Canadian Journal of
pure&applied
sciences

FIRE AND POPULATION DYNAMICS OF WOODY PLANT SPECIES IN A GUINEA SAVANNA VEGETATION IN MOLE NATIONAL PARK, GHANA: MATRIX MODEL PROJECTIONS

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ABSTRACT

Recurrent fires have a considerable potential to influence the structure and composition of savanna vegetation. In Mole National Park in Ghana, the policy is to burn the vegetation annually, early in the dry season. This paper examines the likely effects of these regular fires on the population dynamics of five tree species in the park using matrix model projections. The matrix manipulations were programmed using the Microsoft Excel spreadsheet software. The model is based on analyses and data put forward in Sackey (2006), as well as data on fire impacts and seedling production and growth of woody species recently obtained by Sackey and Imoro (unpublished study) from a savanna vegetation near Mole National Park. The model results show that annual burns will lead to changes in the relative abundance, as well as a decline in the density of all five tree species. The results also show that Burkea africana and Terminalia spp. require a minimum fire-free interval of > 2 years for their persistence, while 2 years minimum burning interval is required for the maintenance of Acacia dudgeoni, Combretum adenogonium and Vitellaria paradoxa. A minimum fire-free interval of > 3 years on a rotational system is suggested for the persistence of the majority of the woody plant species in the park.

Keywords: Grupe camp, fire impacts, matrix models, vegetation transformation.

INTRODUCTION

Plants differ widely in their tolerance of fire and their capacity to recover afterwards. As a result, recurrent fires have considerable potential to influence the structure and composition of vegetation (Trapnell, 1959; Charter and Keay, 1960; Ramsay and Rose-Innes, 1963; Hopkins, 1965; Rose-Innes, 1972; Brookman-Amissah *et al*., 1980; Frost and Robertson, 1987; Swaine *et al*., 1992; Ben-Shahar, 1998; Sackey, 2006; Sackey and Hale, 2008). The extent to which this occurs depends not only on differences in the sensitivity of different species but also on the fire regime (type, frequency and intensity of fire) of the area, and on the physiological and developmental states of individual plants at the time of burning.

In Mole National Park, the policy is to burn the vegetation annually early in the dry season when the grass fuel is still moist, presumably to achieve low fire intensity and, thus, minimise its impact on the Park's vegetation. It is, however, certain that late dry season fires occur regularly over large areas of the Park. Sackey and Hale (2008) and Sackey (2006) in a recent study showed that these regular dry season fires are causing mortality and topkill to trees ≥ 2 m tall in the Guinea savanna near Grupe camp of the Park. A matrix population model is a valuable tool for predicting population response to burning (Silva *et al*., 1991; Hoffmann, 1999) and is used in the present study to

predict the long-term effects of the regular fires on the population dynamics of five main tree species (*Acacia dudgeoni*, *Burkea africana*, *Combretum adenogonium*, *Terminalia* spp. and *Vitellaria paradoxa*) in the south-western section of the Mole National Park, Ghana, near Grupe camp. The model is based on analyses and data put forward in Sackey (2006), as well as data on fire impacts and seedling production and growth of woody species recently obtained by Sackey and Imoro (unpublished study) from a savanna vegetation near Mole National Park. The mathematical workability of the matrix model can be found in Lefkovitch (1965). Further description of matrix models can be found in Hartshorn (1975), Caswell (1982), Crouse *et al*. (1987), Enright and Watson (1991) and Desmet *et al*. (1996).

MATERIALS AND METHODS

METHODS
Study Area
Mole National Park is situated in northern Ghana between 9º 12' - 10º 06' North and 1º 25' - 2º 17' West and covers an area of approximately 4840 km². The Mole and Lovi rivers are the most significant among the numerous rivers which cross or originate in the Park. A climatic diagram for the nearest meteorological station, Damongo, about 18 km south of Mole is shown in figure 1. More than 95% of the mean annual rain (1098.1 ± 78.3 mm) falls during the single rainy season from April to October, with maxima occurring in June and the prime peak in September. The

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five consecutive months of the dry season (November – March) have a mean total rainfall of 49.7 ± 3.2 mm. The mean annual temperature of 27.7ºC varies little from month to month (25.7-31.0ºC), while the average diurnal range is 13.3ºC.

The Park lies in the Guinea savanna zone. The dominant vegetation type is the open savanna woodland with a grass layer that can reach up to 3 m tall during the rainy season and which is burnt annually. Hall and Jeník (1968) have recognised four savanna vegetation types in the West Gonja District, which includes the Park. These are the *Terminalia macroptera-Loudetiopsis thoroldi*-type in badly-drained and seasonally flooded plains, the

Mitragyna inermis-Andropogon gayanus var. gayanus-type in valley bottoms along streams, the *Isoberlinia doka-Loudetiopsis scaethae-Hyperrhenia subplumosa*-type on gentle slopes and well-drained plains and the *Loudetiopsis kerstingii-Polycarpea tenuifolia*-type on iron stone plateaux.

There are about 94 species of mammals (including bats) and over 300 species of birds in the Park (Hossain and Hall, 1996). The distribution of large mammals, particularly elephants, is concentrated in the south-eastern section of the Park. This study was conducted in the south-western section of the Park where elephants as well as other large mammals are virtually absent for most of
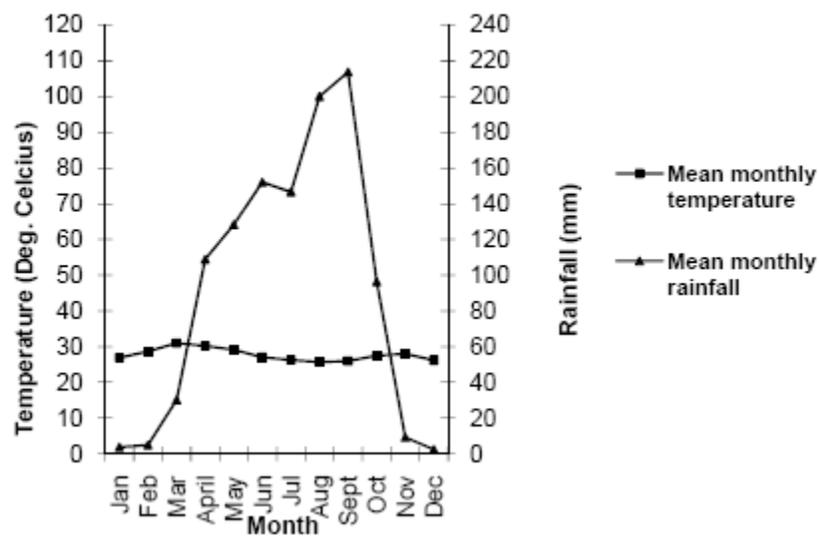

Fig. 1. Climatic diagram for Damongo, Ghana, based on rainfall data from 1985-2003 and temperature data from 1998-2003. Source of data: Ghana Meteorological Services.
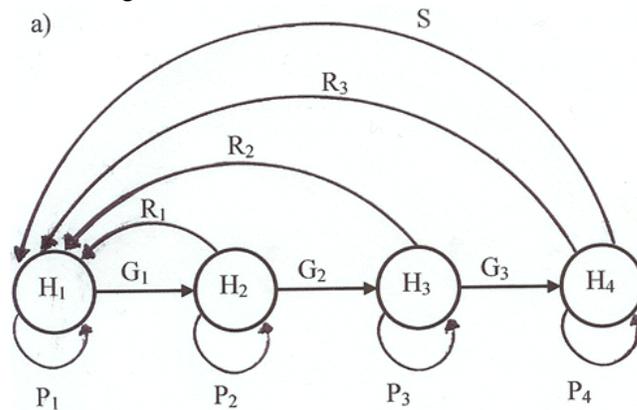

Fig. 2. Generalised life-stage graph of savanna tree species with arrows representing all the possible life-history transitions. H: height stages; *S*: seedling production; *R*: the probability of reversing to height stage H_1; *P*: the probability of remaining in the same height stage; and *G*: the probability of progressing to the next height stage within the time period of the model.

Table 1. Top-kill and mortality rates of the five tree species in one fire season according to height class.

Plant species	Top-kill (%)				Mortality (%)			
	< 1 m	1 – 2 m	2 – 5 m	> 5 m	< 1 m	1 – 2 m	2 – 5 m	> 5 m
Acacia dudgeoni	39.30	63.00	0.07	0.67	52.20	21.60	0.25	9.33
Burkea africana	37.50	59.70	0.10	0.50	60.50	32.50	1.38	5.35
Combretum adenogonium	31.10	67.30	0.32	0.14	65.30	19.40	0.37	1.02
Terminalia spp.	35.30	66.20	2.88	2.20	57.30	17.20	0.97	1.11
Vitellaria paradoxa	33.70	57.10	0.47	0.36	61.10	15.30	0.27	1.52

the year. The savanna vegetation in the area is largely the *Isoberlinia doka-Loudetiopsis scaethae-Hyperrhenia subplumosa* subtype of Hall and Jeník (1968). Further details of the Mole National Park are included in Sackey (2006).

The Matrix Models
The absence of large mammalian herbivores in the savanna near the Grupe camp makes fire the major factor directly influencing the population structure of the component woody species and, hence, the entire woody plant community structure. A stage-based matrix model was, therefore, developed to gain some quantitative insight into the effects of fire on the dynamics of five tree species' populations. A simple matrix based on the division of the life-history of the tree species into four height-classes (H: < 1 m, 1-2 m, 2-5 m and > 5 m) was used. Life-stage graph (Fig. 2) representing all the possible transitions (growth, stasis and reversal) an individual tree in any of the height classes (H) can make in any one time period, as well as seedling production by trees > 5 m tall, was drawn. The effect of climatic changes upon seedling production and tree survival and growth rates, as well as the density-dependent effects of tree numbers upon seedling survival (population-regulation mechanisms) and grass production and, hence, fire intensity has not been considered.

Fire was incorporated in the model in two ways: fire impact and burn frequency. Regarding fire impact, fire was programmed to operate at height-specific rates upon the four delineated height classes of the individual tree species (acting as a mortality or reversal agent), while burn frequency was incorporated as an annual event and as regular two- to four-year burn intervals. The model assumed that the population of a given height-class is exposed to either height-specific mortality rate or height-specific reversal rate (R) due to the impact of fire. Thus only two categories of fire damage were recognised, namely, tree totally killed, i.e., fire acting as a mortality agent, and tree top-killed, i.e., fire acting as a reversal agent reversing tree height. Field observations indicate that fire impact is most severe at tree bole bases (below 1.5 m in height) and re-sprouting of dead stems

commonly occurs from root-collars or stumps below 1 m (Sackey, 2006). Thus the model assumed that all fire-induced height reversals were to the lowest height-class, that is, < 1 m. All living trees with moderate fire damage involving slight scorching of the lower canopy or bark were considered as survivors. The procedure by Desmet *et al*. (1996) was followed to estimate the proportion of these survivors that will progress to the next higher height class (G) and the proportion that will remain or persist in the same height class (Stasis or P) in one year time period. Seedling input (S) was modelled as 'viable seedlings produced per tree' rather than seed production and survival.

Model Parameterization
The following parameter estimates were used in deriving the transition probabilities for the construction of the matrix models for the tree species:

Mortality and top-kill rates of tree species
Top-kill and mortality rates used for the model are summarised in table 1. Data for height classes 2 – 5m and > 5m are derived from Sackey (2006), while data for height classes < 1 m and 1 – 2 m are derived from an unpublished study by I. Sackey and A-W. M. Imoro in savanna vegetation within the 20 km buffer zone of the Mole National Park. The methods used in the unpublished study involved tagging individual plants of height < 1 m and 1-2 m tall, belonging to the five study species in vegetation near Larabanga. The number of individual plants tagged ranged from 55 to 70, depending on their availability for the season, and the vegetation burnt annually in November for three consecutive years, from 2007 to 2009. Fourteen days after each burn, the growth condition of the individual plants were assessed as dead or top-killed or living. The data were analysed in the form of proportions and averaged over the three burning seasons.

Seedling production rates
Seedling production rates of the tree species are derived from an unpublished study by Sackey and Imoro (Table 2). In this study, three trees of reproductive height (> 5 m tall) were selected for each of the five study species.

Table 2. Annual seedling production per tree estimated over three years for the five tree species incorporated in the model. (Source: Unpublished study by Sackey and Imoro).

Plant species	№ of seedlings
Acacia dudgeoni	10.71
Burkea africana	1.30
Combretum adenogonium	3.71
Terminalia spp.	1.08
Vitellaria paradoxa	4.21

Tree growth rates
Values for the growth of savanna trees vary widely, and are measured in a variety of ways. Herlocker estimated annual growth of young *Acacia tortilis* as 30 cm (Croze, 1974). Thomson (1975) indicated that *Brachystegia boehmii* regrowth can reach > 2 m high in 5 years under complete fire protection. Pellew (1983) found annual height increment of *Acacia tortilis* plants of < 0.95 m and 1.0-1.95 m in height to be 50.0 cm and 33.0 cm, respectively, while for trees 2.0-4.95 m tall, the mean annual increment was 46.7 cm, all without giraffe browsing. Lewis (1987) measured annual vertical growth in re-sprouted *Colophospermum mopane* trees in Luangwa Valley, Zambia, as 13.4-19.2 cm. From field observations, Dublin *et al.* (1990) found that height classes of *Acacia gerrardii* were roughly equivalent to

age such that plants reach 15 cm in approximately 1 year, 1 m in 6 years, 2 m in 11 years and 3 m in 15 years. Thus trees of *Acacia gerrardii* progress through height classes 1, 2 and 3 m in an average period of approximately 5 years each. Although the present model concerns different tree species to *Acacia gerrardii*, a similar height-class:age equivalence was assumed, as this represents the best match. Thus 5 years was used in the model as the average period for tree progression from one height class to the next higher height class. The following assumptions were also made that, during the five-year period: all trees would progress to the next higher height class, except those in the highest height class; and that within 5 years no tree would progress in height beyond the next higher height class.

Initial tree densities
The initial densities of trees (stems/ha) used for the construction of the column vectors of the model are values obtained by Sackey (2006) (Table 3).

The transition matrices
The parameter estimates of tree height reversal, growth, survival (derived from mortality and topkill data in Sackey (2006) and unpublished study by Sackey and Imoro) and seedling production (Table 3) were used to construct the transition matrices for the population models. Two transition matrices were constructed per species, each simulating the tree population dynamics at a

Table 3. Observed stage (height) class distribution of the tree populations used for the respective matrix vectors, expressed as number of stems/ha and relative percentage (in brackets).

Plant species	< 1 m	1 – 2 m	2 – 5 m	> 5 m
Acacia dudgeoni	923 (94.86)	15 (1.54)	15 (3.08)	5 (0.51)
Burkea africana	260 (84.42)	0 (0.00)	10 (3.25)	38 (12.34)
Combretum adenogonium	733 (83.96)	75 (8.59)	40 (4.58)	25 (2.86)
Terminalia spp.	350 (97.77)	8 (2.23)	0 (0.00)	0 (0.00)
Vitellaria paradoxa	2128 (93.17)	53 (2.32)	65 (2.85)	38 (1.66)

Table 4. The matrix cell reference labels for transition matrices **B** (a) and **U** (b) corresponding to the transitions on the life-history graph for the tree species in figure 2.

a
$$\begin{pmatrix} P_1 & R_1 & R_2 & R_3 + S \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix}$$

b
$$\begin{pmatrix} P_1 & 0 & 0 & S \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix}$$

different stage of the fire cycle. The probabilities for the two matrices (**B** and **U**) were calculated using the matrix cell reference labels presented in Table 4. *G* in all cases was estimated as the reciprocal of the duration of the height stages (assumed to be 5 years for all the height stages) in accord with Desmet *et al.* (1996); thus in 1 year, 1/5 or 20% of individual trees in height classes < 1 m, 1-2 m and 2-5 m would progress to the next higher height class. P_1, P_2 and P_3 were calculated as 1 minus the stage-specific mortality and topkill (or height reversal, *R*) and the relevant growth probability, *G*. P_4 was calculated as 1 minus the stage-specific mortality and topkill since it corresponds to the highest height stage. *R* in all cases represents individuals experiencing topkill and subsequently re-sprouting. Matrix **B** (Table 5) simulates dynamics in the year each respective tree population is burned. Burning occurs at the beginning of the one-year period simulated by **B**; so re-sprouting of topkilled individuals would occur during the period. Matrix **U** (Table 6) simulates the dynamics of unburned populations. The time period for the model was 1 year. Therefore, the calculated transition probabilities are expressed as the probability of a transition occurring during that time period. The derived transition matrices were subsequently analysed following the procedure outlined in Enright and Watson (1991) and Desmet *et al.* (1996).

Population projections
The transition matrices **B** and **U** were used to simulate the effects of different fire frequencies on the population dynamics of the five tree species. For instance, to simulate the population dynamics during a 4-year period in which burning occurs only in the fourth year, we use
$N_4 = \mathbf{B.U.U.U.N_0}$,
where $\mathbf{N_0}$ and $\mathbf{N_4}$ are the population vectors at year 0 and year 4, respectively.

To project the future population growth, the matrix manipulations were programmed using the Microsoft Excel spreadsheet software. With the spreadsheet software, the finite rate of natural increase, λ, never really stabilizes but changes constantly with time at a decimal accuracy beyond that required for a simple population model (Desmet *et al.*, 1996). Thus this did not constitute a drawback. Besides, the major object was to examine the behaviour of the transition matrix and the population vector elements over time and to determine the direction of change in the tree populations and how this change might respond to changes in fire frequency and impact. In order to avoid the interpretational problems associated with periodic matrix models as noted by Caswell and Trevisan (1994), the matrix manipulations were programmed with the transition matrices in tables 5 and 6 to simulate the exact burning frequencies instead of using the products of these matrices. For instance, to simulate the population dynamics under biennial fire frequency in

which burning occurs in the second year, the transition matrix **U** was multiplied by $\mathbf{N_0}$ (the population vector at year 0). The resulting population vector, $\mathbf{N_1}$, was then multiplied by the transition matrix **B** to obtain $\mathbf{N_2}$. This sequence of matrix manipulations was repeated until the change in λ was < 0.00005.

Table 5. Transition matrix (**B**) and column vectors for the five tree species simulating dynamics in the year each respective tree population is burned. The values in the columns for height classes 2 -5 m and > 5 m, and column vectors are derived from Sackey (2006), while those for height classes < 1 m and 1 − 2 m are from an unpublished study by Sackey and Imoro.

a) *Acacia dudgeoni*

Height class	< 1 m	1-2 m	2-5 m	> 5 m
< 1 m	0.4610	0.6300	0.0007	10.7167
1 – 2 m	0.0170	0.1232	0.0000	0.0000
2 – 5 m	0.0000	0.0308	0.7974	0.0000
> 5 m	0.0000	0.0000	0.1994	0.9000

b) *Burkea africana*

Height class	< 1 m	1 – 2 m	2 – 5 m	> 5 m
< 1 m	0.3910	0.5970	0.0010	1.3050
1 – 2 m	0.0040	0.0624	0.0000	0.0000
2 – 5 m	0.0000	0.0156	0.7882	0.0000
> 5 m	0.0000	0.0000	0.1970	0.9415

c) *Combretum adenogonium*

Height class	< 1 m	1 – 2 m	2 – 5 m	> 5 m
< 1 m	0.3398	0.6730	0.0032	3.7114
1 – 2 m	0.0072	0.1064	0.0000	0.0000
2 – 5 m	0.0000	0.0266	0.7945	0.0000
> 5 m	0.0000	0.0000	0.1982	0.9884

d) *Vitellaria paradoxa*

Height class	< 1 m	1 – 2 m	2 – 5 m	> 5 m
< 1 m	0.3786	0.5710	0.0047	4.2136
1 – 2 m	0.0104	0.2208	0.0000	0.0000
2 – 5 m	0.0000	0.0552	0.7941	0.0000
> 5 m	0.0000	0.0000	0.1985	0.9812

e) *Terminalia* spp.

Height class	< 1 m	1 – 2 m	2 – 5 m	> 5 m
< 1 m	0.4122	0.6620	0.0288	1.1020
1 – 2 m	0.0148	0.0083	0.0000	0.0000
2 – 5 m	0.0000	0.0332	0.7692	0.0000
> 5 m	0.0000	0.0000	0.1923	0.9667

Table 6. Transition matrix (**U**) for the five tree species simulating dynamics in an unburned year for each respective tree population.

a) *Acacia dudgeoni*

Height class	< 1 m	1 – 2 m	2 – 5 m	> 5 m
< 1 m	0.8000	0.0000	0.0000	10.7100
1 – 2 m	0.2000	0.8000	0.0000	0.0000
2 – 5 m	0.0000	0.2000	0.8000	0.0000
> 5 m	0.0000	0.0000	0.2000	1.0000

b) *Burkea africana*

Height class	< 1 m	1 – 2 m	2 – 5 m	> 5 m
< 1 m	0.8000	0.0000	0.0000	1.3000
1 – 2 m	0.2000	0.8000	0.0000	0.0000
2 – 5 m	0.0000	0.2000	0.8000	0.0000
> 5 m	0.0000	0.0000	0.2000	1.0000

c) *Combretum adenogonium*

Height class	< 1 m	1 – 2 m	2 – 5 m	> 5 m
< 1 m	0.8000	0.0000	0.0000	3.7100
1 – 2 m	0.2000	0.8000	0.0000	0.0000
2 – 5 m	0.0000	0.2000	0.8000	0.0000
> 5 m	0.0000	0.0000	0.2000	1.0000

d) *Terminalia* spp.

Height class	< 1 m	1 – 2 m	2 – 5 m	> 5 m
< 1 m	0.8000	0.0000	0.0000	1.0800
1 – 2 m	0.2000	0.8000	0.0000	0.0000
2 – 5 m	0.0000	0.2000	0.8000	0.0000
> 5 m	0.0000	0.0000	0.2000	1.0000

e) *Vitellaria paradoxa*

Height class	< 1 m	1 – 2 m	2 – 5 m	> 5 m
< 1 m	0.8000	0.0000	0.0000	4.2100
1 – 2 m	0.2000	0.8000	0.0000	0.0000
2 – 5 m	0.0000	0.2000	0.8000	0.0000
> 5 m	0.0000	0.0000	0.2000	1.0000

RESULTS

The intrinsic (r) and finite (λ) rates of increase, as well as the stable stage distribution (**w**) for the matrices in tables 5 and 6 are presented in tables 7 and 8. Generally, the results show that fire has an unambiguous effect on the population dynamics of all the study species.

Effect of fire frequency on population growth rate (λ)
The growth rate of all the species increased with decreasing fire frequency or increasing fire return interval. Qualitatively, the model results are similar for all the species under annual, triennial and quadrennial burning frequencies. The growth rate (λ) of all the species is < 1.00 under an annual burning event; thus all the species are predicted to decline, while λ > 1.00 is found under triennial and quadrennial fire frequencies and the

tree populations are predicted to increase. Despite these similarities in trend, there are important quantitative differences in the rates of population growth among the species. *Acacia dudgeoni* had the lowest growth rate under annual fire (0.924) and is expected to experience the steepest decline, while under triennial and quadrennial burning frequencies, it had the highest growth rates (1.694 and 2.433, respectively) and is predicted to experience the fastest increase in numbers. Generally, *Burkea africana* and *Terminalia* spp. are predicted to have the slowest increase in numbers under triennial and quadrennial fire frequencies.

The model outcome is, however, mixed for the species under biennial fire frequency. *Burkea africana* and *Terminalia* spp. are predicted to decline, while *Acacia dudgeoni, Combretum adenogonium* and *Vitellaria paradoxa* are expected to increase marginally. In summary, the model results indicate that the minimum fire return interval that will permit the persistence of *Burkea africana* and *Terminalia* spp. is 3 years, while that for *Acacia dudgeoni, Combretum adenogonium* and *Vitellaria paradoxa* is 2 years.

Effect of fire frequency on the stable stage (height) distribution (w)
The model results show a paucity of individuals (< 2.0%) in height classes 1-2 m and 2-5 m under annual burning for all the study species. The stable height distributions of *Acacia dudgeoni, Combretum adenogonium* and *Vitellaria paradoxa* are quite similar for all the burning frequencies, and have the typical inverted-J shape, while those of *Burkea africana* and *Terminalia* spp. have a pronounced U-shape under annual burning, becoming less of a pronounced U-shape with increasing fire return interval. This is partly due to the very low mortality and topkill rates of mature trees. The predicted height distributions of all the species were significantly different (Chi-square tests, P < 0.001) from the observed height distributions (Table 3) under all the four burning frequencies. Therefore, the predictions are that the current height distribution is not stable, whatever the burning regime in the future.

DISCUSSION

The model results predict that annual burning of the savanna near Grupe camp will lead to a decline in the woody plant density as predicted by Sackey (2006). All five study tree species are predicted to decline under annual burning. Although different in design and less sophisticated than the systems models of Norton-Griffiths (1979) and Pellew (1983), these model predictions broadly agree with those of these authors. The model of Norton-Griffiths (1979) predicted a rapid decline of the density of mature trees over 3m tall under 50% burning. Similarly, Pellew (1983) predicted a rapid reduction in the

total population of *Acacia tortilis* towards an eventual extinction under annual fire frequency. From matrix model projections, Hoffmann (1999) also predicted declines in the density of five woody plants under annual and biennial burning in the Brazilian cerrado.

The model results show that the minimum fire-free seasons required for the persistence of woody plants vary from one species to another, in agreement with the model predictions of Hoffmann (1999). In this regard, two species, *Burkea africana* and *Terminalia* spp. are the most critical, requiring a minimum fire-return interval of > 2 years, while 2 years minimum burning interval is predicted for the maintenance of *Acacia dudgeoni*, *Combretum adenogonium* and *Vitellaria paradoxa* populations. These differences in critical fire frequencies probably represent variations in fire susceptibility among the species and could be explored through further studies to formulate burning policy for the Park.

The discrepancies between the observed and predicted height distributions for all the species under all the simulated fire frequency regimes suggest that the tree populations are not in balance with the measured rates of growth, survival or reproduction or may well indicate that the life-history parameters of the tree species (tree survival, growth and seedling production) and, by inference, the environmental factors influencing them (e.g. rainfall, fire intensity and frequency) have not been constant as implied in the models, but have varied over time. The discrepancies could possibly indicate inaccuracies in the transition matrix elements arising from the fact that the estimated rates for tree survival derived from data presented in Sackey (2006) were not an accurate reflection of reality. Transition matrices derived from detailed, long-term population life-history data may be required to resolve this interpretational uncertainty.

Deterministic transition matrix models are concerned with revealing demographic information about the population under present conditions, rather than portraying the likely future appearance of the population under study (Enright and Watson, 1991). Thus, what can be concluded from the model results is that the savanna near Grupe camp will decline towards an open, grassy vegetation under annual or biennial burning, given that the measured rates for growth, survival and reproduction in the woody plants will remain constant through time. This conclusion raises one important question about the future of the woody vegetation of the area: will it be possible for the woody plants to persist under annual burning if the rates of growth, survival and reproduction vary over time? The most plausible answer to this question is yes. Within a relatively small vegetation unit, burning can be expected to be thorough. However, in large vegetation units there is bound to be increased variability in site conditions, and burning is more likely than not to be patchy and random.

Under such a site-specific random fire regime, there could be occasional fire-free intervals of long enough duration to permit occasional tree recruitment to ensure the maintenance of the woody plant populations even under frequent fires. As the model predictions suggest, fire-free intervals of up to 4 years may be enough to ensure the persistence of the woody plant populations. Such a circumstance has been demonstrated for *Miconia albicans* in the Brazilian cerrado by Hoffmann (1999).

The model results pose an important question about the future of the vegetation near Grupe camp *vis-à-vis* the annual burning policy of the Park management, as well as suggesting several important lines of further research. The model construction relied on some data that were collected at only one time instance, as well as several important assumptions. A larger series of matrices constructed with detailed long-term population life-history data that incorporate fire as a stochastic event would be an improvement. Also, the data incorporated in the model did not permit the examination of other sources of environmental variability, which may have possibly accounted for the discrepancies found between the observed and predicted stage class distributions. It would, therefore, be helpful to characterize the tree population response to other factors (e.g. rainfall) in addition to fire. Lastly, the model analyses did not address the important issue of density-dependent and competitive effects (population-regulation mechanisms) upon the life-history parameters of the tree populations, which may well be important.

Management implications of the results
In the Guinea savanna vegetation near Grupe camp with negligible numbers of large mammalian herbivores to reduce grass fuel, abundant regeneration of woody plants and poor recruitment of trees into large individuals, fire control remains the main viable measure to prevent the inevitable extermination of fire-sensitive woody species such as *Sterculia setigera* and *Parkia biglobosa* and vegetation transformation towards an open grassland, with a few scattered large trees. Although fire and elephant depredation are both regarded as natural ecological factors which have played significant parts in the realization of savanna plant communities, and are thus indispensable to their maintenance and survival, such extreme vegetation transformation is certainly at variance with the Park's objective of ensuring the conservation of wild genetic materials.

It is not certain what the burning frequency and intensity of the vegetation were before the designation of the area as a Game Reserve in 1958 and later a National Park in 1971, as no fire history exists for the entire area. Historically, the area which is now the National Park was fairly heavily populated by the Bole Division of the West Gonja tribe before 1870 (Hossain and Hall, 1996).

Table 7. Intrinsic rate of increase (*r*), finite rate of increase (λ) and the stable stage distribution (**w**) for the five trees species under different fire frequencies.

a) Annual fire frequency.

Plant species	*r*	λ	Stable stage distribution (%)			
			< 1 m	1-2 m	2-5 m	> 5 m
Acacia dudgeoni	-0.030	0.924	93.60	1.99	0.48	3.93
Burkea africana	-0.060	0.942	70.18	0.32	0.03	29.47
Combretum adenogonium	-0.010	0.990	84.54	0.69	0.09	14.68
Terminalia spp.	-0.032	0.968	66.11	1.12	0.17	32.71
Vitellaria paradoxa	-0.013	0.987	86.21	1.17	0.34	12.28

b) Biennial fire frequency

Plant species	*r*	λ	Stable stage distribution (%)			
			< 1 m	1-2 m	2-5 m	> 5 m
Acacia dudgeoni	0.160	1.173	90.37	3.80	2.35	3.47
Burkea africana	-0.034	0.967	75.49	1.41	1.42	21.68
Combretum adenogonium	0.067	1.069	84.59	2.61	2.12	10.67
Terminalia spp.	-0.004	0.996	72.46	1.38	1.92	24.24
Vitellaria paradoxa	0.134	1.144	82.06	4.88	3.73	9.34

c) Triennial fire frequency

Plant species	*r*	λ	Stable stage distribution (%)			
			< 1 m	1-2 m	2-5 m	> 5 m
Acacia dudgeoni	0.527	1.694	87.63	4.23	4.29	3.85
Burkea africana	0.107	1.113	73.47	2.00	5.40	19.13
Combretum adenogonium	0.298	1.347	81.39	3.46	5.26	9.88
Terminalia spp.	0.113	1.120	72.45	1.03	5.46	21.14
Vitellaria paradoxa	0.386	1.471	78.43	6.36	6.37	8.85

d) Quadrennial fire frequency

Plant species	*r*	λ	Stable stage distribution (%)			
			< 1 m	1-2 m	2-5 m	> 5 m
Acacia dudgeoni	0.889	2.433	85.96	4.36	5.53	4.15
Burkea africana	0.280	1.322	71.22	2.25	8.13	18.40
Combretum adenogonium	0.554	1.740	79.09	3.80	7.31	9.80
Terminalia spp.	0.271	1.312	70.38	1.31	8.23	20.09
Vitellaria paradoxa	0.650	1.915	76.21	6.97	8.00	8.81

Table 8. The population growth rate of the five tree species under the different burning frequencies.

Plant species	Population growth rate (λ)			
	Annual burn	Biennial burn	Triennial burn	Quadrennial burn
Acacia dudgeoni	0.924	1.173	1.694	2.433
Burkea africana	0.942	0.967	1.113	1.322
Combretum adenogonium	0.990	1.069	1.347	1.740
Terminalia spp.	0.968	0.996	1.120	1.312
Vitellaria paradoxa	0.987	1.144	1.471	1.915

According to Norton-Griffiths (1979), in the African savannas, other potent forces of disruption to vegetation succession besides elephants and fire are generated following the creation of new national parks, and for Mole, the sudden removal of human impacts (cattle grazing and harvesting of grass as thatch for roofing of houses) may have constituted a major disruptive force. Additionally, the skewed distribution of large mammalian herbivores towards the south-eastern section of the Park, where they are better protected from harassment by poachers, has meant very low grass off-take, and therefore, large amount of grass fuel to support annual intense fires in the vegetation to the southwest near Grupe camp and other areas. It is, therefore, plausible that fire intensities and extent have generally increased since the creation of the Park.

The most important question regarding burning in Mole concerns the frequency. There is every indication that fire frequency and intensity in the savanna near Grupe camp are high and detrimental and, therefore, require management action to reduce them if the Park's objectives are to be met. Complete protection of the entire savanna near Grupe camp, as well as other areas for which the findings of this study may be relevant over an extended period, is a counsel of perfection that will most certainly be rendered virtually unattainable by administrative and practical difficulties. In addition, an inappropriate fire regime may itself constitute a disruptive force to vegetation succession.

As the matrix population projection results suggest, a minimum fire-free interval of 3 years may be sufficient to ensure the maintenance of the main woody species. However, given the fact that other woody species (e.g. *Parkia biglobosa* and *Sterculia setigera*) are less fire-tolerant than the five study species, a minimum fire return interval of > 3 years may be required to permit the persistence of the majority of the woody species. It would, therefore, seem feasible to attempt complete protection in relatively small blocks on a rotational system that would achieve a burning frequency of 3-5 years, depending on the conditions of the vegetation and other factors such as rainfall. This will allow the abundant coppice re-sprouts adequate time to attain a size that will make them less sensitive to fire impacts, thereby increasing tree recruitment potential. Additionally, seedling input will increase through increased seed production and seedling survival rate. In this regard, the existing fire-break at the south-western boundary of the Park should be properly maintained and extended further northwards to prevent uncontrolled anthropogenic fires from outside the park boundary escaping into the Park. Additional fire-breaks should be created and properly maintained around the demarcated vegetation blocks.

Also, regular monitoring of the area should be undertaken during the dry season so as to deter poachers who constitute the major cause of wildfire that is started within the Park and also to deal with any fires from accidental causes (e.g. spotting[1]) or fires from natural causes such as lightning.

CONCLUSION

In Mole National Park, the policy is to burn the vegetation annually early in the dry season. The long-term effect of this annual burning policy of the Park's management is likely to be a vegetation transformation from a savanna woodland to a grassland with only a few woody elements. This prediction is supported by the matrix model projections, and is consistent with the results of several studies (e.g. Trapnell, 1959; Charter and Keay, 1960; Ramsay and Rose-Innes, 1963; Hopkins, 1965; Brookman-Amissah *et al.*, 1980; Hoffmann, 1999). The model results also suggest that the minimum fire-free interval required for tree population maintenance varies from species to species, and demonstrate the potential of matrix population models as a tool for determining appropriate burning frequencies for different vegetation units in conservation areas located within the savanna ecosystem. The findings indicate a minimum fire-free interval of at least two years for the maintenance of all the five tree species.

ACKNOWLEDGEMENT

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[1] The initiation of a new fire ahead of a main fire by an airborne firebrand or ember (Luke and McArthur, 1978).

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