan, R., Moss, G. (Eds.), Proceedings of the MEDECOS XI 2007 Conference, Perth, Australia. Kings Park and Botanic Garden, Perth, Australia, pp. 191–192.

Raftoyannis, Y., Radoglou, K., 2001. Crown condition of a fir forest in Karpenisi, Central Greece. International Conference on Forest Research "A challenge for an integrated European approach" NAGREF, Forest Research Institute, Thessaloniki. Greece, pp. 317–320.

Raftoyannis, Y., Spanos, I., Radoglou, K., 2008. The decline of Greek fir (*Abies cephalonica* Loudon): Relationships with root condition. Plant Biosystems 142, 386–390.

Sala, O., Chapin Stuart, F., Armesto, J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L., Jackson, R., Kinzig, A., Leemns, R., Lodge, D., Mooney, H.A., Oesterheld, M., Poff, N., Sykes, M., Walker, B., Walker, M., Wall, D., 2000. Global Biodiversity Scenarios for the Year 2100. Science 287, 1770–1774.

Samios, K.M., 1908. Ta dasi tis Kefallinias. National Publications Office, Athens, pp. 120–131 (in Greek).

Stamatopoulos, E., 1995. Regeneration of Abies cephalonica in Mountain Parnitha National Park. Ph.D. Thesis. University of Thessaloniki (in Greek with an English summary).

Steinberg, G., Colla, P., 1995. CART: tree-structured non-parametric data analysis. Salford Systems, San Diego, CA.

Stephenson, N.L., van Mantgem, P.J., 2005. Forest turnover rates follow global and regional patterns of productivity. Ecology Letters 8, 524–531.

Takahashi, K., 1997. Regeneration and coexistence of two subalpine conifer species in relation to dwarf bamboo in the understorey. Journal of Vegetation Science 8, 529–536.

Tsopelas, P., Angelopoulos, A., Economou, A., Voulala, M., Xanthopoulou, E., 2001. Monitoring crown defoliation and tree mortality in the fir forest of Mount Parnis, Greece. International Conference on Forest Research, "A challenge for an integrated European approach" NAGREF, Forest Research Institute, Thessaloniki. Greece, pp. 253–258.