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Forest Ecology and Management 225 (2006) 359–367

Forest Ecology and Management

www.elsevier.com/locate/foreco

Effect of fire season, aspect and pre-fire plant size on the growth of *Arbutus unedo* L. (strawberry tree) resprouts

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Received 4 May 2005; received in revised form 4 November 2005; accepted 2 January 2006

Abstract

Resprouting is an important survival strategy for many plant species that allows their survival after fire. The time of fire has been identified as one of the factors affecting the ability and vigor of resprouting in a variety of ways. It is believed that plants recovering after spring fire have a comparative advantage over those recovering after autumn fire due to the larger pool of stored carbohydrates in the beginning of the growing season which can lead in more vigor resprouting. In the current study we present the results of an experiment on the effect of fire season, aspect and pre-fire plant size on the resprout growth of the common Mediterranean shrub *Arbutus unedo* L. The growth parameters of height and diameter were monitored every 3 months for the total of 3 years after fire. Fire season has no immediate effect on resprout height by the end of the first post-fire growing season. It has however an effect on resprout diameter with plants recovering after spring fire reaching bigger diameter by the end of the first post-fire growing season. Aspect has an important effect on both height and diameter of resprouts. The pre-fire plant size was also found to be affecting growth of resprouts especially after the second post-fire growing season.

Keywords: *Arbutus unedo*; Mediterranean; Resprouting; Regeneration; Strawberry tree; Wildfire

1. Introduction

In Mediterranean regions, fire is an important ecological factor, and has a significant role in shaping the landscape and determining ecosystem and species distribution (Naveh, 1975, 1990). The manner in which a given plant species survives fires, the post-fire vegetation dynamics and growth rates have been the subject of many studies in Mediterranean-type ecosystems around the world (e.g. Canadell et al., 1991; Farano et al., 1993; Moreno and Oechel, 1994), including Greece (e.g. Konstantinidis and Chatziphilippidis, 1993; Zagas, 1994; Arianoutsou and Thanos, 1996; Hatzistathis et al., 1999; Theodoropoulos et al., 2002; Konstantinidis et al., 2005).

Most shrub and tree species growing in Mediterranean areas, in which fire, herbivore activity and clear-cutting are common disturbances, possess certain traits that make subsequent survival, regeneration and/or reproduction possible. Plants growing in fire prone environments exhibit a wide range of survival strategies that allow them to overcome the immediate effects of fire (Gill, 1981; Mooney and Hobbs, 1986). Fire-stimulated flowering, seed storage on the plant and fire-stimulated dehiscence, fire-stimulated germination of seeds stored in the soil and resprouting from protected buds are the most well documented of these strategies. The last is a very common survival strategy in many Mediterranean plants which resprout vigorously within the first months or even days after the fire (Hanes, 1971; Keeley and Zedler, 1978; Bond and Midgley, 2001). Resprouting ability can have major impacts on species composition of plant communities: population turnover is reduced and the effects of fire caused disturbance are also reduced (Bond and Midgley, 2001), since burned areas are rapidly reoccupied by species with the ability to resprout (Naveh, 1975; Trabaud, 1987; Pausas et al., 1999) leaving little opportunity for new species to establish themselves in the mid- and long-term.

Resprouting usually occurs from under-ground dormant buds which are stimulated when the above ground part is removed by fire or other disturbance (James, 1984; Lloret and Vilà, 1997; El Omari et al., 2003). A wide range of Mediterranean plants have swelling structures at the base of the stem, the lignotubers or burls, which are a source of new meristems (Malanson and Trabaud, 1987; Zammit, 1988;

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doi:10.1016/j.foreco.2006.01.011

Moreno and Oechel, 1994; Canadell and López-Soria, 1998). Lignotubers are also important storage organs of non-structural carbohydrates, sugars and nutrients which are mobilized after fire and support the initial regrowth of plants (Canadell and López-Soria, 1998). This role of lignotubers has long been considered to be the most important factor determining to a great extent the post-fire vigor of resprouting suggesting that higher amounts of stored carbohydrates and nutrients lead to more vigorous resprouting (Rundel et al., 1987; Malanson and Trabaud, 1988). Hence, variation in the amount of stored carbohydrates and nutrients is expected to cause variations in the resprouting vigor of plants after disturbance.

Fire season has been addressed in the literature as one of the factors which affects the vigor of resprouting and the recovery process of plants. The amount of stored carbohydrates in the lignotuber fluctuates widely during the year with the highest amounts observed in early spring before the onset of the new growing season while significantly lower amounts are stored in early autumn (Cruz and Moreno, 2001). This seasonal fluctuation of stored carbohydrates is considered by many authors to be one of the main reasons for the more vigorous resprouting of plants after a spring fire than after an autumn fire (Rundel et al., 1987; Malanson and Trabaud, 1988; Bowen and Pate, 1993). Some studies, however, have questioned the primary role of lignotuber-stored carbohydrates in determining the vigor of resprouting and they suggest that other factors relating mainly to the post-fire environment play a more important role in the resprouting vigor and vegetation recovery after fire (Cruz et al., 2002, 2003a,b). If the role of post-fire environment is important in determining the vigor of resprouting then it would be expected that the growth of resprouts will differ between aspects, reflecting their differences in soil moisture (Espelta et al., 1999). Different fire season results in a different post-fire environment, which may also affect the vigor of resprouting. Malanson and Trabaud (1988) attributed differences in resprouting vigor, between spring and autumn fires, to the differences in temperature (lower in autumn) and daylight (shorter in autumn) following the fire events. The size and vigor of the tree before fire has been found to be related to the vigor of resprouts for some species, with the general view being that larger plants suffer less damage by fire and subsequently they resprout better (Pausas, 1997; Espelta et al., 1999). The extent of this effect, however, and its duration has not yet been established.

Despite the research which has been conducted on the effects of fire season, post-fire environment and pre-fire plant size on the recovery process of plants questions still remain regarding both the magnitude of those effects as well as the mechanism by which they are achieved. Further, resprouting as a survival and persistence strategy of plants is still under-represented in the literature and in research related to plant regeneration and conservation as opposed to recruitment and seed ecology (Bond and Midgley, 2001).

The present work deals with the post-fire resprouting ability of the typical evergreen Mediterranean species, *Arbutus unedo* (strawberry tree). *A. unedo* has a contrasting regeneration pattern: it is absent from the soil seed banks and it is rarely found as seedlings, despite the fact that it is well represented in many shrublands or forest understoreys (Dvaz-Villa et al., 2003). It is an obligate resprouter and its survival after fire depends entirely on resprouting, since seedlings can only be established several years after fire (Mesleard and Lepard, 1989). Strawberry tree can be found growing in rocky places and has a wide distribution in the Mediterranean region (Athanasiadis, 1986).

The aim of the current study is to investigate the role of fire season, aspect and pre-fire plant size on the resprouting dynamics of *A. unedo*. The growth of resprouts was monitored for 3 years after fire in two sites sharing similar ecological characteristics. The first site was burned at the beginning of the growing season (May 1994) while the second site was burned towards the end of it (September 1994), as a result of two separate wildfires.

2. Materials and methods

2.1. Study area

The study area has already been described, in a publication dealing with the resprout of *Quercus coccifera*, by the authors in a previous issue of this journal (Konstantinidis et al., 2005). Here, only the main characteristics are presented which are necessary for the coherence of the present paper. The area was located in a typical *Pinus halepensis* L. forest (49 years old) with an understorey of dense Mediterranean maquis in the northern part of the Sithonia Peninsula in north Greece. The average canopy closure was 50% for the tree layer and 80% for the shrubby understorey layer. The mean height was 14 and 2 m for the layers of trees and shrubs, respectively. The relief of the area is gentle with low slopes. Substrates are acidic granites, and the soils derived from igneous rocks are shallow and stony.

The climate is typical thermo-Mediterranean characterized by 100–150 biologically ‘‘dry’’ days according to Bagnouls and Gaussen (1957), with a dry period from May to September. Mean annual precipitation is 471 mm with the majority of them (80%) falling during winter (December–April). Minimum temperatures are rarely below 5 °C, while maximum temperatures reach about 30 °C.

Two experimental plots have been established immediately after two wildfire incidents in the area. The first fire happened at the beginning of the vegetative period (Site 1—May 1994), and the second one at the end of the growing season (Site 2—September) of the same year. The first experimental plot was located at an altitude of about 150 m and at a distance of 1 km from the sea, while the second one was 3 km away from the first, at an altitude of 200 m and at 1.5 km distance from the sea. Both plots were deliberately established on areas protected from any kind of post-fire disturbance (property of a local monastery), especially grazing.

The soils on both plots are dry and acidic (pH 5.5–5.7), with sandy-clay textures and poor in organic matter and macro elements. Despite their low fertility and level of water penetration and air, they are suitable for the growth of a

Table 1
Mean monthly precipitation (mm) recorded at the N. Marmaras meteorological station (1968–1975)

Year(s)	Monthly precipitation (mm)												
	J	F	M	A	M	J	J	A	S	O	N	D	Total
1968–1975	68	59	60	33	25	31	24	20	35	41	18	54	471
1994						0	9	3	2	190	64	51	
1995	236	5	74	11	6	0	46	122	66	7	39	173	785
1996	74	101	39	33	27	79	4	1	20	80	45	37	540

Monthly precipitation (mm) recorded at the local meteorological station during the study (1994–1996) (Sithonia, Greece).

Mediterranean evergreen vegetation of pines and typical sclerophyllous shrubs.

Data from a meteorological station, installed in 1994 (Kalabokidis et al., 2002), located between the two experimental plots, were used during the experiment, as well as long-term climatic data from the station of N. Marmaras, 20 km away (Table 1).

2.2. Experimental sampling

A total of 100 burned individuals were randomly selected on each site, 25 at each of the main four aspects (north, east, south and west). The tallest burned shoot of each shrub was marked, and its height and ground level diameter measured which represent the size of the maternal plant. Three months after each fire, both sites were revisited and the longest resprout of the selected shrubs was marked, and measurements of its height and diameter at ground level were taken. These measurements were repeated on both sites every 3 months, until December 1996, to give height and diameter growth of the selected resprouts.

The number of resprouts influences their height and thickness (Sennerby-Forsse and Zsuffa, 1995; Riba, 1998; Cruz et al., 2003b). Therefore, care should be taken to keep the number of resprouts constant, by removing some of them. Mayor and Rodá (1993) consider 50% of the resprouts is a suitable number to be removed, while Ducrey and Turrel (1992) recommend a 75% to be removed. We decided to keep three resprouts as an alternative solution in case of partial destruction, while new eventual resprouts were removed. This decision was bolstered later by Espelta et al. (2003), who found that there is no statistical difference between one and three retained resprouts.

2.3. Statistical analysis

Data are in the form of repeated measures; the same individuals are sampled nine times starting December 1994, every 3 months, and going up to December 1996. The whole experiment can be treated as a split-plot design where the different fire season and the different aspects are the between-subject factors and time of measurement is the within subject factor. The repeated-measures ANOVA model was employed (Von Ende, 2001) which allows the examination of the effect of each treatment alone (fire season and aspect) as well as their interaction with time which is of the greatest interest and corresponds to the effect of the experimental manipulation over time. Despite the fact that in every measurement the time since fire is different for the two treatments (3 months more in the spring fire), it was considered more important and ecologically more meaningful, to compare the effect of the main treatments at the same month of year rather than based on the actual time since the fire event. The reason for doing that was to ensure that the identified difference in the growth of resprouts is the effect of the two different fire treatments and not the effect of the different physiological status of the plant at the time of measurement.

The effect of maternal sprout on the post-fire plant growth was investigated by applying simple linear regression between maternal sprouts and post-fire resprouts for each of the nine time periods. The independent variable was the maternal sprout height or diameter and the dependent variable was the resprout height or diameter, respectively.

3. Results

3.1. Effect of fire season and aspect on post-fire plant height

Table 2 shows the results of repeated measures ANOVA. There is a statistically significant effect of fire season × time interaction as well as of aspect × time interaction ($p < 0.001$) which indicates that both treatments have a significant effect on post-fire plant height over time. The interaction between both treatments together and time is also significant indicating that the effect of fire season is affected by the different aspect and vice versa.

Fig. 1 shows that at the first measure (December 1994), which occurs in the end of the first post-fire growing season, there is no difference in plant height between plants resprouting after spring or autumn fire. After June 1995 (second post-fire growing season) plants burned in spring reach a greater height than those burned in autumn. This difference is greatest at the beginning of the third growing season and decreases by the end. This effect, however, is strongly dependent on aspects as shown in Fig. 2. While differences in plant height after the beginning of the second growing season is the case in north and east aspects, in west and south aspects there is no such an effect and plants grow identically irrespective of the season of burn throughout the duration of the experiment. Fig. 2 also shows that plants growing in north or east aspects, and especially those growing after the spring fire, grow much faster than plants growing in south or west aspects irrespective of the season of burn. Differences also exist between north and east aspects.

Table 2
Table of repeated measures ANOVA for post-fire plant height

Source	DF	MS	*F*	*p*
(A) Between-subjects				
Fire season	1	6086	4.686	0.032
Aspect	3	19427	14.959	0.000
Fire season × aspect	3	1593	1.227	0.301
Error	195	1299		

Source	DF	MS	*F*	*p*	Adj *p*	
					G–G	H–F
(B) Within subject						
Time	8	154058	2850.519	0.000	0.000	0.000
Time × fire season	8	846	15.648	0.000	0.000	0.000
Time × aspect	24	1745	32.281	0.000	0.000	0.000
Time × fire season × aspect	24	460	8.505	0.000	0.000	0.000
Error	1560	54				

Columns 6 and 7 show the adjusted *p*-values when the shift of data from the sphericity condition is taken into account.

While on the latter the effect of fire season decreases dramatically in the middle and end of the third growing season, on the former this effect is maintained at the same extent throughout the third post-fire growing season and it possibly continues thereafter.

3.2. Effect of fire season and aspect on post-fire plant diameter

In the case of post-fire plant diameter there is also a highly significant fire season × time as well as aspect × time interaction ($p < 0.001$) which indicates that both treatments have significant effect overtime as shown in Table 3. The interaction between the two treatments together and the time factor is also highly significant ($p < 0.01$) indicating the effect of each treatment on the other treatment's effect. The fact that the aspect main effect is not statistically significant as shown in the first part of Table 3 is not unusual since its interaction with time is highly significant (Von Ende, 2001).

Plant diameter responds entirely different than plant height on fire season over the study period. Fig. 3 shows that the maximum difference between plants burned in spring and those burned in autumn occurs at the end of the first post-fire growing season with the former having a bigger diameter than the latter. This difference gradually decreases and almost disappears by the end of the study period, which corresponds to the end of the third post-fire growing season. When the effect of fire season is studied in relation to the different aspects (Fig. 4) we see that the diameter response to the season of burn depends strongly on the aspect. While the maximum difference between spring and autumn resprouts occur at the end of the first post-fire growing season irrespective of the aspect, in south and west aspects no difference can be seen in plant diameter after the end of the second post-fire growing season. In north and east aspects on the other hand the plants burned in spring have a greater diameter which is sustained until the beginning of the third growing season on the north aspects and until the end of it on east aspects.

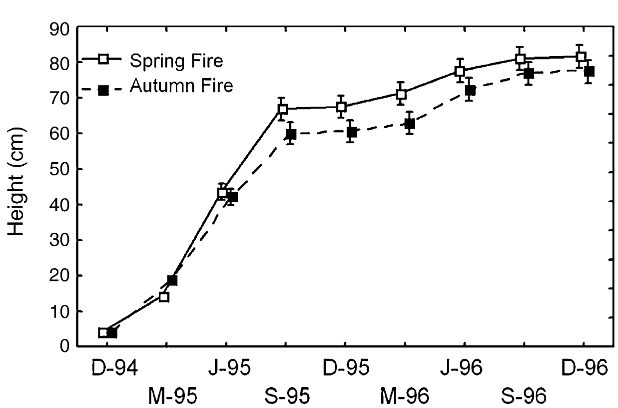

Fig. 1. Growth in height of plants burned on different seasons ($p < 0.001$). The vertical bars show 95% confidence interval.

3.3. Effect of maternal sprout on post-fire resprout height and diameter

The height of the maternal sprout affects the height of the post-fire resprout throughout the study period (Table 4). It remains significant from the first measure in December following the fire events to the last in December 1996. As indicated from the coefficient of determination (R^2) this effect is most important at the beginning of the second post-fire growing season since at that time the height of maternal sprouts accounts for 17.3% of the variation in the resprouts height.

In the case of diameter the effect of maternal sprout on post-fire resprout becomes significant in the beginning of the second post-fire growing season as shown in Table 5. It remains significant for the rest of the study period and the highest effect occurs in the end of the third post-fire growing season. At that time, as indicated from the R^2 of the last two measurements (September and December 1996) the maternal sprout diameter accounts for more than 20% of the resprout diameter variation.

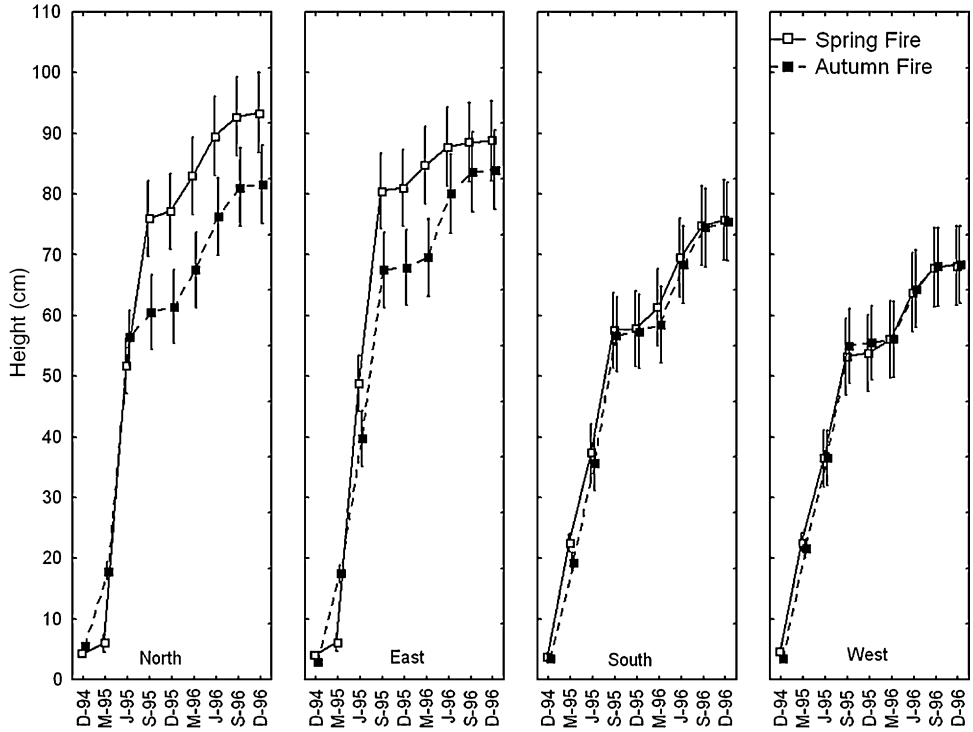

Fig. 2. Growth in height of plants burned on different seasons and growing on different aspects ($p < 0.001$). The vertical bars show 95% confidence interval.

Table 3
Table of repeated measures ANOVA for post-fire plant diameter

Source	DF	MS	*F*	*p*	Adj *p* G–G	Adj *p* H–F
(A) Between-subjects						
Fire season	1	1.079	8.946	0.003		
Aspect	3	0.165	1.371	0.253		
Fire season × Aspect	3	0.047	0.393	0.758		
Error	195	0.121				
(B) Within subject						
TIME	8	11.640	1769.680	0.000	0.000	0.000
TIME × Fire season	8	0.052	7.877	0.000	0.000	0.000
TIME × Aspect	24	0.038	5.722	0.000	0.000	0.000
TIME × Fire season × Aspect	24	0.020	3.110	0.000	0.003	0.002
Error	1560	0.007				

Columns 6 and 7 show the adjusted *p*-value when the shift of data from the sphericity condition is taken into account.

4. Discussion

In the current study, *A. unedo* resprouts vigorously after fire in both sites and no mortality in any of the selected plants has been observed throughout the duration of the experiment. By the end of the first post-fire growing season plants have completed the first stage of their survival strategy, which is to form a sufficient above ground part that will enable them to sustain themselves through the process of photosynthesis. At this time, no difference in the height of resprout, related to the season of burn, was found. This suggests that there are sufficient carbohydrate reserves to be mobilized and support regrowth, even after an autumn fire. Thus, the current study does not support the hypothesis that spring burned plants recover better than autumn burned plants after fire (Rundel et al., 1987; Malanson and Trabaud, 1988; Bowen and Pate, 1993). Cruz et al. (2003b) affirmed that plants store carbohydrates in excess of their needs and only a proportion needs to be mobilized in the early stages of development. This is also confirmed by the fact that plants are able to continuously resprout, even after sequential removal of the produced resprouts (Canadell and López-Soria, 1998).

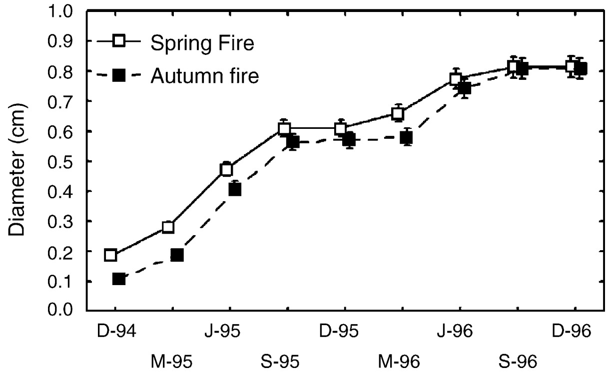

Fig. 3. Diameter growth of plants burned on different seasons ($p < 0.001$). The vertical bars show 95% confidence interval.

Growth in height for *A. unedo* occurs during spring and early summer, followed by a period of reduced photosynthetic activity due to water stress during mid-summer, and continuous again at late summer and early autumn (Castell et al., 1994). Hence, spring burned plants would be expected to be higher than autumn burned plants at the end of the first post-fire growing season, as a result of exploiting the two growing periods. According to Castell et al. (1994), however, autumn resprouts of *A. unedo* grow in height three times as fast as spring resprouts. This enables autumn resprouts to compensate for missing the spring and early summer growing period and reach the height of the spring resprouts by the end of the first post-fire growing season.

From the beginning of the second post-fire growing season and for the rest of the experiment's duration plants growing on north or east aspects are always higher than plants growing on south or west aspects, irrespective of the season of burn. This can only be attributed to the better soil moisture conditions prevailing on those orientations especially during the summer drought period (Espelta et al., 1999). The role of favorable soil moisture conditions in resprout growth has been documented in many studies (e.g. López-Soria and Castell, 1992; Castell et al., 1994; Castell and Terradas, 1994; Cruz et al., 2002, 2003a). Here, the favorable soil moisture conditions on north and east aspects affect the height of resprouts only after the beginning of the second post-fire growing season. This late response is not in accordance with other studies, which reported a positive effect of improved soil moisture conditions on the height of resprouts of *Erica australis* and *A. unedo*, during the first summer after experimental clipping (Cruz et al., 2002; Castell et al., 1994). It does agree, however, with the findings of Cruz et al. (2003a), where the positive effect was only observed 1 year after experimental clipping of *E. australis*. In the latter case, it was attributed to the severe water stress conditions, prevailing during the summer following the disturbance, which may have caused the relative difference in soil moisture to be maintained during the following year. This explanation of the late response of plants to increasing soil moisture fits perfectly with the conditions of the current study too, since the summer of 1994 where both fires occurred was exceptionally dry as shown in Table 1. Moreover, under severe water stress conditions, *A. unedo* was found to show no immediate growth related response to an increase in soil moisture by irrigation, because its stomata are largely controlled by the very high vapor pressure and fail to respond to an increase in soil water potential (Castell and Terradas, 1994). Another possible explanation of the late response to the better conditions of the north and east aspects could be that improved soil moisture conditions have no impact

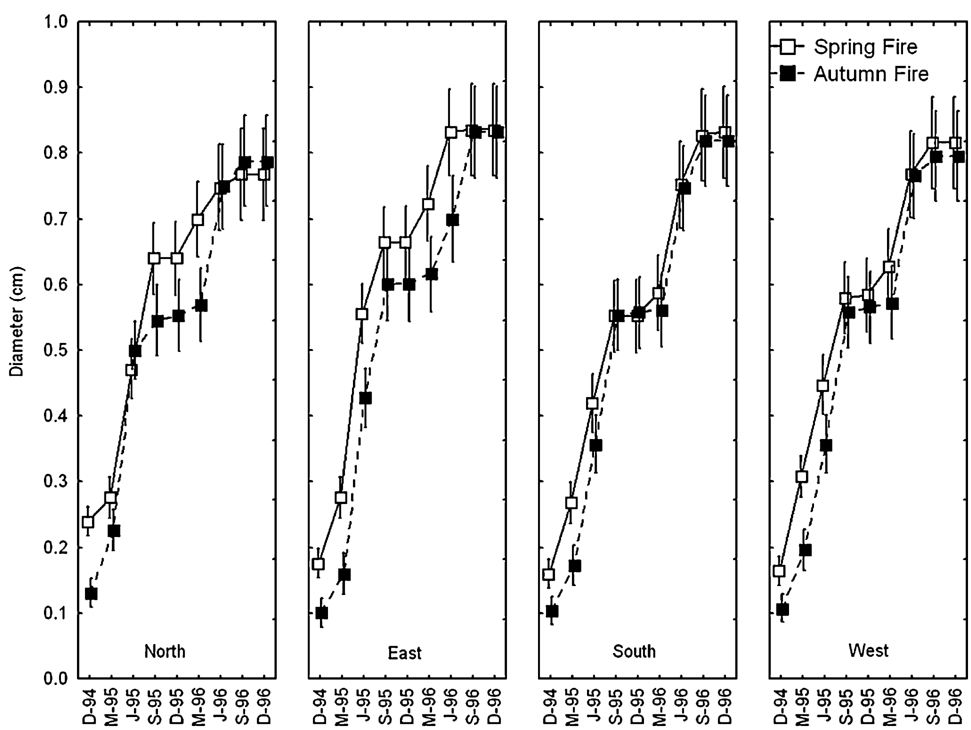

Fig. 4. Diameter growth of plants burned on different seasons and growing on different aspects ($p < 0.001$). The vertical bars show 95% confidence interval.

Table 4
Regression parameters and significance measures for the effect of maternal sprout height on the post-fire resprout height

Time	Intercept	Coefficient	R^2	p
December 1994	3.372	0.004	0.031	0.012
March 1995	7.282	0.054	0.173	0.000
June 1995	31.150	0.066	0.074	0.000
September 1995	47.765	0.088	0.076	0.000
December 1995	48.884	0.085	0.070	0.000
March 1996	53.423	0.076	0.052	0.001
June 1996	58.326	0.094	0.081	0.000
September 1996	60.949	0.101	0.099	0.000
December 1996	61.157	0.103	0.102	0.000

on the resprouts height during the very early stages of development in the case of *A. unedo* in this area. The latter, however, would require much more precise measures of soil moisture during that period in order to be confirmed. It should be noted here that the late response to the better conditions of north and east aspects contrasts with the behavior of the non-lignotuberous species *Q. coccifera* (kermes oak), which was examined in the same area, where resprouts of the two sites show significant differences in height between the different aspects by the end of the first post-fire growing season (Konstantinidis et al., 2005).

Plants resprouting after the autumn fire mobilize lignotuber-stored carbohydrates for the initial growth during the autumn growing period (Castell et al., 1994). Spring resprouts recharge carbohydrate storage during mid- and late summer and also during autumn (Cruz and Moreno, 2001; Castell et al., 1994), where their growth is only 1/3 of the growth of autumn resprouts. Given that lignotuber stored carbohydrates do not increase during winter (Cruz and Moreno, 2001), at the beginning of the second growing season spring burned plants are expected to have much higher carbohydrate concentration in their lignotuber to support the much more demanding spring growth. This explains the difference in height between spring and autumn burned plants observed on east and north aspects at the middle of the second post-fire growing season. This difference does not increase thereafter but it is sustained more or less at the same level suggesting that after this point spring and autumn burned plants grow in height at the same rate. The fact that the same effect is not observed on south and west aspects was rather unexpected. It could only be explained by the fact that the severe drought conditions of the first summer following the spring fire (Table 1), which are even more severe on those two aspects, did not allow the plants to recharge during summer, part of the stored carbohydrates consumed to support the spring resprouting.

Table 5
Regression parameters and significance measures for the effect of pre-fire plant diameter on the post-fire resprout diameter

Time	Intercept	Coefficient	R^2	p
December 1994	0.150	−0.0006	0.000	0.92
March 1995	0.165	0.015	0.019	0.051
June 1995	0.262	0.040	0.066	0.000
September 1995	0.342	0.054	0.099	0.000
December 1995	0.343	0.054	0.099	0.000
March 1996	0.376	0.053	0.084	0.000
June 1996	0.420	0.074	0.137	0.000
September 1996	0.374	0.096	0.206	0.000
December 1996	0.378	0.095	0.203	0.000

Diameter growth of resprouts follows different pattern than height. The biggest difference between spring and autumn burned plants appears at the end of the first post-fire growing season and gradually decreases thereafter until it diminishes by the end of the experiment. Fig. 4 shows that radial growth in the resprouts takes place mainly in spring between March and June, less but still substantial during summer (June–September) and not at all during autumn between September and December, irrespective of the aspect or season of burn. Subsequently, the big difference in diameter between spring and autumn resprouts, at the end of the first post-fire growing season, is explained by the fact that autumn resprouts have missed the period of substantial radial growth. After the start of the second growing season, autumn resprouts start recovering some of that difference and in south and west aspects, they reach the diameter of spring resprouts by the end of the second post-fire growing season. In north aspects, although that in late spring of the second post-fire growing season (June 1995), spring and autumn resprouts have no difference in diameter, during summer the former grow at a much faster rate and they appear to have a bigger diameter in September, which is sustained until the beginning of the third post-fire growing season. It appears that during the second post-fire summer, plants recovering after a spring fire can better exploit the favorable soil moisture conditions of the north aspects than plants recovering after an autumn fire. Similarly on east aspects the spring resprouts sustain the difference gained after the first post-fire growing season until the middle of the third post-fire growing season.

Pre-fire plant size was determined in the current study by measuring the height and diameter of the tallest dead shoot. Although this does not give a precise measurement of the plant size before fire, a high correlation is expected between the two. A similar approach was adopted by Pausas (1997) for *Quercus suber*.

Pre-fire plant size was found to have a significant effect on post-fire size of resprouts throughout the study period for both the growth parameters of height and diameter. The role of pre-fire plant size on the recovery process was reported in other studies too (e.g. Auld, 1990; Lloret and López-Soria, 1993; Pausas, 1997; Hoffmann and Solbrig, 2003). Auld (1990) demonstrated that resprouting vigor in *Angophora hispida* is proportional to plant size, which can be regarded as an index of resource accumulation. Hoffmann and Solbrig (2003) also found a strong positive relationship between pre-burn stem diameter and stem diameter of resprouts of savannas woody species 1 year after burning. The results of the current study suggest that the strongest effect of pre-fire plant size is not observed during the very early stages of plant recovery process but from the second post-fire growing season and onwards. For height the strongest effect occurs at the beginning of the second post-fire growing season where the pre-fire plant height accounts for about 17% of the variation on resprouts height at that stage. Pre-fire plant diameter affects significantly the diameter of the resprouts only after late spring of the second post-fire growing season. Its effect gradually increases thereafter and it reaches its maximum at the end of the third post-fire growing season where more than 20% of the variation on resprouts diameter can be explained by the variation in pre-fire plant diameter. Similar results about the delayed effect of pre-fire plant size on post-fire growth were presented by Lloret and López-Soria (1993). They suggested that at the very early stages, regeneration is mainly determined by the availability of meristematic tissues, while at later stages differential carbohydrate storage between plants with different size can drive a more vigor growth. The previous suggestion assumes a positive correlation between above ground plant size before fire and the ability to mobilize resources after fire from below ground organs. A greater rooting system, which is possibly the case in bigger size plants, provides a richer pool of nutrients and, in addition, offers more surface area for water and nutrient uptake (Kennard et al., 2002). The rooting system plays more important role during the later stages of development where plant growth depends on the uptake of nutrients and water from the soil rather than during the early stages where growth depends mainly on stored carbohydrates. The significant linear relationship between plant size before fire and size of resprouts may also indicate a common response of the two values to the micro-environmental conditions. This means that the relationship between pre-fire plant size and resprout size may not be causal. It could rather mean that the same favorable micro-environmental conditions, such as soil moisture and nutrients, that lead to larger plants before fire also lead to larger resprouts.

5. Conclusion

The results of the present study conclude that the presumed seasonal variation in lignotuber stored carbohydrates cannot ensure a more vigor resprouting on plants burned in spring over plants burned in autumn during the early periods of plant growth. Any effect of fire season is indirect and more related to the environmental conditions prevailed on the site after the disturbance, rather than directly related to the physiological condition of the plant at the time of disturbance. Aspect has a very significant role on resprout growth as a result of the better soil moisture conditions associated with north and east aspects. Finally pre-fire plant size also affects post-fire growth mainly at the later stages of plant development. The results of the current study are of course species and area specific and they are conclusive only for the first 3 years following the fire event. In order to generalize these findings further research is needed including more species in the same study area as well as the same species in different areas. An expansion of the monitoring period beyond the 3 years monitored in the current study could also provide useful insights on the resprouting behavior of Mediterranean shrubs and the possible survival advantages and disadvantages caused by different burning seasons.

Acknowledgements

This research has been carried out in the frame of the project ''Improvement of the efficiency of the prevention and suppression system in Greece'', co-funded by NATO (Science and Stability), the Greek Agricultural Ministry and the Greek Science and Research General Secretary. The authors would like to thank Prof. N. Stamou, scientific responsible of the program, for facilities provided.

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