ELSEVIER

Ecological Modelling 142 (2001) 261–283

ECOLOGICAL MODELLING

www.elsevier.com/locate/ecolmodel

Simulating the effects of different fire regimes on plant functional groups in Southern California

Janet Franklin [a,*], Alexandra D. Syphard [a], David J. Mladenoff [b], Hong S. He [c], Dena K. Simons [a], Ross P. Martin [a], Douglas Deutschman [d], John F. O'Leary [a]

[a] Department of Geography, San Diego State University, San Diego, CA 92182-4493 USA

[b] Department of Forest Ecology and Management, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706 USA

[c] School of Natural Resources, University of Missouri-Columbia, 203M ABNR Building, Columbia, MO 65211 USA

[d] Department of Biology, San Diego State University, San Diego, CA 92182-4614, USA

Received 4 April 2000; received in revised form 12 December 2000; accepted 14 March 2001

Abstract

A spatially explicit landscape model of disturbance and vegetation succession, LANDIS, was used to examine the effect of fire regime on landscape patterns of functional group dominance in the shrublands and forests of the southern California foothills and mountains. Three model treatments, frequent (35 year), moderate (70 year), and infrequent (1050 year) fire cycles, were applied to the landscape for 500 year. The model was calibrated and tested using a dataset representing an initial random distribution of six plant functional groups on an even-aged landscape. Calibration of the three fire regime treatments resulted in simulation of fire cycles within 7% of these intended values when fire cycles were averaged across ten replicated model runs per treatment. Within individual 500-year model runs, the error in the simulated fire cycle (average area burned per decade) reached 11% for the moderate and frequent fire cycle treatments and 53% for infrequent. The infrequent fire regime resulted in an old landscape dominated by the three most shade tolerant and long-lived functional groups, while shorter-lived and less shade tolerant seeders and resprouters disappeared from the landscape. The moderate fire regime, similar to what is considered the current fire regime in the southern California foothills, resulted in a younger landscape where the facultative resprouter persisted along with the long-lived shade tolerant functional groups, but the obligate seeder with low fire tolerance disappeared, despite its moderate shade tolerance. The frequent fire regime resulted in the persistence of all functional groups on the landscape with more even cover, but the same rank order as under the moderate regime. The model, originally developed for northern temperate forests, appears to be useful for simulating the disturbance regime in this fire-prone Mediterranean-type ecosystem.

Keywords: Chaparral; Disturbance; Fire; Mediterranean-type ecosystem; Succession; Spatially explicit landscape model

* Corresponding author. fax: + 1-619-594-4938.
E-mail address: janet.franklin@sdsu.edu (J. Franklin).

PII: S0304-3800(01)00286-1

1. Introduction

Climate, land use, and resource management affect the disturbance regimes that shape ecosystem structure and function (Torn and Fried, 1992; Westman and Malanson, 1992; Baker, 1995; Davis and Michaelsen, 1995; Malanson and O'Leary, 1995; Suffling, 1995; Gardner et al., 1996; Larsen, 1997; Flannigan et al., 1998). A disturbance regime such as fire or flooding is characterized by frequency, size, seasonal timing and intensity (Godron and Forman, 1983; Pickett and White, 1985; Pickett et al., 1989; Johnson and Gutsell, 1994). While much of the literature on environmental change focuses on future (anthropogenic) climate and land use change (Meyer and Turner, 1994; Houghton, 1997), the fire regimes in the world's Mediterranean-type ecosystems have been affected by centuries to millennia of landscape alteration due to intensive and extensive land use, and deliberate use and suppression of fire (Naveh and Dan, 1973; Naveh, 1975; Moreno and Oechel, 1992, 1994, 1995; Pausas, 1999a).

Within the last century the shrub- and forest-dominated Mediterranean-type ecosystems of southern California's foothills and mountains have been subjected to changing patterns and intensities of land use, as well as policies regarding fire suppression and management (Minnich, 1983, 1991a,b; Chou et al., 1993; Minnich et al., 1995; Keeley et al., 1999). For almost a century a land management policy of fire suppression has been in effect throughout most of the region (Minnich, 1983; Keeley et al., 1999). Conversion of shrubland and forest to agricultural and urban land use alters the flammability of certain parts of the landscape (e.g., converted to non-native grassland for grazing). It also affects the location, frequency, and timing of human-caused ignition (accidental and deliberate) in proximity to densely settled areas (Keeley et al., 1999). These land cover alterations can change vegetation composition via the effect of landscape fragmentation on plant species dispersal and gene flow (Saunders et al., 1991; Soule et al., 1991) and invasion by non-native species (Alberts et al., 1993).

There is controversy in the literature about the 'natural' disturbance regime in the region, and the effect of fire suppression on the fire regime. Zedler (1995b) asserted that because climate, human population, and land use and resource management practices have fluctuated widely over the past 10 000 years, it is doubtful that the fire cycle has been stable for more than a few decades or centuries. Further, Keeley et al. (1989) noted that certain chaparral species, those for whom seedling recruitment is dependent upon fire, are threatened if the time between fires is extremely short (less than the time required for a plant to reach maturity). However, both authors also concluded that the fire interval rarely exceeds the longevity of these 'obligate seeders' (that can survive for a century), and that chaparral communities are resilient to a wide range of fire return intervals (fire cycles).

Minnich and his colleagues (Minnich and Chou, 1997, and references therein) compared chaparral-dominated landscapes in southern California, where fire suppression has been practiced since ca. 1900, to northern Baja California, Mexico, where suppression has been very limited. Their results suggested that the chaparral fire cycle (the time required to burn an area equivalent to the area under consideration) is similar ($\sim$70 year) in both regions because fire in chaparral is fuel limited (there is an age-dependent combustion threshold). They concluded that fire suppression in southern California has reduced fire frequency and increased fire size, restricting fires to extreme weather. They also attributed the fine grained patch structure in Baja to the lack of fire suppression there.

Keeley et al. (1999), on the other hand, found no evidence for larger, less frequent fires resulting from suppression during the 20th century in southern California shrublands. Their analysis showed that the average fire size decreased while the number of fires increased (which they attributed to increased anthropogenic ignitions), leading to a shorter return interval (on the order of 30–40 year) in the second half of the century. Nor did they find evidence that fire in shrublands was fuel limited (that younger age classes prevented fire spread), and therefore they concluded that the greatest ecological threat from this increased fire frequency is the replacement of shrublands by nonnative grasslands. Both Minnich's and Keeley's analyses of shrublands were based on relatively short (~ 30–80 year) air photo and fire history records, respectively.

In contrast with the conflicting evidence regarding the effect of fire suppression on shrublands, the story for southern California's montane forests is more straightforward. Research based on dendrochronological reconstructions of fire history, and repeat sampling of historical vegetation plots, indicates that fire suppression in the montane conifer zone of southern California and elsewhere in the western US has caused profound changes in stand structure including increased density of shade tolerant trees in the subcanopy (Savage, 1991; Minnich et al., 1995; Stephenson and Calcarone, 1999; reviewed in Keeley et al., 1999 and Miller and Urban 2000a).

To explore the effects of different disturbance regimes on vegetation patterns over long time spans, models that are capable of explicitly simulating landscape-scale spatial processes over large areas — fire spread and plant dispersal — are effective tools (Mladenoff and Baker, 1999). A previous model of southern California shrubland succession as a function of disturbance regime, climate change, and plant life history traits, did not provide spatial predictions of landscape patterns (Malanson et al., 1992). Recent models of patch dynamics (spatial patterns of landscape age structure) as related to climate and fire regime (Baker et al., 1991; Baker, 1995; Davis and Michaelsen, 1995), as well as Markov models of patch recovery (Turner et al., 1994; Gardner et al., 1996), have not addressed succession or changes in species composition. The FATE model of Moore and Noble (1990), and a first-order Markov model developed by Rego et al. (1993), both simulate multiple pathways of succession as a function of the timing and/or seasonality of stochastic fire disturbances; however, these models are not spatially explicit. A non-spatial gap-type model was developed to examine effects of fire on woody invasions of grasslands in Texas (Fuhlendorf et al., 1996). Another gap model, FM, was recently developed to address forest responses to changes in the fire regime in the southern Sierra Nevada (Miller and Urban, 1999a,b, 2000a,b). FM, derived from the ZELIG model, simulates surface fires, and has certain spatially explicit components.

Detailed models of fire spread (Rothermel, 1972; Albini, 1976) embody physical realism in simulating fire behavior as a function of vegetation characteristics, meteorological conditions, and topography, for discrete fire events (Kessell, 1979; Kessell et al., 1984; Kessell, 1990 and see Wu et al., 1996). However, these models are not usually capable of simulating long-term fire regimes for large areas (Baker et al., 1991; Vasconcelos and Guertin, 1992; Davis and Burrows, 1994). On the other hand, landscape models have been developed that use stochastic approaches to simulate repeated disturbances. The majority of these existing landscape models focus on one landscape process, typically fire, assuming that landscape processes can overwrite fine-scale vegetation dynamics (e.g., Green, 1989; Baker et al., 1991; Gardner et al., 1996). Keane et al. (1997) developed the FIRE-BGC model, linking a gap model of succession to a mechanistic fire behavior model, and simulated ecological and ecosystem processes from the tree to the landscape scale. This model is limited by intensive computation and parameterization (more than a thousand parameters) requirements.

LANDIS (LANdscape DIsturbance and Succession), a spatially explicit model, was designed to represent a heterogeneous forested landscape that is subject to disturbance events (fire, windthrow and timber harvest) and to simulate how these events influence plant succession over decades or centuries (Mladenoff et al., 1996; He and Mladenoff, 1999a,b; He et al., 1999a,b; Mladenoff and He, 1999). LANDIS allows succession to take multiple pathways (Cattelino et al., 1979; Noble and Slatyer, 1980; Vasconcelos and Zeigler, 1993), and is based on the interaction between species life history traits, site conditions, and the disturbance or management regime on the landscape.

The purpose of this research was to use the LANDIS model to study the responses of key dominant plant species in southern California (modeled as functional groups) to different disturbance regimes. We conducted modeling experiments to address the following research questions: (a) Can LANDIS be calibrated to simulate a specified fire regime for this landscape? (b) What does the LANDIS model predict will be the effect of long, medium, and short fire return intervals on the extent and patch structure of the functional groups and age classes on the landscape? (c) Are the predicted patterns reasonable in light of what is known about community dynamics in these systems? LANDIS was developed and tested for forests with longer fire return intervals (He and Mladenoff, 1999a,b). Although the model effectively simulated these other forested ecosystems (Gustafson et al., 2000; Shifley et al., 2000), we wanted to test its ability to simulate fire regimes characteristic of the southern California landscape. If LANDIS can produce logical predictions using a highly simplified dataset, it gives us the confidence to use it to explore alternative disturbance regimes with data representing more realistic landscape patterns of species composition and site conditions.

2. The LANDIS model

The LANDIS model has been extensively described elsewhere (He and Mladenoff, 1999a,b; He et al., 1999a,b; Mladenoff and He, 1999), and will only be outlined briefly here. LANDIS implements a spatially explicit raster-based simulation of the stochastically driven interactions between plant life-history behaviors, site conditions, and disturbance regimes. The vegetated landscape is characterized by a map that contains (for each grid cell) presence and absence information for individual species (or functional groups) in 10-year age cohorts. Multiple species and age cohorts can be present within a cell. Environmental conditions associated with these species, i.e., conditions that facilitate the establishment, growth, and relative dominance of a species, are approximated by a landtype map. For each landtype, establishment probabilities are assigned to each species, indicating the potential for a species' successful establishment on that landtype (cf. Roberts, 1996). Establishment probabilities should reflect what is known about the environmental factors affecting potential establishment and growth — the species' response function or fundamental niche. Each landtype is also characterized by a mean fire-return interval, and a pattern of fuel accumulation and decomposition (potential fire severity) over time, where fire severity is approximated by an ordinal variable (1–5).

When exposed to different fire return intervals a plant community may demonstrate different seral stages. This process, referred to as 'multiple pathways of succession,' results from differing species' life-history attributes (Cattelino et al., 1979; Noble and Slatyer, 1980; Moore and Noble, 1990; Noble and Gitay, 1996; Pausas, 1999a,b). Because LANDIS utilizes life-history information, the model can simulate the effects of different fire regimes on succession. Each species in the model is associated with life history parameters including longevity, age of first reproduction, potential seed dispersal distance, ability to resprout, shade tolerance, and tolerance of fires of varying severity (the last two are ordinal variables ranging from 1–5).

In LANDIS, the probability of fire ignition occurring in a grid cell is spatially stochastic, but increases with the time since the last fire at a rate determined by the fire-return interval for each landtype. Fire size is also stochastic, but related to a specified mean and log-normal distribution function with small fires occurring more frequently than large fires. Successional dynamics are simulated by growth, death, dispersal, establishment, and competition of species in burned and unburned cells in each time step. Fire is treated as a 'bottom up' process. In other words, when an ignition occurs, or fire spreads from another cell, the fire severity is determined by the time since the last fire. Fire-induced mortality depends upon the age-dependent fire tolerance of the species (e.g. a fire of severity class 2 will kill all but the oldest cohort of a species of fire tolerance 2).

Dispersal of any species to any cell in each time step can occur if there is a source of propagules within the dispersal distance for that species. Species establishment occurs as a function of the probability of establishment on the landtype as well as the shade tolerance of the potentially establishing species relative to the age-dependent shade tolerance of the species already present in a cell. For example, a species of shade tolerance 2 might establish on a landtype for which it has a high probability of establishment if there is a species of shade tolerance 3 already on the site but only in very young age classes. All of these processes (ignition, fire spread, dispersal, establishment, mortality) are stochastic. Thus, LANDIS simulates dispersal and succession, even in the absence of disturbance, and it simulates differential mortality of species age cohorts as a function of fire severity and the time between fires.

In its temporal and spatial capacity, LANDIS is semi-explicit because it uses discrete time units of 10 years per iteration to record the occurrence of fire and the age of the species cohorts in each grid cell. Therefore, neither the age of individual plants nor the occurrence of single fires is simulated by the model. Rather, groups of individual fires (collectively referred to as a 'fire entity') can occur in a time step, and species are treated as present or absent in age cohorts within grid cells. These cohorts subsequently age by decades as the simulation progresses (growth is not simulated explicitly in terms of biomass accumulation or relative dominance). This approach reduces the complexity of the data needed to run the model and subsequently allows broad-scale, long-term simulations over hundreds of years and millions of hectares (He and Mladenoff, 1999a) while maintaining attention to certain aspects of fine grain detail.

3. Materials and methods

There are multiple dominant plant species in southern California's fire-prone vegetation types (Barbour and Major, 1990; Gordon and White, 1994; Davis et al., 1995; Stephenson and Calcarone, 1999). Post-fire succession in these shrub and forest communities is strongly tied to the life history traits parameterized in LANDIS (Zedler, 1981, 1995a,b; Keeley, 1986, 1991a, 1995; Keeley and Keeley, 1984; Keeley et al., 1989; Thorne, 1990; Zedler and Zammit, 1989; and references therein). Because the effect of any fire-regime upon a given community is strongly tied to the varying life-history responses of the species found there, it has been proposed that most if not all species should be considered in simulating the community's dynamics (Zedler, 1995a). However, it is the goal of modeling to incorporate only the essential detail required to reproduce observed patterns in an ecological system, and not to attempt to capture all of the details of the system (Levin, 1992). Therefore, in this study, a limited number of functional groups (representing the dominant life-history behaviors of the plant species in the study area) were modeled rather than species (see also Pausas, 1999a,b). We developed a dataset with key characteristics of plant communities in the southern California foothills and mountains. This dataset enabled us to define plant functional groups, their life history attributes, and alternative fire regime scenarios.

3.1. Functional groups and their attributes

A list of dominant species in the foothill and montane plant communities of the Peninsular Ranges in California was derived from quantitative community descriptions (Gordon and White, 1994). A literature review of the life-history traits of these dominant species allowed a profile of the most common life-history strategies to be matched with the functional group classification of Noble and Slatyer (1980). Functional groups were established by determining four 'vital attributes' (from Noble and Slatyer, 1980; Noble and Gitay, 1996):

1. The method of arrival or persistence of propagules at the site following a disturbance.
2. The conditions needed to establish and grow to maturity.
3. The time required to reach critical life history stages.
4. The size, growth rate, and mortality of the species.

Because Noble and Slatyer (1980) consider the first two attributes to be fundamental to describing the successional role of species, we used these to define our functional groups (see Table 1). The third and fourth attributes were then defined as parameters of those functional groups (Table 2).

Table 1
Functional Groups life history strategies and disturbance response of dominant species in the southern California mountains and foothills, classified by the first two vital attributes of Noble and Gitay (1996): method of persistence and conditions for establishment

	Methods of persistence				
Conditions for Establishment	W (Withstands disturbance if mature)	V (Vegetative resprouting)	S (Persistent Seed Pool)	C (Short-lived seed pool)	D (Dispersers, propagules available all sites)
I (Shade-intolerant, can only establish after disturbance)				Obligate Seeder A: *Ceanothus greggii* (Keeley, 1977, 1986; Lariguaderie et al., 1990; Bullock, 1991; Zammit and Zedler, 1992; Zedler, 1995b); *Arctostaphylous glauca* (Keeley, 1977; Fulton and Carpenter, 1979; Zedler et al., 1983)	Pioneer: *Lotus scoparius* (Hanes, 1971; Haidinger and Keeley, 1993; Keeley, 1995); *Artemisia californica* (Hanes, 1971; Zedler, 1981, 1982; Zedler et al., 1983; Malanson and Westman, 1985; Keeley, 1995)
T (Can establish after disturbance and as canopy closes)	Fire Tolerant: *Pinus jeffreyi* (Minnich, 1988, 1991a,b; Vander Wall, 1993); *Quercus agrifolia* (Keeley, 1977; Calloway and Davis, 1993)	Facultative Resprouter: *Adenostoma fasciculatum* (Barro and Conard, 1991; Hanes, 1971; Hilbert and Larigaurderie, 1990; Keeley, 1981, 1986, 1991a, 1995; Keeley et al., 1989; Parker and Kelly, 1989; Zedler et al., 1983; Zedler, 1995b)		Obligate Seeder B: *Adenostoma fasciculatum* (seeding subpopulation)	
R (Requires a canopy to establish, shade-tolerant, late successional)		Obligate Resprouter: *Quercus berberidifolia* (Hanes, 1971; Keeley, 1981, 1986, 1991a; Zedler, 1995b)			

Table 2
Species life history attributes used in LANDIS, and values of these parameters used for each Functional Group (see Table 1)

Parameter (units)	Functional Groups					
	Pioneer	Obligate SeederA	Obligate SeederB	Facultative Resprouter	Fire Tolerant	Obligate Resprouter
Longevity (year)	10	60	90	90	300	120
Age of maturity (year)	1	20	10	20	50	30
Shade tolerance[a]	1	2	3	3	4	5
Fire tolerance[a]	1	3	2	2	5	4
Effective seed dispersal distance (m)	−1[b]	50	100	50	100	500
Maximum seed dispersal distance (m)	−1[b]	100	200	100	750	1000
Probability of vegetative propagation (0–1)	0	0	0	1	0	1
Minimum age of resprouting (year)	0	0	0	1	0	1
Reclass coefficient[c] (0–1)	0.25	0.50	0.50	0.5	1.0	0.75

[a] Parameter is represented by ordinal classes 1–5.
[b] Dispersal distances of '−1' in LANDIS mean that propagules are available at all locations at any time.
[c] Reclass Coefficient (relative dominance of mature plant) is only used if output maps of species assemblages are produced.

Although Noble and Gitay (1996) recognize several basic methods of persistence, only the following were used to define a set of functional groups for our simulated area (Table 1):

- **W**: The mature form of the species withstands disturbance (e.g., thick-barked adults but vulnerable juveniles).
- **V**: Juvenile or mature individuals survive the disturbance but revert to a juvenile state (vegetative resprouting).
- **S**: Persistence by seeds with long viability stored in the soil.
- **C**: Juveniles are only produced if adult was present on site before disturbance. Seeds with short viability often survive the disturbance within protective fruits or cones, stored in the canopy or soil.
- **D**: Species with sufficient dispersal distances that propagules are always available at all sites.

The following categories describe conditions required for establishment:

- **I**: Shade-intolerant, early-successional species, able to establish only immediately after a disturbance when competition is reduced.
- **T**: Shade-tolerant, mid-successional species, able to establish at any time, immediately after disturbance but also as the canopy closes.
- **R**: Shade-requiring, late-successional species, usually unable to establish immediately after a disturbance, but able to become established once individuals of either the same species or another species have established.

Based on the predominant post-disturbance recovery strategies of dominant species in the Peninsular Ranges, the following functional groups were defined for the simulations: Fire Tolerant (WT), Facultative Resprouter (VT), late-successional Obligate Resprouter (VR), early-successional Obligate Seeder A (CI), mid-successional Obligate Seeder B, and Pioneer (DI) (Table 1). A dataset was then developed with these functional groups occurring in the map and parameter inputs to LANDIS. The life history parameters for each functional group are encoded in LANDIS' species attribute file (Table 2). These attributes were derived from the literature (Table 1). In some cases precise values for some of these attributes have been published (e.g. Keeley, 1981). In other cases only generalized or qualitative estimates were available in the literature. Therefore, descriptions of these attributes were composited for several species (Table 1) in order to parameterize the functional groups (Table 2).

Because functional groups represent combined behaviors of several species, the generalized attributes for these groups may not precisely fit a particular species (Table 1). For example, in the Pioneer functional group, *Lotus scoparius* is actually not widely dispersed but rather has a long-lived seed bank with fire-stimulated germination, and therefore may be better described as an S or G species in Noble's framework. On the other hand, *Artemesia californica* has widely dispersed seeds and is shade-intolerant, although it is not usually thought of as a 'Pioneer' species within its plant community. However, the dynamics of more typical Pioneers such as fire-following native ephemerals and non-native 'weedy' or 'invasive' annuals are not easy to capture with LANDIS' current temporal resolution (10 year). In the Fire Tolerant functional group, *Pinus jeffreyi* is not 'shade tolerant' per se, but is probably accurately captured by Noble's establishment type T, because it can establish after disturbance and also as the canopy closes. Furthermore, LANDIS is not yet able to truly simulate some of the methods of persistence found in the study region, such as fire-stimulated germination from a long- or short-lived seed pool. Therefore, Obligate Seeders A and B must establish from seeds dispersed from other cells following fire, and the performance of these functional groups in response to fire will be underestimated. Also note that we characterized the widespread and dominant *Adenostoma fasciculatum* as two separate functional groups (pseudo-species) representing geographically distinct subpopulations that predominantly regenerate either by seeding or by sprouting (Keeley and Soderstrom, 1986).

A 250×250 cell map (where a cell represents a 50×50 m area — 62 500 cells or 15 625 ha) was generated with an initial random distribution of four map classes containing one- to two-species assemblages of the functional groups (Fig. 1, Table 3). The age distribution of the landscape was initially set uniformly to 10 year (Fig. 1).

3.2. Landtypes and their attributes

Four landtypes were defined in order to capture the elevation- and terrain-related gradients of temperature and available moisture occurring in the study area. A map representing the spatial distribution of the landtypes was created by dividing the map area into four equally-sized rectilinear sections (Fig. 1) representing the north–south trending elevational zones of the Peninsular Ranges, e.g., the low elevation (warm, xeric) coastal sage scrub zone, mid-elevation xeric (south facing slopes) dominated by mixed chaparral, mid-elevation mesic (north facing slopes) characterized by scrub oak chaparral, and the high elevation (cool, mesic) conifer forest zone (Table 3a). This map was overlaid with the species and age maps, so that the spatial input to LANDIS contained information on species presence by age cohort, time since last fire, and landtype class, for every cell (site).

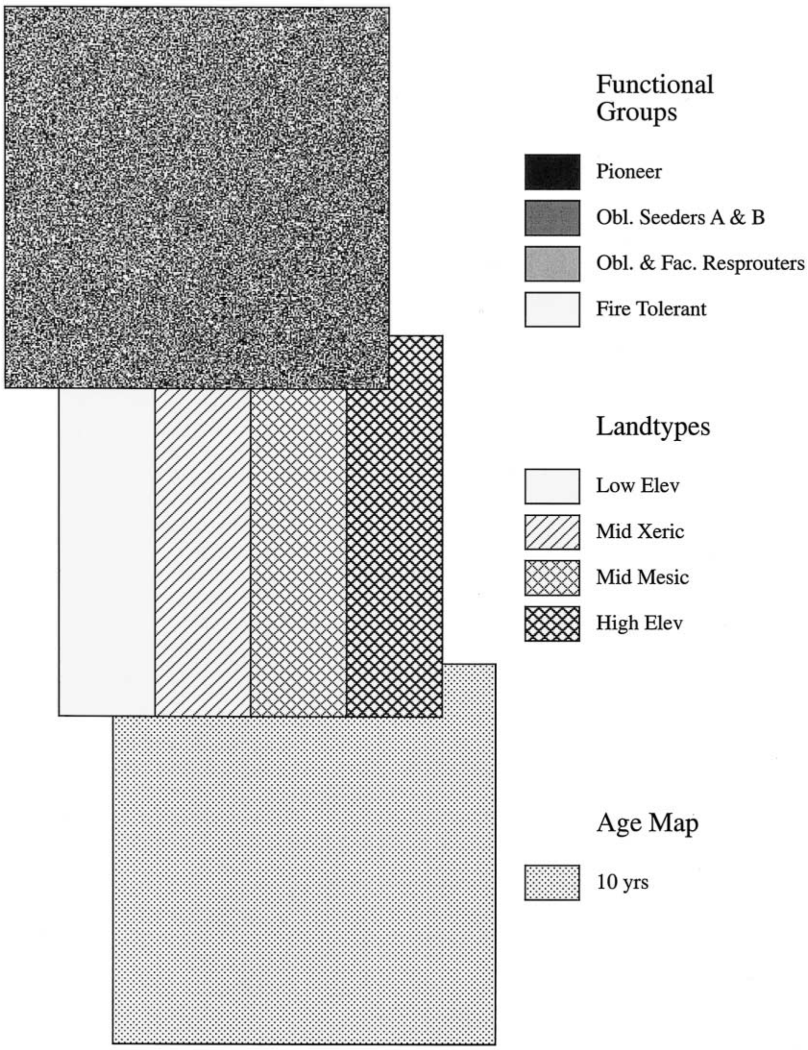

Fig. 1. Landscape used in LANDIS simulations: initial random distribution of four map classes containing functional groups, regular distribution of landtypes and uniform age distribution.

Table 3
(a) Functional group probability of establishment by landtype, and initial assignment of functional groups into four map classes (see Fig. 1); (b) Fire severity curves (year fire severity class is reached)

(a)

Landtypes	Functional groups					
	Pioneer	Obligate SeederA	Obligate SeederB	Facultative Resprouter	Fire Tolerant	Obligate Resprouter
Low elevation	1.0	0.5	0.2	0.1	0.2	0.001
Mid xeric	0.7	1.0	0.5	0.3	0.3	0.01
Mid mesic	0.3	0.5	0.3	0.5	0.7	0.01
High elevation	0.2	0.2	0.1	0.2	1.0	0.01
Functional group map class	1	2	2	3	4	3

(b)

Landtypes	Fire severity class				
	1	2	3	4	5
Low elevation	0	–	10	20	30
Mid xeric	20	30	50	80	130
Mid mesic	20	30	50	80	130
High elevation	30	50	80	130	210

The probability of establishment of each functional group on each landtype represents the functional groups' ability to establish and grow under different site conditions. A species' fundamental niche would be expected to be broader than the realized niche (based on observed distributions), with probabilities of establishment remaining high on sites more favorable for establishment and growth than the empirically observed 'optimum.' In a gap model of shrub communities in this region, the fundamental niche was modeled by assuming that precipitation greater than the optimum value would result in growth rates equal to those at the optimum value, although no such assumption was made for temperature (Malanson et al., 1992). He et al. (1999b), using a forest gap model, showed that species growth rates vary across landtypes, and they are not highest on a single landtype for all species.

In our simulated area, while we might expect landtypes with high potential soil moisture and mild temperatures to be most suitable for all species, temperature and precipitation gradients are confounded, and temperature is related to both water stress and optimum temperatures for growth. Although precipitation increases with elevation on the landtypes, species that find optimum conditions for growth and establishment on the low elevation landtype would be limited by minimum temperatures at high elevation. For these reasons we parameterized the species establishment probabilities with values interpreted from the literature (Table 3). The establishment probabilities remained constant under all fire-regime treatments. Because the map was initialized with a random distribution of functional groups, we deliberately gave at least one functional group a high affinity for each landtype to see how the model simulated the effect of dispersal and establishment. We parameterized the Obligate Resprouter as having a large dispersal distance (Table 2), but extremely low probability of establishment from seed on any landtype (Table 3a), approximating the persistence method of *Quercus berberidifolia*.

The fire severity curves, representing the temporal accumulation of fuel, are also controlled by the landtype. Landtype fire severity classes are shown in Table 3b. Xeric landtypes with slower decomposition rates accumulate fuel more rapidly than mesic sites (He and Mladenoff, 1999a).

3.3. Calibration and modeling experiment

In LANDIS, a fire regime is specified by the mean return interval. The mean return interval is the time required to completely burn an area equivalent to a landtype and can be calculated from the average area burned per time interval (Johnson, 1992; Li et al., 1997). Calibration is carried out by comparing the observed average area burned, as well as the return interval for a model run to specified values for those parameters. Therefore, to reduce the fire cycle error, fire coefficients were systematically adjusted until observed approximated specified fire cycle. The burn area coefficient, (a), is a scalar that relates the simulated burn area to the specified value, where disturbance sizes follow a lognormal distribution. The fire probability coefficient, (b), scales the probability of ignition to the specified return interval (He and Mladenoff, 1999a). Because the modeling experiment consisted of three treatments (fire cycles), each had to be calibrated separately. Initially, default values of the fire regime parameters were used ($a = 50$, $b = 100$). For each treatment first b, and then a, were systematically varied, and the average area burned and return interval were calculated, until no further improvements in the calibration were observed (10–20 calibration runs per treatment). Final values of these parameters were then used in the replicate runs. Once each treatment was calibrated (using a fixed random number seed), ten replicated 500-year simulations (with varying random number seeds) were performed for each treatment to examine the variability of model predictions.

The three simulated fire-regimes (Table 4) were labeled Infrequent, Moderate and Frequent return intervals. The Moderate and Frequent treatments (Table 4) correspond roughly to estimated historical fire regimes reviewed Section 1, a 70-year return interval (Minnich and Chou, 1997), and a 35-year return interval (Keeley et al., 1999) averaged across landtypes. A return interval of 100 and 50 year, respectively (Table 5), was specified in these two treatments for the High-Elevation landtype, dominated by the Fire Tolerant functional group. These values are less frequent than values of 15–50 year given in the literature for conifer forests in southern California, northern Baja California, and the southern Sierra Nevada prior to fire suppression (Minnich et al., 1995). In fact, because fire suppression has been so effective in the conifer zone, it is estimated for the San Bernardino Mountains that the fire regime of the last 70 years would correspond to a 700 year return interval (Minnich et al., 1995). Therefore,

Table 4
Calibration of fire cycle treatments[a]

	Fire regime treatment		
	Infrequent	Moderate	Frequent
Expected area burned per decade, ha (%)	156 (1%)	2188 (14%)	4688 (30%)
Mean observed area burned per decade, ha (%)[b]	160 (1%)	2133 (14%)	4778 (31%)
S.D.	369 (2%)	1210 (12%)	1625 (10%)
S.E.	17 (0%)	86 (1%)	73 (0%)
Error	+3%	−3%	+2%
Range of error (ten replicates)	−32% to +53%	−11% to +9%	−7% to +6%
Expected return interval (year)	1050	70	35
Mean observed return interval	975	73	33
Error[c]	−7%	+5%	−7%

[a] The simulated area consisted of 250 × 250 (62 500) 50 × 50 m (0.25 ha) cells (15 625 ha).
[b] Mean area burned and return interval is calculated from 50 time steps (500 years) × 10 iterations (replicates).
[c] Error, expressed as percent, is [(Observed − Expected)/Expected] * 100.

Table 5
Simulated mean fire return intervals for landtypes[a]

Fire Regime	Landtype	Expected	Mean observed	Range
Infrequent	Low elevation	600	536	388–823
	Mid xeric	900	806	512–1443
	Mid mesic	1200	1388	738–4264
	High elevation	1500	3622	1812–8768
Moderate	Low elevation	40	32	27–35
	Mid xeric	60	97	89–108
	Mid mesic	80	120	112–131
	High elevation	100	227	185–261
Frequent	Low elevation	20	12	11–14
	Mid xeric	30	49	47–49
	Mid mesic	40	79	76–85
	High elevation	50	175	168–183

[a] Mean and range are based on ten replicate model runs.

the Infrequent regime was included to represent this extreme condition of very effective fire suppression (a 1050 year return interval averaged across the landscape).

Analyses comparing the effect of the three fire regimes focused on the spatial location and extent of the functional groups over time. Trends in the age structure of the study area were examined to determine whether the three fire-regime treatments created a landscape of predominantly old, young, or mixed-aged patches. Patterns of cover and age structure over time were analyzed with the APACK (Analysis PACKage) software (Mladenoff and DeZonia, 1999; ftp://flel.forest.wisc.edu/APACK/VERSION213/). Developed to analyze the spatial output of the LANDIS model and other maps, APACK examines the model's ERDAS 7.4 GIS output files for each time step and can calculate many landscape indices and metrics.

4. Results

4.1. Calibration

Error in the simulated area burned was +3 to −3%, and in return interval was +5 to −7%, for the three treatments (averaged for 50 time steps and ten replicate runs; Table 4). The distribution of burned area per decade is shown (Fig. 2) for the replicate runs with the fire return interval closest to the specified value (averaging burned area by decade over the ten replicates would have been meaningless).

Despite this good overall fit between specified and simulated fire cycle, the distribution of return intervals across landtypes was often quite different than expected (Table 5). For each treatment, the return interval increased across the four landtypes, as specified, but the return interval on the low elevation landtype was always shorter than specified, while it was longer than expected on the mid-elevation mesic and high elevation landtypes. The range of average return intervals across the replicate model runs showed that the variability was quite high for Infrequent (not surprising for a 500-year run and a 1050-year return interval) and low for Frequent. Infrequent fire events generally have greater variability than frequent events (He and Mladenoff, 1999a). It was anticipated that the model would simulate the unnatural fire regime (Johnson, 1992) of a small average area burned and a long fire-cycle (Infrequent) with high variability. Despite the high variability, under the Infrequent treatment LANDIS effectively emulated conditions where fire is very infrequent relative to the other treatments.

4.2. Effect of fire regimes on the distribution of functional groups on the landscape

To examine the effect of different fire regimes on the trajectory of the functional groups, the proportion of the study area occupied by each functional group in each time step was summarized in output maps for each functional group (Fig. 3). Table 6 summarizes the average proportion the landscape occupied by each functional group for years 110–500, after cover dynamics had stabilized (Fig. 3). Fig. 4–6 show maps of functional group presence/absence in year 500 for each treatment.

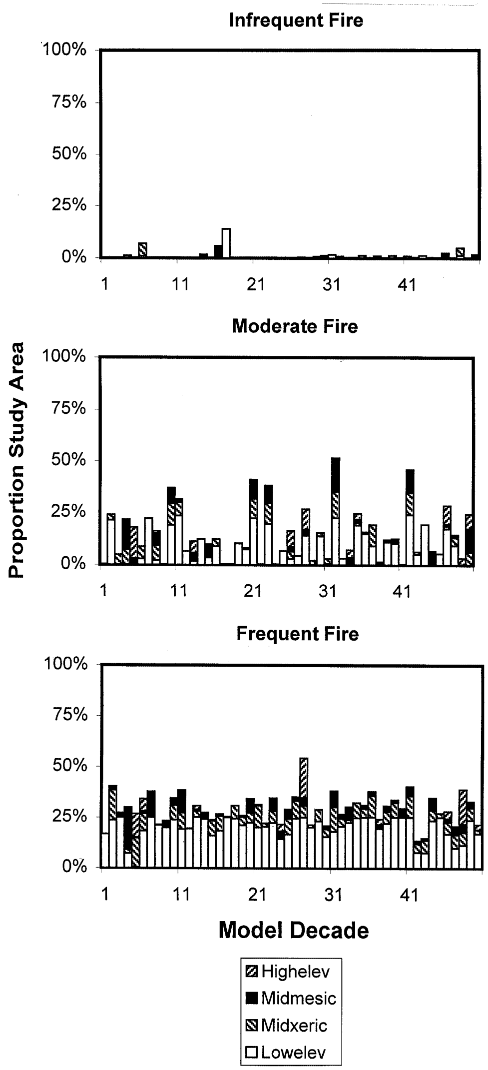

Fig. 2. Relative (%) area of landscape burned per time step (decade) for three fire regime treatments: Infrequent, Moderate, and Frequent (shown for the best-calibrated single model run).

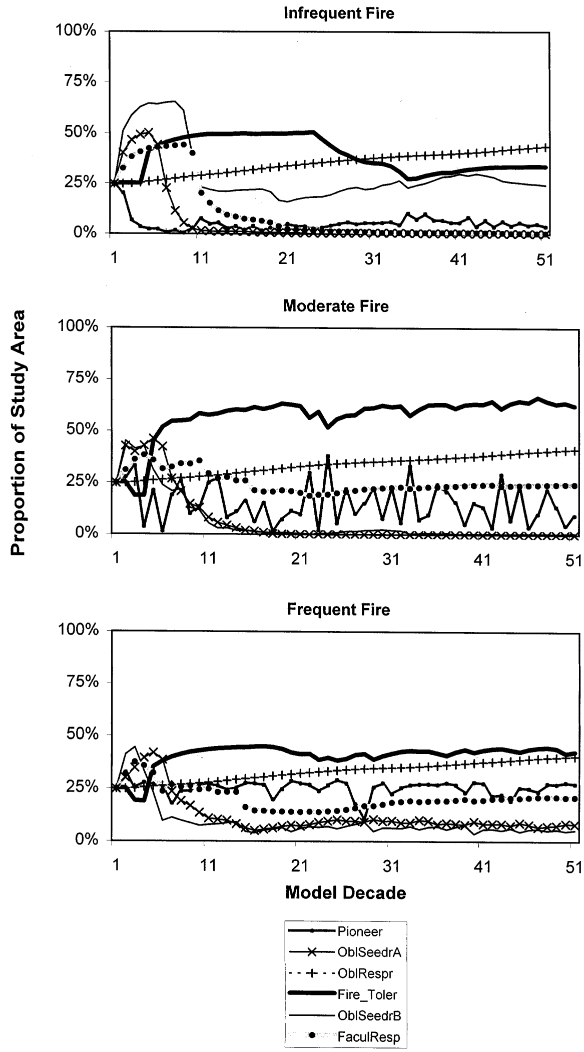

Fig. 3. Relative (%) area of landscape covered by each functional group (Table 1) per time step (decade) for three fire regime treatments: Infrequent, Moderate, and Frequent (shown for the best-calibrated single model run).

Under the Infrequent fire regime, the landscape experienced few fire events (Fig. 2). The functional groups demonstrated seral stages of landscape dominance in the first 100 years (Fig. 3).

Obligate Seeder B (early-maturing, a good disperser) covered the greatest extent of the landscape until the initial cohort began to senesce (longevity is 60), and then, on average, covered 23% of the landscape (Table 6). After several hundred years it was located on the landtypes for which it has the greatest establishment probabilities (especially mid-elevation xeric), where patterns of seeding into burned patches from the initial random distribution can be seen (Fig. 4). The extent of the Pioneer functional group closely tracked the area burned in all treatments, and therefore was low and variable in this regime (Table 6), and it was found on the low elevation landtype (Fig. 4) that experienced the most fire (Table 5). The Obligate Seeder A and Facultative Resprouter declined rapidly as they reached the age of senescence in this landscape without fire (Fig. 3). These two functional groups declined to very low levels and did not recover (Table 6) because of their low shade tolerance, longevity, and dispersal ability, relative to Obligate Seeder B. The Fire Tolerant (WT) functional group expanded after it reached maturity (because it is long-lived and shade tolerant). By the end of the simulation the WT group was found preferentially on the mid-elevation mesic and high elevation landtypes (highest establishment probabilities), both dispersing out from its initial random pattern, and in burned patches where it lacked competition from the Obligate Resprouter (Fig. 4). The Obligate Resprouter expanded steadily through the simulation (Fig. 3), because it was parameterized to be shade requiring/tolerant. Therefore, it can continually resprout in the cells where it was initially placed, as well as expand its cover slightly (Fig. 4), in spite of its low establishment probability, because of its good dispersal ability and the lack of competition.

Under the Moderate regime, where burned area is higher (Fig. 2), Pioneer flourished for 1–2 decades following a fire (Fig. 3), located wherever a fire had recently occurred, but typically at low elevation (Fig. 5). Obligate Seeders A and B initially expanded in the absence of competition, but declined precipitously after initial cohort senescence, similar to the response under the Infrequent treatment (Fig. 3; Table 6), and for the same reasons (relatively short-lived, low shade-tolerance). Because LANDIS cannot yet simulate fire-cued germination from stored seeds after adults are killed by fire on a site, a strategy commonly found in 'Obligate Seeders' in these shrub communities, these functional groups perform worse than would be expected under this fire regime. The Facultative Resprouter maintained higher cover under the Moderate than the Infrequent Regime (Fig. 3; Table 6), although it occurred on the landtype with the greatest fire frequency, low elevation (Fig. 5), rather than on the other landtypes where it had a higher probability of establishment (Table 3), but is faced with greater competition. The Obligate Resprouter showed much the same pattern as under the Infrequent regime for the reasons outlined in the discussion of that treatment. Fire Tolerant had

Table 6
Extent of map (cover) occupied by each functional group under each fire regime[a]

Functional group	Infrequent			Moderate			Frequent		
	Mean	S.E.	CV	Mean	S.E.	CV	Mean	S.E.	CV
Pioneer	859 (6%)	18	41%	2264 (14%)	69	61%	3900 (25%)	34	17%
Obligate SeederA	88 (1%)	3	68%	113 (1%)	16	280%	1319 (8%)	12	18%
Obligate SeederB	3618 (23%)	29	16%	224 (1%)	11	95%	844 (5%)	12	29%
Facultative Resprouter	440 (3%)	26	116%	3433 (22%)	16	9%	3135 (20%)	24	15%
Fire Tolerant	6101 (39%)	63	21%	9546 (61%)	27	6%	6516 (42%)	17	5%
Obligate Resprouter	5797 (37%)	31	11%	5567 (36%)	28	10%	5453 (35%)	26	10%

[a] Mean in ha (and percent of map area), Standard Error (s.e.) and Coefficient of Variation (CV, standard deviation/mean, percent) for 40 time steps (starting at year 110) $\times$ 10 replicates.

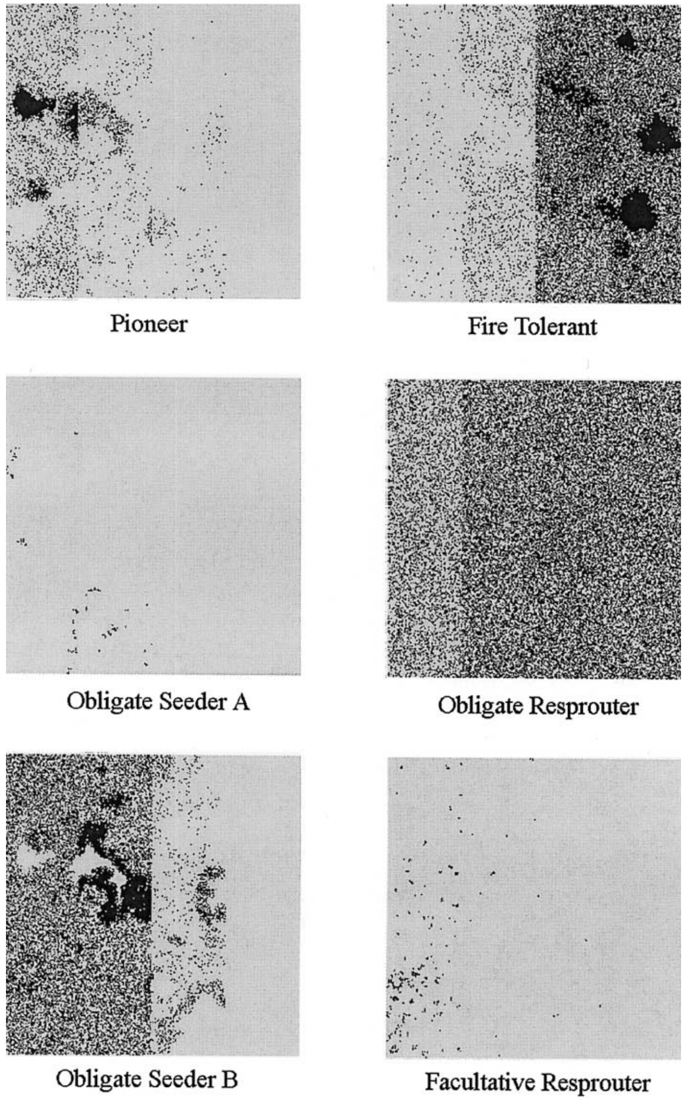

Fig. 4. Map of each functional group at model year 500 for Infrequent fire regime (shown for the best-calibrated single model run).

greatest cover under this regime (Table 6) because it is long-lived and shade- and fire-tolerant. It dominated different landtypes proportional to its establishment probabilities (Table 3), and the pattern of dispersal is obvious on landtypes where it experienced little competition under this regime (Fig. 5).

To achieve the return interval specified under the Frequent regime, large areas of the landscape burned in each time step (Fig. 2). The Pioneer group completely covered the low elevation landtype (Fig. 6) which burned completely in almost every time step (Fig. 2). As a result, it had low temporal variability in cover (CV; Table 6). This Frequent fire regime allowed Obligate Seeders A and B to persist, although at low cover (Table 6; Fig. 3), on the mid-elevation xeric land type (Fig. 6) where they had the highest establishment probabilities (Table 3). The Facultative Resprouter had about the same average cover under this regime as under Moderate (Table 6; Fig. 3), although it was distributed differently (Fig. 6). It was found on the two landtypes with most frequent disturbance, low elevation and mid-elevation xeric, rather than only on the low elevation landtype (as under the Moderate regime), or on the landtype with the highest establishment probability (mid-elevation mesic), where it was usually out-competed. Fire Tolerant had lower cover than under the Moderate regime (Table 6), and was concentrated on mid-elevation mesic and high elevation landtypes (Fig. 6), where it had higher establishment probabilities and experienced less frequent fire. The Obligate Resprouter performed much the same as before, for reasons already discussed.

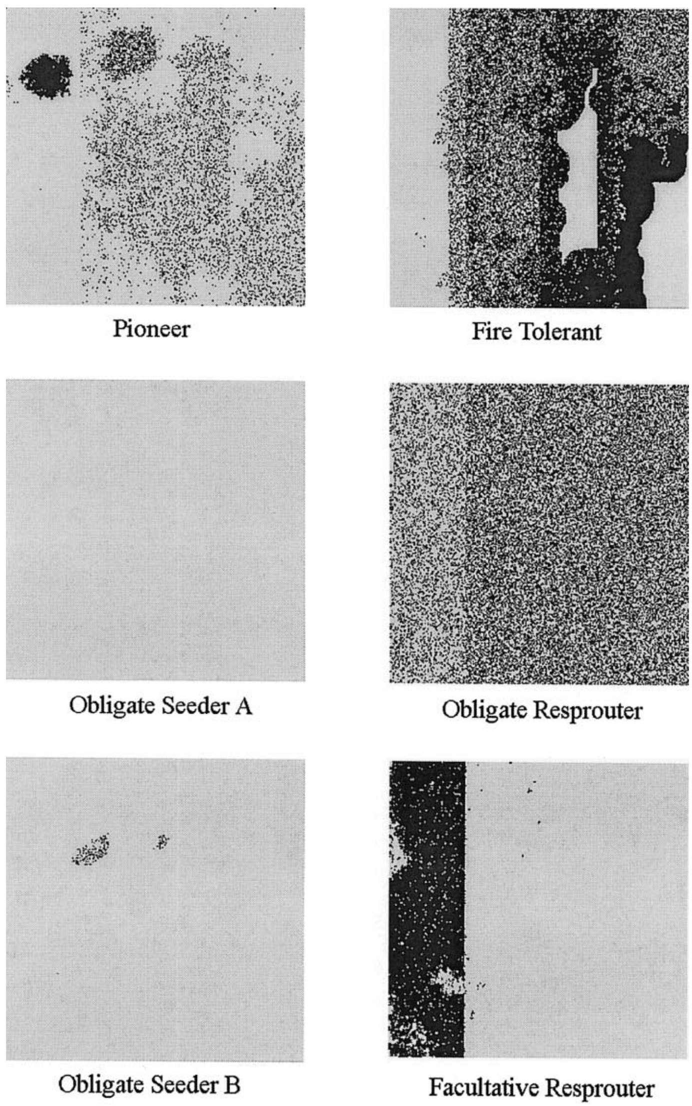

Fig. 5. Map of each functional group at model year 500 for Moderate fire regime (shown for the best-calibrated single model run).

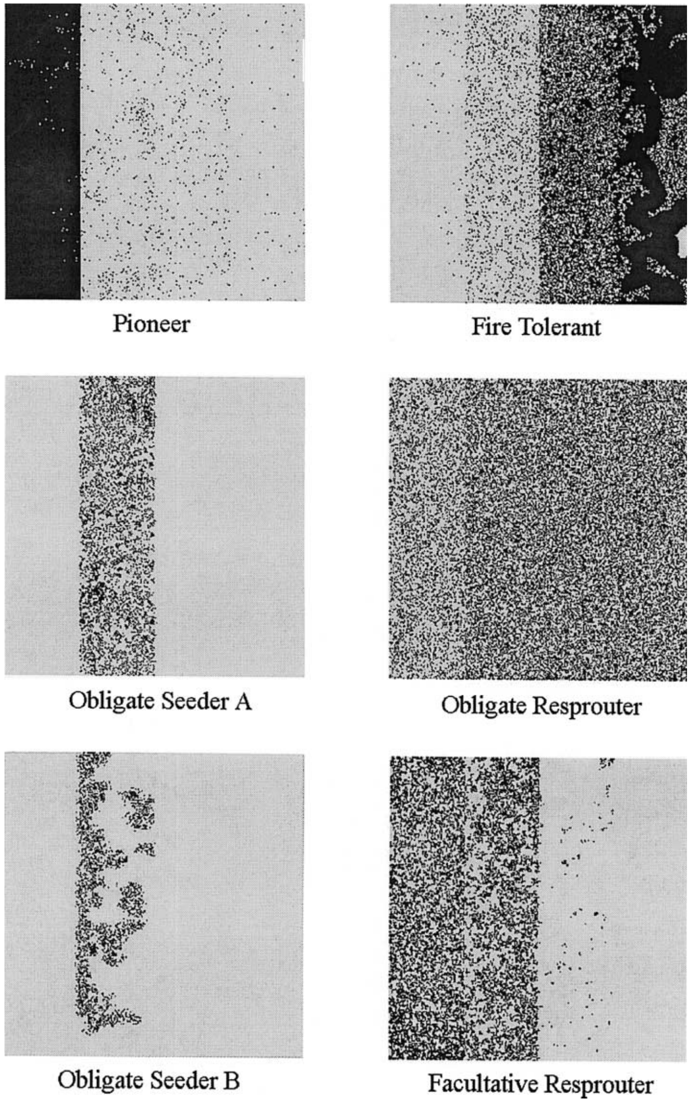

Fig. 6. Map of each functional group at model year 500 for Frequent fire regime (shown for the best-calibrated single model run).

4.3. Age

Because of the infrequent occurrence of high intensity fires, the Small-Infrequent regime permitted the landscape to grow old with a peak in the 91–120 year age class (Fig. 7). The limiting factor controlling maximum age was senescence of the Fire Tolerant group. Moreover, because this long-lived, shade-tolerant functional group continued to recruit once it reached maturity, a temporal gap in succession never occurred after a cohort senesced unlike the other two regimes. Fire regimes with Moderate to Frequent fire-cycles had younger landscapes than the Infrequent regime (Fig. 7). After several hundred years, the Moderate regime tended to produce a landscape where most of the area was 0–180 years old, with a small proportion of the landscape in older age classes (181–300 year). The Frequent regime produced a more skewed landscape age distribution, with most of the landscape in younger age classes (0–120 year) .

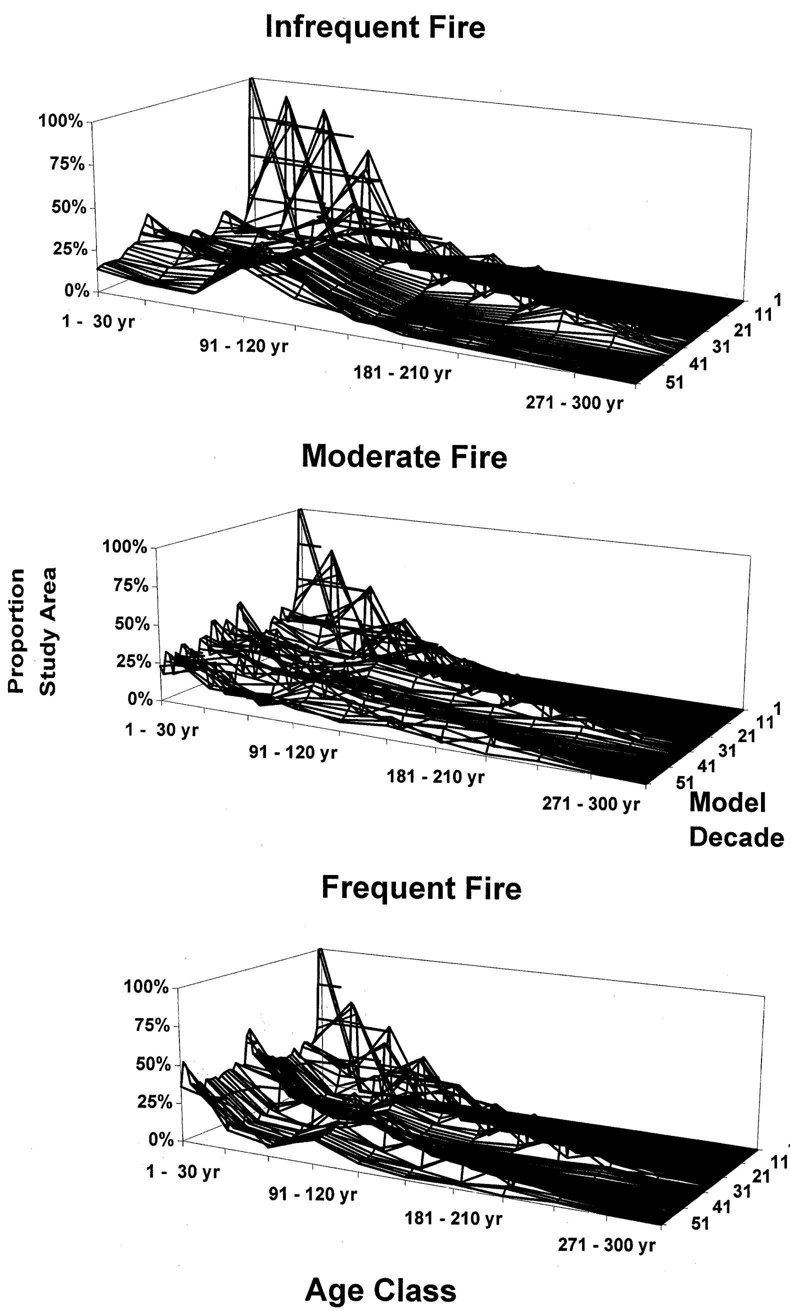

Fig. 7. Age distribution of landscape per time step for three fire regime treatments: Infrequent, Moderate, and Frequent (shown for the best-calibrated single model run).

5. Discussion and conclusion

We were able to calibrate LANDIS to simulate fire cycles within 7% of the specified values. This indicates that the model, developed for forests with longer return intervals, can be applied to the southern California landscape with its shorter fire cycles. Although the fit between observed and expected fire cycle was good when averaged across the entire simulated area the observed return interval was often shorter than specified on the low elevation landtype, and longer than expected on the mid- and high elevation landtypes. This discrepancy occurred because the simulated pattern of fire results from the distribution of stand age and fire severity class, and the availability of fuel (age-dependent fire tolerance of species). Variability in simulated fire cycles was high, as expected, for the Infrequent fire cycles, but low for Frequent because there are a limited number of ways in which the simulated landscape can burn, given the initial conditions, and achieve such a high average proportion of burning for each time step.

Another purpose of the modeling experiment was to determine if the effects of the different fire regime treatments on the plant functional groups were consistent with those described from shorter-term field studies of one or a few species. Under all fire regimes, the dynamics of the Pioneer functional group, parameterized as a short-lived, well dispersed, shade intolerant species, was closely tied to fire events. Its average cover was directly related to fire frequency and the area burned per time step.

In contrast, the Fire Tolerant group was parameterized to be extremely fire-tolerant, long-lived, and able to recruit after disturbance as well as between disturbances. Therefore, under the Infrequent regime, competition and succession controlled the overall landscape pattern of functional group cover, with the Fire Tolerant group dominating after 110 year. After the original Fire Tolerant cohorts began to senesce, this group was outcompeted by the shade-tolerant and vegetatively reproducing Obligate Resprouter on certain landtypes. The Fire Tolerant group also covered a large portion of the landscape under the Moderate and Frequent fire regime, owing to its fire tolerance, competitive ability and longevity.

The Facultative Resprouter was not maintained on the landscape in the absence of fire (Infrequent), but was more successful when Moderate or Frequent fire provided a ‘regeneration niche’ where it could propagate by post-fire resprouting. The three moderately shade tolerant (mid-successional) functional groups, Facultative Resprouter, Obligate Seeder A, and Obligate Seeder B, were maintained with the greatest cover and on the appropriate landtypes under the Frequent fire regime.

The maintenance of all functional groups under the Frequent fire regime is consistent with the literature that suggests a fairly high natural fire frequency and diverse community composition for chaparral. However, previous studies would also suggest that the fire cycle, in the long term, is much more variable than the Frequent regime that was simulated. Further, the results for some functional groups seem inconsistent with other modeling and small-scale studies that found mid-successional species maintained by intermediate disturbance frequencies (e.g., Denslow, 1980; He and Mladenoff, 1999b). The literature for southern California shrub communities also predicts that intermediate fire frequencies will maintain all of the functional groups used in our simulations, while very long ($>>100$ year), or very short ($<<10$ year) return intervals would favor resprouters over obligate seeders (Zedler et al., 1983; Keeley, 1991b).

There are two factors that affect the realism of our modelling results. First, two of these functional groups, the Obligate Seeders, recruit primarily from fire-cued germination from a seed bank following stand-replacing fire (when adults on the site are killed). Because it is not yet possible to simulate this strategy in LANDIS, these functional groups were dependent upon dispersing from cells where adults had survived. Therefore, the performance of these short-lived, poorly dispersing groups under the Moderate and Frequent regimes was underestimated. Second, the initial random placement of the extremely shade-tolerant Obligate Resprouter meant that this group was always maintained by continuous post-fire resprouting in cells where it was initially placed (no matter what the disturbance regime) and also by limited dispersal. Therefore the Obligate Resprouter excluded other functional groups from establishing, to some extent, under all fire regimes.

Simulations were initiated with a random distribution of functional groups (predominantly single- or few-cell patches) in order to see the effects of dispersal and establishment. After 50–100 year larger patches tended to coalesce related to both fire patterns and the dispersal and establishment of functional groups onto landtypes for which they have high establishment probabilities. The exception was the Obligate Resprouter, owing to its low probability of establishment on any landype. The spatial pattern of fires and functional group patches over a model run was strongly related to the pattern of landtypes and landscape age (previous fires). The dataset developed for this simulation, in addition to being simple to interpret, illustrated the degree to which the spatial patterns predicted by the model are controlled by patterns of species and landtype. Initially, with a random distribution of functional groups and uniform age, fires tended to be circular (this can be seen for some functional groups in Fig. 4 and Fig. 5). However, once functional groups dispersed to landtypes for which they had strong affinities, fire boundaries coincided with landtype boundaries, as well as old fire scars (patches of particular ages and fire severity class). This pattern is characteristic of fuel-driven fire cycles (Chou et al., 1993) that can also show spatial patterning (fire shape) related to wind direction and terrain (Minnich and Chou, 1997). However, some studies have suggested that the fire regime is not fuel-driven in this region (Keeley et al., 1999; Zedler and Seiger, 2000).

LANDIS does not simulate individual fire behavior, and it is not clear to what extent this will limit its ability to simulate landscape level patterns of fire and succession in southern California given that fire behavior is strongly tied to topography and weather (Zedler and Seiger, 2000). However, terrain can be used to define landtypes, and the model's fire severity curves can be modified (flattened) to reflect the ability of even young shrub stands to burn in California, given the right conditions. These modifications, as well as simulating fire-stimulated germination from a seed bank, will be the subject of future research, when LANDIS is applied to more realistic landscape patterns in southern California.

Acknowledgements

We are grateful to J. Keeley, R. Minnich, and P. Zedler for their guidance and comments, and to C. Coulter, H. Johnson, J. Miller, D. McKinsey and D. Shaari for their assistance. This work was funded by NSF grant SBR-9818665 to JF.

References

Alberts, A.C., Richman, A.D., Tran, D., Sauvajot, R., McCalvin, C., Bolger, D.T., 1993. Effects of habitat fragmentation of native and exotic plants in southern California coastal sage scrub. In: Keeley, J.E. (Ed.), Interface Between Ecology and Land Development in California. Southern California Academy of Sciences, Los Angeles, pp. 103–110.

Albini F.A. 1976, Estimating wildfire behavior and effects. USDA Forest Service General Technical Report INT-30. Inter-Mountain Forest and Range Experiment Station, Ogden, UT, 92 pp.

Baker, W.L., 1995. Long term response of disturbance landscapes to human intervention and global change. Landsc. Ecol. 10, 143–159.

Baker, W.L., Egbert, S.L., Frazier, G.F., 1991. A spatial model for studying the effects of climatic change on the structure of landscapes subject to large disturbances. Ecol. Modell. 56, 109–125.

Barbour, M.J., Major, J., 1990. In: Barbour, M.J., Major, J. (Eds.), Terrestrial Vegetation of California. California Native Plant Society, Sacramento, CA, p. 1002.

Barro, S.C., Conard, S.G., 1991. Fire effects on California chaparral systems: an overview. Environ. Int. 17, 135–149.

Bullock, S.H., 1991. Herbivory and the demography of the chaparral shrub *Ceanothus greggii* (Rhamnaceae). Madroño 38, 63–72.

Calloway, R.M., Davis, F.W., 1993. Vegetation dynamics, fire, and the physical environment in coastal central California. Ecology 74, 1567–1578.

Cattelino, P.J., Noble, I.R., Slatyer, R.O., Kessell, S.R., 1979. Predicting the multiple pathways of plant succession. Environ. Manage. 3, 41–50.

Chou, Y.H., Minnich, R.A., Dezzani, R.J., 1993. Do fire sizes differ between southern California and Baja California? For. Sci. 39, 835–844.

Davis, F.W., Burrows, D.A., 1994. Spatial simulation of fire regime in Mediterranean-climate landscapes. In: Moreno, J., Oechel, W.C. (Eds.), The Role of Fire in Mediterranean-Type Ecosystems. Springer-Verlag, New York, pp. 117–139.

Davis, F.W., Michaelsen, J., 1995. Sensitivity of fire regime in chaparral ecosystems to global climate change. In: Moreno, J.M., Oechel, W.C. (Eds.), Global Change and Mediterranean-Type Ecosystems. Springer-Verlag, New York, pp. 435–456.

Davis, F.W., Stine, P.A., Stoms, D.M., Borchert, M.I., Hollander, A., 1995. Gap analysis of the actual vegetation of California: 1. The southwestern region. Madroño 42, 40–78.

Denslow, J.S., 1980. Patterns of plant species diversity during succession under different disturbance regimes. Oecologia 46, 18–21.

Flannigan, M.D., Bergeron, Y., Engelmark, O., Wotton, B.M., 1998. Future wildfire in circumboreal forests in relation to global warming. J. Veg. Sci. 9, 469–476.

Fuhlendorf, S.D., Smeins, F.E., Grant, W.E., 1996. Simulation of a fire-sensitive ecological threshold: a case study of Ashe juniper on the Edwards Plateau of Texas, USA. Ecol. Modell. 90, 245–255.

Fulton, R.E., Carpenter, F.L., 1979. Pollination, reproduction, and fire in California *Arctostaphylos*. Oecologia 38, 147–157.

Gardner, R.H., Hargrove, W.W., Turner, M.G., Romme, W.H., 1996. Climate change, disturbances and landscape dynamics. In: Walker, B., Steffen, W. (Eds.), Global Change and Terrestrial Ecosystems. Cambridge University Press, Cambridge, pp. 149–172.

Godron, M., Forman, R.T.T., 1983. Landscape modifications and changing ecological characteristics. In: Mooney, H.A., Godron, M. (Eds.), Disturbance and Ecosystems. Springer-Verlag, New York, pp. 12–27.

Gordon, H., White, T.C., 1994. Ecological Guide to Southern California Chaparral Plant Series. USDA Forest Service, Pacific Southwest Region, San Diego, CA.

Green, D.G., 1989. Simulated effects of fire, dispersal and spatial pattern on competition within forest mosaics. Vegetatio 82, 139–153.

Gustafson, E.J., Shifley, S.R., Mladenoff, M.J., Nimerfro, K.K., He, H.S., 2000. Spatial simulation of forest succession and harvesting using LANDIS. Can. J. For. Res. 30, 32–43.

Haidinger, T.L., Keeley, J.E., 1993. Role of high fire frequency in destruction of mixed chaparral. Madroño 40, 141–147.

Hanes, T.L., 1971. Succession after fire in the chaparral of Southern California. Ecol. Monogr. 41, 27–52.

He, H.S., Mladenoff, D.J., 1999a. The effects of seed dispersal on the simulation of long-term forest landscape change. Ecosystems 2, 308–319.

He, H.S., Mladenoff, D.J., 1999b. Spatially explicit and stochastic simulation of forest-landscape fire disturbance and succession. Ecology 80, 81–90.

He, H.S., Mladenoff, D.J., Boeder, J., 1999a. An object-oriented forest landscape model and its representation of tree species. Ecol. Modell. 119, 1–19.

He, H.S., Mladenoff, D.J., Crow, T.R., 1999b. Linking an ecosystem model and a landscape model to a study of forest species response to climate change. Ecol. Modell. 114, 213–233.

Hilbert, D.W., Larigaurderie, A., 1990. The concept of stand senescence in chaparral and other mediterranean type ecosystems. Acta Oecol. 11, 181–190.

Houghton, J., 1997. In: Global Warming: Houghton, J. (Ed.), The Complete Briefing, 2nd. Cambridge University Press, Cambridge.

Johnson, E.A., 1992. Fire and Vegetation Dynamics, Studies from the North American Boreal Forest. Cambridge University Press, Cambridge, UK.

Johnson, E.A., Gutsell, S.L., 1994. Fire frequency models, methods and interpretations. Adv. Ecol. Res. 25, 239–286.

Keane, R.E., Hardy, C.C., Ryan, K.C., Finney, M.A., 1997. Simulating effects of fire on gaseous emissions and atmospheric carbon fluxes from coniferous forest landscapes. World Resour. Rev. 9, 177–205.

Keeley, J.E., 1977. Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and nonsprouting chaparral shrubs. Ecology 58, 820–829.

Keeley J.E. 1981, Reproductive cycles and fire regimes. In: Proceedings of the Conference Fire Regimes and Ecosystem Properties, General Technical Report WO-26. USDA, Washington, pp. 231–277.

Keeley, J.E., 1986. Resilience of mediterranean shrub communities to fire. In: Dell, B., Hopkins, A.J.M., Lamont, B.B. (Eds.), Resilience in Mediterranean-Type Ecosystems. Dr W. Junk, Dordrecht, pp. 95–112.

Keeley J.E. 1991, Fire management for maximum diversity in California chaparral. In: Nodvin, S.C., Waldrop T.A. (Eds.), Fire and the Environment: Ecological and Cultural Perspectives, General Technical Report SE-69. USDA Forest Service, Southern Forest Experiment Station, Asheville, NC, pp. 11–14.

Keeley, J.E., 1991b. Seed germination and life history syndromes in the California chaparral. Botan. Rev. 57, 81–116.

Keeley, J.E., 1995. Seed germination patterns in fire-prone Mediterranean-climate regions. In: Arroyo, M.T.K., Zedler, P.A., Fox, M.D. (Eds.), Ecology and Biogeography of Mediterranean Ecosystems in Chile, California, and Australia. Springer-Verlag, New York, pp. 239–273.

Keeley, J.E., Keeley, S.C., 1984. Postfire recovery of California coastal sage scrub. Amer. Midl. Natur. 111, 105–117.

Keeley, J.E., Soderstrom, T.J., 1986. Postfire recovery of chaparral along an elevational gradient in southern California. Southwest Natur. 31, 177–184.

Keeley, J.E., Zedler, P.H., Zammit, C.A., Stohlgren, T.J., 1989. Fire and demography. In: Keeley, S.C. (Ed.), The California Chaparral: Paradigms Reexamined. Natural History Museum of Los Angeles County, Los Angeles, pp. 151–153.

Keeley, J.E., Fotheringham, C.J., Morais, M., 1999. Reexamining fire suppression impacts on brushland fire regimes. Science 284, 1829–1832.

Kessell, S.R., 1979. Gradient Modeling: Resource and Fire Management. Springer-Verlag, New York.

Kessell, S.R., 1990. An Australian geographic information and modeling system for natural areas management. Int. J. Geogr. Inf. Syst. 4, 333–362.

Kessell, S.R., Good, R.B., Hopkins, A.J.M., 1984. Implementation of two new resource management information systems in Australia. Environ. Manage. 8, 251–270.

Lariguaderie, S., Hubbard, T.W., Kummerow, J., 1990. Growth dynamics of two chaparral shrub species with time after fire. Madroño 37, 225–236.

Larsen, C.P.S., 1997. Spatial and temporal variations in boreal forest fire frequency in northern Alberta. J. Biogeogr. 24, 663–673.

Levin, S.A., 1992. The problem of pattern and scale in ecology. Ecology 73, 1943–1967.

Li, C., Ter-Mikaelian, M., Perera, A., 1997. Temporal fire disturbance patterns on a forest landscape. Ecol. Modell. 99, 137–150.

Malanson, G.P., O'Leary, J.F., 1995. The coastal sage scrub-chaparral boundary and response to global climate change. In: Moreno, J.M., Oechel, W.C. (Eds.), Global Change and Mediterranean-Type Ecosystems. Springer-Verlag, New York, pp. 203–224.

Malanson, G.P., Westman, W.E., 1985. Postfire succession in Californian coastal sage scrub: the role of continuous basal sprouting. Amer. Midl. Natur. 113, 309–318.

Malanson, G.P., Westman, W.E., Yan, Y.-L., 1992. Realized versus fundamental niche functions in a model of chaparral response to climate change. Ecol. Modell. 64, 261–277.

Meyer, W.B., Turner, B.L. II (Eds.), 1994. Changes in land use and land cover: a global perspective. Cambridge University Press, Cambridge.

Miller, C., Urban, D.L., 1999a. A model of surface fire, climate and forest pattern in Sierra Nevada, California. Ecol. Modell. 114, 113–135.

Miller, C., Urban, D.L., 1999b. Interactions between forest heterogeneity and surface fire regimes in the southern Sierra Nevada. Can. J. For. Res. 29, 202–212.

Miller, C., Urban, D.L., 2000a. Modeling the effects of fire management alterations on Sierra Nevada mixed-conifer forest. Ecol. Appl. 10, 85–94.

Miller, C., Urban, D.L., 2000b. Connectivity of forest fuels and surface fire regimes. Landsc. Ecol. 15, 145–154.

Minnich, R.A., 1983. Fire mosaics in Southern California and Northern Baja California. Science 219, 1287–1294.

Minnich, R.A., 1988. The biogeography of fire in the San Bernardino Mountains in California: a historical study. University of California Publications in Geography 27, 1–121.

Minnich, R.A., 1991a. Conifer forest fire dynamics and distribution in the mountains of southern California, part 1. Crossosoma 17, 1–11.

Minnich, R.A., 1991b. Conifer forest fire dynamics and distribution in the mountains of southern California, part 2. Crossosoma 17, 1–9.

Minnich, R.A., Barbour, M.G., Burk, J.H., Fernau, R.F., 1995. Sixty years of change in Californian conifer forests of the San Bernadino Mountains. Conserv. Biol. 9, 902–914.

Minnich, R.A., Chou, Y.H., 1997. Wildland fire patch dynamics in the chaparral of southern California and northern Baja California. Int. J. Wildland Fire 7, 221–248.

Mladenoff, D.J., Baker, W.L., 1999. Development of forest and landscape modeling approaches. In: Mladenoff, D.J., Baker, W.L. (Eds.), Spatial Modeling of Forest Landscape Change: Approaches and Applications. Cambridge University Press, Cambridge, pp. 1–13.

Mladenoff, D.J., DeZonia, B., 1999. APACK 2.11 Analysis Software User's Guide. University of Wisconsin, Madison, 50 pp.

Mladenoff, D.J., He, H.S., 1999. Design, behavior and application of LANDIS, as object-oriented model of forest landscape disturbance and succession. In: Mladenoff, D.J., Baker, W.L. (Eds.), Spatial Modeling of Forest Landscape Change: Approaches and Applications. Cambridge University Press, Cambridge, pp. 125–162.

Mladenoff, D.J., Host, G.E., Boeder, J., Crow, T.R., 1996. LANDIS: A spatial model of forest landscape disturbance, succession, and management. In: Goodchild, M.F., Steyaert, L.T., Parks, B.O. (Eds.), GIS and Environmental Modeling: Progress and Research Issues. GIS World, Ft. Collins, CO, pp. 175–179.

Moore, A.D., Noble, I.R., 1990. An individualistic model of vegetation stand dynamics. Journal of Environ. Manage. 31, 61–81.

Moreno J.M., Oechel W.C. 1992, Anticipated effects of a changing global environment on Mediterranean-type ecosystems. Report and recommendations of the symposium and workshop held in Valencia, Spain, 14-17 September, 1992, sponsored by Universidad Internacional Menendez Pelayo and Centro de Estudiod Medioambientales de Mediterraneo.

Moreno J.M., Oechel W.C. (Eds.) 1994, In: The Role of Fire in Mediterranean-Type Ecosystems. Ecological Studies Volume 107. Springer-Verlag, New York, 201 pp.

Moreno J.M., Oechel W.C. (Eds.) 1995, Global Change and Mediterranean-Type Ecosystems. Ecological Studies Volume 117. Springer-Verlag, New York, 427 pp.

Naveh, Z., 1975. The evolutionary significance of fire in the Mediterranean region. Vegetatio 29, 199–208.

Naveh, Z., Dan, J., 1973. The human degradation of Mediterranean landscapes in Israel. In: Di Castri, F., Mooney, H.A. (Eds.), Mediterranean-Type Ecosystems, Origin and Structure. Springer-Verlag, Berlin, pp. 373–390.

Noble, I.R., Gitay, H., 1996. A functional group classification for predicting the dynamics of landscapes. J. Veg. Sci. 7, 329–336.

Noble, I.R., Slatyer, R.O., 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43, 5–21.

Parker, V.T., Kelly, V.R., 1989. Seed banks in California chaparral and other Mediterranean climate shrublands. In: Leck, M.A., Parker, V.T., Simpson, R.L. (Eds.), Ecology of Soil Seed Banks. Academic Press, New York, pp. 231–255.

Pausas, J.G., 1999a. Mediterranean vegetation dynamics: modeling problems and functional types. Plant Ecol. 140, 27–39.

Pausas, J.G., 1999b. Response of plant functional types to changes in the fire regime in Mediterranean type ecosystems: a simulation approach. J. Veg. Sci. 10, 717–722.

Pickett, S.T.A., White, P.S., 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York, NY.

Pickett, S.T.A., Amesto, J.J., Collins, S.L., 1989. The ecological concept of disturbance and its expression at various hierarchical levels. Oikos 54, 129–136.

Rego, F., Periera, J., Trabaud, L., 1993. Modelling community dynamics of a *Quercus coccifera* L. garrigue in relation to fire using Markov chains. Ecol. Modell. 66, 251–260.

Roberts, D.W., 1996. Modeling forest dynamics with vital attributes and fuzzy systems theory. Ecol. Modell. 90, 161–173.

Rothermel, R.C., 1972. A mathematical model for predicting fire spread in wildland fuels. USDA Forest Service Research Paper INT-115. Inter-Mountain Forest and Range Experiment Station, Ogden, UT, 40 pp.

Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. Conserv. Biol. 5, 18–32.

Savage, M., 1991. Structural dynamics of a southwestern pine forest under chronic human influence. Ann. Assoc. Am. Geogr. 81, 271–289.

Shifley, S.R., Thompson, F.R. I.I.I., Larsen, D.R., Dijak, W.D., 2000. Modeling forest landscape change in the Missouri Ozarks under alternative management practices. Comp. Electron. Agric. 27, 7–27.

Soule, M.E., Alberts, A.C., Bolger, D.T., 1991. The effects of habitat fragmentation on chaparral plants and vertebrates. Oikos 63, 39–47.

Stephenson J., Calcarone G.M. 1999, Southern California mountains and foothills assessment: habitat and species conservation issues. General Technical Report PSW-GTR-172, USDA Forest Service, Pacific Southwest Research Station, Albany, CA, 402 pp.

Suffling, R., 1995. Can disturbance determine vegetation distribution during climate warming? A boreal test. J. Biogeogr. 22, 501–508.

Thorne, R.F., 1990. Montane and subalpine forests of the Transverse and Peninsular Ranges. In: Barbour, M.G., Major, J. (Eds.), Terrestrial Vegetation of California. California Native Plant Society, Sacramento, pp. 537–558.

Torn, M.S., Fried, J.S., 1992. Predicting the impacts of global warming on wildland fire. Clim. Chang. 21, 257–274.

Turner, M.G., Romme, W.H., Gardner, R.H., 1994. Landscape disturbance models and the long-term dynamics of natural areas. Nat. Areas J. 14, 3–11.

Vander Wall, S.B., 1993. Cache site selection by chipmunks and its influence on the effectiveness of seed dispersal in Jeffrey Pine (*Pinus jeffreyi*). Oecologia 96, 246–252.

Vasconcelos, M.J., Guertin, D.P., 1992. FIREMAP — simulation of fire growth with a Geographic Information System. Int. J. Wildland Fire 3, 87–96.

Vasconcelos, M.J., Zeigler, B.P., 1993. Discrete-event simulation of forest landscape response to fire disturbances. Ecol. Modell. 65, 177–198.

Westman, W.E., Malanson, G.P., 1992. Effects of climate change on Mediterranean-type ecosystems in California and Baja California. In: Peters, R.L., Lovejoy, T.E. (Eds.), Global Warming and Biological Diversity. Yale University Press, New Haven, CT, pp. 258–276.

Wu, Y., Sklar, F.H., Gopu, K., Rutchey, K., 1996. Fire simulations in the Everglades landscape using parallel programming. Ecol. Modell. 93, 113–124.

Zammit, C.A., Zedler, P.H., 1992. Size structure and seed production in even-aged populations of *Ceanothus greggii* in mixed chaparral. J. Ecol. 81, 499–511.

Zedler, P.H., 1981. Vegetation change in chaparral and desert communities in San Diego County, California. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.), Forest Succession. Springer-Verlag, New York, pp. 406–430.

Zedler P.H. 1982, Plant demography and chaparral management in Southern California. In: Dynamics and management of Mediterranean-type ecosystems, General Technical Report PSW-58. Pacific Southwest Forest and Range Experiment Station, USDA Forest Service, Berkeley, CA, pp. 123–127.

Zedler, P.H., 1995a. Fire frequency in southern California shrublands: biological effects and management options. In: Keeley, J.E., Scott, T.A. (Eds.), Brushfires in California Wildlands: Ecology and Resource Management. International Association of Wildland Fire, Fairfield, WA, pp. 101–112.

Zedler, P.H., 1995b. Plant life history and dynamic specialization in the chaparral/coastal sage shrub flora in southern California. In: Arroyo, M.T.K., Zedler, P.A., Fox, M.D. (Eds.), Ecology and Biogeography of Mediterranean Ecosystems in Chile, California, and Australia. Springer-Verlag, New York, pp. 89–115.

Zedler, P.H., Seiger, L.A., 2000. Age mosaics and fire size in chaparral: a simulation study. In: Keeley, J.E., Baer-Keeley, M., Fotheringham, C.J. (Eds.), 2nd Interface Between Ecology and Land Development in California. International Association of Wildland Fires, Fairfield, WA, pp. 9–18.

Zedler, P.H., Zammit, C.A., 1989. A population-based critique of concepts of change in the chaparral. In: Keeley, S.C. (Ed.), The California Chaparral: Paradigms Reexamined. Natural History Museum of Los Angeles County, Los Angeles, pp. 73–83.

Zedler, P.H., Gautier, C.R., McMaster, G.S., 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. Ecology 64, 809–818.