SATELLITE EVIDENCE OF DECREASING RESILIENCE IN MEDITERRANEAN PLANT COMMUNITIES AFTER RECURRENT WILDFIRES

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Abstract. Vegetation recovery from fire has been widely studied at the stand level in many types of terrestrial ecosystems, but factors controlling regeneration at the landscape scale are less well known. Over large areas, fire history, climate, topography, and dominant type of vegetation may affect postfire response. Increased fire frequency, as is occurring in some mediterranean-type ecosystems, may reduce ecosystem resilience, i.e., the ability to recover the pre-disturbance state. We used the Normalized Difference Vegetation Index (NDVI) from Landsat imagery to monitor vegetation recovery after successive fires in a 32 100-km^2 area of Catalonia (northeastern Spain) between 1975 and 1993. In areas burned twice, NDVI patterns indicated that regrowth after 70 mo was lower after the second fire than after the first. This trend was observed several years after burning, but not immediately following fire. Green biomass after the second fire significantly increased with longer intervals of time between fires. There was also a positive correlation between postfire NDVI and mean rainfall, whereas a negative correlation was found between NDVI and solar radiation. Forests dominated by resprouting *Quercus* spp. were more resilient to fire, but they showed a larger decrease in resilience after the second fire than did forests dominated by *Pinus* spp. that regenerate from seed. We conclude that the use of time series satellite images may help to gain further insights in postfire vegetation dynamics over large regions and long time periods.

Key words: Catalonia; fire regime; Landsat; Mediterranean Basin; mediterranean plant communities; NDVI; Normalized Difference Vegetation Index; postfire regeneration; resilience; Spain; wildfire.

INTRODUCTION

Fire has a powerful influence on ecosystem dynamics and function across a large variety of biomes (Kozlowski and Ahlgren 1974, Attiwill 1994). Fire-induced changes in ecosystem functioning and in plant and animal species composition mostly occur as a consequence of biomass loss and alterations of soil properties. These changes imply increasing light arriving to the soil surface, loss of carbon and other nutrients from the overall ecosystem, together with a transitory fertilization effect on soils (Seastedt et al. 1991, Christensen 1993, Kasischke et al. 1995, Whelan 1995). Although fires may be considered as a natural disturbance, shifts in current fire regime in relation to historical records have been observed in some regions. Reduced fire recurrence has been shown in circumboreal forests (Flannigan et al. 1998), coniferous forests of western North America (Heyerdahl et al. 2001), and temperate forests of North America and Mexico (Covington and Moore 1994, Fulé and Covington 1999). On the other hand, higher fire recurrence, higher fire intensity, or

larger burned area has been reported for tropical forests (Goldammer 1999) and some mediterranean shrublands and forests (Moreno et al. 1998, Keeley et al. 1999). Global warming may increase fire occurrence in these ecosystems (Rambal and Hoff 1998, Goldammer 1999). Therefore, a great concern has arisen about the effects of changes in disturbance regime on ecosystems, and particularly on the ecosystem-level consequences of increased fire frequency (Lavorel et al. 1998, Cochrane et al. 1999, Keeley et al. 1999).

We investigated the relationship between fire recurrence and postfire revegetation in a coastal area of the Mediterranean Basin. We considered this revegetation in terms of green biomass resilience, that is, the level of postfire green biomass in relation to pre-fire levels. We also examined the role of several environmental parameters, such as climate, topography, and dominant overstory species, in determining ecosystem resilience. The study was carried out by monitoring NDVI (Normalized Difference Vegetation Index) values from detailed satellite remote sensing images of forests and woodlands of Catalonia (northeastern Spain) over the period 1975–1993.

Ecosystem resilience may be defined as the ability of an ecosystem or community to return to pre-disturbance conditions (Westman 1986), and it has been ap-

plied in a fire ecology context (Keeley 1986, Westman and O'Leary 1986, Malanson 1987, Malanson and Trabaud 1987). Although the equilibrium assumption of this concept does not apply in many cases, resilience is useful for evaluating the effects of disturbance on ecosystem properties. For a given ecosystem parameter, resilience may be estimated at a given time as the ratio between the postdisturbance and the pre-disturbance measurements of this parameter (Tilman and Downing 1994). This ratio can be applied to investigate environmental controls on the response of the ecosystem to disturbances and the effects of increasing disturbance frequency.

Vegetation composition and structure in mediterranean-type ecosystems are strongly shaped by the fire regime. In some of these communities, fire has operated as a selective force increasing species diversity (Cowling et al. 1996), or as a filter favoring the dominance of some species (Lloret et al. 1999). The extent of burned areas and the frequency of fires are now increasing in some mediterranean-type ecosystems, such as some shrublands and forests of California, Chile, and the Mediterranean Basin (Avila et al. 1988, Moreno et al. 1998, Keeley et al. 1999). In Spain, fires increased moderately with Roman settlement, then decreased for centuries, and then increased again in recent decades (Riera-Mora and Esteban-Amat 1994).

Mediterranean-type ecosystems are generally recognized as resilient to fire, given that many species are able to survive or reestablish after fire (Trabaud and Lepart 1980, Keeley 1986, Malanson 1987). However, some studies suggest that a shift in species composition and structure may occur with changes in the fire regime (Zedler et al. 1983). We hypothesized that ecosystem resilience would decrease with increasing fire frequency. This hypothesis is based on (1) nutrient losses by volatilization (Debano and Conrad 1978, Wells et al. 1979), (2) postfire soil erosion as a consequence of the loss of plant cover (Wells et al. 1979), and (3) the loss of species with life histories that do not fit the disturbance regime (Zedler et al. 1983). Available evidence to test this hypothesis is mainly based on local, stand-level studies, but such changes are better examined over larger areas and longer time scales to account for landscape heterogeneity (Zedler et al. 1983, Trabaud 1991). Long-term, detailed field surveys covering large areas are impractical. On the other hand, optical imagery from satellite-borne sensors has been shown to be an efficient methodology to identify burned areas and to monitor the regeneration of plant cover after fire (Minnich 1983, Malingreau et al. 1985, Viedma et al. 1997, Chuvieco and Martín 2001). Based on this experience, we undertook an extensive analysis of archival satellite imagery to test empirically whether ecosystem resilience was related to the time interval between fires in mediterranean vegetation.

STUDY AREA

The study region (Catalonia) includes an area of ~32 100 km² in the northeast of the Iberian Peninsula, beside the Mediterranean Sea (Fig. 1). Shrublands and forests cover ~60% of this region. Agricultural lands cover most of the remainder, contributing to the fragmentation of natural vegetation. Most of the study area has a Mediterranean climate, with moist, mild winters and dry, hot summers (Clavero et al. 1996), which favor wildfires. The region is typical of fire-prone ecosystems in that many species have a recognized ability to regenerate after fire (Trabaud 1987). In the last 3–4 decades, fire occurrence has increased in this region as a consequence of land use changes and increasing climatic risk of fire (Piñol et al. 1998, Díaz-Delgado and Pons 2001).

METHODS

Burned areas detection and characterization

More than 100 Multi-Spectral Scanner (MSS) images for 1975–1993 from Landsat (1, 2, 3, 4, and 5) satellites (spatial resolution 79 × 59 m) were employed after applying geometric (Palà and Pons 1995) and radiometric corrections (Pons and Solé-Sugrañes 1994). MSS images were resampled to 60 × 60 m. A Digital Elevation Model was used in these processes to achieve a better geometric accuracy as well as to correct topographic effects on viewing geometry and solar illumination. The images were radiometrically rectified to allow comparisons across different sensors, dates, and atmospheric conditions by scene normalization using "scene-invariant" training areas (Hall et al. 1991). Near-infrared and red bands were used to calculate NDVI images (Normalized Difference Vegetation Index; Mather 1999).

The NDVI measure exploits the high absorptance of vegetation in the red portion and the high reflectance of vegetation in the near-infrared (NIR) portion of the electromagnetic spectrum. It is simple to compute from reflectance images as (NIR − RED)/(NIR + RED) and, in many cases, exhibits a strong relationship with a number of vegetation characteristics, notably green leaf area index (LAI), green biomass, and fractional absorbed photosynthetically active radiation, FPAR (e.g., Tucker 1979, Hardisky et al. 1984, Hatfield et al. 1985, Peterson et al. 1987, Anderson et al. 1993, Benedetti and Rossini 1993). In particular, and because of its general response to levels of green biomass irrespective of plant species (Blackburn and Milton 1995, Gamon et al. 1995), it has been used to quantify the total vegetation cover (Anderson et al. 1993, Duncan et al. 1993). Moreover, like other spectral band ratios, NDVI significantly attenuates undesirable effects caused by topographic relief.

Despite its wide use, NDVI has well-documented limitations and uncertainties. The relationships between vegetation variables and NDVI are often non-
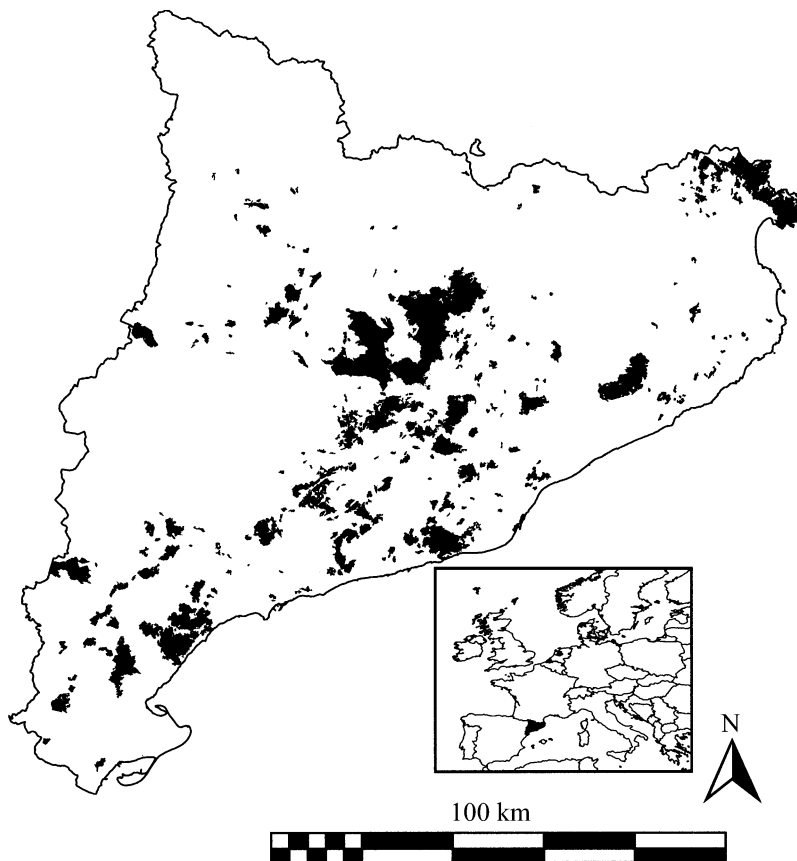
FIG. 1.   Map of fire recurrence (1975–1998) in Catalonia (northeastern Iberian Peninsula). Dark shading indicates burned areas; note the unburned areas within the fire perimeters.

linear. This is especially true with increasing biomass, because NDVI reaches a threshold level (saturation) before the maximum biomass is reached. As vegetation grows, shadows can even decrease NDVI while actual biomass increases. Background soil properties such as surface soil color affect NDVI, as do viewing geometry and the non-lambertian reflectance of plant canopies and topography. (We accounted for topographic effects using a 45-m resolution Digital Elevation Model). Examples of these kinds of problems can be found in Huete et al. (1985), Peterson et al. (1987), Baret and Guyot (1991), Wiegand et al. (1991), Bégué (1993), Oi et al. (1993), Danson and Plummer (1995), and Steininger (1996). Despite these limitations, there is good evidence that NDVI is well correlated with FPAR and, thus, with leaf area, leaf biomass, and photosynthetic potential (Zhou et al. 2001; see also Myneni et al. 1995).

Landsat Multispectral Scanner (MSS) data offer an incomparable way of studying vegetation dynamics over large areas since 1972, and the 60-m image resolution and high frequency of image acquisition (16–18 d) are especially useful for examining the relationship between vegetation and wildfire over a region.

Although other metrics can be derived from MSS

imagery, we use NDVI and assume that it provides a reasonable proxy for green biomass, with the following caveats: (1) NDVI data do not provide a basis for a highly detailed interpretation, but can reveal broad patterns and trends in relative vegetation amount. (2) When high levels of green biomass are present, NDVI saturation will not reflect the variations in that biomass, and the error level will be higher. (3) We will do a transformation on the NDVI values to reduce some problems related to phenological and meteorological variability.

In our study, areas >0.3 km^2, which was the minimum burned area discriminated ($\sim$83 MSS pixels of 60×60 m) were considered to have burned when the subtraction of consecutive NDVI images was greater than threshold values, i.e., all pixels exceeded the threshold value. Thresholds were obtained from empirical regression models based on 21 fires. For more details on methods, see Salvador et al. (2000). This procedure allows recognition of areas that have burned more than once during the study period (Figs. 1 and 2). For each burned area, fire size and perimeter (ranging from 0.3 to 68 km^2 and from 6.03 km to 341.73 km, respectively), and time interval between two fires
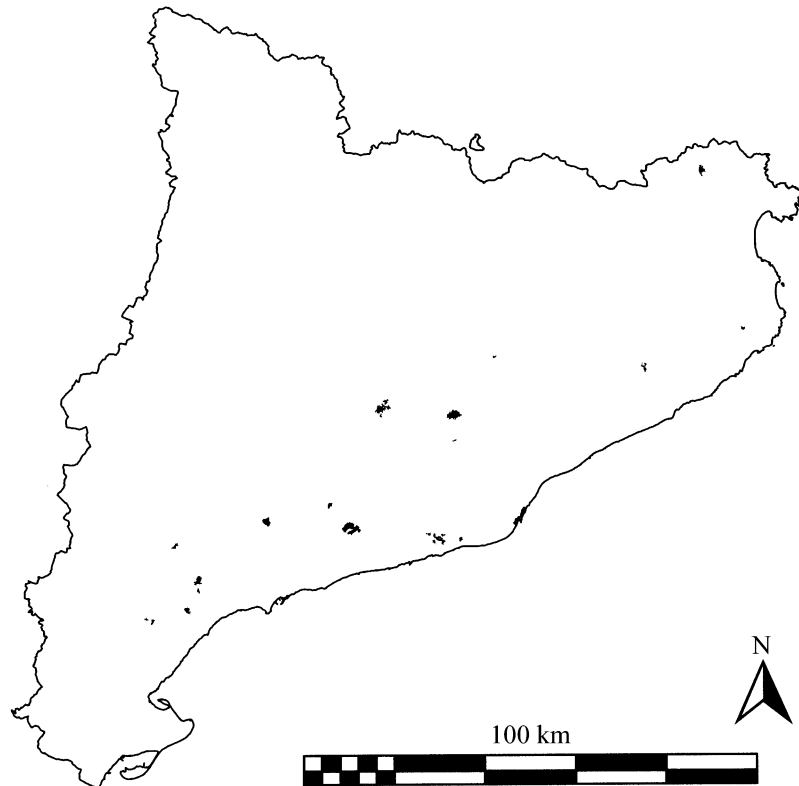
FIG. 2. Areas that burned twice between 1975 and 1993 and were employed in the study.

(4–11 yr) were also measured in order to check the influence of such fire regime parameters on resilience.

We selected, from the total of 473 detected fires, those areas in which our satellite record provided a period of ≥70 mo after the last fire. This selection process produced a data bank of 139 areas that burned once and 25 areas that burned twice during the study period (Figs. 1 and 2).

Nine different geological substrates and eight different vegetation types were considered after grouping the 224 categories of the geological map of Catalonia (ICC 1989; 1:250 000) and the 68 categories of the 1978 land use–land cover map (MAPA 1980; 1:50 000), respectively. The most abundant geological substrate and the dominant vegetation type of each burned area were assigned to each particular fire. The nine substrate types included marl, siliceous, basaltic, sandstone, clay, non-cemented alluvial, limestone, cemented alluvial, and miscellaneous (not assigned in the geological map). These categories were expected to vary in erodability, nutrients, and water availability. The eight vegetation types were forests dominated by the evergreen oaks *Quercus suber* and *Q. ilex*, the pines *Pinus halepensis*, *P. sylvestris*, and *P. nigra*, mixed forests of pines and oaks, shrublands, and *Eucalyptus* plantations.

Several topoclimatic variables for areas affected by just one fire, were extracted from different GIS layers

(ICC-DARP 1993, Clavero et al. 1996) to elucidate the role played by them in plant retrieval after fire. These variables were mean annual solar radiation (ranging from 138.8 to 185.1 $W \cdot m^{-2} \cdot d^{-1}$), mean altitude (from 54 to 1589 m), mean annual rainfall (from 425 to 975 mm, extracted from an empirical model developed by Ninyerola et al. 2000) and rainfall of the year immediately after fire (from 322 to 1175 mm). Estimation of mean solar radiation took into account several parameters: the Sun's path through the day, the Sun–Earth distance, the atmospheric attenuation, the incident angles on each point, and the cast-shadow effects on each point. Some of these parameters were extracted from the 45-m resolution digital elevation model of Catalonia. Cloudiness from meteorological stations was used to adjust the potential radiation model to a real one (Pons 1996). Data on total rainfall during the year following fire were obtained from the regional network of meteorological stations.

Regeneration monitoring

Because wildfires produce a clear drop in NDVI values, and resilience can be defined as the return to predisturbance conditions, regeneration could be evaluated simply by monitoring NDVI recovery after fire. However, results would be affected by seasonal and interannual variations in phenology (note that images are not always available at the same period because of

cloud coverage) and by the particular climatic conditions of each year. In order to minimize these effects, we calculated, for each date and in each burned area, the quotient between the average NDVI measurements of burned areas and the average NDVI measurements of unburned, neighboring areas. This quotient is referred to as Q_{NDVI} and provides revegetation monitoring that is more independent of year and period of year. Unburned areas were selected adjacent to burned ones by experienced photointerpreters and from land use–land cover 1:50 000 cartography, corresponding to the late 1970s (MAPA 1980). These unburned areas were selected to have surficial geology, topography, and vegetation similar to that of adjacent burned areas.

Resilience can be measured with reference to total aboveground biomass (Hobbs and Mooney 1985, MacGillivray and Grime 1995). Therefore we estimated resilience as the proportion of pre-fire Q_{NDVI} (average NDVI measurements of burned areas scaled by average NDVI measurements from neighboring unburned areas) attained by postfire Q_{NDVI} at several intervals of time. Pre-fire Q_{NDVI} values were extracted from the three consecutive measurements prior to fire. Postfire Q_{NDVI} values were also obtained from the three consecutive measurements following that interval.

The effect of recurrence on postfire resilience was evaluated in the 25 twice-burned areas by comparing the values obtained from rating the Q_{NDVI} after the first and after the second fire, respectively, to the Q_{NDVI} obtained before the first fire (Fig. 3).

Q_{NDVI} values were compared at 38, 44, 57, and 70 mo after the first and second fires. Thus a different year period was analyzed for resilience following the first fire than following the second fire. That is, the regeneration period considered for the first fires ranges from 1975 to 1984 vs. from 1983 to 1993 for the second fires.

We tested for any systematic differences in climate between the early and more recent observation periods by analyzing climate data (mean annual temperature and annual rainfall) from all the available meteorological stations in the area in the 1975–1993 period. Only stations with complete series were used. The averages of mean annual temperature ($n = 12$ stations) and annual rainfall ($n = 20$ stations) did not show a significant increase or decrease during the period (correlation between years and meteorological parameters: $r = 0.329$, $P = 0.170$ for mean temperature; $r = 0.045$, $P = 0.854$ for rainfall; Fig. 4). Therefore, we rejected the hypothesis of different climatic conditions after the first and the second fires, and we assumed that the recovery differences at the same site after the first vs. the second fire would be due to fire recurrence.

To evaluate the effects of geological substrate, vegetation type, climate, altitude, and fire magnitude on green biomass after fire, we computed the ratio of postfire Q_{NDVI} to the respective pre-fire Q_{NDVI} on the 139 areas that only burned once. The effect of geological substrate and vegetation type on postfire resilience was assessed by one-way ANOVAs, whereas the effects of topoclimatic variables (altitude, solar radiation, mean rainfall, rainfall in the year following fire) and fire variables (fire extent and fire perimeter) were evaluated using multiple regression models.

RESULTS

Fire recurrence

After 70 mo, resilience after the second fire was significantly lower than after the first fire (two-tailed paired t test, $t = 2.79$, $P = 0.01$, $n = 11$ fires). These differences were not significant at earlier stages of recovery (38 mo, $t = 1.47$, $P = 0.15$, $n = 25$ fires; 44 mo, $t = 0.64$ $P = 0.52$, $n = 23$ fires; 57 mo, $t = 0.46$, $P = 0.64$, $n = 16$ fires). This type of response fits a logarithmic model (Díaz-Delgado et al. 1998) in which the asymptote value is lower after the second fire than after the first one (Fig. 3).

We found a significant positive correlation between resilience after the first fire and resilience after the second fire at 38 mo after each fire, which is the minimum period of time available for all of the twice-burned areas ($r = 0.40$, $P = 0.04$, $n = 25$).

Resilience was also positively correlated with the time interval between consecutive fires (Fig. 5), which ranged from 1552 to 4099 d (~4 to 11 yr) ($r = 0.44$, $P = 0.02$, $n = 25$, measurements at 38 mo following the second fire; Fig. 5).

Differences were also found in the recovery after the second fire between the two main types of forests: those dominated by resprouting oaks (*Quercus ilex* and *Q. suber*) and those dominated by non-resprouting pines (*Pinus halepensis*, *P. sylvestris*, and *P. nigra*). Oak forests showed higher resilience values than former pine forests after the second fire (one-way ANOVA, $F_{1,23} = 8.8$, $P = 0.006$, $n = 25$; measurements at 38 mo after fire). However, when comparing resilience after the first and second fires, we observed that the ability to regenerate after the second fire decreased less in pine forests than in oak forests (measurements at 38 mo after the fire: pines, two-tailed paired t test, $t = 1.05$, $P = 0.36$, $n = 4$ fires; oaks, two-tailed paired t test, $t = 2.65$, $P = 0.037$, $n = 7$ fires; Fig. 6).

Once-burned areas

In areas where only one fire occurred, resilience estimated at 70 mo after fire was significantly affected by the dominant geological substrate (one-way ANOVA, $F_{8, 137} = 5.0$, $P < 0.001$; Fig. 7A), and by the vegetation type (one-way ANOVA, $F_{7, 137} = 2.3$, $P = 0.0285$; Fig. 7B).

Climate and altitude had significant effects on postfire resilience (see Table 1). Nonetheless, rainfall in the year following fires was not significantly correlated with postfire resilience (standardized regression coefficient β $= 0.49$, $P > 0.05$). Parameters related to fire magnitude,
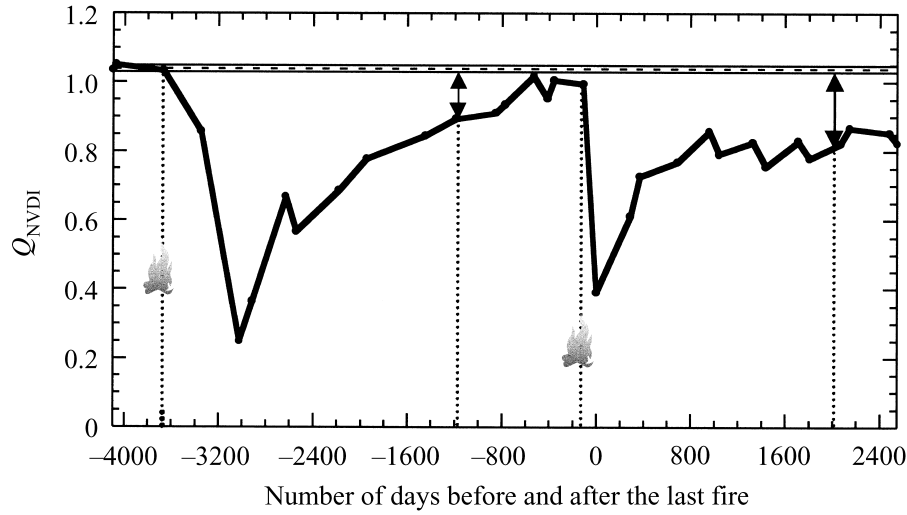
FIG. 3. Plant cover resilience (plant ability to recover, measured as green biomass) after consecutive fires. The figure shows Q_{NDVI} variations after two fires occurred in 1976 and 1985 in a forest dominated by *Quercus suber*, an oak that shows postfire resprouting ability from epicormic tissues and stumps. Arrows indicate the first and the second fire; note the difference between Q_{NDVI} values before fire and at 2096 d (69 mo) after. Q_{NDVI} is the quotient of average Normalized Difference Vegetation Index values for burned areas divided by average NDVI values for neighboring unburned areas. The upper horizontal dashed line and solid-line bounds represent the pre-fire phenological values (mean $\pm$ 1 SD).
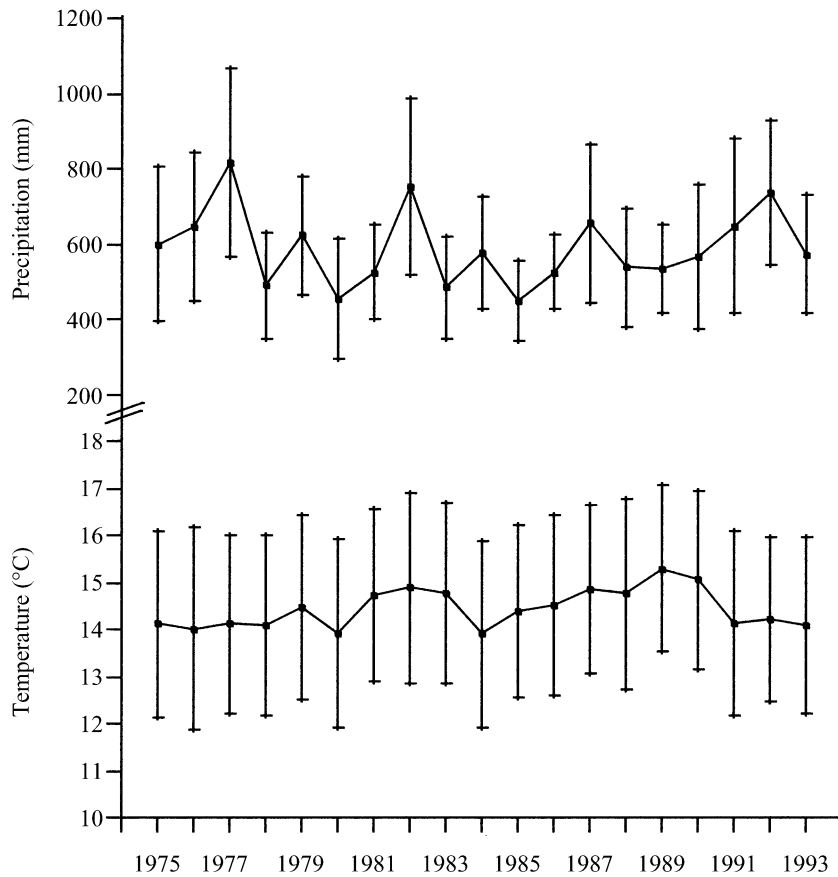

FIG. 4. Temporal variation in average precipitation and temperature in Catalonia during the 1975–1993 period of the study. Error bars indicate ± 1 SD.

FIG. 5. Relationship between plant cover resilience 38 months after the second fire and the fire interval. In this case, all of the twice-burned areas were considered. The regression equation is: resilience at 38 mo = 0.44 + 0.00009 (fire interval); $r = 0.44$, $n = 25$, $P = 0.02$.
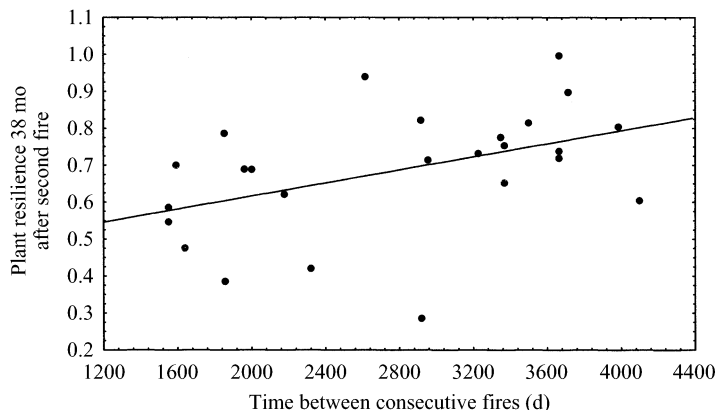
such as fire extent and fire perimeter, were not correlated with postfire resilience (see also Table 1).

DISCUSSION

Many studies have reported postdisturbance regeneration of vegetation after fire in mediterranean-type ecosystems. They have usually considered stands of vegetation and the role of regeneration mechanisms at the individual or species level. These studies have provided the basis for a sound theory of plant response centered on regeneration strategies and life-history traits (Whelan 1995, Zedler 1995, Bond and van Wilgen 1996). The development of models based on life-history traits allows the prediction of trajectories of vegetation composition and structure as a result of different fire regimes, including increasing fire recurrence (Noble and Slayter 1980, Moore and Noble 1990). However, there are scant empirical data on the relationship between fire regime and revegetation dynamics at landscape-to-regional scales.

Our study provides evidence of a slower recovery of NDVI after the second of two successive fires separated by <11 yr. To the extent that NDVI measures green plant biomass, which is associated with important ecosystem processes such as surface energy and water balance, nutrient cycling, erosion, and habitat structure, our results also imply lowered ecosystem resilience with higher fire frequency.

This result is observed in a mediterranean-type ecosystem, where plants regenerate by resprouting or from seed banks after wildfires (Hanes 1971, Trabaud 1987, Moreno and Oechel 1995). We note that the effect of fire recurrence on resilience is not detectable until several years after the fire. In this type of ecosystem, the ground is rapidly covered after fire by germinating plants, among which ephemeral, short-lived species are abundant (Trabaud and Lepart 1980), or by resprouting plants that were previously established, among which grasses may also play an important role (Pausas et al. 1999). Ephemeral species may emerge from the soil seed bank, which is rapidly filled after fire. Seeds of some of these species may also arrive from unburned,

neighboring areas. In both cases, recurrent fires may not significantly alter these processes. Grass resprouting is often enhanced by fire, even under high-recurrence fire regimes (Vilà et al. 2001). Our study is not able to discriminate the relative importance of the seeder and resprouting response of short-lived species in early regeneration, but we know that later cover is mainly due to long-lived, dominant trees and shrubs, which are able to exclude short-lived, smaller species (Escarré et al. 1983). Some studies have shown that large, long-lived resprouters may have a decreasing ability to grow after consecutive fires (Zedler et al. 1983, Trabaud 1991). Decreasing underground reserves may explain this declining response (Canadell and López-Soria 1998). Although bud bank depletion after frequent disturbances has been reported (Zammit 1998), further research is needed to investigate if this reduction is effective at the time scale in which fire recurrence occurs in our area. However, long-lived seeder species, such as *Pinus halepensis*, which is dominant in the region and often shows a very good regeneration after fire, may be sensitive to recurrent fires that limit seed storage (Thanos and Daskalakou 2000).

Green biomass diminishes significantly when disturbances occur at short intervals of time (<11 yr). Although life-history traits of dominant species may
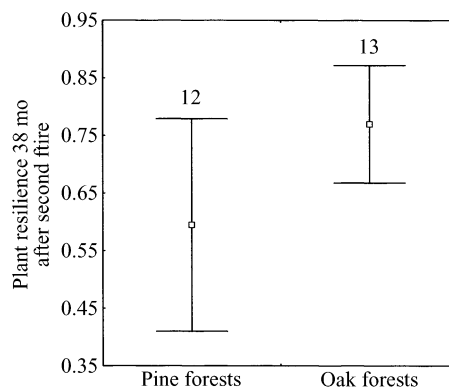

FIG. 6. Pine and oak forest resilience (mean ± 1 SD) after recurrent fires.
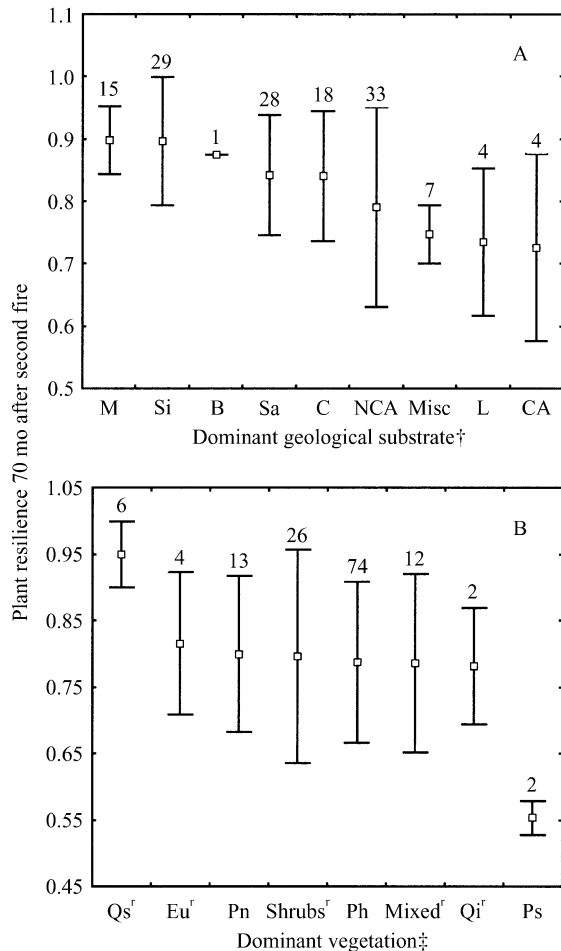
FIG. 7. Fire resilience (mean ± 1 SD, *n* values above bars) of once-burned areas in relation to (A) geological substrate and (B) dominant vegetation. Categories with a superscript r are resprouting species.

†Abbreviations: M, marl; Si, siliceous; B, basalt; Sa, sandstone; C, clay; NCA, non-cemented alluvial; Misc, miscellaneous; L, limestone; CA, cemented alluvial.

‡Abbreviations: Qs, *Quercus suber*; Eu, *Eucalyptus* sp.; Pn, *Pinus nigra*; shrubs, shrubland; Ph, *P. halepensis*; Mixed, mixed forest; Qi, *Q. ilex*; Ps, *P. sylvestris*.

explain the observed pattern, time between fires only explains ~20% of the total variance of resilience. It is highly probable that the same factors affecting fire resilience at once-burned areas (rainfall, radiation, geological substrate, vegetation) also contribute to explaining this variance. Fire history previous to 1975 may also explain part of this variance.

In once-burned areas, resilience is higher in communities dominated by resprouting species (*Quercus suber*, *Q. ilex*, *Eucalyptus* sp.) than in communities dominated by non-resprouting pines, some of which (*Pinus sylvestris*, *P. nigra*) may be sensitive to fire (Habrouk et al. 1999). In the communities that were dominated by pines before fire, green biomass after burning would mostly be due to the recruitment of

seedlings of short-lived species or to the regrowth of resprouters existing in the understory.

There are also different resilience patterns in pine and holm-oak forests after recurrent fires. Overall, resilience is higher in holm-oak forests, but pine forests show lower resilience decrease after the second fire. Holm-oak forests are, in general, a dense community, dominated by woody resprouters that regenerate quickly after fire. The rate of recovery might decrease after the second fire because of lower resprouting success and because of the absence of a fast-growing herbaceous layer in these communities. In contrast, pine forests may show lower resilience after six years because tree canopy development from seedlings initially is slower than from re-sprouts. However, open pine forests in the region have greater understory green biomass than do evergreen oak forests. Data from the Spanish Forest Inventory (IFN 1997) show that the mean understory cover is 62% in pine forests (*n* = 1945 stands) and 40% in holm-oak forests (*n* = 1518 stands). The first years after fire, before germinating pines reach to build a new forest canopy, these pine forests become shrublands or grasslands, which may remain as permanent communities if a short interval between fires prevents pines from reaching their full reproductive stage. These secondary communities, with an important herbaceous layer, may grow again rapidly after a second fire (Vilà et al. 2001).

Site characteristics also contribute to explaining postfire regeneration (López-Soria and Castell 1992, Christensen 1993). The positive relationship found between the resilience values after the first and second fires suggests that the same factors determining postfire recovery (site productivity and biological potential to regenerate, i.e., life-history characteristics of the species present in the community) are operating at both times. This result also indicates that good regeneration after the first fire is not at the expense of the regenerative potential after the second fire.

Rainfall, in particular, plays an important role in the ecosystem response to fire, as shown by the positive correlation between resilience and mean rainfall. In mediterranean ecosystems, seedling establishment has a seasonal pattern because it requires moist conditions

TABLE 1. Overall results for the multiple regression model between vegetation resilience (measured at 70 months after fire) and topoclimatic and fire magnitude parameters.

Parameters	β	P
A) Topoclimatic (r^2 = 0.23, P < 0.0001, n = 139 fires)		
Mean rainfall (mm)	0.22	<0.05
Mean solar radiation ($W \cdot m^{-2} \cdot d^{-1}$)	−0.22	<0.05
Mean altitude (m)	−0.27	<0.05
B) Fire (r^2 = 0.017, P = 0.311, n = 139 fires)		
Fire extent (m²)	−0.31	>0.05
Fire perimeter (m)	0.24	>0.05

(Specht et al. 1983, Keeley 1986). However, short-term effects of rainfall in the year immediately following the fire event have not been correlated to resilience, probably because resprouting is highly determined by resources previously stored in underground organs (Canadell and López-Soria 1998). The negative correlation between postfire resilience and solar radiation is possibly explained because rising solar radiation increases evapotranspiration, which might cause water stress for plant establishment and growth. The negative correlation between altitude and postfire resilience may be due to the different distribution of the dominant tree species, with different response to fire. Data from the Spanish Forest Inventory (IFN 1997) show that most populations (~80%) of the resprouters *Q. ilex* and *Q. suber* and the seeder *P. halepensis*, which successfully establish after fire, are distributed at low altitudes (240–985 m, 115–940 m, and 140–650 m, respectively). However, the populations of *P. nigra* and *P. sylvestris* are distributed at higher altitudes, 450–1000 m and 700–1600 m, respectively. These two species are neither able to resprout nor to establish significant seedlings after fire.

Soil characteristics may also be important in postfire regeneration processes (Malanson and O'Leary 1985). Nutrient availability and soil susceptibility to erosion are particularly dependent on the type of geological substrate. We found that postfire NDVI values were significantly different among geological substrates. However, our data do not permit us to distinguish the effect of soil on vegetation cover from the effect of soil reflectance, which has been reported to influence NDVI estimations (Huete et al. 1985). Because the different vegetation types were similarly distributed in the dominant substrates, we do not expect that the differences of resilience among the main types of vegetation were actually caused by the geological substrate.

From our study, we can conclude that at least three kinds of factors contribute to postfire resilience: fire regime, dominant life-history traits of vegetation, and postfire conditions. The fit between fire regime, and particularly fire recurrence, and the regenerative type of dominant species, coupled with the traits of suitable species to replace them, determines the biotic potential of regeneration. More research is needed, however, to understand how the regional patterns of resilience are explained by responses at the stand level. For example, in our study, extensive field work would be needed to elucidate which processes explain the differences in green biomass between holm-oak and pine forests after a second fire. Finally, postfire conditions, determined by site characteristics such as climate and geological substrate, have been proved to determine resilience at a regional scale. These characteristics are associated with site productivity, which appears to be positively correlated with resilience.

Previous studies have shown the relevance of site productivity and species composition on ecosystem response to fire at the stand level. Here we have shown the suitability of satellite NDVI measurements to obtain large-scale estimates over extended periods of time. NDVI provides good monitoring of green biomass, which is a parameter well associated with other important properties of ecosystems. Large-scale spatial and temporal remote sensing monitoring can be used to asses regional and global models and can greatly contribute to a better representation of the response of terrestrial ecosystems to disturbances. Our study points out the importance of life-history traits associated with the dominant species in determining vegetation patterns under specific disturbance regimes.

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