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Early post-fire regeneration in *Pinus brutia* forest ecosystems of Samos island (Greece)

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ABSTRACT

The recovery of the burnt pine (*Pinus brutia*) forests of Samos island was followed during the first three post-fire years. Samos is characterised by a Mediterranean-type climate with a mild, subhumid winter and a long xerothermic period.

The natural regeneration of *P. brutia* is realised exclusively by seeds and is enhanced by a number of adaptations to fire: (i) the cones are serotinous and xerochasic, so most seeds survive inside the cones and are disseminated by the strong winds immediately after fire; (ii) the seeds are non-dormant and can germinate throughout the rainy season, though two frequency peaks were observed (a major one in spring and a minor one in late autumn); (iii) the heliophilous nature of both seed germination and seedling establishment is promoted by the opening of habitats produced by fire; (iv) from the survival curve it is evident that pine seedlings show a considerable drought tolerance and, once settled, their survival chance is quite high. The average density of pine seedlings measured after 15 months was 0.30 seedlings/m^2, high enough to result in complete natural reforestation for most of the area burnt.

The ecosystem recovery was additionally characterised by a prolific regeneration through both seed germination and resprouting. Among the reseeders, an eminent role was allocated to *Cistus* spp. and many leguminous plants. Resprouting was also very important and was especially impressive among the evergreen sclerophylls, the geophytes-hemicryptophytes and several phryganic shrubs.

KEY WORDS: fire, mediterranean forest, *Pinus brutia*, regeneration, resprouting, seed germination, seedling survival.

RÉSUMÉ

La récupération à la suite d'un incendie d'une forêt de *Pinus brutia* de l'île de Samos a fait l'objet d'un suivi pendant les 3 premières années. L'île de Samos est caractérisée par un climat de type méditerranéen à hiver subhumide et doux et une longue période de sècheresse estivale.

La régénération naturelle de *P. brutia* se fait exclusivement par graines et est favorisée par un certain nombre d'adaptation au feu. Premièrement, les graines sont conservées dans les cônes, et disséminées par le vent immédiatement après incendie. Deuxièmement, les graines ne sont pas dormantes, et susceptibles de germer tout au long de la saison des pluies, mais avec deux pics : un pic principal au printemps et un pic secondaire à la fin de l'automne. Troisièmement, le caractère héliophile de la germination des graines et de l'établissement des plantules favorise l'installation dans trouées provoquées par le feu. Quatrièmement, il ressort des courbes de survie que les plantules ont une résistance à la sécheresse considérable et, une fois installées, ont de très grandes chances de survie. La densité moyenne de plantules, établie 15 mois après le feu, est de 0,3 plantules par mètre carré, nombre suffisant pour assurer la reforestation dans de bonnes conditions de la majeure partie de la zone incendiée.

La récupération de l'écosystème est, en outre, caractérisée par une régénération prolifique par voie sexuée (germinations) aussi bien que végétative (rejets). La reproduction par graines joue un grand rôle dans différentes espèces du genre *Cistus* et de légumineuses, tandis que la reproduction par rejets joue un rôle particulièrement important parmi les sclérophylles sempervirentes, les géophytes, les hémicryptophytes et différents arbustes de la phrygane.

MOTS CLÉS : *Pinus brutia*, incendie, régénération, germination, repousse, survie des plantules, forêt méditerranéenne.

INTRODUCTION

Samos is among the largest (477.2 km^2) islands of Greece. It is situated at the central and eastern part of the Aegean Sea, only a few miles off the Minor Asian coast of Turkey and is enclosed by N. Lat. 37°38′-37°49′ and E. Long. 26°34′-27°04′. The major part of the island (nearly 70%) is considered as mountainous (higher summit 1440 m) and in contrast to most Aegean Sea islands, Samos is largely cultivated (about 33.5% of total area). In addition, a considerable part (21.4%) of the island is wooded while another large fraction (40.5%) is characterised as rangeland though most of it is dominated by evergreen sclerophylls (the rest being covered by phrygana).

The Calabrian pine (*Pinus brutia* Ten.) dominates the overwhelming majority of the forests of Samos, with the exception of several, spontaneously growing, unmixed stands of Mediterranean cypress (*Cupressus sempervirens* L.) and a narrow zone of Corsican pine (*Pinus nigra* Arnold ssp. *pallasiana* [Lamb.] Holmboe) restricted to higher altitudes (800-1,000 m). The total forest area covered by *P. brutia* amounts to nearly 10,000 ha (located mainly at the central part of the long, east-west axis of the island) and constitutes about 8% of the total area covered by *P. brutia* in Greece. In Samos, only in a few cases *P. brutia* is mixed with either the Mediterranean cypress or the Corsican pine; it is usually the only tree dominating the *Quercion ilicis* vegetation belt (250-700 m of altitude) though it is found growing all over the island, from sea level to about 1,000 m (CHRISTODOULAKIS, 1986). The forest shrub layer is very variable but is generally occupied by evergreen sclerophylls and in some cases by phryganic low shrubs or both. In the ground layer, the presence of geophytes and therophytes is always considerable, as expected for a mediterranean-type ecosystem.

Pine forests around the Mediterranean basin are well known to be highly flammable and thousands of hectares are burnt every year, especially during the dry and hot summer months. Nevertheless it seems that wildfire constitutes an integral part of the mediterranean-type climate and this is justified by the routinely observed dramatic post-fire regeneration capacity of the burnt mediterranean-type ecosystems (*e.g.* NAVEH, 1974; PURDIE, 1977 *a*; PURDIE, 1977 *b*; ARIANOUTSOU-FARAGGITAKI & MARGARIS, 1981; RUNDEL, 1981; TRABAUD *et al.*, 1985 *a*; TRABAUD *et al.*, 1985 *b*). Because of their long subjection to recurring fires, these ecosystems were characterised by SHANTZ (1947) as "fire type" or "fire climax". Moreover, NAVEH (1975) suggests that the role of fire is a long-term and important stress factor and selective force in Mediterranean ecosystems. The post-fire positive feedback of the ecosystem is brought about chiefly by a vigorous regeneration. Many individual plant species have been adapted to fire by developing a resprouting strategy (either obligatory or facultative) while others have evolved as obligatory seed regenerators. Both pine species belong to the latter group and this fact was already known in the ancient times, as recorded by THEOPHRASTUS (Book II, II, 2); pine seed germination and seedling establishment may be so prolific after a wildfire that "according to some, resprouting is possible as when happened for instance at the burnt pine forest on the mountain near the (ancient) city of Pyrrha, in Lesbos island" (Book III, IX, 5).

In the decade of 1940s, during the World War II and the subsequent Greek Civil War, the largest part of the pine forests of Samos island was burnt for military purposes. At present, no evidence from those fires can be easily detected, due to the prolific, natural reforestation of the whole area. Of course, a considerable number of fires occur regularly every year (11.6 ± 1.0 fires corresponding to a total burnt area of 150 ± 40 ha per year for the period 1973-1982). During August 1983, two very destructive fires occurred and lasted for 3 and 2 days, respectively, burning a total area of more than 2,500 ha, of which about 2,000 ha were, mainly, unmixed forests of *P. brutia*. It was on this area that the present work was undertaken shortly afterwards and its aim was to investigate some of the characteristics of the early regeneration responses of the burnt forest ecosystems.

MATERIALS AND METHODS

The main meteorological data of Samos island (compiled from ANDREAKOS, 1978, and National Meteorological Service of Greece, 1953-1984) are presented in tables I and II. The climate of Samos island belongs to the Mediterranean-type family of climates and is further characterised by a rather humid and mild rainy season (October-April) followed by a rather long and intensely xerothermic period (May-September). The monthly distribution of precipitation (table I) shows a marked, Mediterranean-type, seasonal periodicity. During 1982-1983 only 596.5 mm of rain were measured while, on the other hand, a total of 1,037.2 mm was measured during the following year 1983-1984 (*i. e.* 29.2% below and 23.1% above the mean value, respectively). Table II contains the temperature data of Samos. It is quite clear that the winter is very mild and while it seems somewhat colder during 1982-1983, compared to 1983-1984, the average yearly values are very close both to each other and to the mean values for the period 1953-1984. From the data of tables I and II, the xerothermic season of Samos is shown to occur (to a varying extent) during the period May-September.

The present work was carried out in randomly selected sites of the *Pinus brutia* forest ecosystems of Samos island burnt in two different fires, which lasted from 7-9 and 28-29, August 1983, respectively. The first fire was very destructive (a total of 2,000 ha burnt) and all the data presented in tables III-VI and VIII were obtained from or refer to various sites of the corresponding burnt area. The forests burnt in August 1981 and August 1982 (data reported in tables VI and VII) are both located near Pagondas village.

TABLE I. — *Monthly distribution of precipitation (mm) on Samos island.*

	1953-1984 *	% of total	1982-1983	1983-1984
September	16.1	1.9	.0	.0
October	51.7	6.1	52.0	.6
November	118.2	14.0	73.6	201.7
December	184.5	21.9	150.6	191.3
January	178.8	21.2	53.4	227.3
February	120.4	14.3	174.3	219.6
March	86.5	10.3	49.1	114.0
April	50.1	5.9	9.7	74.9
May	27.7	3.4	13.3	2.6
June	6.3	.7	3.3	.0
July	1.6	.2	2.5	5.2
August	.7	.1	14.7	.0
TOTAL	842.6	100.0	596.5	1037.2

(*) Mean monthly values ($n=31$-32).

TABLE II. — *Mean (m), minimum (min) and maximum (max) monthly temperatures (°C) on Samos island.*

	1953-1984 *			1982-1983			1983-1984		
	m	min	max	m	min	max	m	min	max
September	23.1	19.7	26.0	25.7	21.5	27.8	23.8	19.6	26.2
October	19.3	16.5	22.0	19.4	16.6	21.7	17.9	14.5	19.9
November	15.9	13.4	18.3	14.2	11.7	15.8	14.8	11.8	16.3
December	12.6	10.3	14.9	11.9	8.7	13.3	12.5	9.8	14.3
January	10.7	8.2	13.1	8.5	5.7	9.9	11.5	8.7	13.0
February	11.0	8.4	13.5	8.4	5.7	10.0	11.3	8.4	12.8
March	12.5	9.6	15.0	11.6	8.7	13.2	12.1	9.4	13.5
April	15.8	12.5	18.3	16.8	13.1	18.7	14.2	10.6	15.9
May	20.0	16.4	22.9	21.2	16.9	22.8	21.1	16.4	22.7
June	23.8	20.3	26.9	24.0	23.4	27.7	24.5	19.7	26.3
July	26.0	22.0	28.9	27.9	23.4	29.7	27.1	22.4	29.0
August	25.8	22.1	28.7	26.7	22.6	28.7	26.3	22.1	28.1
Mean Yearly	18.0	15.0	20.7	18.0	14.8	19.9	18.1	14.5	19.8

(*) Mean monthly values ($n=24$-30).

TABLE III. — *The density of* P. brutia *seeds found on the burnt ground at 5 different sites of the burnt pine forest. (Measurements were taken on 6 & 7 Oct.* 1983).

Site	Seeds/m² (*)
1	47
2	68
3	22
4	35
5	41
$m \pm SE$	43 ± 8

(*) Values are means of seeds found on 50 randomly sampled surfaces (0.04 m^2) from each site.

Surveys were conducted randomly with various sampling areas, ranging from 0.1 to 1 m^2, depending on the research object. The area and the number of quadrats used are appropriately mentioned in each table. Values are generally presented as means ±SE (standard error).

Germination tests were carried out in Petri dishes, in temperature controlled chambers, where in all cases temperature was kept constant within ±0.5°C. The intermittent Far Red, FR, (broad band) light source consisted of 8 white incandescent tubes (Philips Philinea 6276×60 W) and 3 sheets of plexiglas filters (two blue, 527, and one red, 601, 3 mm thick; Röhm GmbH, W. Germany). Total fluence rate at the region 675-800 nm was 4.5 W m^{-2}.

The growth chambers were equipped with a white light source of an emission spectrum quite similar to natural daylight ($Q_{660}/Q_{730}=1.00$). The source consisted of 4 white fluorescent tubes (Sylvania, Cool White F48T12/CW/HO, 60 W) and 8 white incandescent bulbs (Osram 40 W) and the total fluence rate in the range 400-800 nm was 16.7 W m^{-2}. When this light was filtered through the 3 sheets of plexiglas filters described above, a broad band FR light was obtained (total fluence rate 1.7 W m^{-2} in the range 675-800 nm). Total fluence rates were estimated by integration of the spectral fluence rate curves constructed after the measurements taken with a spectroradiometer (ISCO SR, U.S.A.). All manipulations of imbibed seeds were carried out under a dim green safelight (green fluorescent tube F 15T8.G.6, 15 W Green-Photo, General Electric; 2 sheets of plexiglas filter, 3 mm thick each, one red orange, 478, and one green, 700, Röhm GmbH, W. Germany; emission at 525-575 nm, maximum at 550 nm, total fluence rate 10 mW m^{-2}). In order to simulate the conditions prevailing in nature at November and December, an alternating temperature regime was applied: 10 hours at 15°C and 14 hours at 10°C with white light (or broad band continuous Far Red light) given during the warm period (daytime) (THANOS & SKORDILIS, 1987).

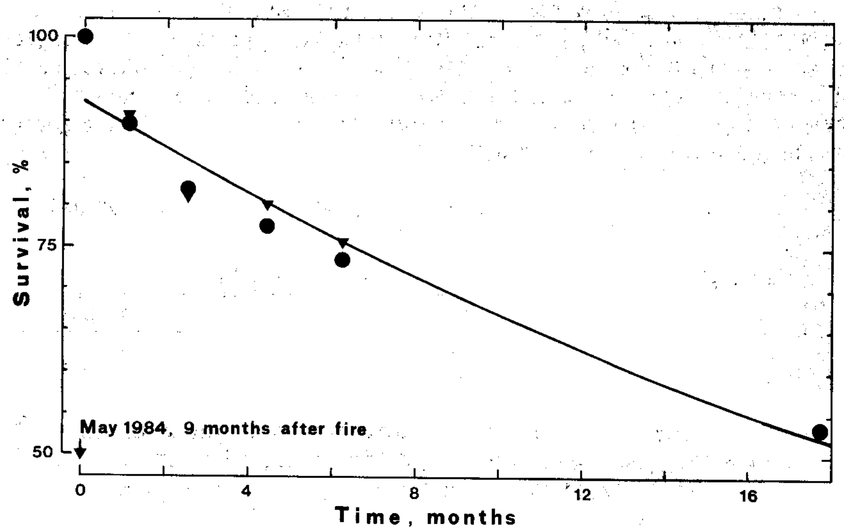

FIG. 1. – The survival curve of *P. brutia* and *C. sempervirens* seedlings for the period May 1984-Nov. 1985. The percentages have been estimated from an initial total of 452 pine (●) and 76 cypress (▼) seedlings, marked at 12 and 5, respectively, different burnt locations.

Survival measurements (fig. 1) were made possible by securing colour, plastic rings around the stem of pine and cypress seedlings growing in several, randomly chosen, burnt sites. A total of 452 pine seedlings and 76 cypress ones were ringed at 12 and 5 sites of the burnt area of the fire of 7-9 August, 1983.

The floristic data (tables IX-XI) were obtained from the burnt areas of both fires of August 1983. The botanical nomenclature of this work follows that of "Flora Europaea" (TUTIN *et al.*, 1964-1980) and/or that of "Flora of Turkey and the East Aegean Islands" (DAVIS, 1965-1985) with certain recent revisions mentioned by CHRISTODOULAKIS (1986).

RESULTS

a. SEED GERMINATION AND SEEDLING ESTABLISHMENT OF *Pinus brutia*

Less than two months after the fire of 7-9 August 1983, a careful sampling on the surface of the bare, burnt soil resulted in the discovery of a considerable number of pine seeds. The density of the seeds is shown in table III and does not seem to vary largely among the five, randomly chosen, sampling sites. The majority of the seeds found still carried their wing and since a number of charred seeds were also found (especially inside the ash layer) it is quite clear that the former landed after the fire.

Next step was to test the germinability of these seeds and compare it to that of seeds collected from unburnt sites. Final germination in darkness at continuous 15 or 20°C turned out to be 80 and 83%, respectively, for seeds from burnt sites and only 58 and 35% for those from unburnt sites. In a subsequent experiment the natural conditions prevailing during December have been simulated in the lab. Final germination was now somewhat reduced (presumably as a result of lower temperatures): 51 and 33% for seeds from burnt and unburnt sites, respectively. However, when daylight was filtered through a Far Red filter (simulating conditions of thick shading under dense canopy) no seeds were able to germinate. In a third experiment after one year of storage at room temperature (20 ± 5°C) the germinability was tested again at 15, 20 and 25°C (table IV). An overall decrease of final

TABLE IV. — *Final dark germination levels (% ± SE) of* P. brutia *seeds collected from burnt and unburnt pine forest locations.*

Seed origin	Temperature (°C)		
	15	20	25
Burnt sites	47 ± 6	65 ± 5	47 ± 5
Unburnt sites	34 ± 4	38 ± 4	16 ± 3

germination (probably due to storage) was observed compared to the values reported above. With only one exception (at 15°C of table IV), the final germination differences between the seed lots from burnt and unburnt sites were statistically significant at the 5% level.

Pine seedlings had emerged on the burnt ground as early as December 1983, about one month after the start of the rainy season. On the basis of unquantified observations, the number of germinating seeds was rather limited, although more frequent in humid microhabitats, like runoff ditches. During January and February 1984, seedling emergence was even more scanty while a burst of germination was observed from mid March until the end of the rainy season (beginning of May). Table V contains the density measurements of *P. brutia* seedlings carried out in November 1984, at a seedling age of between 6 and 11 months (and early enough for the manifestation of second-year germination). The sites sampled were selected randomly and were distributed all over the burnt area. The calculation of

TABLE V. — *The density of* P. brutia *seedlings in various sites of the burnt pine forest.* (Measurements were taken in Nov. 1984.)

Site	Seedlings/m² (*)
1	0.76±0.19
2	0.31±0.07
3	0.14±0.05
4	0.00±0.00
5	0.74±0.21
6	0.54±0.16
7	0.04±0.03
8	0.18±0.08
9	0.38±0.14
10	0.16±0.06
11	0.04±0.03

(*) Values are means (±SE) of seedlings found on 50 randomly sampled surfaces (1 m^2) from each site.

the gross average for the 11 sites gives a value of 0.30 seedlings/m^2. The seedling density varied between 0.14 and 0.76 seedlings/m^2, with the exception of sites 4, 7 and 11. The reasons for the low densities of those latter sites were evident: heavy grazing for the first case, steep slope and calcareous, poor soil for the other two.

The survival curve of the pine seedlings in shown in figure 1. Time 0 is set at the start of the observation period, in May 1984, 9 months after the fire and at the end of the rainy season when no more germination was expected. The seedlings marked were 1-5 months old though most were, presumably, 2-3 months old and were forming their primary needles at that time. The shape of the curve seems to fit well to a negative exponential curve of the formula:

$$S = 92.457\, e^{-0.032\, T}$$

(S: survival, as % of the initial value; T: time, in months; $r^2 = 0.955$.) Mortality of pine seedlings in the periods May-November 1984 and November 1984-November 1985 was estimated to be around 25% for both cases. In addition to the *P. brutia* seedlings, a considerable number of *Cupressus sempervirens* seedlings were also identified, especially in sites where a mixed forest stand existed prior to fire. It is interesting that a much smaller sample of cypress seedlings, marked at only 5 of the above mentioned 12 sites, gave survival values surprisingly close to those of pine seedlings (fig. 1).

The vegetative growth of pine seedlings in three forest areas, burnt in different years, is shown in table VI. By comparing the corresponding heights in consecutive measurements during January, June and November 1984, it is evident that vegetative growth occurs exclusively during springtime and so January and June measurements can be compiled together with those of nearest November. Therefore, after 1, 2, 3 and 4 growth (spring) seasons, mean heights of pine seedling are 5.9, 12.6, 21.7 and 37.6 cm, respectively. The absolute yearly increment increases progressively while, in relative terms, a doubling (or nearly) of total height is scored each year.

TABLE VI. — *The height (cm) of* P. brutia *seedlings grown in three burnt, pine forest areas.*

Date of fire	Date of measurements			
	Jan. 1984	Jun. 1984	Nov. 1984	Nov. 1985
Aug. 1981	14.4±0.5	23.3±0.9	22.7±0.9	37.6±0.9
Aug. 1982	5.7±0.3	11.7±0.6	12.8±0.9	19.1±0.7
Aug. 1983	–	–	6.1±0.3	11.4±0.4

Values are means (±SE) from at least 50 seedlings.

b. RECOVERY OF BURNT FOREST ECOSYSTEMS

For the forests which were previously burnt during 1981 and 1982, some vegetation characteristics are presented in table VII. Both sampled areas (and

TABLE VII. — *Characteristics of natural regeneration in two pine forest ecosystems burnt on Aug.* 1982 (*a*) *and Aug.* 1981 (*b*). (Measurements were taken in Jan. 1984.)

	Seedlings/m²	Coverage (%)	Height (cm)	Grazed (%)
(*a*)				
Pinus brutia	0.54±0.14	0.04	5.7±0.3	39
Cistus spp.	5.84±0.99	10.	–	–
Sarcopoterium spinosum	2.38±0.49	4.	–	–
(*b*)				
Pinus brutia (2-yrs-old)	2.60±0.47	–	14.4±0.5	44
Pinus brutia (1-yr-old)	0.60±0.16	–	–	–
Pinus brutia (total)	3.20±0.50	4	–	–
Cistus spp.	3.90±0.70	19	–	–

Values are means (±SE) from 50 randomly sampled surfaces (1 m²); the percentage of grazed seedlings was determined from one sample of 100, for each case.

especially the second) were located relatively near to unburnt pine stands. The considerable presence of *Cistus* seedlings in both cases and of *Sarcopoterium spinosum* in the former are noteworthy. Another interesting feature is the rather high proportion of grazed but still growing pine seedlings. Grazing (presumably by goats) was easily detected in 1st-year seedlings by the absence of the apical primary needles and the concurrent necrosis of the apical part of the stem. The survival and recovery of grazed seedlings was achieved (to an unknown degree) by the growth of one or two lateral stems and this resulted to badly shaped seedlings and trees, later on.

Soon after the start of the rainy season a green carpet of seedlings covered the burnt soil. Although the measurements were taken rather early, the average density of seedlings was quite high, ranging from 190 to 1,660 per m² (data of table VIII). The number of *Cistus* seedlings ranged from 50 to 1,640 per m² and in certain spots reached incredible values; nearly 29,000 seedlings per m² were counted in a very impressive case. The density of the other seedlings was also very variable and seems to correlate negatively with the *Cistus* densities.

All the dicotyledonous seedlings of table VIII were at the early growth stage of cotyledon expansion when measurements took place. A small number of plants

TABLE VIII. — *Density of seedling emergence in various sites of the burnt pine forest.* (*Measurements were taken in Dec.* 1983.)

Site	*Cistus* spp./10^{-2} m^2	Other seedlings/10^{-2} m^2
1	1.3±0.3	11.5±1.9
2	5.3±0.9	2.2±0.5
3	3.0±0.5	0.9±0.3
4	0.5±0.1	1.4±0.4
5	16.4±2.8	0.2±0.1

Values are means (±SE) of seedlings found in 40 randomly sampled surfaces (0.01 m^2) on each site.

from each morphologically different type were transplanted and transferred to a rudimentary nursery where they were eventually identified when flowering occurred.

TABLE IX. — *List of species germinating promptly* (*Nov.-Dec.* 1983) *in burnt sites. The seedlings were transplanted into pots and identified when flowering occurred.*

Plant species	Family
Anemone pavonina Lam.	Ranunculaceae
Lathyrus aphaca L.	Leguminosae
L. sphaericus Retz.	Leguminosae
Medicago disciformis DC.	Leguminosae
M. polymorpha L.	Leguminosae
Scorpiurus muricatus L.	Leguminosae
Trifolium campestre Schreber	Leguminosae
T. clypeatum L.	Leguminosae
T. grandiflorum Schreber	Leguminosae
T. tomentosum L.	Leguminosae
Vicia cuspidata Boiss.	Leguminosae

Table IX contains a list of these species which, all but one, belong to the family Leguminosae. An additional list of plants regenerating from seeds was compiled in the following spring: this time the species were identified *in situ* (table X).

A great number of either obligatory or facultative resprouting plants was observed in the burnt area of Samos and table XI shows a list of the most frequently encountered. Among them, most impressive were the evergreen sclerophyllous shrubs and the group of geophytes and hemicryptophytes. The former started to root-sprout immediately after the fires and at the time when the first rains occurred the new shoots were already around 10-20 cm high; in the following autumn (1984) the shoots were often higher than 1 m. The first signs of recovery in the latter group were represented, also very early, by the emergence of the flowering stalk, of the autumn- and winter-flowering species (*Urginea maritima*, *Crocus* spp., *Colchicum variegatum*, *Scilla autumnalis*, *Taraxacum megalorrhizon*). It was during winter that the vegetative growth of the spring-flowering species was triggered, and this growth was eventually followed by normal flowering during spring 1984.

DISCUSSION

A factor which probably considerably affected the intensity and spread of the August 1983 fires was the relative dryness of the preceding year 1982-1983 (table I).

TABLE X. — *List of species regenerating from seeds and observed in burnt sites during spring* 1984.

Plant species	Family
Anagallis arvensis L.	Primulaceae
Anthemis chia L.	Compositae
Arabis verna (L.) R. Br.	Cruciferae
Astragalus spp.	Leguminosae
Dorycnium hirsutum (L.) Ser.	Leguminosae
Fumaria sp.	Papaveraceae
Galium sp.	Rubiaceae
Geranium molle L.	Geraniaceae
G. rotundifolium L.	Geraniaceae
Lamium amplexicaule L.	Labiatae
Lotus spp.	Leguminosae
Papaver rhoeas L.	Papaveraceae
Ranunculus sp.	Ranunculaceae
Sarcopoterium spinosum (L.) Spach	Rosaceae
Sherardia arvensis L.	Rubiaceae

This fact in combination with the relative dryness especially during spring 1983 (only 72.1 mm, 12.1% of the yearly total rainfall compared to the average value of 166.1 mm or 19.5%, *i. e.* a 56.6% decrease) and the somewhat higher temperatures in the period April-July could contribute significantly to a considerable flammability increase of pine forests, during summer 1983.

The climatological conditions which prevailed during the post-fire year 1983-1984 presented only minor deviations from the average values. The slightly higher temperatures during January and February 1984 (table II) as well as the increase of precipitation (table I) might contribute to a better recovery of the burnt areas. On the other hand, the increased rainfalls might also increase (by enhancing overland flow) the short-term erosional effects of fire (RUNDEL, 1981), as actually observed in several cases of steep slope on Samos island.

For many species of pines it is well known that their cones are serotinous and xerochasic (RUNDEL, 1981). This is also the case for *Pinus brutia* (NAVEH, 1974) where the seeds are already ripe, since late spring, but the cones open gradually only during late summer and autumn. Moreover, it has been observed that a percentage of cones remain closed for months or even years and the extent of this might be correlated with the local values of temperature and/or humidity (PANETSOS, 1981). Xerochasy (opening in dry air) is apparent only in the anemochorous species of *Pinus* (PIJL, 1972). It is certain that during midsummer, when most of the highly destructive fires take place, the great majority of the *P. brutia* cones are either completely or partially closed. Due to the high temperatures developed by the fire, the cones burst open and a massive dissemination of the seeds occurs. This was also verified in this case of Samos fires from a survey of the scorched pine cones, found either on the tree skeletons or on the bare soil, but still containing some safe and sound seeds.

The strong northern winds blowing in the Aegean Sea during summer (called etesian or meltemi) show a peak during July and August and this facilitates not only the spread of the fire but also the post-fire dissemination of the winged pine

TABLE XI. — *List of species regenerating vegetatively in burnt sites of pine forest ecosystems of Samos island.*

Plant species	Family
Evergreen sclerophylls:	
Arbutus andrachne L.	Ericaceae
A. unedo L.	Ericaceae
Ceratonia siliqua L.	Leguminosae
Erica arborea L.	Ericaceae
Olea europaea L. var. *sylvestris* (Miller) Lehr.	Oleaceae
Myrtus communis L.	Myrtaceae
Phillyrea latifolia L.	Oleaceae
Pistacia lentiscus L.	Anacardiaceae
Quercus coccifera L.	Fagaceae
Deciduous (shrubs and trees):	
Cercis siliquastrum L.	Leguminosae
Pistacia terebinthus L.	Anacardiaceae
Quercus pubescens Willd.	Fagaceae
Spartium junceum L.	Leguminosae
Styrax officinalis L.	Styracaceae
Vitex agnus-castus L.	Verbenaceae
Phryganic shrubs:	
Anthyllis hermanniae L.	Leguminosae
Genista acanthoclada DC.	Leguminosae
Euphorbia acanthothamnos Heldr. & Sart. ex Boiss.	Euphorbiaceae
Hypericum empetrifolium Willd.	Guttiferae
Sarcopoterium spinosum (L.) Spach	Rosaceae
Geophytes and hemicryptophytes:	
Asphodelus aestivus Brot.	Liliaceae
Colchicum variegatum L.	Liliaceae
Crocus spp.	Iridaceae
Cyclamen spp.	Primulaceae
Daucus sp.	Umbelliferae
Gagea graeca (L.) A. Terracc.	Liliaceae
Gynandriris sisyrinchium (L.) Parl.	Iridaceae
Muscari comosum (L.) Miller	Liliaceae
M. neglectum Guss.	Liliaceae
Neotinea maculata (Desf.) Stearn	Orchidaceae
Ophrys spp.	Orchidaceae
Orchis spp.	Orchidaceae
Ornithogalum montanum Cyr.	Liliaceae
Scilla autumnalis L.	Liliaceae
Taraxacum megalorrhizon (Forsk.) Hand.-Mazz. (s. l.)	Compositae
Urginea maritima (L.) Baker	Liliaceae
Miscellaneous:	
Asparagus acutifolius L.	Liliaceae
Brachypodium retusum (Pers.) Beauv.	Gramineae
Rubia tenuifolia D'Urv.	Rubiaceae
Rubus sp.	Rosaceae
Smilax aspera L.	Liliaceae

seeds, to distances in the range of hundreds (and probably thousands) of meters away from the mother plant. MULLER (1955) presented some verified data for the wind dispersal of seeds during storms and recorded a distance of 2 km for seeds of *Pinus sylvestris* L. Thus the origin of the seeds found on the burnt ground (table III) may be attributed both to unburnt cones of the local burnt trees and to unburnt trees from the nearby stands. The ratio of the contribution of these two sources is thought to be primarily determined by the intensity of the fire and the distance of the neighbouring unburnt wood. Concerning with table III, each sampling site was more than 200 m away from the nearest unburnt pine tree and so it is concluded that most of the seeds found on the ground should have come from the burnt trees. Therefore, on the occasions where live pine trees keep growing in the vicinity, the post-fire, soil seed bank might be considerably enriched. This suggestion is supported in an indirect way by the data shown in table VII, concerning the forest site burnt in 1981. Both the relatively high density of pine seedlings and the considerable second-year germination (probably due mostly to newly dispersed seeds) could be attributed to the presence of unburnt trees in the vicinity of the sampled area.

From the germination data described in the Results section and presented in table IV it is clear that the lot of seeds collected from the surface of the burnt soil was viable to a high degree while its germinability was certainly not lower in comparison with that of "normal" seeds. Moreover, it could be argued that fire has a promotive effect on *P. brutia* seed germination, probably through seed coat scarification in a portion of the seed population. THALOUARN (1976) reported an enhancement of germination of *P. halepensis* through a stimulation mechanism which renders the seed coat more water-permeable. To our knowledge, this is the single evidence published about a seed coat effect on the germination of a *Pinus* species. The possibility of fire stimulation in *P. brutia* seed germination is still an unresolved matter. The statistically significant germinability differences between the lots from burnt and unburnt sites could be viewed alternatively as a result of natural heterogeneity (SHAFIQ & OMER, 1969; PANETSOS, 1981; THANOS & SKORDILIS, 1987). A very interesting characteristic is the complete inhibition of germination under simulated conditions of dense canopy, thus verifying the heliophilous nature of *P. brutia* seed germination and seedling growth (already suggested by SHAFIQ, 1979 and CALAMASSI, 1982, and further investigated by THANOS & SKORDILIS, 1987).

The germination characteristics of the seeds collected from both burnt and unburnt sites of Samos island did not show any type of primary dormancy. In certain occasions, for seeds from certain provenances, a chilling requirement was necessary for *P. brutia* seed germination (SHAFIQ & OMER, 1969; SKORDILIS & THANOS, unpublished), but this does not seem to be the case for Samos. Moreover, both the laboratory tested temperature range of germination and the actual, field observations lead to the conclusion that seed germination of *P. brutia* is possible throughout the rainy season. However, an empirical approach to the germination frequency in nature (under the specified meteorological conditions of Samos) seems to support a bimodal pattern, with a lower peak in December and a much higher one in April. This bimodal pattern is presumably imposed by the inhibitory temperatures of winter.

From the field observations it was quite clear that pine seed germination and seedling establishment was favoured by the presence of a pine needle layer. Though all of the litter present was consumed by the fire, in several occasions a new layer of fallen, scorched or simply dried, pine needles had formed soon afterwards. This layer seemed beneficial for pine seed germination presumably through providing better water conditions while at the same time drastically decreasing competition from other species (probably due to its acid pH). The existence of such a layer could additionally imply a larger supply of pine seeds as a result of the reduced fire intensity.

The number of seeds found on the burnt ground might be considered maximal since the survey was carried out early in October 1983, by when seed dispersal had presumably been concluded. In addition, the rains had not started yet (a factor which would promote runoff and burial of seeds) while the activity of seed consuming animals must have been kept low. Practically no seed coat "beds" or seed remains were found at sampling time while this was a common encounter during the first rainy months. By using the equation of the survival curve of figure 1 and based on the average seedling density of table V, we can calculate a density of 0.41 and 0.20 seedlings/m^2 for May 1984 and November 1985, respectively. Thus only 1 out of 100 seeds found on the burnt ground in October 1983 (table III) germinated and established successfully by the end of the rainy season, in May 1984. A certain proportion, probably ranging between 10 and 20% of the initial population, was comprised of unsound and dead seeds. Assuming that all viable seeds had germinated during the first rainy season after their dispersal, a high mortality rate (79-89%) was observed. This ought to be attributed to seed predation, seed deterioration and unsuccessful germination or establishment. Though the individual contribution of each factor is unknown it is believed that all are important. Pine seeds are thought to be consumed by animals even at an early stage of post-germination growth; the seed coat (containing the megagametophyte and enclosing part of the cotyledons) was frequently observed missing (and presumably was eaten).

The mortality curve of figure 1 is surprisingly smooth, without any apparent seasonal effect, especially during the first drought period (from May to November 1984). It seems that, at the end of the rainy season, those pine seedlings already established successfully have a high probability (about 75%) of surviving the first dry period of their life span. This is also supported by the fact that even though their average height is, at that time, around 6 cm (table VI) they have already developed a strong and long (about 20 cm) main root. The overall probability of survival is again 75% but for the entire second year and is assumed to increase progressively during the following years. By adopting a rather moderate, average survival probability of 90%, from the second year and onwards, the calculated mean density of pines (data of table V) would be about 0.13 and 0.08 after 5 and 10 years, respectively. Even in the extreme case that no further supply of seeds would be provided by the unburnt trees from the vicinity, the densities computed above are quite sufficient for the complete tree coverage of the area. Naturally, there is a number of exceptional cases, especially in sites with steep slopes or poor soil which are heavily affected by erosion. Other factors contributing to the non recovery of the pine forest are of course: grazing, additional subsequent fires and human management.

In a large survey of the recovery of previously (1-30 years ago) burnt *P. halepensis* forests, TRABAUD *et al.* (1985 *b*) found that during the first five years after fire the number of seedlings is rather stable, around 1,000 stems/ha (or 0.1 seedlings/m^2). Afterwards (5-15 years) the density increases gradually to a peak value of about 10,000 stems/ha and then decreases again to a plateau value, equal to the initial one of 1,000 stems/ha, maintained during the third period (15-30 years after fire). The density increase was furthermore attributed to and fairly correlated with the density of adult trees in adjacent unburnt stands. This pattern of recovery might be applied to the previously burnt ecosystems of Samos (presented in tables VI and VII) and particularly for the area burnt in 1981 it seems that during the second year there was already a significant increase of density. On the other hand, there is an evident absence of adjacent unburnt trees for the majority of sites in the vast area burnt during the summer of 1983. Thus it is doubtful whether this pattern would be followed in these cases.

The height of the 1-year-old *P. brutia* seedlings (5.9 cm) measured in burnt areas of Samos island is somewhat higher than the values measured by PANETSOS (1981) in nursery tests of 4 different provenances (values ranging from 4.45-4.83 cm). The growth rates of *P. brutia* are clearly lower than those manifested by *P. halepensis*, at least during the first 4-5 years (PANETSOS, 1981; TRABAUD *et al.*, 1985 *b*). A noteworthy feature for the 1- and 2-years-old *P. brutia* seedlings is their apparent grazing-tolerance (table VII), though both the extent of this tolerance and the long term effects of non-lethal grazing are unknown.

Among the post-fire obligatory reseeders around the Mediterranean basin are the active pyrophytes belonging to the genus *Cistus* (*e.g.* SHANTZ, 1947; LE HOUEROU, 1974; NAVEH, 1974; ARIANOUTSOU & MARGARIS, 1981; TRABAUD, 1984). LE HOUEROU (1974) mentioned 12 different species of *Cistus* as typical pyrophytes regenerating exclusively by seeds and creating pure and extended stands after fire. The species encountered in Samos are *C. incanus* ssp. *creticus* (L.) Heywood and *C. salvifolius* L., the former being far more common than the latter. The post-fire *Cistus* seedling density is very variable (table VIII), presumably depending upon the size of the available, soil seed bank while after 1 or 2 years there is a dramatic decrease of surviving plants, as shown in table VII. These perennial *Cistus* were accompanied in their pioneering post-fire role in Samos by a considerable number of annual leguminous species (table IX). The family of Leguminosae is very well known and notable for the water impermeability of seeds (hard seededness or hard coatedness) in many of its members (BALLARD, 1973; ROLSTON, 1978). It is nevertheless surprising that the ecophysiological role of fire in the release from the coat-imposed dormancy (by "softening" of the seed coats) is only marginally discussed and acknowledged by the seed physiologists. The post-fire development of an impressive leguminous flora and vegetation has been noted several times (*e.g.* NAVEH, 1974; ARIANOUTSOU-FARAGGITAKI & MARGARIS, 1981). Because legumes can fix nitrogen, their presence is obviously beneficial for the replenishment of the burnt ecosystem nitrogen, up to 96% of which was estimated to be lost in the smoke of a fire (ARIANOUTSOU-FARAGGITAKI & MARGARIS, 1981).

The lists presented in tables IX, X and XI are not meant to be exhaustive though they contain the most important plant species for each plant group. A closer investigation might eventually transfer some of the species of table X (as well as additional ones) to table IX. This seems to be the case for *Sarcopoterium* *spinosum*, the seed regeneration of which is indirectly triggered by fire through the destruction of shading vegetation and the concurrent improvement of the light regime on the soil surface. Seed germination of *S. spinosum* has been shown to be free of any dormancy but is inhibited by moderate or dense shading (ROY & ARIANOUTSOU-FARAGGITAKI, 1985). This is presumably the reason for the 10-fold increase of post-fire observed germination in a burnt phryganic ecosystem (ARIANOUTSOU & MARGARIS, 1981) and also for the considerable density of *S. spinosum* seedlings in the burnt site presented first in table VII.

The other important phenomenon which contributes to the recovery of the Mediterranean-type ecosystems and complements seed germination, is of course resprouting (*e.g.* NAVEH, 1974; PURDIE, 1977*a*; ARIANOUTSOU-FARAGGITAKI & MARGARIS, 1981). Most of the perennial species found in the understorey of *P. brutia* forests, in Samos, have evolved towards fire a very efficient vegetative, regenerative strategy. This adaptation, though essentially conservative, has proved of greater survival value in ecosystems with a higher fire frequency (TRABAUD, 1984). Most geophytes and hemicryptophytes are fire-tolerant plants since their reproductive organs are generally not affected by fire.

A final note should focus on fire-stimulated flowering (RUNDEL, 1981). This is the case with *Cistus* spp. and *Sarcopoterium spinosum* which normally flower only in the second year. Nevertheless, a small proportion of these plants were seen to flower during summer 1984, in agreement with previous observations (NAVEH, 1974; ARIANOUTSOU-FARAGGITAKI & MARGARIS, 1981). On the other hand, none of the early-spring-flowering resprouted phanerophytes was seen flowering during the first spring after the fire (as already reported by NAVEH, 1975). This is attributed to a fire-stimulated elongation of the growth period (RUNDEL, 1981) resulting in an extended juvenile phase; eventually (November 1984, 15 months after fire) the manifestation of late-season flowering was observed in the resproutings of the late-spring/early-summer-flowering *Myrtus communis* and the autumn-flowering *Arbutus unedo* and *Smilax aspera.*

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