Ecological and Simulation Studies of the Responses of *Miconia albicans* and *Clidemia sericea* Populations to Prescribed Burning

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ABSTRACT

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Computer simulation modelling is offered as one solution to the problem of evaluating long-term effects on shrub populations of prescribed burning programmes with data collected in short-term studies. The population dynamics of two melastomataceous shrubs, *Miconia albicans* and *Clidemia sericea*, in a *Pinus caribaea* savanna in Belize subjected to controlled burning, were investigated with the objective of developing a simulation model and predicting long-term consequences of continued regular burning. Simulation results suggested that, while both annual burning and total fire-suppression would result in eventual extinction of both shrub populations, burn cycles of 2-5 years would allow maintenance of *Miconia* populations and an increase in *Clidemia* populations.

INTRODUCTION

Prescribed burning has been recommended for management of timber stands to control understory species (Cunningham and Cremer, 1965), as well as of rangelands to control invasion by woody species (Phillips, 1965; Langlands, 1967; Daubenmire, 1968; Trollope, 1982). In areas where the management goal is maintenance of animal populations dependent on grass and shrubs for food, prescribed burning has been suggested for maintaining and rejuvenating shrub populations and also for maintaining an adequate grass-shrub balance in the vegetation (Lay, 1956; Leege and Hickey, 1971; Christensen and Kimber, 1975; Orme and Leege, 1976; Barrett and Arno, 1982; Merrill et al., 1982; Trollope,

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1982). Depending on the burning regime, fires can be used for elimination, control, or maintenance of shrub populations.

The choice of a specific prescribed-burning programme depends on the particular management goals for the vegetation of an area, and requires an understanding of the effects of such a burning programme on the plant populations present. Due to the tendency of most shrub species to sprout after burning, the long-term effects of a particular burning regime may not always be apparent from the results of a short-term study. Furthermore, because of the variable results of any burning regime on different species under different conditions (Thomas and Pratt, 1967), the specific results and recommendations from the few long-term studies which have been conducted (Trapnell, 1959; Charter and Keay, 1960; Kennan, 1971; Lewis and Harshbarger, 1976) cannot be generalized. Conducting a long-term study in each area prior to selection and establishment of a vegetation management programme is impractical. One solution suggested for this type of problem is the use of computer models to simulate the slow ecological processes affecting vegetation under different management practices (Strayer et al., 1986).

Computer models have been developed to simulate forest succession under different environmental conditions, as well as to predict the expected long-term effects of various management practices on temperate mixed-forest stands (Botkin et al., 1972; Shugart and West, 1977; El-Bayoumi et al., 1984). These models are based on data on growth, reproduction and mortality of the tree species involved. Such data has been collected for a number of tree species over the years by foresters and ecologists. The lack of similar models for the shrub understory may be due, to some extent, to the notable lack of information on the demography and ecology of shrub species (Harper, 1977; Silvertown, 1982). We present in this paper an example of the development of a species- and site-specific computer model, to simulate the long-term dynamics of shrub populations under varying burning regimes, based on data from a short-term study. By obtaining estimates of rates of recruitment, growth and mortality, and the effects of burning on these rates for any given shrub population, a model simulating its population dynamics under various burning regimes can be developed.

The specific objective of the present study was to develop a model to simulate population responses of two shrub species, *Miconia albicans* and *Clidemia sericea*, to regular prescribed burning and then to evaluate the burning regimes by determining which burn cycles allowed population maintenance and which resulted in population increase or decline.

A project to study the effectiveness of burning cycles of 1–5 years in reducing fuel accumulation was established in 1976 by the Belize Forestry Department (Hudson, 1976). Although discontinued in 1982, the project plots located in the Mountain Pine Ridge Forest Reserve, Belize, provided an opportunity to investigate a shrub understory which had been subjected to a range of pre-

scribed burning regimes over a 7-year period. The shrub understory of this pine savanna is dominated by two species, *Miconia albicans* (Schwartz) Triana and *Clidemia sericea* D. Don (Kellman, 1976; Miyanishi, 1984).

The effects of a prescribed-burning programme on the population dynamics of these two species are of interest to managers of this forest reserve since the broadleaf shrub canopy and resulting litter may control pine regeneration. It has also been suggested that the shrubs may play a role in nutrient accumulation in extremely infertile environments such as this neotropical pine savanna (Kellman, 1979; Kellman et al., 1987). In such sites, the soils are often deeply weathered to depths beyond the rooting zone of the pines and the major source of mineral nutrient input is from the atmosphere (Kellman and Hudson, 1982). The soils surrounding some of the savanna hardwood species in Belize, including *M. albicans*, were found to be enriched in comparison with the soils under open grassland (Kellman, 1979). Furthermore, nutrients from the shrub biomass would be released after burning and the shrubs may thus be utilized as a mechanism for trapping and recycling mineral nutrients from atmospheric inputs. Prescribed burning could potentially be used simultaneously to control the growth of the shrub understory and to allow release of the nutrients from the shrub biomass, temporarily enriching the soil and increasing the nutrient availability to the pines.

SITE DESCRIPTION

The study was conducted in the Mountain Pine Ridge Forest Reserve which occupies 560 km^2 in west-central Belize (lat. 17°N, long. 89°W). Within the reserve, stands of *Pinus caribaea* Morelet occur on infertile Ultisols developed from granitic parent material (Johnson and Chaffey, 1973). Annual precipitation averages 1560 mm (Walker, 1973). The thunderstorms which signal the end of the 3–4 month dry season (February to May) constitute a significant wildfire hazard. More than half the fires occurring in the past decade have been caused by lightning (Hudson, 1976). The relatively recent establishment of dense pine stands in areas formerly covered by open savanna coincides with the establishment of fire-control measures in 1945 (Lundell, 1940; Hunt, 1970). In a 1974 survey of the shrub understory which recorded a mean density of 6053 stems ha^{-1}, the two most abundant species were found to be *M. albicans* and *C. sericea* (Kellman, 1976), both of which are widely distributed in the Neotropics from Mexico to Paraguay (Wurdack, 1973). Although the heat-sensitive shoots of both species are killed even by low-intensity burns, their root crowns sprout prolifically after burning and post-burn shoots generally attain pre-burn sizes within 5 years (Miyanishi, 1984).

The Belize Forestry Department prescribed-burning project involved 20 plots (40 m × 25 m) in a randomized block design of 20 factorial treatments (five burning cycles × two burning seasons × two burning intensities) plus five con-

TABLE 1

Actual burn histories of the plots in the Belize Forestry Department Prescribed Burning Project

Burn cycle	Year							
	1976	1977	1978	1979	1980	1981	1982	1983
Control	X							
One	X	X	X	X	X		X	
Two	X		X			X	X	
Three	X			X			X	
Four	X				X			
Five	X					X		

As indicated by the X's which represent each burn, not all of the treatment plots were burned according to schedule.

trol plots. This design was replicated at four sites (Hudson, 1976). Only plots assigned to the end-of-dry-season (May/June) burn treatment were used in our study. Since fire intensity had no apparent effect on sprouting or survivorship of *Miconia* and *Clidemia* (Miyanishi, 1984), the two intensity treatments were simply considered as replicates of the burn-cycle/burn-season treatment. Two of the five control plots were randomly selected to provide a balanced design. The shrub populations at two of the four sites (called A and B) were studied. Both sites were reasonably uniform in fuels, topography and stocking of *Pinus caribaea* (Hudson, 1976). By 1976, these sites had been under effective fire protection for 20 years. No wildfires had occurred in that period at site A which was thinned in 1964. Site B had a wildfire in 1972 and was thinned in 1973. Data for model development were collected from the 12 plots (two plots for each of the five burn cycles plus two controls) at site A during the summers (May–July) of 1981–1983. Data for model evaluation were collected from the corresponding 12 plots at site B in 1983. The plots were not always burned on schedule but the actual burn histories for each plot were recorded (Table 1). Since topkill and subsequent resprouting were 100% in both species following each burn, and since virtually all sprouting occurred within 2–3 months after a burn, the ages of all shoots were equal to the time since the last burn.

DATA COLLECTION

In order to develop models simulating shrub population dynamics, estimates of rates of mortality, growth, fecundity and recruitment were required. Furthermore, for the models to simulate burning of such populations, the effects of burning on these demographic rates were also necessary. As indicated by Table 1, during the 3 years of this study (1981–1983), it was possible to examine the response of *Miconia* and *Clidemia* populations to burning from 1 to

7 years after a burn. Only the 4th year after a burn was not represented in this time period. Also, since two of the plots had been burned for 5 consecutive years, we were able to look at the effects of repeated annual burns on these population parameters.

Survivorship/mortality was monitored on 20 tagged plants of each species in each plot (40 plants per species per burn cycle per year). During the 3 years of study no actual mortality of shrubs ≥ 75 mm in height was observed either with or without a burn. However, a small number of tagged individuals could not be found in subsequent years and it was assumed that such shrubs had died, although it is possible that the tags had been removed. The number of missing individuals was used as an estimate of annual mortality, which was 2.2% for both species.

Because of the lack of post-burn mortality in larger shrubs, two subpopulations were defined on the basis of this criterion. 'Established' fire-tolerant shrubs were those that exhibited 100% post-burn sprouting with no apparent mortality due to burning, while 'seedlings' were plants that exhibited less than 100% post-burn sprouting as well as a significant size-dependent post-burn mortality. Since shrubs ≥ 75 mm in height neither failed to sprout nor exhibited post-burn mortality, this was taken as a conservative estimate for the minimum size of a fire-tolerant shrub. 'Seedlings' were thus all plants with shoots < 75 mm in height prior to a burn.

Because of the low density of seedlings in the burn plots and the difficulties of finding the same individuals of such small stature after a burn, seedling survivorship after burning was monitored in separate seedling burning experiments which were reported in a previous paper (Miyanishi and Kellman, 1986a). Sprouting ability and post-burn mortality of seedlings were both found to be size-dependent. Therefore, estimates for post-burn survivorship were obtained by size class. Survivorship of seedlings in the absence of burning was monitored in neighbouring areas beyond the experimental plots. Non-burn seedling survivorship was not size-dependent for seedlings beyond 4 mm in height, and appeared to be primarily due to dessication during the dry season. Mean annual mortality of seedlings in a non-burn year was estimated to be 9.4% for *Miconia* and 5.0% for *Clidemia*.

Shoot growth height was monitored on the same shrubs which were tagged for the survivorship study. Thus, growth was measured on shrubs with 1–6-year-old sprouts within the burn plots. Empirical growth functions were then derived for these shoots. Shoot growth rates changed during the first 3 years following a burn, declining from year to year but becoming constant 4 or more years following a burn (Miyanishi, 1984). Thus, the growth curve for plants 4 or more years after a burn was identical to that for unburned shrubs, and was continuous for seedlings and mature shrubs ranging in size from 2 mm to 2340 mm in height in both species.

Separate functions for annual height growth were derived for sprouts 1–3

years old. Only annual burning was expected to result in a steadily declining root and shoot growth rate with each successive burn cycle due to a cumulative net decline in root starch reserves (Miyanishi and Kellman, 1986b). The growth of 1-year-old sprouts for all burn cycles longer than 1 year was not a function of the number of burns and was dependent only on root size.

For unburned plants, growth rate of roots was assumed to be constant and proportional to shoot growth rate. This assumption was justified on the basis of the strong relationship over a wide range of sizes between root crown diameter and shoot height ($r = 0.98$ for *Miconia*, $r = 0.91$ for *Clidemia*, $P < 0.0001$ for both species). Measured shoot growth was converted to estimated annual growth in root-crown diameter using this highly significant relationship between height and root-crown diameter. Increase in biomass could also be estimated since height was highly significantly correlated with shoot fresh weight ($r = 0.95$ for *Miconia*, $r = 0.85$ for *Clidemia*, $P < 0.0001$ for both).

Density of established shrubs was estimated in 1981 in all 12 plots by the point-centred quarter method (Cottam and Curtis, 1956) using a correction for empty quadrants (Warde and Petranka, 1981). The estimated mean density at site A of *Miconia* was 82 plants per 100 m^2 and of *Clidemia* was 41 plants per 100 m^2. The size distribution for each species population was obtained by measuring the root-crown diameter on a random sample of 20 plants of each species in each plot ($n = 240$). Density of seedlings in 'unburned' plots was estimated by sampling twenty randomly located 0.25-m^2 quadrats within each plot that represented 5 or more years after a burn. The mean densities were 100 seedlings per 100 m^2 for *Miconia* and 38 seedlings per 100 m^2 for *Clidemia*. All seedlings sampled also had their heights recorded so that seedling size distributions could be developed.

Detailed data on post-burn seed production and seedling establishment were presented in Miyanishi and Kellman (1986a). Since seedling establishment was not found to be limited by seed availability except in the 1st year following a burn in *Miconia*, data on fecundity were not used in developing the model. The density and height distribution of seedlings in unburned plots as well as in the experimental plots 1–6 years after a burn were also measured. Figure 1 shows the mean seedling establishment obtained 1–7 years after a burn. The value for the 4th year was obtained by interpolation while those for periods after 7 years, which would only be required for simulation of the control population, were obtained by extrapolation.

MODEL DEVELOPMENT AND DESCRIPTION

A computer model was then developed to simulate the birth, growth and death of individuals within each species population assigned to burn cycles of 1–5 years, or to the control treatment which was a single burn at initiation of the project. Due to the constraints imposed by the computer memory available,
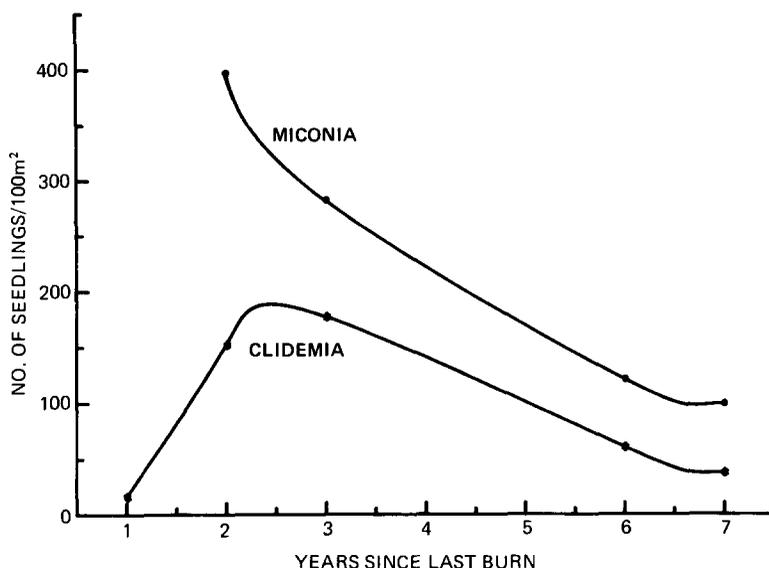
Fig. 1. Mean seedling density (plants per 100 m²) of *Miconia* and *Clidemia* found in plots 1–7 years following a burn.

the programs could not manage populations on areas the size of the experimental plots (1000 m²) so used, instead, an area of 100 m². The programs were written in APL and run in an interactive mode. A general flow diagram for the model is given in Fig. 2.

After input of the simulation period and burn cycle, the model begins by generating a random subpopulation of established shrubs comparable in density and root-crown diameter distribution to those which would have been found at the start of the burning project in 1976. The initial size-distribution was obtained by using the size-distribution recorded in 1981 and then adjusting for the expected growth from 1976 to 1981 using the derived growth-functions. The model also generates a random subpopulation of seedlings with a density and height distribution similar to that found in sites 5 or more years after a burn. The subroutine developed to generate these non-uniform random distributions, RPGENER, uses the inverse transformation method described by Gordon (1978). This combined population of mature shrubs and seedlings is then taken through the various sections of the program (MORT, GROW, MOVE, RECRUIT) for each simulated year.

Since mortality in the absence of burning was not found to be size-related, removal of established shrubs by the subroutine MORT is completely random. The subroutine MORT also randomly removes seedlings but uses either the size-dependent or size-independent mortality rates for a burn year or a non-burn year, respectively.
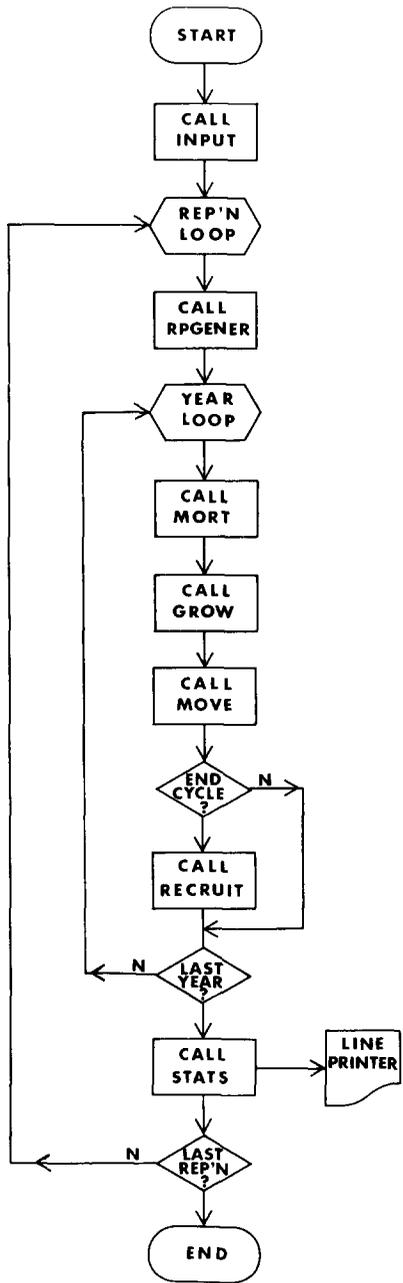
Fig. 2.General flow diagram for the shrub population computer model.

The decline in shoot growth rate measured over five annual burns was used to obtain a rate of decline to predict future growth of 1-year sprouts with continued annual burning. When the roots fail to produce a sprout of 1 mm height, they are considered dead. The subroutine GROW was developed to grow each plant according to the shoot and root growth appropriate for the particular time since the last burn and the particular burn cycle.

The subroutine MOVE then selects seedlings which have reached the minimum size criterion for fire-tolerance (the expected root-crown diameter of a seedling 75 mm in height, which was 2.7 mm for *Miconia* and 2.9 mm for *Clidemia*) and moves them from the seedling subpopulation into the established-shrub subpopulation.

Since it was not possible to obtain data on seedling establishment occurring during each year within all burn cycles, and data was only collected on seedling density and height distribution at the end of each burn cycle (Miyanishi and Kellman, 1986a), the model only allows seedling establishment at the end of each burn cycle. The convenience of adding seedlings only at the end of a burn cycle just prior to a burn does not create any special problems, particularly over long-term simulations. It does, however, affect the values for mean plant size (root-crown diameter, shoot height and shoot fresh weight), and results in a minor drop in the mean values for the final year within each burn cycle, due to the addition of these small plants. The subroutine RECRUIT adds the appropriate number and height-distribution of seedlings.

An annual accounting is conducted of the numbers, mean height, mean shoot fresh weight and total biomass (combined shoot fresh weights) of the total population as well as of the subpopulations of seedlings and mature shrubs. The number of deaths and additions to the established population are also recorded. These population statistics are printed out at the end of the total simulation period.

SIMULATION RESULTS

Mean results are presented for ten runs of each model through 70-year simulations for each of the five burn cycles plus the control.

Because of the ephemeral nature of seedlings, the dynamics of the subpopulation of established fire-tolerant shrubs was of greatest concern. Annual mortality and recruitment for this subpopulation of established fire-tolerant shrubs appear to reach dynamic equilibrium for *Miconia* populations subjected to burn cycles of 2–5 years, indicating population stabilization (Fig. 3). For the *Clidemia* populations subjected to these burn cycles recruitment is greater than mortality, indicating increasing populations. With the 1-year burn cycles, recruitment does not occur in populations of either species, while mortality rises as root reserves are depleted (Miyanishi and Kellman, 1986a).

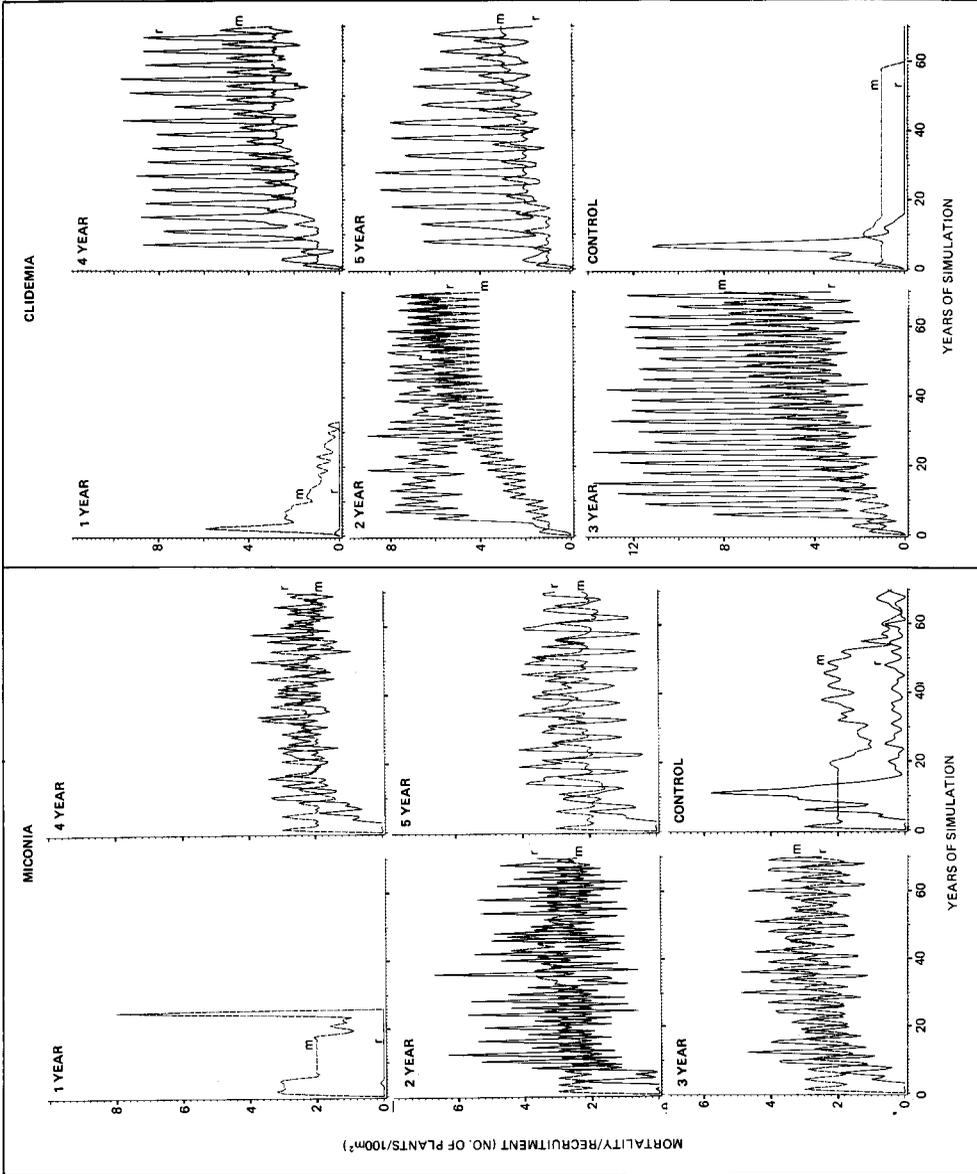Complete fire suppression (the Control treatment) results in declining

Fig. 3. Mean mortality and recruitment (plants per 100 m²) in the population of established *Miconia* and *Clidemia* over 70 years of simulated burning at burn cycles of 1–5 years, and the control. Mean values represent the results of ten runs.

recruitment after an initial peak 6–7 years following the first burn. Since seedling recruitment declines to, or very close to, zero in the control populations, it can be concluded that these shrub populations will eventually go extinct without any further burning. The time required for extinction would depend on the longevity of each species.

The mean population numbers each year under the different burning regimes are plotted in Fig. 4. Simulations of the 1-year burn cycle resulted in population extinction after 26 years for *Miconia* and after 33 years for *Clidemia*. Simulations of burn cycles of 2 and 3 years resulted in *Miconia* populations stabilizing at densities similar to those at the initiation of the burning treatment, approximately 8000 plants ha^{-1}. Burn cycles of 4 and 5 years resulted in populations stabilizing at slightly lower densities of about 7000 plants ha^{-1}. Frequent burning had a noticeably different effect on *Clidemia* populations. Burn cycles of 2–5 years resulted in increasing populations which appeared to start to level off slightly after 50 years of simulated burning. The 3-year burn cycle produced the highest, and the 5-year burn cycle the lowest, stable population density. These results suggest that, although burn cycles of 2–5 years do not have any deleterious effect on either species populations, *Clidemia* appears to respond more favourably to frequent burning than *Miconia*.

Fluctuations in total above-ground live biomass are also plotted for the two shrub species in Fig. 4. Total shoot biomass of *Miconia* populations, although showing the expected fluctuations within each burn cycle, are relatively stable and similar for burn cycles of 2–5 years. Live shrub biomass in the annually burned plots was extremely low since no year-to-year accumulation took place, and since shoot growth was declining with each burn (Miyanishi and Kellman, 1986a). Under complete fire suppression, the total shoot biomass of *Miconia* increased to very high levels. However, this would eventually decline as each large individual died and was not replaced. In comparison, total shoot biomass of *Clidemia* populations was higher in the plots burned at 2–5-year intervals than in the control plots. Although *Miconia* shrubs do exhibit annual die-back of some branches, particularly those bearing inflorescences, the main stem remains intact and there is an overall net annual accumulation of shoot biomass in the absence of burning. The main stems of *Clidemia* shoots, on the other hand, become brittle with age and tend to break readily, resulting in a net loss of biomass. Therefore, in the absence of shoot renewal by post-burn sprouting, total biomass of *Clidemia* shrubs declines with long fire-free intervals.

EVALUATION OF THE MODELS

Unfortunately, the predictions of the model could not be rigorously tested since there were no areas in the Mountain Pine Ridge which had experienced such frequent and regular burning over any extended period. However, we attempted to evaluate the reasonableness of the model outputs by comparing
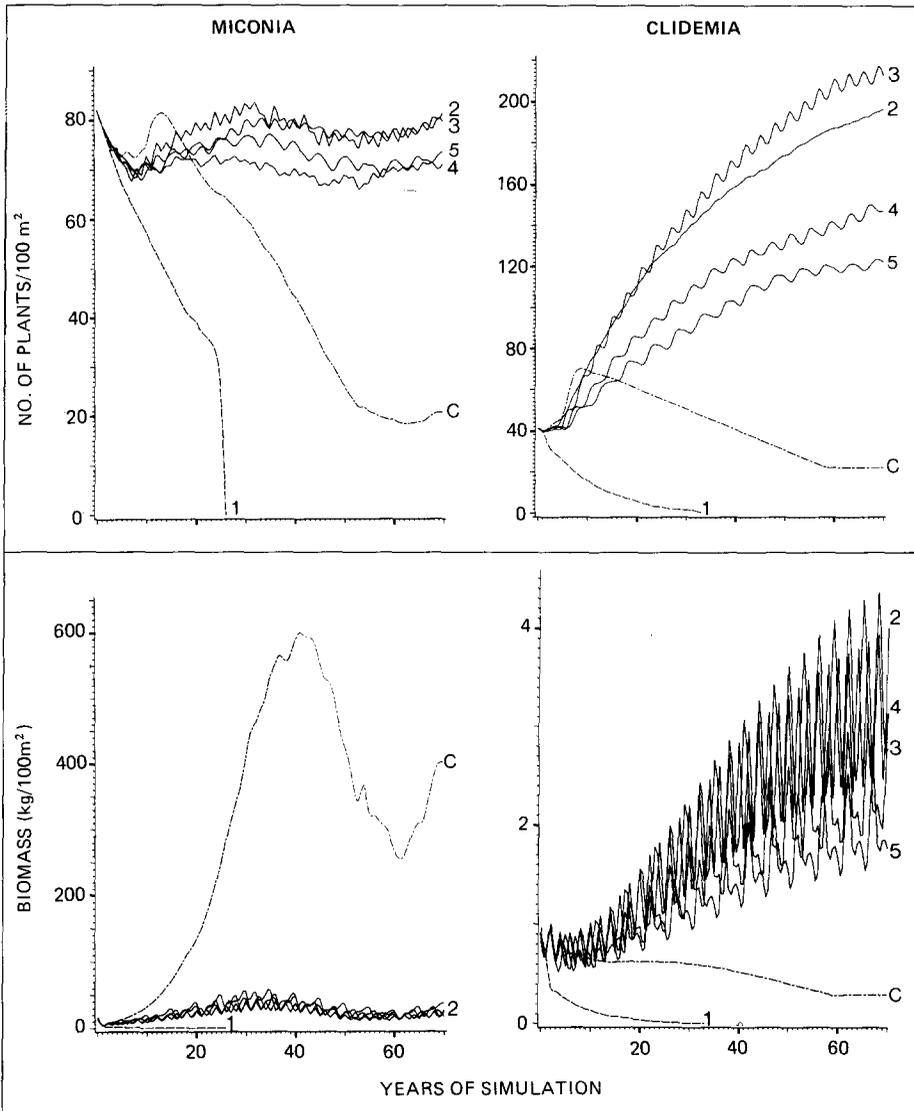
Fig. 4. Mean number of established plants per 100 m², and mean total biomass in kg per 100 m², of *Miconia* and *Clidemia* during 70 years of simulated burning at intervals of 1–5 years and the control. Means represent the results of ten runs.

some of the short-term predictions with data collected in 1983 on the shrub populations at a second site of the same burning project. Data on the established shrub population at this site were not used in any part of the development of either model. Since the only plots which were burned according to schedule were those assigned the 3-, 4- and 5-year burn cycles, these plots plus

TABLE 2

Comparison between (a) mean plant height (mm) and (b) mean shoot fresh weight (g) $\pm$ SE of each species predicted by the model for the 3-, 4- and 5-year burn cycles and controls in 1983 and actual values obtained from the shrubs in plots at the B site

Species	Burn cycle	Mean height (mm)		t	$P > t$
		Predicted	Actual		
(a)					
Miconia	3	462 ± 12	428 ± 46	0.677	ns
	4	897 ± 19	785 ± 63	1.361	ns
	5	760 ± 18	813 ± 52	−0.709	ns
	Control	1044 ± 23	1366 ± 104	−3.241	<0.01
Clidemia	3	310 ± 7	335 ± 31	−0.962	ns
	4	722 ± 13	640 ± 49	1.674	ns
	5	616 ± 11	598 ± 36	0.472	ns
	Control	583 ± 12	697 ± 68	−2.278	<0.05
(b)					
Miconia	3	99 ± 5	92 ± 17	0.302	ns
	4	159 ± 9	151 ± 35	0.190	ns
	5	165 ± 9	213 ± 39	−1.265	ns
	Control	265 ± 14	480 ± 98	−3.356	<0.001
Clidemia	3	11 ± 1	11 ± 2	0	ns
	4	13 ± 1	19 ± 4	−1.368	ns
	5	20 ± 1	11 ± 1	3.404	<0.001
	Control	11 ± 1	13 ± 3	−1.143	ns

Sample sizes were 40 for the actual values, while those for the predicted values ranged from 692 to 729 for Miconia and from 444 to 653 for Clidemia.
ns = not significant.

the controls were used in the comparison. The mean plant height and mean shoot fresh weight predicted by the models for these particular treatments 7 years after initiation of the burning treatments were compared with the data obtained from the second site in 1983. The predictions were based on the means generated for 1983 from the ten simulation runs of the models discussed previously. The significance of differences between the two sets of means were tested using two sample t-tests.

Of the eight comparisons between predicted and actual mean plant height, six were not significantly different (Table 2). The mean heights predicted for Miconia and Clidemia in the control treatment underestimated the mean heights for the shrubs in the control B plots. Of the eight comparisons between predicted and actual mean shoot fresh weight, six were not significantly different (Table 2). The mean shoot weight of Miconia predicted for the control was an

underestimate while that of *Clidemia* predicted for the 5-year burn cycles was an overestimate. Since the models were based on data from the shrub populations in one site, part of the discrepancy may be due to differences between the two sites with respect to the mean age of the two populations. Furthermore, although the two sites did not differ significantly in soil fertility (Miyanishi, 1984) they may have differed in factors which were not measured, such as soil moisture availability, pine canopy cover, or density of other broad-leaved species. Despite these possible differences in site characteristics, lack of significant differences between predicted and actual mean shoot sizes in the three burn treatments for both species supports the importance of fire history as the major factor determining shoot sizes of shrubs in this environment.

The prediction of gradual decline of populations of both *Miconia* and *Clidemia* in the absence of burning is supported by field observations of areas in the Mountain Pine Ridge, particularly on more-fertile soils which had not been burned for 35 years or more. Such sites have high stockings of pine, increasing populations of woody dicots, no grass layer and a deepening litter layer. Although some large individuals of either or both shrub species still remain, these shrubs have been overtopped by a closing canopy of taller broad-leaved trees. Canopy closure, as well as accumulation of the broad-leaved litter, have most likely been responsible for suppression of the grass layer as well as failure in recruitment of the shrub species. At these sites there are no seedlings or intermediate-sized saplings of *Miconia* or *Clidemia* present. Therefore, maintenance of populations of these savanna shrub species requires the occurrence of fire before the remaining individuals succumb to natural senescence or to the effects of shading by the canopy of taller species.

DISCUSSION

The results of the simulations imply that these shrubs, once established, can be maintained with minimal recruitment as long as the fire cycles are longer than 1 year. The outcome showing that population responses to burning in terms of population numbers is not very different for short burn cycles suggests that these shrubs, particularly *Miconia*, are adapted to a range of burn frequencies.

Although previous studies of the demography of short-lived herbaceous plants infrequently disturbed environments have recognized the importance of density-independent factors in population regulation, demographic studies of trees have tended to concentrate on the effects of intra- and inter-specific competition in survivorship, growth and fecundity (Harper, 1977). In illustrating the key role of fire in controlling numbers and sizes of individuals in savanna shrub populations, the present study has offered an example of populations of long-lived woody species that appear to be controlled largely by disturbance frequency rather than competitive interactions. Under present shrub-density

conditions, one factor alone, namely time since the last burn, could account for most of the variance in shoot size, seed production and seedling density of these species within the burn plots.

With no visible signs of predation or disease, senescence may be the major cause of death among these shrub populations. Shrubs within dense hardwood thickets showed no signs of suppression or mortality due to the effects of shading or other competitive interactions, either intra- or inter-specific. The persistence of shrubs of both species in the understorey within unthinned unburned sites with a closed canopy further suggests that population decline in the absence of fire over long periods is due primarily to annual attrition not being compensated by recruitment, rather than to mortality due to competitive interactions.

Populations of *Miconia* and *Clidemia* are regulated by opportunities for seedling establishment and recruitment. Such opportunities are primarily controlled by the occurrence of fire. While seed production may remain reasonably constant from year to year, recruitment is episodic, occurring within a 'window' of several years following a burn. Populations would therefore be expected to fluctuate in a lagged response to fire. However, with prescribed burns occurring at regular short intervals of 2–5 years, these fluctuations would be damped since recruitment would no longer be episodic but virtually continuous.

Recruitment to the established population is the net result of post-fire seedling establishment and post-burn mortality, since mortality of seedlings in non-burn years is relatively low. With *Miconia* populations, the model simulations indicate that recruitment following burning and fire-independent mortality within the established population balance out within the period of each burn cycle, such that populations can be maintained at close to present densities. It would be interesting to run simulations of much longer burn cycles to discover if *Miconia* populations can be increased substantially with appropriate regular burn frequencies. With *Clidemia* populations, burn cycles of 2–5 years resulted in recruitment rates greater than the annual non-fire mortality in the similated populations such that the populations continued to increase, suggesting that density-dependent mortality among mature plants may eventually become important to population regulation. This increase was not expected to occur until after burning treatments had continued for longer than 6 years. Since the prescribed-burn project was discontinued after 6 years, such increases could not be observed. Consequently, it was not possible to investigate the possibility that density dependence would begin to play a major role if *Clidemia* populations continued to increase at the rates shown by the simulation output.

Simulation models, such as the one presented here, provide a means of predicting long-term consequences of various vegetation management programmes. While a study over a 5-year period would indicate no change in population numbers with annual burning, the model predicts that, over longer periods, annual burning would result in population extinction for both species.

Models such as this may be applicable to other shrub situations such as range or wildlife management, where the primary concern is whether the management programmes are having an effect in either controlling or maintaining shrub populations.

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