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Pinus halepensis invasion in *Pinus pinea* habitat in Strofylia forest (Site of NATURA 2000 network), southern Greece

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Summary

Pinus halepensis invasion to *P. pinea* biotope, which is included in the Annex I of the Directive 92/43 of European Union for nature conservation, has been observed in many cases within the Mediterranean region. Strofylia forest, southern Greece, belongs to the Natura 2000 European network, the Ramsar Convention, and in the Special Protected Zones for birds according to E.U. Directive 79/407/EEC. The forest is characterised by the invasion of *P. halepensis* to *P. pinea* biotope for many decades which resulted in the gradual replacement of the species. This study aims to investigate the invasion process by analysing stand structural data, species seed production, and species growth patterns using the stem analysis method. Data analysis showed that *P. pinea* stands are even-aged, approximately 115-130 years old, with a very low stand density. *P. halepensis* invasion started approximately 50 years ago and still continues to the present day. Seed production of *P. pinea* is limited, while *P. halepensis* produces a large number of seeds. Both pine species are quite fast growing during the first 20-30 years of tree age, regardless of the difference of 70 years in the time they established. Comparatively, at the same ages, *P. halepensis* has significantly larger height growth than *P. pinea*, while *P. pinea* shows greater diameter growth. The comparatively high growth rates of *P. halepensis* in combination with high seed production and seed dispersal traits should be considered significant factors favouring the species invasion and contribute to an increased possibility for future dominance of *P. halepensis* in *P. pinea* habitat.

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Introduction

Ecological succession takes place in many circumstances around the world. Usually, during succession, late successional species invade an area occupied by early successional species and gradually replace them. Many models have been used to explain succession, pointing out the importance of competition between individual plants, which is based on the species physiological traits, such as shade tolerance and growth rates (Barbour et al. 1999; Huston & Smith 1987). Quite often, seed dispersal and land use history, play an important role (Botkin 1981; Kimmins 1997). While, according to Oliver and Larson (1996) invasion patterns are the result of regeneration mechanisms, growth rates, mortality rates and shade tolerances.

Pinus pinea is a Mediterranean pine species whose natural range is impossible to determine due to early human use and expansion (Martinez & Montero 2004). It is a species that has commonly been used from ancient times for wood and (mainly) for nuts production (Calama et al. 2003; Moussouris & Regato 1999). It is geographically distributed along the Mediterranean basin, and its habitat is included in the Annex I of the Directive 92/43 of European Union for nature conservation. *Pinus halepensis* is a Mediterranean pine which forms extensive natural forests along the Mediterranean basin (Quezel 2000). This species is considered one of the most invasive pines, threatening native biodiversity in various habitats (Nathan & Ne'eman 2004; Richardson 2000). It is a well-known post-fire colonisation tree species due to the serotinous cones. On the contrary, post-fire regeneration of *P. pinea* is poor and it seems unlikely that forests of the species can recover after a fire; therefore, action is recommended to restore their ecosystems (Perula et al. 2003).

Strofylia forest lies in Western Peloponnese and together with nearby sand-dune and wetland areas belong to the European NATURA 2000 network of protected areas and is also designated under the Ramsar Convention. Furthermore, it is a Special Protected Zone for birds according to E.U. Directive 79/407/EEC. Limitation of *P. pinea* habitat by invasion of the species *P. halepensis* has been observed in the area for many decades (Ganatsas & Tsakaldimi 2007; Moussouris & Regato 1999), as well as in many cases around the Mediterranean basin (Barbero et al. 1998; Tapias et al. 2004). This results in a long-term reduction of *P. pinea* habitat due to the forest succession phenomenon.

Until now, not much is known on stand dynamics of *P. pinea* forest invaded by *P. halepensis* and the drivers forcing this process. Seed production and dispersal of the two species may be the critical factors, but tree growth rates may also play a decisive role.

Growth rate of tree species in temperate ecosystems can be determined through the reconstructive growth course of the trees, precisely estimated using the stem analysis method. Stem analysis is a very useful technique in forest ecosystems, and it finds multiple uses in forestry and especially in stands productivity assessment and discrimination of site qualities (Bravo-Oviedo et al. 2004; Salas & Garcıa 2006; Thanasis 2004). The constructed growth curves have a wide biological, ecophysiological, silvicultural and practical importance in forestry (Kariuki 2002). Beyond this implementation, stem analysis is a useful tool for studying biological phenomena such as invasion process (Webster et al. 2005). Also, it has recently been used in the development of models related to climate change and carbon sequestration possibilities in forest ecosystems (Lopez-Serrano et al. 2005; Magnani et al. 2004).

This paper deals with the estimation of stand dynamics of *P. pinea* forest invaded by *P. halepensis*, based on the analysis of stand structural data, and tries to estimate the role of seed production and tree growth rates of the two pine species in the invasion process. The time of invasion, and the tree growth rates in height and diameter for the two species were examined thoroughly with the reconstruction of tree growth curves.

Materials and methods

Area description

The research was conducted in Strofylia forest in Western Peloponnese, southern Greece (Figure 1). The forest covers a north-south coastal strip with a length of 15 km and an average width of 1.5 km. *P. halepensis*, *P. pinea* and *Quercus aegilops* are the dominant plant species in the area, and they form pure and mixed stands. *P. halepensis* occupies the greater part of the forest, while *P. pinea* appears in the eastern part of the forest. *Q. aegilops* occupies only a small part in the centre of the area. *P. pinea* population in the area is considered natural (Georgiadis et al. 1990). All the area is almost flat with a low altitude 1-10 m; the soils appear to have sandy to loamy sand texture with high water table, estimated 1.5 m (Papamichos 1986). The climate is Mediterranean with long dry periods which reach up to five months. The vegetation belongs to *Quercetalia ilicis* zone (Athanasiadis & Gerasimidis
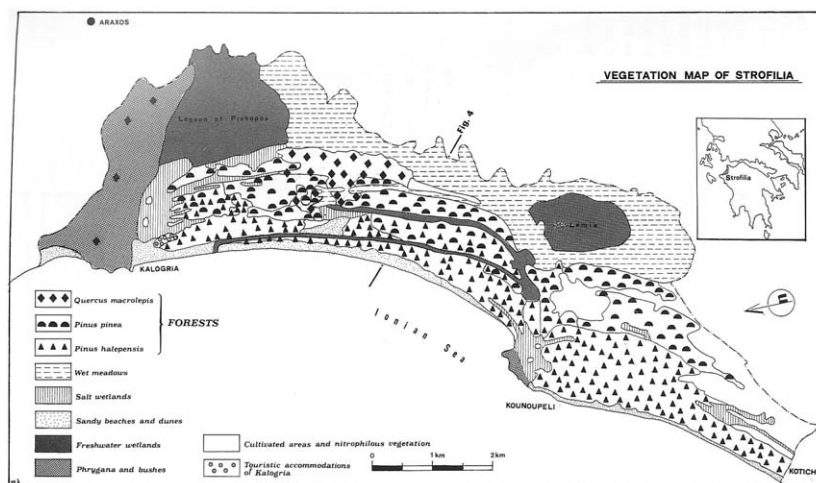
Figure 1. Map of the study area. Vegetation mapping was taken by Georgiadis et al. (1990).

1986). The whole area receives tourist pressures every summer, a fact that contributes to some degradation of the ecosystems. The population of *P. pinea* occupies rather uniform site conditions; the habitat area is characterised by flat surfaces lying on sandy-dune formations, at an altitude of a few metres (1-5 m) above sea level.

Methods

Stand structure of *P. pinea* forest in the area was evaluated by taking a sample of 20 rectangular permanent plots of 0.6-1.8 ha, distributed along the area the species occupies, based on the habitat map of the Natura 2000 network. However, we did not sample in a small part of the area that is covered by young artificial stands 25 years old, and a few open over-mature stands (Ganatsas et al. 2008). All the plots were established in the field in 2004, and their geographic coordinates were recorded and placed on a map. In each plot, the following data were collected: i) tree dimensions (diameter at breast height (DBH) and total height) of all the trees with DBH above 4 cm were measured for all species; and ii) tree age was measured in a number of three dominant trees per plot by taking tree cores and measuring tree annual rings in the laboratory.

Then, based on the species stem distribution, the stands were distinguished in four stages in regards to *P. halepensis* invasion, which in a chronosequence approach can be considered as different seral stages of forest succession (Barbour et al. 1999; Foster & Tilman 2000). These stages are: a) pure *P. pinea* stands; b) early successional stage with low *P. halepensis* invasion; c) advanced invasion stage; and d) late successional stage with dominance of *P. halepensis* (Figure 2a, b, c, d).

Seed production was estimated by measuring all the cones of 15 mature trees per species (random sampling), selected from stands of the third seral stage for two successive years. As mature trees we considered trees with DBH over 35 cm (Dafis 1990). Then, taking into account, the species stem density, which was estimated by field measurements, and literature data for seed production per cone (Daskalakou (1996) for *P. halepensis*, and Ganatsas et al. (2008) for *P. pinea*), we estimated the seed crop of the two species as follows: Seed crop = number of trees per hectare × number of cones per tree × number of seeds per cone. Seed dispersal of *P. halepensis* was considered to follow the model developed by Nathan and Ne'eman (2004), while for *P. pinea* we accepted that seed dispersal is limited under the parent trees (Barbeito et al. 2008).

Tree sampling was conducted in April 2005 in *P. pinea* stands invaded by *P. halepensis* (third seral stage). Fifteen randomly selected dominant or co-dominant trees were felled for *P. pinea* along the *P. pinea* stands. Trees of *P. halepensis* were selected according to the tree diameter classes of the species. In order to cover any variation in species growth pattern depending on the tree classes, five trees per diameter class for the following classes (Dafis 1990) were felled: i) trees with diameter at beast height (DBH) < 20 cm; ii) trees with DBH 20-35 cm; and iii) trees with DBH > 35 cm. The relatively small number of sampling trees is due to the large dimensions of the trees, and thus the sampling procedure (cutting, felling, splitting up), the stems discs transport and the examination and analysis of annual rings were extremely time-consuming. DBH and total height were measured in all felled trees. Stem discs were taken at section height 0.3 m and 1.3 m and then every 3 m along the
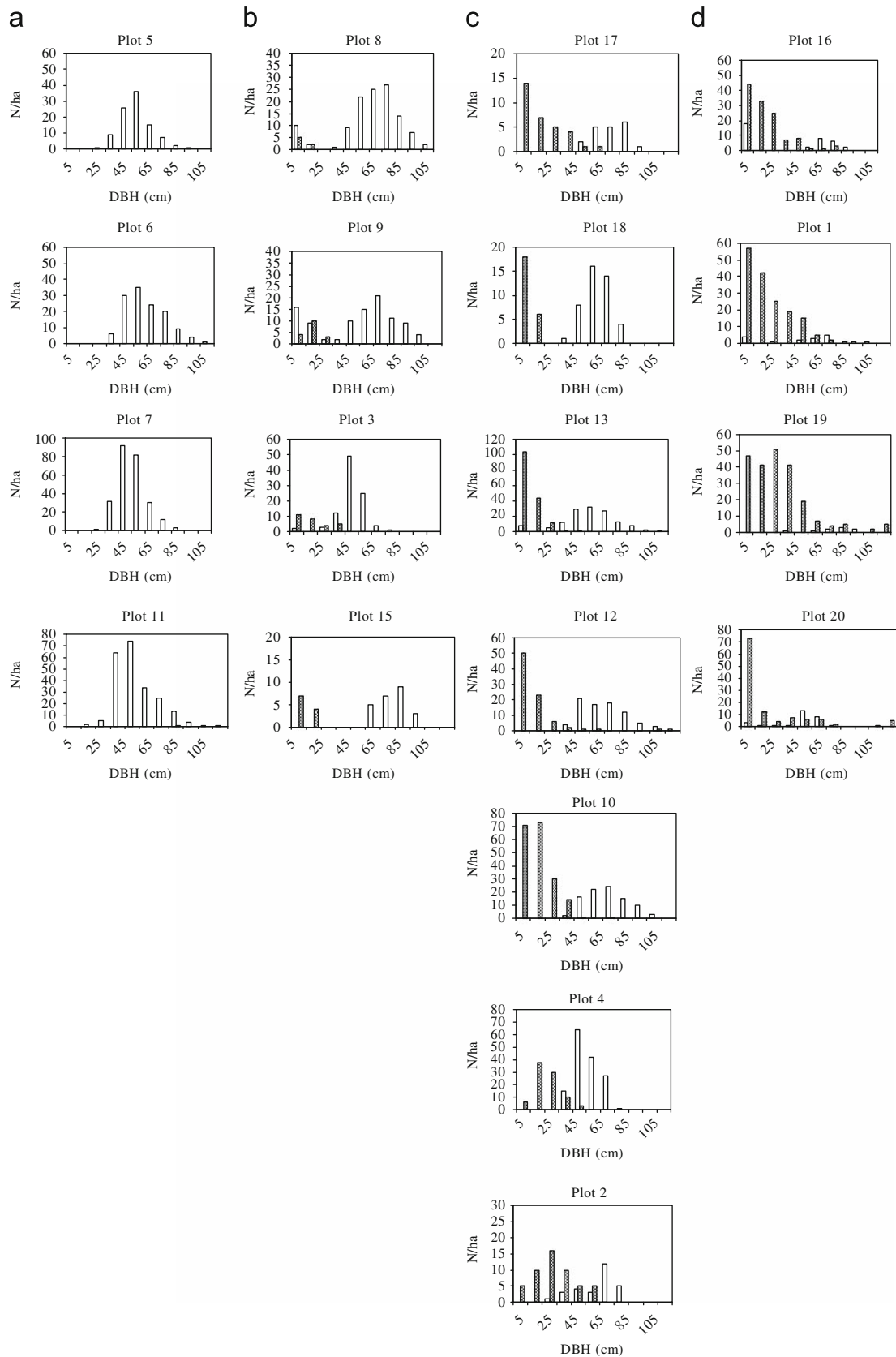
Figure 2. Tree diameter distribution of the two species (*P. pinea* empty bars, *P. halepensis* lined bars) in the sample stands, showing a progressive increase on *P. halepensis* stems, especially in the under storey and middle storey: a) pure *P. pinea* stands; b) stands with low *P. halepensis* invasion; c) stands with advanced *P. halepensis* invasion; and d) stands where *P. halepensis* already dominates.

entire stem until the diameter over bark of 5 cm. The stem discs, 2 cm thick, were transported to the laboratory where they were air-dried and the number and width of annual growth rings were measured, according to mean radial, with a Parker Instrument, Electronic Machine for Measuring Annual Growth Rings-Mod. 3, in an accuracy of 0.01 mm.

Annual height increment and tree height in every stem section was estimated by using the Carmean method (Carmean 1972), which is considered as one of the most accurate methods in stem analysis (Dyer & Bailey 1987; Fabbio et al. 1994; Salas & García 2006; Tsitsoni et al. 2004; Wang & Kimmins 2002). Cumulative growth curves and increment curves (mean annual and current annual) of height and diameter were produced from data obtained from stem analysis for each sample tree. Then, based on the mean values, we constructed the average growth and increment curve for each species. However, in the case of *P. halepensis*, we firstly produced three curves, one for each diameter class; then, due to the similar growth pattern they followed, we homogenised the data of the three classes, and we constructed one curve as the average value of all *P. halepensis* trees. In order to analyse periods of tree suppression and release for each tree, we compared the average tree-ring width over a 10-year period with the average tree-ring width the 10 previous years (Dahir & Lorimer 1996; Groven et al. 2002; Webster et al. 2005). A growth release was defined as 100% or greater increases in radial growth rate for 10 years following 10 years of slow growth. For trees already showing moderate growth before release (>1 mm/year) a 50% increase was applied to define growth release (Groven et al. 2002; Lorimer 1985). The minimum growth rate during a release event is set at 1.0 mm per year. Based on the data analysis we estimated the growth behaviour of the two species and we tried to estimate the invasion process in the area.

Statistical analysis was conducted using the SPSS software (SPSS Inc., Chicago, IL. USA), and the Waller-Duncan criterion was used for means comparison of tree height and diameter among the different seral stages. Values distribution was tested for normality by Kolmogorov-Smirnov criterion and the homogeneity of variances was tested by Levene's test (Norusis 1994; Snedecor & Cochran 1988).

Results

Stand dynamics

The stands of *P. pinea* in the Strofylia forest were found to be even-aged, 115-130 years old, established approximately in 1873-1890. Based on the species composition and their stem density, a progressive increase on *P. halepensis* stems from west and north to east and south was observed (from *a* to *d* column in Figure 2), especially in the understorey and middlestorey, that can be considered as a series showing the rate of *P. halepensis* invasion to *P. pinea* habitat. The stands of first stage (Figure 2a) are even-aged pure *P. pinea* stands without any presence of *P. halepensis* in any storey. Stands of the second seral stage (Figure 2c) consist an early successional stage where *P. halepensis* appears only in the understorey and middlestorey, with relative low stem density (mean tree density 20.7 trees per hectare). All the *P. halepensis* trees are young and they do not exceed the value of 35 cm in DBH and they did not enter in the overstorey. In terms of total stem density, the ratio is approximately 80-20% for *P. pinea* and *P. halepensis* respectively (Figure 3).

The stands of third stage (Figure 2c) consisted of an overstorey of *P. pinea* trees with large dimensions and low density, and a middlestorey and understorey of *P. halepensis*, while some trees of *P. halepensis* have entered the overstorey. *P. pinea* is completely absent in these two storeys which means that, if no silvicultural measure will be taken, the next tree generation will consist only of *P. halepensis*. The mean ratio of species density is 47.6% for *P. pinea* and 52.4% for *P. halepensis*. The total stem density is 142.8 trees per hectare. The fourth stage (Figure 2d) is characterised by the dominance of *P. halepensis* in all storeys, in terms of stem density. In these stands *P. pinea* will disappear after a period that depends on the life of *P. pinea* trees as well as on tree uprooting events that happen periodically in the area (Moussouris & Regato 1999) due to the shallow root system that the species forms in the area. However, presence of
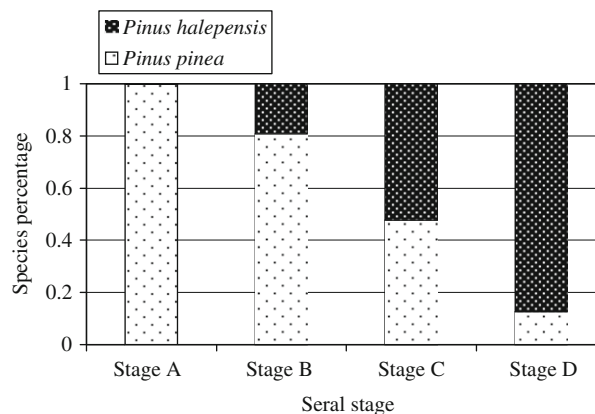
Figure 3. Average species percentage in the four seral stages.

Table 1. Stand characteristics of the *P. pinea* forest in Strofylia, southern Greece, for the four distinguished seral stages.

Stand type	Number of *P. pinea* trees ha-1	Number of *P. halepensis* trees ha-1	Canopy cover (%)	*P. pinea*		*P. halepensis*	
				DBH (cm)	H (m)	DBH (cm)	H (m)
Pure *P. pinea* stands	108.0 (15.0)	0.0 (0.0)	70–80	52.5 (0.5) b	17.4 (0.1) ns	–	–
Stands with low *P. halepensis* invasion	87.2 (16.8)	20.8 (5.1)	50–80	52.7 (0.7) b	17.8 (0.2) ns	13.7 (1.6) a	6.7 (0.4) a
Stands with advanced *P. halepensis* invasion	68.1 (11.3)	74.8 (8.3)	50–80	56.8 (0.4) a	18.0 (0.2) ns	16.1 (2.4) b	9.9 (1.1) b
Stands where *P. halepensis* dominates	37.5 (7.9)	260.8 (32.8)	60–70	43.8 (0.5) c	17.6 (0.2) ns	22.4 (2.0) c	13.1 (1.2) c

Values are the mean and the standard error of the mean (in parenthesis). Values within the same column followed by a different letter are significantly different ($P < 0.05$, Waller-Duncan test). ns: non significant differences.

P. pinea trees presence in the overstorey is quite imposing, even at this very low density, due to their large dimensions, especially crown width.

The tree density of *P. pinea* is at significantly low levels in all stands, exhibiting a mean value of 108 trees per hectare (Table 1) in pure stands, and it is further decreased in invaded stands reaching 37.5 trees per hectare in the fourth seral stage. On the contrary, *P. halepensis* appearance is low in the early successional stage (20.8 trees per hectare in the second seral stage) and it increases with invasion intensity, reaching a mean density 260.8 trees per hectare in the fourth seral stage.

The average diameter of *P. pinea* trees was similar (52.5 cm) in pure stands and stands with low *P. halepensis* invasion, while it was found significantly higher (56.8 cm) in the third seral stage and significantly lower (43.8 cm) in the fourth stage (Table 1). Mean tree height was found to be almost constant in the area, ranged from 17.4 m to 18.0 m, reflecting the similar site conditions existing in the area occupied by the species (Papamichos 1986). Trees of *P. halepensis* exhibited great differences in their dimensions as a result of their age differences. Thus, the trees exhibited significantly higher dimensions (diameter and height) in the stands of the fourth seral stage, medium dimensions in the third seral stage, and lower in the stands with low *P. halepensis* invasion.

Seed production and dispersal traits

Annual seed production of *P. pinea* is low, ranging from 103,174 to 219,450 seeds per hectare depending on tree density (Table 2), while annual seed production of *P. halepensis* is much higher, estimated to be over 1,197,504 seeds per hectare. Concerning seed dispersal, Nathan and Ne'eman (2004) indicated that seed dispersal curves of *P. halepensis*, similar to nearly all other wind-dispersed tree species, show a peak at, or very close to, the source, followed by a rapid decline and a long tail, while, most seeds travel short distances (<30 m). On the contrary, seeds dispersal of *P. pinea* is limited under the parent trees (Barbeito et al. 2008) due to large size of seeds and the very small wing (Ganatsas et al. 2008; Magini 1955). Taking into account either the hump-shaped (Janzen-Connell pattern) or the declining (Hubbell pattern) for plant establishment with distance from seed source (Nathan & Ne'eman 2004), *P. halepensis* has greater possibility for recruitment within a 20-30 m zone from parent trees, while plant recruitment of *P. pinea* is limited under the parent trees. Therefore, in the study

Table 2. Seed production of the pine species in the studied forest.

Species	Number of mature trees per hectare min–max ha-1	Average number of cones per tree	Number of filled seeds per cone	Estimated annual seed crop ha-1
P. pinea	40.0–140.0	62.7–9.8	87.5–75.2[a]	219,450–103,174
P. halepensis	28.0–47.8	810.0	52.8[b]	1,197,504–2,044,310

[a]Values are from Ganatsas et al. (2008).
[b]Values are from Daskalakou (1996) for *P. halepensis* stands in central Greece.

area, it is expected that *P. halepensis* has greater possibility for plant recruitment than *P. pinea*, in the borders of species stands.

Growth of *P. pinea* trees

Firstly, it must be noted that tree sampling was carried out in the stands of the third seral stage (Figure 2c), as in this stage both species coexist in the overstorey. Based on the stem analysis, all the sampled *P. pinea* trees have grown without any suppression period (according to Dahir and Lorimer (1996) criteria) and without great differences between the trees, during their whole life.

The maximum height increment for *P. pinea* is reached early in life, during the period of 5 to 35 years (Figure 4), with a peak in the period of 15-30 years. The tree height increment dramatically decreases after the age of 35 years, and after the age of 70 years it is less than 7-8 cm per year. The diameter growth of *P. pinea* trees follows a similar to height growth pattern; trees present their maximum diameter increment during the period of 5 to 25 years (Figure 5) having a peak in the period of 10 to 20 years, when the mean current annual increment reaches ca. 10 mm. After the age of 30-35 years the diameter growth gradually decreases and at the age of 70 years it reaches low values of annual ring, less than 1 mm, which further decreases at the age of 100 years to approximately 0.5 mm. It can be mentioned that in some cases we recorded annual rings over 15 mm, which means that the species is quite fast growing in the area.

Based on the analysis of both height and diameter growth data and their reconstructive curves it can be said that *P. pinea* trees exhibit, from their early life, a high annual increment of both height and diameter. Based on the cumulative growth curves of diameter and height (Figures 6 and 7), as well as from the current and mean annual increment of height and base diameter (Figures 4 and 5), the growth of *P. pinea* trees can be divided into four developmental stages. There is a clear
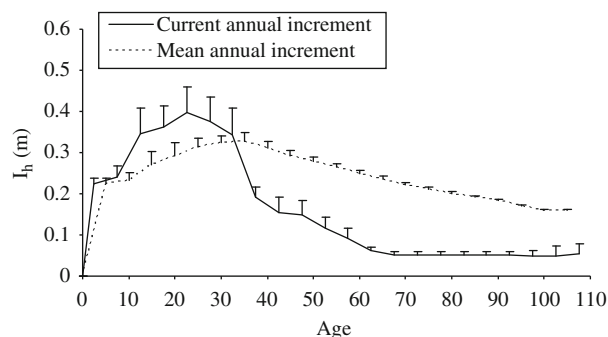

Figure 4. Current annual and mean annual increment of height for *P. pinea*. Vertical bars represent the standard error of means, N = 15.
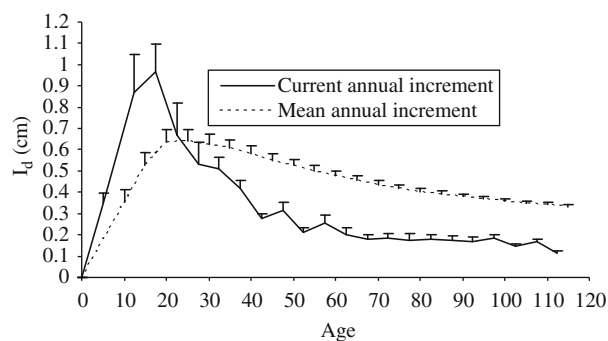

Figure 5. Current annual and mean annual increment of base diameter for *P. pinea*. Vertical bars represent the standard error of means, N = 15.

absence of an early understorey reinitialisation stage, commonly appearing in naturally regenerated forest ecosystems (Oliver & Larson 1996). It is characterised by a low growth of young seedlings, due to the low illumination reaching the forest floor. The first developmental stage starts in the first years of tree life and lasts about 5-6 years. This stage is characterised by a rapid accelerated increase of tree dimensions every year and it can be considered as a growth acceleration stage (Willms et al. 2006). The second stage is characterised by constantly high growth rate both in tree height and diameter and can be characterised as the stage of maximum growth. It lasts about 30 years from the sixth year up to the 35th year when
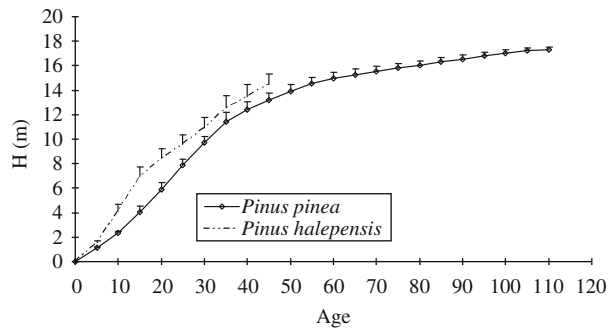
Figure 6. Cumulative growth curve of height for the two species based on stem analysis data. Vertical bars represent the standard error of means, N = 15.
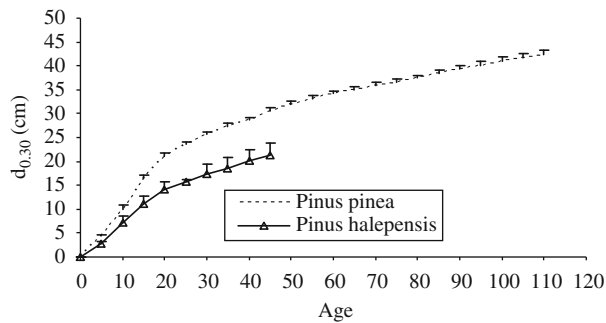

Figure 7. Cumulative growth curve of base diameter for the two species based on stem analysis data. Vertical bars represent the standard error of means, N = 15.

the trees reach a height of 12 m. In this stage the trees show their growth peak; the maximum values recorded were 30 mm and 80 cm for diameter and height growth respectively. The third stage can be characterised as the mature growth phase with a progressively declining radial and height growth that lasts about 35 years. This stage starts from the 35th year of the trees and ends when the trees reach approximately the age of 70 years. During this period even though a gradual reduction of tree growth is observed, the tree volume growth is high because of the large tree diameter and height. The fourth stage starts at approximately 70 years when the tree height increment has been almost stopped or it is strongly reduced (annual increment lower than 7-8 cm), while the radial growth is continued but with a very low rate (annual ring width less than 1 mm). This stage can be characterised as an early over mature stage (Dafis 1990) and may last for the remainder of the tree's life.

Growth of *P. halepensis* trees

The oldest *P. halepensis* trees (trees with DBH above 35 cm) are approximately 50 years old and they seem to comprise the first invasion wave in the

P. pinea biotope. Even though relatively young in age, these trees grew fast and they are now in the overstorey as co-dominant trees. The younger trees (trees with diameter belonging to the classes lower than 20 cm and 20-35 cm), which are now in the middlestorey, invaded the *P. pinea* stand approximately 35 years ago (in 1970). All *P. halepensis* trees, regardless of invasion period, grew without any suppression or release period and grew quite fast during their life (Figures 8 and 9), even though they were established under the canopy of *P. pinea* trees, or more accurately in gaps between the *P. pinea* trees. According to stem analysis the species growth is high in the area, both in height and diameter, almost from the first years of the tree life. The maximum height growth was observed during the period (at the ages) of 5-15 years, and afterwards the growth gradually decreases and remains stable with small fluctuation during the next years. However, at the same tree age, the height growth of *P. halepensis* trees is higher than that of *P. pinea* trees, especially during the first years of trees life. The diameter growth of the trees follows a similar pattern to that for height; thus, trees present their maximum diameter increment during the period of 5 to 15 years, and then
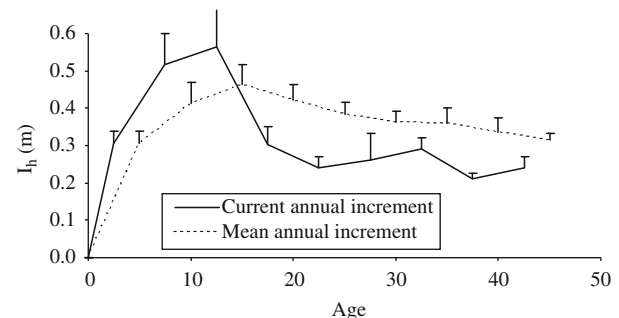
Figure 8. Current annual and mean annual increment of height for *P. halepensis*. Vertical bars represent the standard error of means, N = 15.
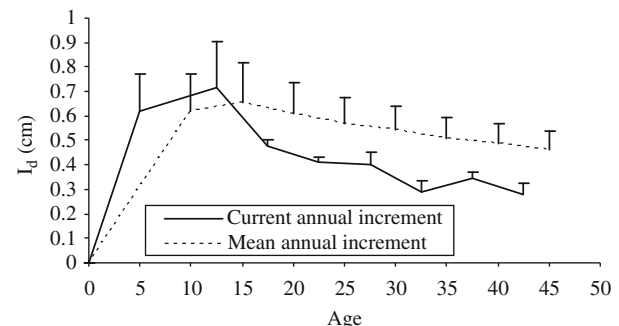
Figure 9. Current annual and mean annual increment of base diameter for *P. halepensis*. Vertical bars represent the standard error of means, N = 15.

the growth gradually decreases to an annual ring of approximately 3 mm and it remains constant afterwards. Comparatively, the diameter growth of *P. halepensis* is lower than that of the *P. pinea* and results in the formation of taller and thinner boles while the trees of *P. pinea* form shorter and wider boles.

Discussion

The analysis of the collected data shows that the *P. pinea* habitat has been invaded by *P. halepensis* for many decades and the gradual replacement of the species is anticipated for most of the forest. Initial invasion has been caused by seeds coming from the adjacent pure *P. halepensis* stands. The invasion has a direction from west and north to east and south. According to the tree age data, the invasion of *P. halepensis* in *P. pinea* habitat seems to have started around the year 1954, and the oldest *P. halepensis* trees that have invaded, are now in the overstorey. However, most of the *P. halepensis* trees are in the middlestorey, while the species dominates in the understorey in many cases too. *P. pinea* tree density is very low, ranging between an average 108 trees per hectare in pure stands, and quite lower (37.5 trees per hectare) in the fourth seral stage. This fact in combination with the absence of species natural regeneration and the low seed production shows that forest succession is anticipated in the area, by the gradual replacement of the *P. pinea* by *P. halepensis*.

The starting time of invasion can be explained by stand dynamics and mainly by the management history of the Strofylia forest. According to the data of the periodical Forest Management Plans of the area, a thinning schedule of the stands started during the period 1954-1959, aimed at opening the stands and favouring *P. pinea* regeneration (Zervas 1954). Until then, any cutting of *P. pinea* trees was prohibited in order to save the species habitat in the area (Zervas 1954). The thinning probably favoured the understorey establishment of *P. halepensis* in the neighbouring *P. pinea* stands, by seeds coming from the adjacent stands; according to Barbeito et al. (2008), even-aged management practices may be behind the failure to encourage natural regeneration of *P. pinea* stands. During that period, the stands were approximately 60 years old, with a dense crown density (90%, Zervas 1954). Under these conditions it can be assumed that, *P. pinea* natural regeneration was limited due to low seed crop and the low understorey illumination that did not favour the estab-

lishment of the light-demanding *P. pinea* (Ciancio et al. 1986); in contrast to a much greater ability of *P. halepensis* for understorey colonisation (Magini 1955). However, after the inclusion of the area in the Ramsar Convention (1975) any tree cutting was again prohibited in the area.

In a chronosequence approach (Foster & Tilman 2000), the present *P. pinea* stands comprise four successional stages in regards to the invasion degree of *P. halepensis*: a) pure stands unaffected by *P. halepensis* that are situated at the greatest distance form the adjacent *P. halepensis* stands; b) stands where the invasion has recently started which are generally close to the stands of the previous stage and they are characterised by the dominance of *P. pinea* and the presence of *P. halepensis* only in the understorey and middlestorey; c) stands where *P. pinea* comprises the understorey while middlestorey and understorey is occupied by *P. halepensis* and additionally few trees have entered in the overstorey; and d) the fourth stage consisting of stands already dominated by *P. halepensis* in all storeys, while *P. pinea* exist only in the overstorey with a few number of trees with large dimensions especially in terms of crown width.

Seed crop estimation and seed dispersal traits verify the above trend for the future stands. *P. halepensis* produces much larger amount of seeds per year in the area, as reported for many areas around the Mediterranean region (Daskalakou 1996; Goubitz et al. 2004; Thanos & Daskalakou 2000), compared to *P. pinea* (approximately 10:1). Seed dispersal capacity of *P. halepensis* is generally high, at least in a distance of 30 m from the parent stands (Nathan & Ne'eman 2004), as opposed to *P. pinea* which is low and limited under the parent trees (Barbeito et al. 2008); while, seed germination is high for both species (Escudero et al. 2002; Ganatsas et al. 2008; Paitaridou et al. 2006). Taking into consideration either the hump-shaped or declining pattern establishment with distance from seed source, we can conclude that, the possibility of *P. halepensis* recruitment in the border of species stands, as well as in a narrow strip (approximately 30 m) along the *P. pinea* stands, is greater than that of *P. pinea*. The earlier fruit production of *P. halepensis* trees, compared to *P. pinea* (Tapias et al. 2001), further increases the possibilities of the higher participation of *P. halepensis* trees in the new generation.

Stem analysis showed that all the studied *P. pinea* trees have grown following a similar typical, hump-shaped form, without any suppression or release period, meaning that they grew without any strong competition during their whole life, leading to the

possibility that the stands may be artificialy established, approximately in 1873-1890. This possibility is in contrast to what Georgiadis et al. (1990) concluded, that the stands of *P. pinea* in the Strofylia area are naturally grown. While, it seems to agree with the latest view about the origin of *P. pinea* stands which supports that almost all the *P. pinea* stands are human established, a fact which explains the very low genetic diversity of the species worldwide (Fady et al. 2004).

Based on stem analysis data, it can be said that *P. halepensis* trees present a high height growth rate and comparatively, at the same tree age, they significantly exceed the trees of *P. pinea* in height. This difference is greater during the early years of tree life and especially during the period of 5th to 15th year and thus, at this age, the trees of *P. halepensis* reach a height of 7-8 m, while the *P. pinea* trees reach a height of 4-5 m. It is characteristic that the curve of mean annual increment crosses the curve of current annual increment at the age of 15 years in *P. halepensis* trees (Figure 8) and quite later in *P. pinea* trees (at the age of 34 years, Figure 4).

On the contrary, the diameter growth of *P. pinea* trees is higher than that of *P. halepensis* trees, and this results in the formation of shorter and thicker trees in *P. pinea* versus taller and thinner trees in *P. halepensis*. Even though diameter growth depends on stand density, this high diameter growth seems to be necessary for the *P. pinea* tree anchorage in the area. The formation of shallow root system due to the high water level and the huge crown dimensions, in combination with the high metacentre (in the vertical axis) of the *P. pinea* trees, make them unstable.

Pine species are generally considered early successional species. *P. halepensis* is a well-known post-fire colonisation tree species which forms extensive natural forests along the Mediterranean basin (Quezel 2000). In contrast, *P. pinea* is a Mediterranean pine that even though it is widespread around the world, its natural origin is considered very limited. This means that most of the occupied areas are human-made ecosystems. These areas are within natural distribution of *P. halepensis* and thus, the danger for the species replacement from *P. halepensis* invasion is high (Athanasiadis & Gerasimidis 1986; Barbero et al. 1998; Tapias et al. 2004). However, the duration of forest succession process in the area will be quite long, determined by the physiological longevity of *P. pinea* trees that due to their huge dimensions resist invasion until maturity, as other forest species (Kimmins 1997). The estimated lifespan of this species is considered to be over 150 years.

To sum up, the findings of this study can contribute to a better understanding of this replacement, and moreover they could be taken into consideration in the forest management of the area. Since the habitat of *P. pinea* is of high importance according to the Directive 92/43/EU and it is included in Annex I, the appropriate silvicultural measures should aim to conserve species habitat. These measures should include: i) gradual transformation of even-aged *P. pinea* stands to more diversified structures (uneven, multi-aged and multistorey stands) in order to favour the species natural regeneration (Barbeito et al. 2008; Calama et al. 2008; Ciancio et al. 1986); ii) grazing control; iii), careful control of the understorey maquis species through the improvement of the moisture conditions in order to favour seedling establishment and growth (Ciancio et al. 1986); and iv) removal of *P. halepensis* trees in the *P. pinea* stands where the species has invaded, as early as possible, and preferably at the age before the trees reach full- reproduction. An uneven-aged management system of low stocking that follows a 25-year schedule could be followed. This, will favour the greater nut producers, will eliminate their competitors and will also preserve maquis species vegetation with low density and open gaps since natural regeneration has already been established (Barbeito et al. 2008; Ciancio et al. 1986).

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References

Athanasiadis, N., & Gerasimidis, A. (1986). *Strofylia ecosystem of NW Peleoponisos and the phytosociological units*, Thessaloniki (in Greek).

Barbeito, I., Pardos, M., Calama, R., & Canellas, I. (2008). Effect of stand structure on Stone pine (*Pinus pinea* L.) regeneration dynamics. *Forestry, 81,* 617–629.

Barbero, M., Loiser, R., Quezel, P., Richardson, D. M., & Romane, F. (1998). Pines of the Mediterranean basin. In D. M. Richardson (Ed.), *Ecology and biogeography of Pinus* (pp. 153–170). Cambridge: Cambridge University Press.

Barbour, M. G., Burk, J. H., Pitts, W. D., Gilliam, F. S., & Schwartz, M. W. (1999). *Terrestrial plant ecology* (3rd

ed.). Menlo Park, CA: Benjamin Cummings, Addison-Wesley, Longman.

Botkin, D. B. (1981). Causality and succession. In D. C. West, H. H. Shugart, & D. B. Botkin (Eds.), *Forest succession: Concepts and applications* (pp. 36–55). New York: Springer.

Bravo-Oviedo, A., Del Rıo, M., & Montero, G. (2004). Site index curves and growth model for Mediterranean maritime pine (*Pinus pinaster* Ait.) in Spain. *Forest Ecology and Management*, *201*, 187–197.

Calama, R., Barbeito, I., Pardos, M., del Rio, M., & Montero, G. (2008). Adapting a model for even-aged *Pinus pinea* L. stands to complex multi-aged structures. *Forest Ecology and Management*, *256*, 1390–1399.

Calama, R., Canadas, N., & Montero, G. (2003). Inter-regional variability in site index models for seven-aged stands of stone pine (*Pinus pinea* L.) in Spain. *Annals of Forest Science*, *60*, 259–269.

Carmean, W. H. (1972). Site index curves for upland oaks in the Central States. *Forest Science*, *18*, 109–120.

Ciancio, O., Cutini, A., Mercurio, R., & Veracini, A. (1986). Sulla struttura della pineta di pino domestico di Alberese. *Annali dell' Istituto Sperimentale della Selvicoltura*, *XVII*, 171–236 Arezzo.

Dafis, S. (1990). *Forest ecology*. Thessaloniki: Giahoudis-Giapoulis Ed. (in Greek).

Dahir, S. E., & Lorimer, C. G. (1996). Variation in canopy gap formation among developmental stages of northern hardwood stands. *Canadian Journal of Forest Research*, *26*, 1875–1892.

Daskalakou, E. (1996). *Ecophysiology and postfire regeneration of Aleppo pine (Pinus halepensis)*. Ph.D. thesis (pp. 181), University of Athens, Department of Biology.

Dyer, M., & Bailey, R. (1987). A test of six methods for estimating true heights from stem analysis data. *Forest Science*, *33*, 3–13.

Escudero, A., Perez-Garcia, F., & Luzuriaga, A. K. (2002). Effects of light, temperature and population variability on the germination of seven Spanish pines. *Seed Science Research*, *12*, 261–271.

Ganatsas, P., & Tsakaldimi, M. (2007). Effect of light conditions and salinity on germination behaviour and early growth of umbrella pine (*Pinus pinea* L.) seed. *Journal of Horticultural Science and Biotechnology*, *82*, 605–610.

Ganatsas, P., Tsakaldimi, M., & Thanos, C. (2008). Seed and cone diversity and seed germination of *Pinus pinea* in Strofylia Site of the Natura 2000 Network. *Biodiversity and Conservation*, *17*, 2427–2439.

Georgiadis, T., Economidou, E., & Christodoulakis, D. (1990). Flora and vegetation of the Strofilia coastal area (NW Peloponnesos – Greece). *Phyton*, *30*, 15–36.

Goubitz, S., Nathan, R., Roitemberg, R., Shmida, A., & Ne'eman, G. (2004). Canopy seed bank structure in relation to: Fire, tree size and density. *Plant Ecology*, *173*, 191–201.

Groven, R., Rolstad, J., Storaunet, K. O., & Rolstad, E. (2002). Using forest stand reconstructions to assess the role of structural continuity for late-successional species. *Forest Ecology and Management*, *164*, 39–55.

Fabbio, G., Frattegiani, M., & Maneti, M. C. (1994). Height estimation in stem analysis using second differences. *Forest Science*, *40*, 329–340.

Fady, B., Fineschi, S., & Vendramin, G. G. (2004). *EUFORGEN technical guidelines for genetic conservation and use for Italian stone pine (Pinus pinea)* (6pp.). Rome: International Plant Genetic Resources Institute.

Foster, B. L., & Tilman, D. (2000). Dynamic and static views of succession: Testing the descriptive power of the chronosequence approach. *Plant Ecology*, *146*, 1–10.

Huston, M., & Smith, T. M. (1987). Plant succession: Life history and competition. *American Naturalist*, *130*, 168–198.

Kariuki, M. (2002). Height estimation in complete stem analysis using annual radial growth measurements. *Forestry*, *75*, 63–74.

Kimmins, J. P. (1997). *Forest ecology: A foundation for sustainable management*. Upper Saddle River, NJ: Prentice-Hall.

Lopez-Serrano, F. R., Garcıa-Morote, A., Andres-Abellan, M., Tendero, A., & Cerro, A. (2005). Site and weather effects in allometries: A simple approach to climate change effect on pines. *Forest Ecology and Management*, *215*, 251–270.

Lorimer, C. G. (1985). Methodological considerations in the analysis of forest disturbance history. *Canadian Journal of Forest Research*, *15*, 200–213.

Magini, E. (1955). Sulle di condizioni di germinaziones del pino d' Aleppo e del pino domestico. *Italia Forestale e Montana*, *3*, 106–124.

Magnani, F., Consiglio, L., Erhard, M., Nole, A., Ripullone, F., & Borghetti, M. (2004). Growth patterns and carbon balance of *Pinus radiata* and *Pseudotsuga menziesii* plantations under climate change scenarios in Italy. *Forest Ecology and Management*, *202*, 93–105.

Martinez, F., & Montero, G. (2004). The *Pinus pinea* L. woodlands along the coast of the South-western Spain: Data for a new geobotanical interpretation. *Plant Ecology*, *175*, 1–18.

Moussouris, Y., & Regato, P. (1999). *Forest harvest: An overview of non timber forest products in the Mediterranean Region* (16pp.). WWF Mediterranean Programme. FAO on-line publications http://www.fao.org/docrep/5593e/x5593e00.htm.

Nathan, R., & Ne'eman, G. (2004). Spatiotemporal dynamics of recruitment in Aleppo pine (*Pinus halepensis* Miller). *Plant Ecology*, *171*, 123–137.

Norusis, M. J. (1994). *SPSS professional statistics 6.1*. Chicago, IL, USA: SPSS Inc.

Oliver, C. D., & Larson, B. C. (1996). *Forest stand dynamics* (update ed.). New York, USA: Wiley, Inc.

Paitaridou, D., Ganatsas, P., Sotiriou, K., Varvarigos, G. (2006). Research on seed quality of four native pine species. In Hellenic Forestry Society (Ed.), *Proceedings of the 12th national conference*, Drama 2–5 October 2005 (pp. 151–158) (in Greek with English summary).

Papamichos, N. (1986). *Ecological study and natural resource utilization of Strofylia forest in NW Peloponisos*. Thessaloniki (in Greek).

Perula, V. G., Cerillo, R., Rebolloo, P. F., & Murillo, G. V. (2003). Postfire regeneration in *Pinus pinea* L. and *Pinus pinaster* Aiton in Andalusia (Spain). *Environmental Management, 31*, 86–99.

Quezel, P. (2000). Taxonomy and biogeography of Mediterranean pines (*Pinus halepensis* and *P. Brutia*). In G. Ne'eman, & L. Trabaud (Eds.), *Ecology, biogeography and management of Pinus halepensis and P. brutia forest ecosystems in the Mediterranean Basin* (pp. 1–12). Leiden, The Netherlands: Backhuys Publishers.

Richardson, D. M. (2000). Mediterranean pines as invaders in the Southern Hemisphere. In G. Ne'eman, & L. Trabaud (Eds.), *Ecology, biogeography and management of Pinus halepensis and P. brutia forest ecosystems in the Mediterranean Basin* (pp. 131–142). Leiden, The Netherlands: Backhuys Publishers.

Salas, C., & Garcıa, O. (2006). Modelling height development of mature *Nothofagus obliqua*. *Forest Ecology and Management, 229*, 1–6.

Snedecor, G. W., & Cochran, W. G. (1988). *Statistical methods*. Ames, IA, USA: The Iowa State University Press.

Tapias, R., Climent, J., Pardos, J. A., & Gill, L. (2004). Life histories of Mediterranean pines. *Plant Ecology, 171*, 53–68.

Tapias, R., Gil, L., Fuentes-Utrilla, P., & Pardos, J. A. (2001). Canopy seed banks in Mediterranean pines of southeastern Spain: A comparison between *Pinus halepensis* Mill., *P. pinaster* Ait., *P. nigra* Arn. and *P. pinea* L. *Journal of Ecology, 89*, 629–638.

Thanasis, G. (2004). *Research on Pinus nigra plantations in the Mt. Olympus area*. Ph.D. thesis (pp. 171), Aristotle University of Thessaloniki (in Greek with English summary).

Thanos, C. A., & Daskalakou, E. N. (2000). Reproduction in *Pinus halepensis* and *P. brutia*. In G. Ne'eman, & L. Trabaud (Eds.), *Ecology, biogeography and management of Pinus halepensis and P. brutia forest ecosystems in the Mediterranean Basin* (pp. 79–90). Leiden, The Netherlands: Backhuys Publishers.

Tsitsoni, T., Ganatsas, P., Zagas, T., & Tsakaldimi, M. (2004). Dynamics of postfire regeneration of *Pinus brutia* Ten. in an artificial forest ecosystem of northern Greece. *Plant Ecology, 171*, 165–174.

Wang, J. R., & Kimmins, J. P. (2002). Height growth and competitive relationship between paper birch and Douglas-fir in coast and interior British Columbia. *Forest Ecology and Management, 165*, 285–293.

Webster, C. R., Nelson, K., & Wangen, S. R. (2005). Stand dynamics of an insular population of an invasive tree, *Acer platanoides*. *Forest Ecology and Management, 208*, 85–99.

Willms, C. R., Pearce, D. W., & Rood, S. B. (2006). Growth of riparian cottonwoods: A developmental pattern and the influence of geomorphic context. *Trees, 20*, 210–218.

Zervas, P. (1954). *Management plan of Strofylia forest*. Forestry Service of Patra, Greece (in Greek).