Journal of Biological Research-Thessaloniki **11**: 83 – 94, 2009
J. Biol. Res.-Thessalon. is available online at http://www.jbr.gr
Indexed in: WoS (Web of Science, ISI Thomson), SCOPUS, CAS (Chemical Abstracts Service) and DOAJ (Directory of Open Access Journals)

The growth ecology of *Juniperus excelsa* Bieb. trees in the central part of the Nestos valley (NE Greece) in the context of anthropogenic disturbances

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Received: 10 July 2008 Accepted after revision: 4 March 2009

In order to analyse the growth of *Juniperus excelsa* Bieb. trees in the stands found in the slopes of Nestos valley, 48 trees growing under different shade and site conditions were studied. Stem analysis was conducted on all trees. The main results of this research indicate that the disturbance regime, shade and site conditions strongly affected the growth of *J. excelsa* trees. *Juniperus excelsa* is a species with significant growth plasticity, which is capable of surviving and growing under various competition and disturbance regimes. It is also capable of exhibiting the maximum height growth rate at various ages. Moreover, it has the ability to attain significant ring width growth increases at an old age. Regardless of the fact that *J. excelsa* behaves as a shade tolerant species which can endure shade for many decades, it is not necessarily a shade demanding species since it can germinate and grow under full light. It seems that the species growth plasticity contributes efficiently to its maintenance in intensely disturbed and severe environments.

Key words: disturbances, facilitation, grazing, growth, shade tolerance.

INTRODUCTION

Juniperus excelsa Bieb. is found in the central and south Balkans, Anatolia, Crimea, central and southwest Asia and east Africa (Athanasiadis, 1986; Boratynski *et al.*, 1992; Christensen, 1997). In Greece it is found in altitudes between 50 and 1600 m. Even though it has been observed in few cases in mixed and pure stands, it is mainly found as a component of degraded scrublands and as scattered individuals or as very small aggregations of trees in open forests. Most studies in the overall area of the species concern the structure and regeneration patterns of *J. excelsa* stands (Ahmed *et al.,* 1989; Ahmed *et al.,* 1990; Hajar *et al.,* 1991; Fisher & Gardner, 1995; Gardner & Fisher, 1996; Carus, 2004; Milios *et al.,* 2007). However, none of them is concerned with stem analyses of *J. excelsa* trees, while Ahmed *et al.* (1989), Ahmed *et al.* (1990) and Milios *et al.* (2007) presented some data regarding the growth of seedlings, saplings and adults of *J. excelsa* trees.

Research and subsequent knowledge regarding the growth of *J. excelsa* trees under various competition regimes will contribute to improved *J. excelsa* forest management.

In the present study, the main objectives were: a) to analyse the growth of *J. excelsa* trees growing under different sites and shade conditions, in stands located in the slopes of the central part of Nestos valley and b) to detect if this growth was affected by the local anthropogenic disturbance regime.

MATERIALS AND METHODS

Study sites

The study was carried out in the central part of the Nestos river valley. This area is located in the south of the central Rhodope mountains in the northwest

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region of Xanthi which lies in NE Greece close to the Bulgarian borders. The central part of Nestos valley (including the surrounding slopes) covers an area of about 9333 ha (41°11′ to 41°15′ N, 24°33′ to 24°41′ E). *Juniperus excelsa* stands are mainly located in the eastern part of the Pascalia public forest. Even though the *J. excelsa* stands are sparsely distributed in many locations on the slopes of Nestos valley, most *J. excelsa* stands, groups and trees appear in a wider area of 895 ha where the altitude ranges from 100 to 800 m. The closest meteorological stations are: a) Echinos, situated at an elevation of 300 m a.s.l. about 43 kilometres away from studied area and b) Xanthi, which lies at an elevation of 50 m a.s.l. approximately 36 kilometres away from studied area. On average the annual rainfall in Echinos is 771 mm and the mean yearly temperature is 12.1°C while the corresponding values for Xanthi are 580.6 mm and 15.4°C.

Juniperus excelsa trees were cut in stands located in the three following site types: a) in moderate most southerly facing slopes (MSFS), b) in extremely steep, most southerly facing slopes (ESSFS) and c) in narrow ridges (NR). The substratum is limestone and the soils are sandy-clay, rocky and shallow (Maragos, 1998). In many cases surface appearances of parent material are observed. The stands in ESSFS are pure. Small mixed stands of *J. excelsa* and species such as *Quercus coccifera*, *Phillyrea latifolia*, *Fraxinus ornus*, *Paliurus spina-christy*, *Juniperus oxycendrus* and *Quercus pubescens* exist in the remaining sites.

In MSFS stands there are three major categories of *J. excelsa* trees: a) scattered, too old, badly-formed and of great dimensions trees, b) dominant (more or less scattered) trees, without any severe competition (in most cases), and c) aggregated trees around and beneath the trees of great dimensions or (in a few cases) around and beneath some dominant trees, and which create dense groups of *J. excelsa* trees with dense branches and foliage that reach the ground (Milios *et al.*, 2007). The soil found under the dense tree crowns is rich in humus. In these groups many *J. excelsa* trees grow in shade or side shade and there are also some dead *J. excelsa* trees in deep shade. An analogous (to MSFS stands) structure and spatial distribution is observed in the stands of narrow ridges (NR stands), but in these stands the groups of *J. excelsa* trees are by far looser. In stands found in the extremely steep, most southerly facing slopes (ESSFS), only scattered single dominant *J. excelsa* trees without competition are observed (Milios *et al.*, 2007). Soil in extremely steep slopes is almost absent; in the ridges it is shallow whereas in moderate slopes it is more or less deeper.

The prevailing disturbances in the entire Nestos Valley area are grazing and illegal cutting of branches and small dimension sprouts for livestock feeding (Milios *et al.*, 2007). These disturbances have taken place over a long period of time with various intensities and intervals. Over the last 20 years, about 1000 goats occasionally grazed in all site type stands with more or less the same intensity (Milios *et al.*, 2007). There is no exact quantitative data available about grazing pressure in the past. According to our information (interviews with elderly shepherds), during the 19th century thousands of goats were (more or less) uniformly grazing in *J. excelsa* stands in all site types.

Sampling

Four *J. excelsa* stands were selected in moderate most southerly facing slopes (MSFS) and four in narrow ridges (NR). In each one of the previously mentioned stands, two sample plots of 200 m^2 (10 m × 20 m) were established at random (16 plots in total).

In the plots which were established in the MSFS stands, 8 dominant (D), under full light, without competition *J. excelsa* trees, 8 shaded (S), 8 side shaded (SS) and 8 dead, under deep shade *J. excelsa* trees (SM) were cut. In particular in each one of the eight plots 1 D, 1 S, 1 SS and 1 SM tree were cut. These trees were selected according to the stratified random sampling method.

In NR stands, only 8 dominant (DR) under full light, without competition *J. excelsa* trees were cut. One DR tree was cut in each one of the eight plots. All the trees that were cut were selected according to the simple random sampling method.

Since it was impossible to take any kind of measurements in stands found in extremely steep, most southerly facing slopes (ESSFS), due to the steep terrain abnormalities, 8 dominant (DST) *J. excelsa* trees were cut which were found under full light, without competition. These trees were selected from trees which were approachable according to the simple random sampling method.

The altitude of the stands where the *J. excelsa* trees were cut ranged from 100 to 350 m.

Stem analysis and anthropogenic disturbance regime investigation

In all the trees the north side of the stem was colour-marked before felling. From each tree, cross-sectional discs were cut and removed from the 0.3 m (stump height) level, the breast height (1.3 m) and at 1 m intervals, up to the bole. The last disc was collected from the 5 cm-bole diameter. When a tree had small dimensions (all S and 3 SM trees) the 0.3 m and the breast height (1.3 m) discs were cut, but in the case of very small trees (5 SM trees) only the 0.3 m disc was used. These discs were taken to the laboratory in order to measure the width of the rings, to the nearest 0.01 mm, with an ADDO instrument (a stereoscope with a ring width measurement device) (Smiris *et al.*, 1998). False rings were easily distinguishable because of their diffuse latewood boundaries (Fritts, 1976; Schweingruber, 1996). Discontinuous rings that had clear boundaries and were well formed were counted as annual rings. Annual ring increments were measured along a mean radius (which had all the rings) orientated approximately in the same direction, in all cross sections, using the color mark as a guide (Milios, 2004). A stem analysis was conducted in all trees. In stem analysis, the mathematical formulas of Regent instruments in Xlstem V1.1 were used (Fortin & Labranche, 1996). The periodic annual height increment (p.a.h.i.) (see Husch *et al.*, 1982) in the different age periods of a tree's life was determined through the process of stem analysis. The p.a.h.i. is calculated if the height difference of sequential cross sections is divided by their age difference (the difference of their total growth ring counts). In fact, it is the periodic annual height increment in the different stem parts of a tree which are separated by the sequential cross sections and furthermore between the last cross section and the top of the tree. The height difference among the sequential cross sections in each tree is known, but the age difference among them (the period of years in our case) varies. As a result the period is not constant.

In each tree the ratio RT was determined (RT = the sum of the widths of the first 10 annual rings of the stump height cross section divided by the sum of the widths of the last 10 annual rings of the same cross section). As a rule, the ring widths of a cross section decrease in size as the age of the tree increases (Fritts, 1976). Thus the ring pattern of a crop tree (even though it has been released through a series of timely thinnings) is one in which ring thicknesses decrease slowly but steadily outward from the pith (Smith *et al.*, 1997). Therefore, the prospective RT for a tree, which had not been subjected to growth space shifts, is well above 1. RT values below 1 indicate a great change in growth space availability (increase) between the young phase of a tree's life and the period just before it is cut. This increase becomes more dramatic as the RT approaches zero or as the diameter of the tree at the time it is cut gets larger.

Statistical analysis

The effect of a) the site type on the height and stem volume of the dominant trees of the three site types (D, DR, and DST trees) and b) shade conditions on the height and stem volume of the trees growing in different shade conditions (D, S, SS and SM trees) in moderate most southerly facing slopes (MSFS), at various ages, was tested using the Duncan test (Toothaker, 1993). When there was heterogeneity of variances, the data were transformed using the formula $Z = \log_{10}(10000X)$, where X equals the volume or height of *J. excelsa* trees and Z represents the transformed variable (Sokal & Rohlf, 1995).

In cases we had 2 samples (comparisons between D and DR trees at the ages of 50, 60, 70 and 80 years) the t-test was used.

Moreover the effect of site type on a) the highest periodic annual height increment (p.a.h.i.), b) the lowest p.a.h.i and c) the young height growth rates (p.a.h.i. between the 0.3 and 1.3 m cross sections) of the dominant trees of the three site types was tested using the Duncan test. Finally the effect of shade conditions on a) the highest p.a.h.i., b) the lowest p.a.h.i and c) the young height growth rates (p.a.h.i. between the 0.3 and 1.3 m cross sections) of the trees growing in different shade conditions (D, SS and S trees) in moderate most southerly facing slopes (MSFS), was tested using the Duncan test. The dead, under deep shade trees (SM) were not included in the analysis since there was only one cross section in a number of them; as a result the highest-lowest p.a.h.i. and the young height growth rates could not have been calculated.

All statistical analysis was carried out using SPSS 12.0 (SPSS Inc., Chicago, IL, USA).

RESULTS

Multiple comparisons among growth means of the J. excelsa trees growing in different shade conditions in MSFS site type

The multiple comparisons between the growth (height and volume) means of the *J. excelsa* trees growing in

TABLE 1. Multiple comparisons among the growth (height and volume) means of *J. excelsa* trees growing under different shade conditions in the moderate most southerly facing slopes (MSFS site type). SS: Side shaded trees; S: Shaded trees; D: Dominant trees, SM: Dead, under deep shade trees

	Height (m)		Volume (dm^3)		Height (m)		Volume (dm^3)		N
	Mean	S. D.[1]	Mean	S. D.[1]	Mean	S. D.[1]	Mean	S. D.[1]	
	Age of 10 years				*Age of 20 years*				
SS	1.196^{a}	0.184	0.043^{a}	0.026	2.101^{a}	0.400	0.379^{a}	0.206	8
S	1.040^{a}	0.230	0.022^{a}	0.017	1.655^{b}	0.328	0.197^{a}	0.143	8
D	0.782^{b}	0.223	0.026^{a}	0.027	1.305^{bc}	0.491	0.318^{a}	0.401	8
SM	0.744^{b}	0.088	0.009^{b}	0.007	1.186^{c}	0.175	0.062^{b}	0.046	8
	Age of 30 years				*Age of 40 years*				
SS	3.140^{a}	0.530	1.527^{a}	0.817	4.016^{a}	0.649	4.012^{a}	2.016	8
S	2.246^{b}	0.439	0.606^{a}	0.378	2.839^{b}	0.560	1.186^{b}	0.606	8
D	2.029^{b}	0.842	1.593^{a}	2.061	3.149^{ab}	1.244	5.216^{a}	5.969	8
	Age of 50 years								
SS	4.901^{a}	0.588	7.570^{a}	2.988					8
S	3.432^{b}	0.687	1.832^{b}	0.811					8
D	4.424^{ab}	1.392	12.397^{a}	12.556					8

Means, in a column, are statistically different at $p < 0.05$, when they share no common letter. The comparisons (for each age class separately) were made using the Duncan test.
[1] S. D. = Standard Deviation

TABLE 2. Multiple comparisons among the growth (height and volume) means of the dominant *J. excelsa* trees growing in the different sites. D: Dominant trees from MSFS site type; DR: Dominant trees from NR site type; DST: Dominant trees from ESSFS site type

	Height (m)		Volume (dm^3)		N	Height (m)		Volume (dm^3)		N
	Mean	S. D.[1]	Mean	S. D.[1]		Mean	S. D.[1]	Mean	S. D.[1]	
	Age of 10 years[2]					*Age of 20 years*[2]				
D	0.782^{a}	0.223	0.026^{a}	0.027	8	1.305^{a}	0.491	0.318^{a}	0.401	8
DR	0.772^{a}	0.179	0.015^{a}	0.007	8	1.296^{a}	0.429	0.296^{a}	0.327	8
DST	0.852^{a}	0.153	0.030^{a}	0.021	8	1.443^{a}	0.309	0.279^{a}	0.194	8
	Age of 30 years[2]					*Age of 40 years*[2]				
D	2.029^{a}	0.843	1.593^{a}	2.061	8	3.149^{a}	1.244	5.216^{a}	5.969	8
DR	2.038^{a}	0.715	1.028^{a}	0.817	8	2.738^{a}	1.034	3.758^{a}	2.739	8
DST	2.165^{a}	0.484	1.283^{a}	0.784	8	2.870^{a}	0.530	3.362^{a}	1.908	8
	Age of 50 years[3]					*Age of 60 years*[3]				
D	4.424^{a}	1.392	12.397^{a}	12.556	8	5.590^{a}	1.227	24.642^{a}	17.829	8
DR	3.460^{a}	1.415	8.561^{a}	6.280	8	4.038^{a}	1.675	16.366^{a}	10.889	8
	Age of 70 years[3]					*Age of 80 years*[3]				
D	6.405^{a}	1.168	42.630^{a}	25.223	8	7.002^{a}	1.154	57.263^{a}	27.240	7
DR	4.659^{b}	1.811	27.408^{a}	17.676	8	5.184^{b}	1.916	44.020^{a}	28.884	8

Means, in a column, are statistically different at $p < 0.05$, when they share no common letter.
[1] S. D. = Standard Deviation
[2] The comparisons were made using the Duncan test (for each age class separately)
[3] The comparisons were made using the t test (for each age class separately)

different shade conditions in the moderate most southerly facing slopes (MSFS site type) are given in Table 1. At the ages of 30, 40, and 50 years, comparisons were made only between the side shaded (SS), the shaded (S) and the dominant (D) trees, since a number of the dead, under deep shade (SM) trees (that were cut) did not attain these ages.

Height

At the ages of 10, 20 and 30 years the side shaded (SS) trees had higher height on average than the dominant (D) trees ($p < 0.05$). Moreover, from the age of 20 years the SS trees had higher height on average than the shaded (S) trees ($p < 0.05$). On the other hand the S trees exhibited on average higher height than the D trees at the age of 10 years ($p < 0.05$).

Volume

At the ages of 10 and 20 years, the dead, under deep shade (SM) trees had the lowest volume compared to the other tree categories ($p < 0.05$). On the other hand there were no statistically significant differences in volume among the side shaded (SS), the shaded (S) and the dominant (D) trees ($p > 0.05$). However, the S trees at the ages of 40 and 50 years exhibited the lowest volume ($p < 0.05$) compared to the D and SS trees.

Multiple comparisons among growth means of the dominant trees

The multiple comparisons between the growth (height and volume) means of the dominant *J. excelsa* trees growing in the different site types are presented in Table 2. At the ages of 50, 60, 70 and 80 years comparisons were made only between the dominant trees (D) from the moderate most southerly facing slopes (MSFS) and those (DR) from the narrow ridges (NR), since the majority of the dominant trees (DST) from the extremely steep, most southerly facing slopes (ESSFS) had a lower age.

Height

No significant difference ($p > 0.05$) was observed in height among the dominant trees in the different site types at the ages of 10, 20, 30, 40, 50 and 60 years. However, at the ages of 70 and 80 years the dominant trees (D) from the MSFS site type had higher height on average than those (DR) from the NR site type ($p < 0.05$).

Volume

No statistical difference in volume was observed among the dominant trees growing in the different site types at all ages ($p > 0.05$).

Growth characteristics of the trees

All the side shaded (SS) trees exhibited the highest p.a.h.i. (periodic annual height increment), throughout their life, between the ages of 21 and 56 years (Table 3), while most of the shaded (S) trees exhibited the highest p.a.h.i. during the first years of their life. On the other hand, there is a great range of ages where the lowest p.a.h.i. was observed, in both tree categories. The 3 dead, under deep shade (SM) trees (in which two cross sections were measured) exhibited low height growth rates, having almost identical p.a.h.i. during their life span.

All the dominant trees (D) from MSFS exhibited the highest p.a.h.i between the ages of 31 and 59 years (Table 4). In the case of the dominant trees (DR) from the narrow ridges (NR) and the extremely steep, most southerly facing slopes (DST trees), there is a large range of ages where the highest p.a.h.i. was observed (Table 4). Almost all the D trees and most of the DR and DST trees, exhibited the lowest p.a.h.i. during the first years of their life (Table 4). However, there is a high variation in the young height growth rates among dominant trees, in each site type (Table 5).

In most of the cases, the side shaded (SS) trees and the shaded (S) trees exhibited higher values for lowest p.a.h.i (periodic annual height increment) than the dominant (D) trees from MSFS (Tables 3 and 4). Significant difference ($p < 0.05$) on average in the lowest p.a.h.i. was detected only between the SS and the D trees (Table 6). Moreover, the D trees exhibited lower young height growth rates (p.a.h.i. between the 0.3 and 1.3 m cross sections) ($p < 0.05$) compared to the SS and S trees (Table 6). On the other hand, the D trees exhibited on average higher values for highest p.a.h.i. ($p < 0.05$) compared to the SS and S trees, while the SS trees exhibited higher values for highest p.a.h.i. than the S trees ($p < 0.05$) (Table 6).

The dominant trees (D) from MSFS exhibited, on average, higher values for highest p.a.h.i. than the dominant trees from the rest of the site types ($p < 0.05$) (Table 7). On the contrary there was no significant difference ($p > 0.05$) in the lowest p.a.h.i. and in the young height growth rates among the dominant trees of the three site types (Table 7).

TABLE 3. Growth characteristics of the side shaded (SS), the shaded (S) and the dead, under deep shade (SM) *J. excelsa* trees. p.a.h.i.: periodic annual height increment; RT: the sum of the widths of the first 10 annual rings of the stump height cross section divided by the sum of the widths of the last 10 annual rings of the same cross section; –: there was only 1 cross section and therefore the lowest and the highest p.a.h.i. could not be computed

	Total age (years)	Total height (m)	Age period of the highest p.a.h.i. (years)	Highest p.a.h.i. (m)	Age period of the lowest p.a.h.i. (years)	Lowest p.a.h.i. (m)	RT	Stump height diameter at the time of cut (m)
				Side shaded (SS) trees				
1	80	6.850	48-49	0.200	50-80	0.069	0.668	0.133
2	83	7.130	49-53	0.200	19-37	0.053	0.508	0.104
3	68	6.500	28-33	0.167	1-19	0.053	0.352	0.110
4	78	6.960	27-31	0.200	38-78	0.048	2.043	0.104
5	91	6.450	47-56	0.100	14-30	0.059	0.288	0.117
6	54	5.360	21-24	0.160	25-54	0.081	0.887	0.072
7	57	5.800	25-30	0.167	11-24	0.071	0.399	0.095
8	53	5.780	22-23	0.140	1-11	0.091	0.570	0.065
				Shaded (S) trees				
1	78	4.150	1-16	0.063	17-78	0.046	0.537	0.044
2	70	3.400	1-14	0.071	15-70	0.038	1.978	0.042
3	52	3.230	19-52	0.057	1-18	0.056	1.280	0.045
4	71	4.340	1-16	0.063	17-71	0.055	0.556	0.054
5	58	5.100	1-8	0.125	9-58	0.076	2.497	0.046
6	65	5.050	1-13	0.077	14-65	0.072	2.480	0.051
7	61	5.000	1-10	0.100	11-61	0.073	2.414	0.045
8	64	3.800	22-64	0.058	1-21	0.048	1.269	0.055
				Dead, under deep shade trees (SM) trees				
1	52	2.210	–	–	–	–	1.735	0.015
2	23	1.440	–	–	–	–	0.703	0.013
3	60	2.880	–	–	–	–	1.018	0.023
4	58	2.200	–	–	–	–	0.769	0.047
5	30	2.000	–	–	–	–	1.975	0.018
6	52	3.130	25-52	0.065	1-24	0.042	2.849	0.027
7	40	2.500	1-18	0.056	19-40	0.055	0.544	0.023
8	60	2.950	27-60	0.049	1-26	0.038	0.489	0.029

All the dominant trees had RT < 1 (Table 4). Seven SS trees had RT < 1 (Table 3). On the other hand, two S trees and four SM trees had RT < 1 (Table 3).

DISCUSSION

Juniperus excelsa is considered to endure shade in its first stages of life. In the valley of Hayl Juwari, most *J. excelsa* trees less than 2 m in height, either grow in the dense shade of a much taller tree or in the northern side of a nurse plant (Fisher & Gardner, 1995). Furthermore, in Balouchistan, *J. excelsa* seedlings occur with a canopy cover of dense shrubs or in the vicinity of groups of parent trees (Ahmed *et al.*, 1989; Ahmed *et al.*, 1990). Ahmed *et al.* (1989) found *J. excelsa* seedlings which were over the age of 50 under dense canopies. These seedlings were over 1 m height. According to our results, *J. excelsa* showed a sustained ability of shade tolerance for many decades. Moreover, in the moderate most southerly facing slopes (MSFS), the shaded (S) *J. excelsa* trees did not exhibit significant height difference compared to the dominant (D) *J. excelsa* trees, with the exception of the age of 10 years, where S trees presented higher height values than D trees.

TABLE 4. Growth characteristics of the dominant *J. excelsa* trees at different site types. p.a.h.i.: periodic annual height increment; RT: the sum of the widths of the first 10 annual rings of the stump height cross section divided by the sum of the widths of the last 10 annual rings of the same cross section

	Total age (years)	Total height (m)	Age period of the highest p.a.h.i. (years)	Highest p.a.h.i. (m)	Age period of the lowest p.a.h.i. (years)	Lowest p.a.h.i. (m)	RT	Stump height diameter at the time of cut (m)
				Dominant (D) trees from the MSFS site type				
1	93	7.860	37-43	0.143	1-16	0.063	0.418	0.249
2	100	7.310	54-58	0.200	1-42	0.024	0.181	0.236
3	73	7.580	31-35	0.200	48-73	0.070	0.562	0.228
4	101	7.090	32-36	0.200	1-31	0.032	0.218	0.183
5	83	8.760	45-48	0.250	1-22	0.045	0.196	0.188
6	103	8.950	36-40	0.200	1-22	0.045	0.171	0.241
7	114	8.710	55-59	0.200	1-38	0.026	0.243	0.191
8	80	7.890	51-53	0.237	1-17	0.059	0.237	0.201
				Dominant (DR) trees from the NR site type				
1	83	5.850	27-34	0.125	1-26	0.038	0.181	0.190
2	136	5.910	80-92	0.077	1-61	0.016	0.133	0.144
3	163	7.220	112-118	0.143	30-98	0.014	0.520	0.192
4	80	7.240	45-51	0.143	1-21	0.048	0.581	0.210
5	93	6.110	19-28	0.100	60-93	0.034	0.166	0.176
6	88	6.950	14-22	0.111	64-88	0.054	0.223	0.218
7	87	6.750	43-51	0.111	1-18	0.056	0.195	0.184
8	86	6.090	51-61	0.091	1-19	0.053	0.246	0.202
				Dominant (DST) trees from ESSFS site type				
1	58	4.780	18-27	0.100	1-17	0.059	0.290	0.126
2	55	4.900	27-34	0.125	1-17	0.059	0.439	0.126
3	72	4.900	1-12	0.083	42-72	0.052	0.499	0.141
4	81	4.870	40-47	0.071	1-23	0.043	0.452	0.111
5	57	3.770	17-24	0.090	25-57	0.053	0.546	0.094
6	86	4.270	26-39	0.071	1-25	0.040	0.278	0.127
7	90	3.900	29-38	0.080	39-90	0.035	0.321	0.130
8	45	3.480	22-45	0.080	1-17	0.059	0.343	0.068

The great age variation of the dead, under deep shade (SM) trees suggests that either they confronted different shade conditions during their life or their death is the result of water deficiency or other biotic factors, such as insects and fungal diseases (Grime, 1966; Augsberger, 1984; Kozlowski *et al.*, 1991).

On the other hand, regardless of the fact that *J. excelsa* behaves as a shade tolerant species, the existence (in our stands) of a) dominant trees growing more or less scattered, without any severe competition and b) seedlings and saplings growing in full light, suggests that *J. excelsa* is not an obligatory shade demanding species.

In the stands of MSFS, the dominant (D) trees exhibited an upward trend in height and volume growth compared to the side shaded (SS) and shaded (S) trees, as the trees became older. As far as height is concerned, this is the result of the lower young height growth rates of D trees compared to those of SS and S trees in combination with the higher values for highest p.a.h.i. (periodic annual height increment) of D trees than that of SS and S trees (Tables 3, 4, 5 and 6). In particular almost all D trees exhibited their highest p.a.h.i. after the age of 31 resulting in the upward trend in height growth. A more or less analogous pattern must have been followed in the volume growth of

TABLE 5. Young height growth rates (p.a.h.i. between the 0.3 and 1.3 m cross sections) of all trees. p.a.h.i.: periodic annual height increment; –: there was only 1 cross section and therefore the p.a.h.i. between the 0.3 and 1.3 m cross sections could not be computed

	Age period (years)	p.a.h.i. between the 0.3 and 1.3 m cross sections (m)	Age period (years)	p.a.h.i. between the 0.3 and 1.3 m cross sections (m)	Age period (years)	p.a.h.i. between the 0.3 and 1.3 m cross sections (m)
	Side shaded (SS) trees		*Shaded (S) trees*		*Dead, under deep shade trees (SM) trees*	
1	1-11	0.091	1-16	0.063	–	–
2	1-10	0.100	1-14	0.071	–	–
3	1-19	0.053	1-18	0.056	–	–
4	1-9	0.111	1-16	0.063	–	–
5	1-13	0.077	1-8	0.125	–	–
6	1-11	0.091	1-13	0.077	1-24	0.042
7	1-10	0.100	1-10	0.100	1-18	0.056
8	1-11	0.091	1-21	0.048	1-26	0.038
	Dominant (D) trees from the MSFS site type		*Dominant (DR) trees from the NR site type*		*Dominant (DST) trees from the ESSFS site type*	
1	1-16	0.063	1-26	0.038	1-17	0.059
2	1-42	0.024	1-61	0.016	1-17	0.059
3	1-11	0.091	1-29	0.034	1-12	0.083
4	1-31	0.032	1-21	0.048	1-23	0.043
5	1-22	0.045	1-18	0.056	1-16	0.063
6	1-22	0.045	1-13	0.077	1-25	0.040
7	1-38	0.026	1-18	0.056	1-28	0.036
8	1-17	0.059	1-19	0.053	1-17	0.059

trees, since volume is related to tree height.

The fact that the vast majority of dominant trees in all site types exhibited the lowest p.a.h.i., during the first years of their life combined with their low RT indicates a negative influence on the growth of dominant trees during the first years of their life. In the case of the dominant trees from the moderate most southerly facing slopes (D trees) 7 out of the 8 trees exhibited the lowest p.a.h.i., during the first years of their life (Table 4).

In all site types, high variation in the young height growth rates among dominant trees was observed (Table 5). Moreover, the dominant trees from the moderate most southerly facing slopes did not exhibit higher young height growth rates or greater lowest p.a.h.i. values than the dominant trees of the other site types (Table 7), as it was expected, since they grew in more productive sites. The assessment of the superiority in site quality of the moderate most southerly facing slopes compared to the other site types is based not only on their soil depth differences but also on the clear differences in the highest p.a.h.i. values among the dominant trees (the D compared to the DR and DST trees) (Tables 4 and 7) (Assmann, 1970).

This indicates that neither the full light conditions (since all the dominant trees in all site types were established and grew in full light) nor the site quality were the causes of low young height growth rates.

Furthermore, the present existence of many grazed seedlings and saplings that grow in full light suggests that grazing was possibly the factor which retarded the growth of many dominant trees in all site types. Furthermore, it must be pointed out that the regeneration plants which grow under the shade of *J. excelsa* groups had no signs of grazing. The dominant trees, which had high young height growth rates, were probably established in periods of low grazing pressure.

Moreover, the absence of significant height and volume differences among dominant trees of the three site types, at least until the age of 40 years, is

TABLE 6. Multiple comparisons among the means of a) highest p.a.h.i., b) lowest p.a.h.i. and c) young height growth rate of the *J. excelsa* trees growing under different shade conditions in the moderate most southerly facing slopes (MSFS site type). Means, in a column, are statistically different at $p < 0.05$, when they share no common letter. The comparisons were made using the Duncan test. p.a.h.i.: periodic annual height increment; SS: Side shaded trees; S: Shaded trees; D: Dominant trees

Trees under different shade conditions	Highest p.a.h.i. (m)		Lowest p.a.h.i. (m)		Young height growth rates (m)[1]		N
	Mean	S. D.[2]	Mean	S. D.[2]	Mean	S. D.[2]	
SS	0.167[b]	0.035	0.066[a]	0.015	0.089[a]	0.018	8
S	0.077[c]	0.024	0.058[ab]	0.014	0.075[a]	0.025	8
D	0.204[a]	0.032	0.046[b]	0.017	0.048[b]	0.022	8

[1] represents p.a.h.i. between the 0.3 and 1.3 m cross sections
[2] S. D. = Standard Deviation

TABLE 7. Multiple comparisons among the means of a) highest p.a.h.i., b) lowest p.a.h.i. and c) young height growth rate of the dominant *J. excelsa* trees growing in the different sites. Means, in a column, are statistically different at $p < 0.05$, when they share no common letter. The comparisons were made using the Duncan test. p.a.h.i.: periodic annual height increment; D: Dominant trees from the MSFS site type; DR: Dominant trees from the NR site type; DST: Dominant trees from the ESSFS site type

Dominant trees of the different sites	Highest p.a.h.i. (m)		Lowest p.a.h.i. (m)		Young height growth rates (m)[1]		N
	Mean	S. D.[2]	Mean	S. D.[2]	Mean	S. D.[2]	
D	0.204[a]	0.032	0.046[a]	0.017	0.048[a]	0.022	8
DR	0.113[b]	0.024	0.039[a]	0.017	0.047[a]	0.018	8
DST	0.088[b]	0.018	0.050[a]	0.090	0.055[a]	0.015	8

[1] represents p.a.h.i. between the 0.3 and 1.3 m cross sections
[2] S. D. = Standard Deviation

probably the result of grazing. The impact of grazing probably masked the influence of the different site characteristics on the growth of the dominant trees. However, after the age of 70, significant height differences between the dominant trees from the moderate most southerly facing slopes (D trees) and those of narrow ridges (DR trees) were traced. At that age, the majority of trees were quite tall and therefore their terminal shoots were protected from grazing.

The potential influence of grazing is indicated by the fact that in one dominant tree from narrow ridges (DR tree), lowest p.a.h.i. of 0.014 m was observed during the age period of 30-98 years. At that age, its height was between 1.3 and 2.3 m. After a few years, at the age period of 112-118 years it exhibited a highest p.a.h.i. of 0.143 m. This indicates that a factor with a strong negative effect on height growth acted intensely for a period of years and later on stopped its action, allowing the tree to exhibit (after a period of a few years) a p.a.h.i. of 0.143 m. If we consider that goats have the ability to cause grazing damages in lateral and terminal shoots in heights over 1.5 m, it is possible that this growth performance was the result of grazing or the cutting of branches.

War and socio-economic events, with the resulting disturbance regimes, influenced the structure, development patterns, species composition and growth of the dominant trees in many forest ecosystems in the mountains of Rhodope in the wider region of Nestos Valley (Milios, 2000; Tsiripidis, 2001; Milios, 2004; Tsiripidis *et al.*, 2005).

Examples from other European areas showed that, in the French Pyrennes, high intensity grazing seems to reduce in a remarkable way the height growth of *Fraxinus excelsior* whereas low intensity grazing disturbs more or less intensively the growth of trees (Julien *et al.*, 2006). Moreover, McEvoy *et al.* (2006) mentioned that in a grazed forest in NW Spain the height of similar aged saplings was found to be significantly greater in ungrazed than in grazed treatments.

Facilitation by herbivory-mediated nurse plants is the decisive ecological process which determines the performance and spatial distribution of plant species in many ecosystems (Callaway, 1992; Bakker *et al.*, 2004; Smit *et al.*, 2006). According to Gomez (2005) herbivory affects not only the performance of plants or their population dynamics but also their habitat distribution and niche structure.

As far as the RT is concerned, the fact that all dominant trees from the three site types and the side shaded trees (SS) in their vast majouirity exhibit an RT < 1, regardless of age period where the lowest p.a.h.i. was observed (Tables 3 and 4) indicates that the *J. excelsa* seedlings and saplings (of those categories), in the first years of their life, showed low ring width growth until the development of a deep root system, which could supply them with the adequate water and mineral nutrients (Fritts, 1976). In addition grazing probably had a negative impact on the ring width growth of dominant trees. Later, as the trees formed robust root systems (and the grazing stopped in dominant trees), a great ring width growth was achieved. In the case of dominant trees from the moderate most southerly facing slopes and the narrow ridges (D and DR trees) this growth was extremely high, since it was observed in trees of an old age and in large diameters. On the contrary, the majority of the shaded trees (S) was established in rich in humus soil under the *J. excelsa* groups (Milios *et al.*, 2007). As a result, the ring width growth was high in the first years of their life compared to that of the last 10 years leading to RT values higher than 1 (in most of the cases) (Table 3). As the shaded trees (S) became older, greater competition was imposed on them by the taller trees, since the needs of shaded trees for growth space increased, in order to maintain a larger biomass. In addition, an analogous height growth performance was observed. Most of the shaded trees (S) exhibited the highest p.a.h.i. in young ages and the lowest p.a.h.i. during the last years before they were cut.

Our results suggest that *J. excelsa* is a species with significant growth plasticity, which is capable of surviving and growing under various competition and disturbance regimes. Moreover, it exhibits the ability to attain the maximum height growth rate at various ages (in some cases after the age of 100 years) (see Table 4) according to prevailing competition and disturbance conditions. In addition, it may exhibit significant ring width growth increases at an old age. Carus (2004) referred that *J. excelsa* resembles *Pinus nigra* (which is a semi shade tolerant species) as far as its shade tolerance is concerned. However, according to our results, despite the fact that *J. excelsa* can grow in full light it can also endure shade for many decades resembling some very shade tolerant species such as beech (*Fagus sylvatica*) and fir (*Abies alba*) (Assmann, 1970).

The dominant trees from the moderate most southerly facing slopes (D trees) exhibit relatively high values for highest p.a.h.i. The moderate most southerly facing slopes (MSFS site type) can not be considered as productive. This implies that in productive sites, *J. excelsa* may attain sufficient high rates of height growth.

To our knowledge, only three studies presented data about *J. excelsa* growth. Ahmed *et al.* (1989) provide, age estimations for various sizes of *J. excelsa* seedlings and saplings, using 6 seedlings from different size classes, in which the ages were determined by a simple ring count. They estimate, that 59 year old seedlings have a dbh diameter (diameter of breast height) of approximately 6 cm. This data cannot be compared to ours, since they did not refer to a) the stem height in which the tree age was determined and b) the growth environment of the seedlings. In any case, some of our trees attained a dbh diameter of 6 cm at younger stump height ages than the trees in Balouchistan and some other at older ages. Moreover, Ahmed *et al.* (1990) analysed the breast height cross sections of 16 randomly selected *J. excelsa* trees from the Zierat site in Balouchistan that had a dbh of 20-30 cm and found that even though there was great variation among individuals, there was a mean annual ring width increment of 1 mm. An almost identical mean annual ring width increment was found in two of our trees, which had a dbh of 20-30 cm. Finally, in the central part of Nestos valley, Milios *et al.* (2007) using ground level cross-sectional discs from various sites found that the Mean Annual Height Increment (MAHI = total height/age at the ground level) of shaded and side shaded seedlings and saplings (which most were up to 60 cm, personal observation) ranged from 0.0069 to 0.0365 m and 0.0070 to 0.0348 m, respectively. These height growth values are by far lower than those presented in this study. One reason for this could be the fact that in their height growth analysis of regeneration plants, the early period of the life of the seedlings is incorporated (period from the emergence of seedlings up to the height of 30 cm). It seems that *J. excelsa* exhibits a very slow height increment in its first years of life, since the lowest MAHI was found in seedlings with a height up to 40 cm personal observation. Moreover, most seedlings used in the study of Milios *et al.* (2007) probably confronted stronger competition during their establishment compared to our S and SS trees, since the seedlings used in the study of Milios *et al.* (2007) had been established much later than our trees and most of them were probably under the competition of more dense groups of *J. excelsa* trees (Milios *et al.*, 2007).

The fact that *J. excelsa* is a site insensitive species, its ability to attain old ages and the facilitation process appear to be the dominant factors, which permit the species establishment and preservation in degrading environments (Ahmed *et al.*, 1989; Ahmed *et al.*, 1990; Fisher & Gardner, 1995; Garcia & Zamora, 2003; Carus, 2004; Milios *et al.*, 2007). It seems that another trait, which contributes efficiently in the species survival in intensely disturbed and severe environments, is the species growth plasticity, since it has the ability to adapt to various growth regimes (from full light to dense shade) and to exhibit growth increases (even at an old age) when the growth conditions are improved.

CONCLUSIONS

The disturbance regime (grazing) and the shade and site conditions strongly affected the growth of *J. excelsa* trees in the Nestos valley.

Juniperus excelsa is capable of surviving and growing under various competition and disturbance regimes, while it has the ability a) to attain the maximum height growth rate at various ages and b) to exhibit significant ring width growth increases at an old age if growth conditions are improved. Moreover it can attain high rates of height growth. Even though *J. excelsa* can germinate and grow in full light, it can also endure shade for many decades.

It seems that the species growth plasticity contributes efficiently in its maintenance in intensely disturbed and severe environments.

ACKNOWLEDGEMENTS

Special thanks to the forest commission of Stavroupolis for their cooperation.

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