

Survival, regeneration and leaf biomass changes in woody plants following spring burns in *Burkea africana*—*Ochna pulchra* Savanna*

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ABSTRACT

Effects of two intensities of spring burn on various aspects of woody plants of a *Burkea africana*—*Ochna pulchra* Savanna after one growth season are given. Mortality of woody plants was very low with, for example, that of individuals of *Ochna pulchra* being between 1 and 5%. Some species where the above-ground parts were often burned away completely, as in *Grewia flavescens*, no mortality of individuals occurred. Basal regeneration shoot mass was found to depend parabolically on plant height while the ratio of leaf to twig mass in basal shoot regeneration varied inversely with plant height in *Ochna pulchra*. The ability of *Ochna pulchra* plants to produce new basal shoots appeared to not only depend on size of the plant but also on the number of basal shoots present prior to the fire. In live *Ochna pulchra* plants basal regeneration shoot biomass per individual was found to increase exponentially with greater reduction in canopy leaf biomass. This relation was also affected by possible direct heat effects. Basal shoot regeneration mass was found to vary greatly with species and varied from 0.7 g/individual for *Dichapetalum cymosum* to 285.6 g/individual for *Euclea natalensis*. There was a clear tendency for non-suffrutex shrub species to have greater mean basal regeneration shoot mass per plant than that of most tree species. There was a compensatory effect in *Ochna pulchra* between number and size of basal regeneration shoots. Standing dead woody plant individuals (before the burn) were either felled by fire or apparently unaffected by fire and there was no selectivity by species. Results of the present study are generally supported by other work on the effects of fire in savanna and some other vegetation types.

RÉSUMÉ

SURVIVANCE, RÉGÉNÉRATION ET CHANGEMENTS DE BIO-MASSA DE FEUILLE DANS LES PLANTES LIGNEUSES À LA SUITE DES BRULÂGES DE PRINTEMPS DANS LA SAVANNE BURKEA AFRICANA—OCHNA PULCHRA

Les effets de brulage de printemps de deux intensités sur les aspects variés de plantes ligneuses de savannes *Burkea africana*—*Ochna pulchra* après une saison de croissance, sont donnés. La mortalité des plantes ligneuses fut très faible avec, par exemple, celle des individus d'*Ochna pulchra* situant entre 1 et 5 %. Certaines espèces dont la partie au dessus du sol était souvent complètement brulée, comme *Grewia flavescens* ne montrèrent aucune mortalité des individus. On trouva que la régénération de base des masses de rejets dépendait paraboliquement de la hauteur de la plante tandis que le rapport de feuille à la masse de brindille dans la régénération des rejets de base variait inversement avec la hauteur de la plante chez l'*Ochna pulchra*. L'aptitude des plantes d'*Ochna pulchra* à produire de nouveaux rejets de base apparait non seulement dépendre sur la taille de la plante mais aussi sur le nombre de rejets de base antérieurement présents au brulage. Chez les plantes d'*Ochna pulchra* en vie, la bio-masse des rejets de régénération de base par individu fut trouvée s'accroître exponentiellement avec une réduction plus grande dans la bio-masse des feuilles du couvert. Cette relation fut aussi effectuée par des effets possibles de chaleur directe. La masse de régénération des rejets de base fut trouvée varier considérablement avec les espèces et elle varia de 0,7 g/individu pour le *Dichapetalum cymosum* à 285, 6 g/individu pour l'*Euclea natalensis*. Il y eut une claire tendance pour les espèces de buissons non-sous-arbriseaux à avoir une plus grande moyenne de masse de rejets de régénération de base par plante que celle de la plupart des trois espèces. Il y eut un effet compensatoire dans l'*Ochna pulchra* entre le nombre et la taille des rejets de régénération de base. Les individus morts de plantes ligneuses debouts (avant le brulage) furent soit abattus par le feu ou apparemment pas atteints par le feu et il n'y avait pas de sélectivité par les espèces. Les résultats de la présente étude sont généralement soutenus par d'autres travaux sur les effets des feux de savanne et certaines autres catégories de végétation.

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1. INTRODUCTION

Fire has probably occurred regularly in the savannas of southern Africa, initiated first by agencies such as lightning and later increasingly by man. The structure of savanna is probably related to this incidence of fire. In the past fire, once started, could spread over vast areas of savanna but more recently fire is often contained by artificial fire breaks such as roads. Fire is used as a veld management tool for both livestock farming and wildlife conservation. The two main objectives of burning savanna for livestock farming are to remove moribund grass and to decrease the woody plant element. In wildlife management these two objectives are also important, but additional reasons include encouraging some form of rotational grazing, reducing the wild-fire hazard and controlling animal diseases and parasites (Trollope *et al.*, in press). In the savannas of the central-northern areas of the Transvaal the current frequency of fire is extremely variable from annually to only every few decades in more protected areas although the more common frequency may be described as between one and five years. Fires in savannas are usually surface fires, and crown fires are very rare although localized burning of canopies can occur. Controlled fires are almost always applied in or near the dry season, usually between May and November in southern African savanna vegetation areas. In these areas it is generally recognized that a fire earlier in this period is less effective in controlling tree growth than a fire later in this period (West, 1965). Effectiveness of late burns as a means of woody plant control is usually ascribed to the fire being hotter and the trees being more susceptible to heat injury at a time when growth has just started. However, Deeming *et al.*, (1972) point out that this stage of plant development (the rapid growth stage) indicates a 'high moisture content throughout the plant' which (as in other living fuels) acts as a heat sink since it takes considerable amounts of energy to dessicate this material. Only after dessication can such material itself act as a heat source. In contrast to burning in the dry season, it has been found (Anon, 1960) in the Transvaal lowveld that very little damage is done to trees and shrubs during late summer (February) veld burning when grass is green.

That fire can fundamentally affect many components of an ecosystem has long been recognized. Interest has been shown in many diverse effects, for example, the cycling of nutrients (Trapnell *et al.*, 1976; Christensen, 1977), changes in the water balance and the possible effects on past carbon dioxide changes in the atmosphere (Reiners & Wright, 1976), while work on woody plants has included classifying savanna woody plant species according to different degrees of fire tolerance with the study of the evolution of pyrophytic habits (Jackson, 1974), derivation of allometric fuel load prediction formulae (Kaul and Jain, 1967), modelling fuel mass (McNab *et al.*, 1978) and determining fire scar tree ring chronologies (Zackrisson, 1977).

The scientific Committee on Problems of the Environment (set up by the International Council of Scientific Unions) informally co-ordinates as part of its mid term project 2 a short term (1977–80) international programme for the review of the ecological effects of fire. South African participation in this programme is co-ordinated by the Working Group for Fire Ecology of the Committee for Terrestrial Ecosystems initiated by the National Programme for Environmental Sciences of the Council for Scientific

and Industrial Research. The present paper forms part of the contribution by the South African Savanna Ecosystem Project on the ecological effects of fire (Anon, 1978). Results of an experimental burn within the South African Savanna Ecosystem Project are being prepared for publication as a synthesis report by M. V. Gandar (in press) where an overview is given of effects of fire on the abiotic, decomposer, primary producer and consumer components of the ecosystem. The present paper is limited to the more detailed effects of fire on the woody plant component.

The South African Savanna Ecosystem Project is being conducted on a portion of the recently-established Nylsvley Nature Reserve (3 120 ha in extent), 10 km south of Naboomspruit in the northern Transvaal. The basic ecological characteristics of the study area are described in Huntley and Morris (1978) while the project's overall objectives and research programme are outlined in Huntley (1978).

The study area lies on the edge of the Springbok flats on a slightly raised plateau at about 1 100 m above sea level. Most of the Waterberg System sandstone bedrock is covered by sandy soils belonging mainly to the Hutton and Clovelly forms (Harmse, 1977). Mean annual rainfall is about 630 mm and occurs mainly in summer. The mean annual air temperature is 18.6°C. The study site's past management has included light summer grazing by cattle with small populations of impala and fluctuating populations of kudu present. The main vegetation type of the study area has been classified as *Eragrostis pallens*—*Burkea africana* Tree Savanna (Coetsee *et al.*, 1976) with the most extensive variation of this being the *Eragrostis pallens*—*Dombeya rotundifolia* variation with dominant trees *Burkea africana* and *Terminalia sericea* and dominant shrubs *Ochna pulchra* and *Grewia flavescens*. Huntley (1977) has suggested that the broad-leaf savanna of the study site is related to the mesic and moist broad-leaf savanna biome of Africa. In the year before the experimental burning, there had been no grazing by cattle in the area to be burned. Since the area had been unburned for some years and had a recent history of very low grazing pressure the graminoid fuel load was probably above average for the given type of vegetation although the nutrient-poor sandy soils may be expected to result in a generally lower heat intensity and slower fire than in several other vegetation types (Anon, 1960). The presence of trees also tends to result in a reduction in graminoid fuel load beneath them so that intensity and frequency of burning may be expected to be reduced by the trees (West, 1965). Given the tree leaf litter input each year (from June to August) and the relatively low decomposition rates (especially for leaves of *Ochna pulchra*), thick layers, sometimes up to 10 cm deep, occurred below certain trees. On the whole, the ground fuel composition of the experimental site was mixed with graminoid, tree leaf litter and some wood pieces of varying dimensions.

The main objectives of the present study were to determine the short term effects of two intensities of spring burn on the individuals of each woody plant species population in a selected area of the Nylsvley study site, with particular attention being given to mortality/survival, degree of canopy reduction, degree of basal regeneration, changes in leaf biomass and to relationships between these aspects.

2. SELECTIVE LITERATURE REVIEW

Work on the effects of fire on individual woody plants in African savanna appears to have been mainly concentrated on mortality or survival of plants after fire. Less attention has been given to effects of fire on plant canopies and the stimulation of basal shoots. Very little work has apparently been done on establishing and quantifying the interrelationships between different plant dimensions and mass components after fire (pyro-allometry). Such relations may be used to predict, for example, the degree of dependency of leaf mass re-distribution within the plant on the size of the plant following fire. The limited effort in this last mentioned respect possibly relates to the difficulties involved in determining the fire effects on the different organs of the woody plant individual and to the variable degree to which ground fires reach into the canopy stratum of woody vegetation as well as to the often very heterogeneous spatial distribution of woody plants in savannas. Published work on the particular fire effects and plant species considered in the present study has included various, sometimes conflicting, findings.

a) Mortality/survival of plants after fire

Relatively low mortality of some woody savanna plants with fire has been indicated by, for example, the classification in Malawi of *Burkea africana* as a 'pyrophytic' species (Jackson, 1974). In the Kavango region of South West Africa, Geldenhuys (1977) tested for mortality in *B. africana* with fire in an analysis of co-variance and despite the high proportion of dead trees (35.3% at Rundu), this was not attributable to treatment. Of the four most common woody plant species in a Nigerian savanna after annual (late winter) burns for five years, only *B. africana* had all individuals (from 4 to 13 m height) survive. *B. africana* increased relative to the other species with fire and it is suggested that it is through better adaptation to fires that certain *B. africana* savannas may have arisen (Hopkins, 1965). In contrast to the above findings, van Rensburg (1971) reported that some *B. africana* trees 'were damaged and killed' in *Terminalia sericea* Woodland on sand in eastern Botswana after an April burn (toward the end of the normal rainy season). However, mortality of *Burkea africana* trees has been reported to be not necessarily linked to the effects of the fire in several areas (Rutherford, in press). Tinley (1966) only refers to coppices of *B. africana* being 'very sensitive to fire' in the northern Okavango Swamps of Botswana.

Effects of long-term application of fire may differ from the expected short-term effects. Thus, for example, in *Terminalia sericea*—*Burkea africana* Savanna at Matopos, Zimbabwe, Kennan (1971) reports fewer trees present in long-term fire treated plots than in fire protected plots. There was also a much smaller proportion of those trees below 0.9 m in height in the fire treatments than in the protected plots. In *Burkea africana*—*Terminalia avicennoides*—*Detarium microcarpum* Savanna Woodland in Nigeria, Afolayan (1978) found that annual 'late' (presumably late in the dry season) burning for four years decreased tree density particularly for trees less than 10 cm girth at breast height.

The effect of fire on seedlings has been observed in Matopos savanna, Zimbabwe, where burning at three year intervals resulted in many tree seedlings being killed (West, 1965).

Other woody plant species in the present study have been characterized on other sites in terms of

their ability to withstand fire. In the Transvaal lowveld, Van Wyk (1971) reported that *Terminalia sericea* and *Dichrostachys cinerea* were to a 'certain extent fire resistant' and despite burning to ground level sprouted vigorously after the burn. In Zambia, Trapnell (1959) found that 'the fire-tolerance of *Dombeya rotundifolia* has been confirmed by repeated field observation', and that *Strychnos pungens* was semi-tolerant with *Lannea discolor* probably also so. Lawton (1978) includes *Ochna pulchra*, *Strychnos pungens* and *Burkea africana* in a group that can survive intense dry season fires in parts of north-eastern Zambia. In Wankie National Park, Zimbabwe, Rushworth (1978) found that *Terminalia sericea* and *Ochna pulchra* were 'strikingly frost hardy' and points out the similar coppicing reaction of some other species due to both frost and fire. Geldenhuys (1977), in two regularly burnt areas of the Kavango region of South West Africa/Namibia, refers to *Ochna pulchra* as a 'fire-sensitive' species. However, it appears that this finding might be limited to trees with measurable diameter at breast height.

Many other woody plant species in African savanna also appear to be relatively tolerant of fire. Thus in *Acacia thornveld* (*A. karroo*) at Matopos, complete killing of woody plants by fire of various fire regimes was extremely rare and nearly all affected plants regrew vigorously from their undamaged bases after the fire (Kennan, 1971). In eastern Cape *Acacia karroo* vegetation, Trollope (1974) found in a spring head fire that mortality of *A. karroo* was 9.9% of which more than three-quarters of the plants were between 1 and 2½ m tall. In the Molopo area of the northern Cape, Donaldson (1966) reported that even with dry grass artificially packed around the base of *Acacia mellifera* subsp. *detinens* plants, the grass burns (at various times of the year) only resulted in a mortality of about 15%. Only when large amounts of wood and twigs were burned at the bases did a 75% mortality obtain here due to much longer duration of heat. In other African savannas, *Pterocarpus angolensis* has been classed as 'fire-tolerant' (Zambia: Trapnell, 1959) and in east Africa *Balanites aegyptiaca* Savanna no evidence was found of the death of mature trees being affected by a mainly annual fire regime (Harrington & Ross, 1974). Although Trapnell (1959) reported the dominant canopy species of *Brachystegia*, *Julbernardia* and *Isobertlinia* (in Zambia) to be 'fire tender' (but not 'fire intolerant'), West (1971) states that some of these are 'extremely fire tolerant' but states that even these will eventually be eliminated by sufficiently regular, intense, late dry season burns every year. At Matopos, Kennan (1971) found 'that burning had much the same effect on the sandveld trees as in the thornveld ...' so that mortality in the sandveld woody plants was presumably also very low. The relatively high fire tolerance of woody plants of the present study and other savanna woody plant species is not limited to Africa. For example, in a Texan *Pinus taeda*—*P. echinata* forest with a head fire, it was found (Stransky & Halls, 1979) that of the 10 most important understorey woody plant species, three (for example, *Cornus florida*) had zero mortality and all others except one had less than 32% mortality.

A possible effective adaptation to fire in savannas is the suffrutex or 'underground tree' form such as that of *Dichapetalum cymosum* that West (1971) has suggested as a possible evolutionary adaptation that resulted in evading fire. The reaction of trees to fire

and the possible fire adaptations have resulted in many savannas being regarded as seriously limiting the effectiveness of fire alone as a woody plant controlling mechanism for management purposes, for example, in eastern Cape *Acacia karroo* Savanna (Du Toit, 1972a) and *Brachystegia spiciformis*—*Julbernardia globiflora* Savanna of the Zimbabwe highveld (Barnes, 1965). In the latter area, burning intervals longer than annually have been found to be ineffective in preventing coppice becoming increasingly vigorous (Barnes, 1965). However, Van Wyk (1971) stated that in *Dichrostachys cinerea*—*Terminalia sericea* Savanna in the Transvaal lowveld, burning as little as every three years resulted in plants seldom escaping the regular damage to reach maturity. It appears that fire as a tool for the management and control of undesirable woody plants differs in its effectiveness according to area and conditions of application.

b) Effects of fire on plant canopies

Fire often greatly affects the canopy of woody savanna plants, particularly those of smaller plants. After a hot November burn in *Burkea africana* Savanna in South West Africa, canopy (but not plant) mortality of the plants less than 2 m tall was greater than 75% for each of the 4 most common woody species (*Burkea africana*, *Terminalia sericea*, *Combretum psidioides* and *Ochna pulchra*) with most (90%) for *Ochna pulchra* (Rutherford, 1975). In the Transvaal lowveld Van Wyk (1971) reported that *Terminalia sericea* (and *Dichrostachys cinerea*) plants of up to about 1,2 m were generally burnt back to ground level although some *Terminalia sericea* trees up to 3,7 m height had also been burned back. In eastern Cape *Acacia karroo*, 95% of canopy mortality after fire was limited to plants under 2,5 m tall (Trollope, 1974). In *Burkea africana* Savanna (regularly burned at the end of the dry season) at Makambu, Kavango in South West Africa, Geldenhuys (1977) found that for shrubs and trees (with stems less than 5 cm DBH) canopy volume dropped by two-thirds relative to that of the control. Mean height of this plant group was 0,9 m compared to 2,2 m of those of the control, that is a decrease of about 60%. That fire generally reduces the canopy heights of lower woody vegetation in many other regions is supported by studies such as that in a Texan forest fire (Stransky & Halls, 1979) where for the ten most important understorey woody species height decreased by 41% from 4,4 m to 2,6 m.

After a hot November burn in a *Burkea africana* Savanna in South West Africa, canopy mortality of *Securidaca longipedunculata* plants greater than 2 m tall was the lowest of six species, namely zero per cent (Rutherford, 1975).

In *Acacia* veld at Matopos, Kennan (1971) states that in the case of larger trees, burning invariably caused complete defoliation ('if they were in leaf when burning took place') but seldom did more than to kill branches up to a height of about 1,8 m. However, in the eastern Cape, it was found that canopy mortality of surviving individuals of *Acacia karroo* was 79% (Trollope, 1974). Donaldson (1966) found with burning *Acacia mellifera* subsp. *detinens* in the northern Cape with fuel (grass, wood, dung or sawdust) at the base of the plants, that generally there were total 'top-growth kills'.

Although it is clear from the evidence that fire may be expected to reduce canopy leaf biomass, it appears that the effect on radial stem growth may be different

since in the Kavango region of South West Africa it was found that there was no significant effect of annual fire treatments on stem basal area increment over a nine year period in *Burkea africana* and other species investigated (Geldenhuys, 1977) while also in Nigerian savanna it was found that controlled burning early in the dry season would permit an increase in established trees' basal area (Kemp, 1963).

c) Fire and basal shoots

In many studies it has been found that the number of stems are likely to increase with fire. For example, in a Texan forest fire mean stem number of the ten most important understorey woody plant species increased from 1,5 to 2,1 with a maximum increase for one species (*Ilex vomitoria*) from 2,2 to 5,1 (Stransky & Halls, 1979). A common phenomenon under total fire protection in savanna, is for woody thickets to tend to develop. However, Harrington (1974) points out that in Uganda despite the densest appearance of *Acacia hockii* in an unburnt treatment (relative to that in several burning regimes) it had the lowest number of stems per bush (and the lowest number of bushes per hectare).

After a hot November fire in a *Burkea africana* savanna in South West Africa, it was found that of the three species *Terminalia sericea*, *Burkea africana* and *Ochna pulchra*, the first mentioned had the greatest percentage of plants with basal regeneration shoots present (Rutherford, 1975). In scrub sand veld savanna in Wankie National Park, Zimbabwe, Rushworth (1975) found that whereas the mean number of new coppice stems produced on *Terminalia sericea* in an area unburned for at least eight years was zero, those burned in just under three months prior to measurement (an early October burn) was 20,33 (versus 0,05 in an area with approximately the same burning history as above but without the October burn). Van Wyk (1971) has reported vigorous sprouting of *Terminalia sericea* after a burn in the Transvaal lowveld. Donaldson (1966) has also commented that the multistemmed *T. sericea* of the Molopo area of the northern Cape have possibly resulted from periodic grassfires in the past.

Interrelationships after fire

After a hot November burn in *Burkea africana* Savanna in South West Africa, data showed that a higher percentage of plants with canopies killed had basal regeneration shoots present than those with canopies that survived for all species investigated (Rutherford, 1975). These included *Burkea africana*, *Terminalia sericea* and *Ochna pulchra*. In eastern Cape savanna, Trollope (1974) showed that after a spring head fire, of those *Acacia karroo* trees that survived and had formed basal regeneration shoots after the fire, 86% had canopies killed leaving only 14% with live canopies. James & Smith (1977) state that 'extensive suckering does not usually occur after low-intensity fires' while Farmer's (1962) work on *Populus tremuloides* demonstrated that suckering was related to the reduction of apical dominance by damage to the above ground parts.

3. METHOD

a) The two burns

Three one hectare square blocks of Camp 2 of the Nylsvley study area were burned separately before the remainder of the camp on September 5, 1978. All work on the woody plant species was done in two of

these hectare blocks which were about 1 km apart. Both areas were ignited at one side of the hectare block with flame-throwers directed at the herbaceous layer which allowed the fires to rapidly attain their maximum intensities. Plot 1 was ignited at 19h01 and plot 2 at 18h00. The mean windspeed at 2.0 m above ground from 12h00 on September 5, 1978 to 07h00 September 6, 1978 was 1.8 ms^{-1} (Harrison, 1978). Both fires were ignited as head fires (burning in the same direction as the wind) although in plot 1 there was some degree of backburning (burning in the opposite direction to the wind) of some islands left unburned after the main flame front had past. At 19h00 (corresponding to time of burn in plot 1) screen climatic data gave: air temperature 17.2°C ; relative humidity 33%; vapour pressure 6.4 mb and saturation vapour pressure deficit 13.1 mb. At 18h00 (corresponding to time of burn in plot 2) screen climatic data gave: air temperature 19.0°C ; relative humidity 28%; vapour pressure 8.5 mb and saturation vapour pressure deficit 13.3 mb (Harrison, 1978). Mean moisture content of plants (mainly grasses) of the herbaceous layer one week prior to the fires was 4.2% (Grunow and Grossman, 1978). Estimated ground fuel loads (see Section 3c) showed more frequent higher levels in plot 2 than in plot 1. Fuel loads were sometimes very localized, for example, typical individuals of the shrub species *Grewia flavescens* (type 1, less than 2.5 m height, — Rutherford, 1979) had $4\,800 \text{ gm}^{-2}$ of thin finely divided standing dead wood on the area they covered. Other areas were sometimes virtually bare, that is, less than 10 g of dry herbaceous material for individual square metres. Data on mean herbaceous layer dry mass per unit ground area are not available for the two plots but from many other clipping studies (Huntley & Morris, 1978) on the study site, the mean mass of the standing dead grass lay between 50 and 125 gm^{-2} . Ladder fuel in larger trees was rare, that is, there was usually no continuous fuel path from the herbaceous layer to the tree canopy.

Differences in the behaviour of the burns are given in Table 1. The burn in plot 2 was more than five times faster, fire temperatures were higher, flame heights were greater and burning on an area basis more complete than in plot 1. Although on the basis of these data the fire in plot 2 might be regarded as more intense than in plot 1, because of difficulties in averaging the great differences in heat intensity at different levels above ground, the fire in plot 1 is referred to as the slower burn and that in plot 2 as the

faster burn. This designation may be appropriate since speed of fire (whether 'self' generated or wind induced) appears to be important to fire behaviour. That head fires are faster than back fires is commonly observable. Trollope (1978) found greater flame lengths in head fires and a positive correlation between rate of spread and flame height and maximum temperatures at grass canopy height in head fires. In laboratory simulated experiments, Gill (1974) indicated an increasing flame height with increasing wind speed (up to 0.48 ms^{-1}). Wind affects fire behaviour by increasing the flow of oxygen to the fire and (in a head fire) wind bends the flames over the unburned fuel and increases the flow of hot gases from the combustion zone; both processes contributing to the pre-heating of the unburned fuels (Deeming *et al.*, 1972) which is particularly important for realizing the potential of water-conducting woody material as fuel.

b) Experimental layout

The two plots selected, contained woody and herbaceous elements that were floristically and structurally typical of the Nylsvley study area vegetation. Since the method of recording certain aspects of the plant was different for tree individuals and multistemmed shrubs (see next section) data were processed separately for these two groups but so as to prevent the same species from occurring in both groups, the groups were defined as the tree species group, that is, individuals that were trees or normally have the potential to grow into tree-sized individuals; and the multistemmed shrub species group whose members seldom form tree-sized individuals on the Nylsvley site. In the slower burn area, tree species were (in order of abundance): *Ochna pulchra*, *Burkea africana*, *Terminalia sericea*, *Strychnos pungens*, *Securidaca longipedunculata*, *Dombeya rotundifolia* and *Dichrostachys cinerea*. The multistemmed shrub and suffrutex species were: *Grewia flavescens*, *Fadogia monticola*, *Lannea discolor*, *Euclea natalensis* and *Vitex pooara*. In the faster burn area tree species were (in order of abundance): *Ochna pulchra*, *Burkea africana*, *Terminalia sericea*, *Vitex rehmannii*, *Dombeya rotundifolia*, *Strychnos pungens*, *Securidaca longipedunculata*, *Combretum molle*, *Strychnos cocculoides*, *Acacia caffra*, *Ximenia caffra*, *Sclerocarya caffra* and *Pappea capensis*. Multistemmed shrub and suffrutex species were: *Grewia flavescens*, *Dichapetalum cymosum*, *Euclea natalensis*, *Fadogia monticola* and

TABLE 1.—Differences in fire behaviour characteristics between two plots

	Time for main flame front to pass over one hectare square block * (minutes)	Mean tempil plate temperature (°C) +	Incidence of aluminium plate ** melting (at 20 cm above ground), i.e. $>660^{\circ}\text{C}$ (%)	Estimated flame height *		Estimated ground level fuel load ***	% of tagged woody plants remaining on unburned islands
				mean (m)	max (m)		
PLOT 1	11	<260	0.52% (n = 407)	1–2	5	low	37
PLOT 2	2	± 350	1.46% (n = 412)	2–3	8	medium	3

* B.J. Huntley (pers. comm.)

+ Harrison (1978)

** Plates described section 3b

*** Estimates described section 3c

Asparagus suaveolens. Typical structural features of the vegetation can be seen in the photographs (Figs. 1–6). At the time of the fire many of the woody plants, particularly those of *Ochna pulchra*, were starting to unfurl new leaves. The most advanced leaves on some individuals of *O. pulchra* were about 2 weeks old. All the more common species (except *Strychnos pungens*) had dropped their old leaves before the fire so that almost all of the woody plant leaves formed in the previous growing season were already added to the fuel load on the ground prior to the fire. Also present at the time of the fire were a few woody plant seedlings, mainly those of *Burkea africana*. The dominant grass in both burn plots was *Eragrostis pallens*.

In each plot a subplot of 30 × 50 m was placed centrally and demarcated. In the subplots all sizes of standing individuals of woody plant species were tagged with numbered aluminium plates (either on 20 cm high stakes at the base of smaller individuals (Fig. 1) or on to the trunk of large individuals) in one half of the area. All individuals equal to or larger than 2 m height were tagged in the other half to increase the

area. The individuals of this new control set were geographically close to the burn treatments, probably had a very similar treatment history in the past and were also measured in exactly the same way and time as the burned individuals. It transpired that the effects of fire were so profound that differences between treatment and control were usually so great that statistical analyses of most differences, especially those concerning basal regeneration, were superfluous. The control in many respects only served to confirm the obvious. References to unburned control data are thus kept to a minimum with more attention being given to the differences between the two burns.

c) Measurements

Recordings of plants were made, (i) shortly before the burns, (ii) just after the burns, (iii) at monthly intervals after the burns and (iv) after completion of one season's growth but before commencement of leaf fall. Most detailed measurements were made in periods (i) and (iv).

One to two weeks before the burns, each woody



FIG. 1.—A view on the 6th September after the fire of part of one of the burned areas revealing aluminium tags marking small woody plants normally largely concealed in the herbaceous layer.

sample size of the larger individuals. All standing dead individuals equal to or larger than 2 m height in the remainder of each one hectare plot were also tagged and numbered. In the slower burn plot there were altogether 607 tagged individuals in the subplot and two additional dead individuals in the rest of the hectare plot. In the faster burn plot 425 individuals were tagged in the subplot and an additional 12 dead individuals in the remainder of the plot. Altogether 1 046 individuals were thus tagged for recording the effects of fire. The day following the burns it was found that in the slower burn area 37% and in the faster burn area 3% of tagged individuals had escaped the fire altogether on large unburned islands with each of these individuals having no vegetation burned on their canopy ground projection area. Since such a relatively high proportion of individuals was altogether untouched by fire, it was decided to use these unburned individuals (from both plots) as a control rather than the originally envisaged tagged individuals already being monitored as part of a separate programme in Camp 3 of the Nylsvley study

plant individual was allocated a numbered aluminium tag, and the tag position was also recorded for relocating the plant later. The species and live or dead state of the plant was recorded. Also measured were height of plant above ground level, number of live basal shoots (these constituted the whole individual in small non-canopied individuals) and number of dead basal shoots. Estimates were made of the proportion of canopy volume that was dead using a five point scale (0–9,9; 10–34,9; 35–64,9; 65–89,9; 90–100%) based on zones of dead twigs. Also estimated was the relative amount and composition of ground layer fuel load under the individual on a three point scale and with 3 type classes, namely, woody plant leaf litter, dead standing grass and pieces of wood material (e.g. Fig. 2). This ground layer fuel classification only applied well to individuals up to about 2½ m height. The area under large individuals was relatively large with often great differences in ground fuel load under the same tree. Photographs of various parts of the vegetation were taken from reference positions.



FIG. 2.—A pair of *Burkea africana* stems to the left of centre; a stem of a *Securidaca longipedunculata* tree on the right; *Ochna pulchra* individuals immediately behind and to both sides of the *Securidaca* stem and dead fallen branches of *Burkea africana* in the right foreground, showing: a, on the 5th September before the burn the relatively high fuel load; b, on 6th September after the burn, the ash production from burned, fallen branches also showing the incomplete burn of other branches; c, on 6th February at the end of the growth season and the basal regeneration from the *Burkea* stems and the appearance of the new grass cover.

One and two days after the burns, all labels were checked for legibility and position and a few replaced where necessary. Whether the plant was burned or totally untouched by fire was recorded as was an estimate of degree of burn namely: burned, for a broad class including plants that fire had touched at least at some point of where ground fire occurred under at least part of the canopy; severely burned for plants where most leaves or other parts of the plant were at least severely scorched; and completely burned where the plant's aboveground parts were completely burned away or at most only a very short stub (1 or 2 cm high) remained. Photographs were taken from the reference positions.

At monthly intervals for six months following the burns, the photographs of selected components of

vegetation were taken from the reference positions. Checks of animal (almost entirely insect) browsing of leaves were made to confirm that this remained at a low level (less than 5%) so that leaf changes could be attributed to fire effects.

Six months after the burns (March), the following were recorded for all tagged individuals: species (a recording check); live or dead state of plant; canopy live or dead; height of top parts of canopies; diameter of stem at 20 cm above ground level (for all stems >1.0 cm diameter); number of new basal shoots; number of old basal shoots still present; number of basal shoots killed by the fire and still present; number of old dead basal shoots that survived the fire; estimation of proportion of original canopy volume dead (this was difficult to apply in species

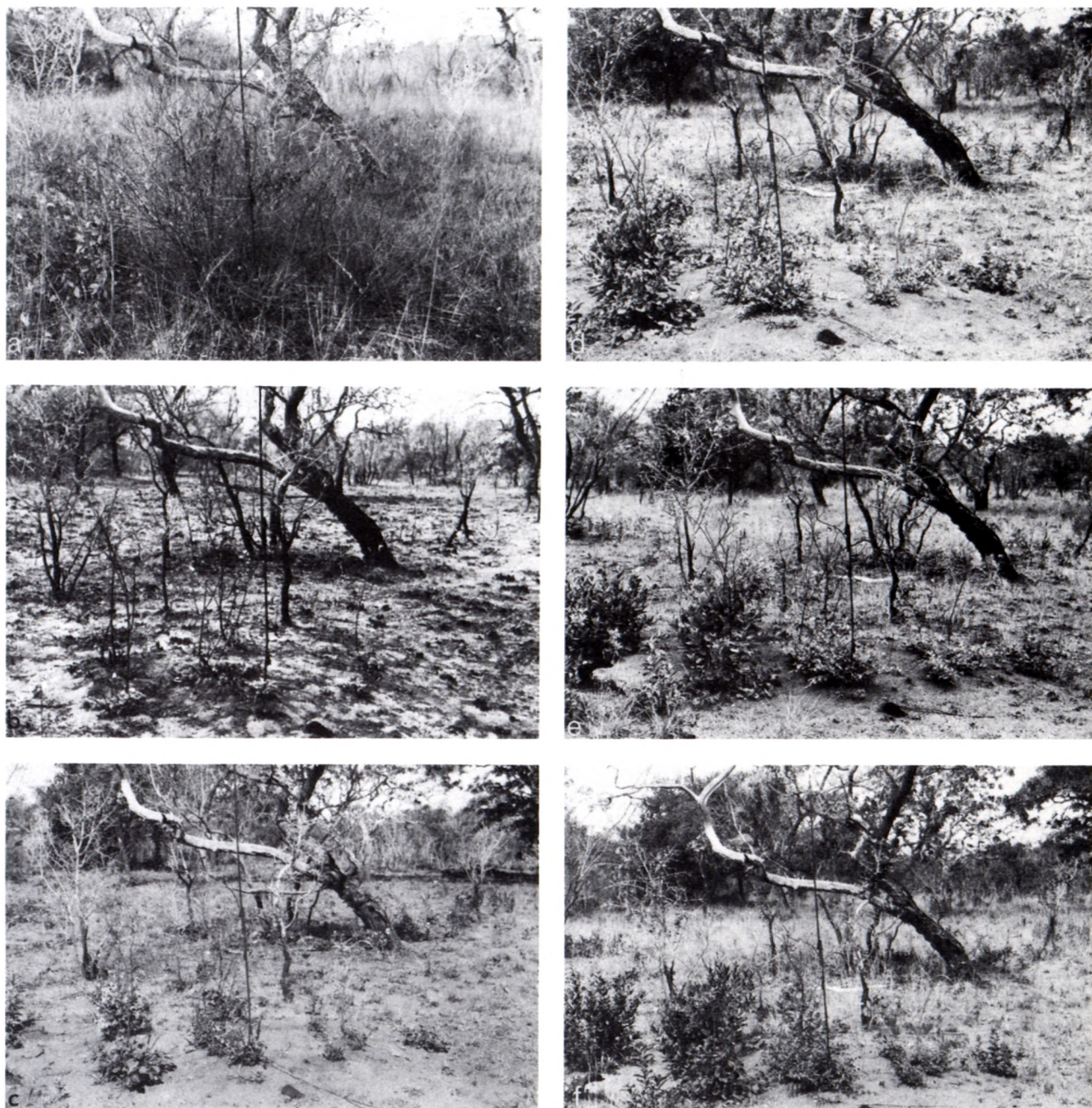


FIG. 3.—A *Grewia flavesces* shrub (with pole): a, on 5th September, before the burn; b, on 5th October, one month after the burn, showing basal regeneration commencing, after virtual total removal of aboveground material by the burn; c, on 7th November, two months after the burn showing basal regeneration at an intermediate stage; d, on 18th December, more than three months after the burn showing basal regeneration virtually complete; e, on 3rd January; f, on 6th February demonstrating that virtually all basal regeneration is completed by the December date. The shrubs on the left of the marked *Grewia* individual are *Euclea natalensis* which regenerated more strongly than did the *Grewia* individuals.

such as *Grewia flavescens*, where the original outline of canopies was usually altogether lost through fire (Fig. 3); biomass of basal twig regeneration (clipped at ground level); biomass of basal leaf regeneration; biomass of all leaves in canopy (for individuals ≤ 5 m height). All biomass data were obtained oven dry at 85°C and total sampling was used, that is, no subsampling was employed.

The diameters of stems were taken for use in already established formulae that predict canopy leaf mass (Rutherford, 1979). These regression formulae were first tested by destructive sampling for each of the more common species in the unburnt control populations since the formulae were derived for populations several kilometres distant and three years previous to the time of fire. If, as was found in the *Ochna pulchra* population, there was very good agreement between predicted canopy leaf mass and actual destructively sampled canopy leaf mass of the unburnt population, the regression formula was applied to the burnt population of the appropriate species (using original plant height if height was reduced by fire) to obtain expected leaf mass had the population not been burned. Therefore, on condition that the regression formulae still proved suitable, this procedure provided a more sensitive measure of the degree of canopy leaf biomass reduction by fire than that provided by using treatments and controls which sometimes had greatly differing distributions of heights within each height class. Canopy leaf biomass reduction per height class was thus calculated in these cases by taking the predicted unburned canopy leaf biomass of the burned individuals and subtracting the actual canopy leaf biomass obtained by direct harvest from the burned individuals.

It should be noted that for practical reasons a small proportion of the individuals included in the sample for numerical counts of stems, mortality and so on were not harvested for biomass. Therefore those numerical non-biomass data concerning differences before and after the fires are not necessarily precisely interrelateable with the biomass data set since there are possible differences in plant size distribution in the whole sample set and in the biomass data subset.

Only some data are tabulated since tabulation of all data for all species, all plant size classes and all the types of possible fire effects, results in many large tables with very many empty cells. This difficulty is inherent in studies such as the present, and arises not only from variation in the natural vegetation composition and structure but also from the inapplicability of some measures of the effects of fire to certain plant growth forms. The very unbalanced total data set resulted in no full analysis of variance being attempted. Instead, for categories where sufficient data existed, all data from the category were used in standard statistical tests of significance between means, often using the non-parametric Wilcoxon test where appropriate. Most data are indicated graphically where use was made of data grouped into classes in the presentation of relations.

4. RESULTS

a) Mortality/survival of plants after the burns

Mortality was defined as the proportion of the number of plant individuals that were alive before the fire but dead (above ground) six months after the fire ('Root kill' of Niering *et al.*, 1970). It is possible that mortality includes individuals that survived or regenerated after fire but died from other causes within the six month period following the fire.

That mortality of unburned individuals would be close to zero was confirmed by the data for the control that showed a mortality of 1% of the tree species group's individuals and 0% of the multistemmed shrub species group's individuals. In the slower burn area mortality of the tree species individuals was 5% which was significantly greater ($P=0.005$) than that of the unburned control. For the shrub species individuals mortality was 0%. In the faster burn area mortality of the tree species individuals was 2% which was not significantly different from that of the control. The mortality of the multistemmed shrub species individuals was significantly greater than that of the unburned control. This mortality is, however, subject to further interpretation since one species was involved, namely, *Dichapetalum cymosum*, where a mortality of 64% for its individuals up to 25 cm tall was indicated. Re-examination in August of most of these individuals recorded as dead in March showed that although most had no aboveground parts visible there were live belowground parts that were in the process of initiating new shoot growth. In these cases, therefore, fire possibly only delayed new growth by one growth season. However, given the extensive underground branching and interconnections between 'individuals' of this geoxylic suffruticose species, new regenerative growth possibly occurred after the fire but not in the immediate vicinity of the labelled 'individual'. Rushworth (1978) also found that woody suffrutices such as *D. cymosum* did, contrary to other woody plants, not produce additional stems per plant unit after fire in Wankie National Park, Zimbabwe. That the high mortality of 'individuals' of *D. cymosum* is merely an apparent mortality, means that, in fact, the mortality values for the multistemmed shrub species individuals was very close to zero.

Despite individuals of *Grewia flavescens* having the highest fuel loads within the plant and that many plants were completely consumed by the fire (Fig. 3), there was no mortality within these populations in either burn. Mortality of *Ochna pulchra* plants in the slow burn (5%) was significantly greater ($P=0.005$) than that in the faster burn (1%). However, when grouped into plant height classes (Table 2) there was no significant difference in mortality for those plants taller than 0.25 m but only for the group below 0.25 m height. In *Burkea africana*, mortality was limited to small plants under 10 cm tall, that is, 54% for those of both burns. Most of these plants killed were seedlings.

b) Effects of fire on plant canopies

Plants were defined as canopied where leaves were carried on stems more than one year old. Non-canopied individuals were thus made up of only (young) basal shoots whereas canopied individuals had an older main stem bearing the canopy leaves with or without basal shoots present. Because of some difficulties in ageing basal shoots before the burns a few non-canopied individuals possibly had basal shoots slightly older than one year but such basal shoots were morphologically similar to one-year old shoots. The effects of the burns on canopies are of course limited to the canopied plants. The effects of fire on canopies can be expressed in various ways, depending upon the canopy attribute considered. Canopy mortality occurs where the whole canopy dies, but where the plant still survives in the form of basal regeneration shoots ('Stem kill' of Niering *et al.*, 1970) (Fig. 4). The occurrence of abnormal leaf growth refers to the amount of leaves

TABLE 2.—Mortality of woody plant individuals following fire according to plant height class

Plant Height Classes (cm)	Tree Species Group			Multistemmed Shrub Group		Ochna pulchra	
	Slow burn (%)	Fast burn (%)	Control (%)	Slow burn (%)	Fast burn (%)	Slow burn (%)	Fast burn (%)
0 – 9,9	13	9	0	0	69	12	0
10 – 24,9	7	0	0	0	60	8	0
25 – 49,9	0	1	5	0	0	0	0
50 – 99,9	5	0	0	0	0	0	0
100 – 149,9	0	5	5	0	0	0	9
150 – 199,9	0	0	0	0	0	0	0
200 – 249,9	6	6	0	0	0	6	7
250 – 499,9	2	0	0	0	0	0	0
>500	0	0	0	—	—	0	0
All	5	2	1	0	38	5	1

that have grown in a convoluted manner and are usually produced not from terminal twigs but from thicker, older wood parts (Fig. 5). Also in terms of shoot extension in Ugandan savanna, Harrington (1974) refers to the tops of taller burned bushes behaving similarly to bushes in an unburnt controlled treatment. Changes in the height and canopy volume of plants refers to measurements as described in the section on methods. Another attribute used is the change in the total amount of leaf biomass in the canopy.

i) Canopy Mortality

Only 0,7% of the unburned control tree species plants' canopies died. In the faster burn, 43,2% canopies were killed of which 92,1% were under 2 m tall with none taller than 5 m. In the faster burn, these plants up to 1,5 m tall had 9,2 canopies killed to each one that survived. For those over 1,5 m tall there were only 0,2 canopies killed for each surviving canopy. In the slower burn, 23,5% canopies were killed of which 90,1% were under 2,5 m tall and also

with none taller than 5 m. In the slower burn, those plants up to 1 m tall had 1,6 canopies killed for each one that survived. For plants between 1 and 1,5 m tall the ratio was about 1 : 1 while for those more than 1,5 m tall there were also only 0,2 canopies killed for each surviving canopy. Relative to the control tree species plants, therefore, canopy mortality in both burns was highly significant particularly for individuals less than 2 or 2,5 m tall.

In the *Ochna pulchra* population, canopy mortality was 32,0% in the slower burn and 44,1% in the faster burn. Only in one species, namely *Vitex rehmannii* was it clear that tall individuals had a relatively high canopy mortality, that is, 64,3% for individuals between 2,5 and 5,0 m tall. Despite the sensitivity of canopies of *V. rehmannii* to fire, no plants of this species died after fire. The hollow main stem of one tree individual, *Securidaca longipedunculata*, was observed to burn vigorously for several hours after the main flame front had passed, but at the end of the growth season the canopy showed no obvious effects of the fire (Fig. 6).

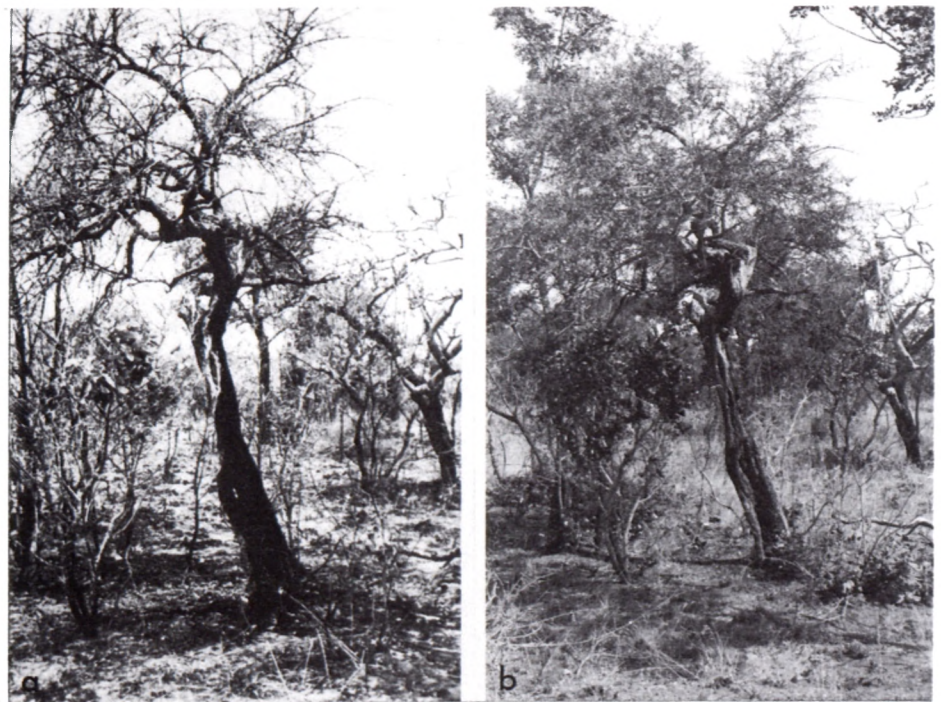


FIG. 4.—A group of *Ochna pulchra* individuals with most canopies killed by the burn but with prolific basal regeneration.

FIG. 5.—a, An *Ochna pulchra* individual showing areas of missing foliage in lower parts of former canopy and the predominantly normally formed leaves at the extremities of the highest branches; b, an *Ochna pulchra* individual showing reduction of foliage in former canopy areas and the predominantly abnormally formed leaves clustered and produced directly from areas of thicker branches and stem and not at the branch extremities.



FIG. 6.—A *Securidaca longipedunculata* tree: a, one day after the burn (6th September) with a hollow stem that was observed to burn vigorously for several hours after the burn; b, five months after the burn (6th February) indicating the canopy that shows no obvious reduction and appears as unaffected as that of a normal unburned individual of this species.



ii) Occurrence of abnormal canopy leaf growth

Apart from observing that the incidence of abnormal canopy leaf growth was generally higher in the faster burn than in the slower burn, the mere presence of abnormal leaf growth was found to be less informative than the actual value of abnormal leaf biomass compared to that of normal leaf biomass. Since a clear qualitative recognition of this abnormality is required for expressing such ratios, consideration was limited to the *Ochna pulchra* population where such distinction was most reliable (Fig. 5). The ratio of normal to abnormal canopy leaf biomass was found to increase exponentially with plant height (Fig. 7) and is discussed further in Section 4e.

iii) Changes in canopy height and canopy volume

For the unburned tree species control plants, mean change in height was +4% with the greatest relative reduction in any height class being -2%. Although in unburned plants height appeared to be unimportant in affecting tree height changes, in both burns canopied plants of the lowest height classes had the greatest relative reduction in height (about 100%) with tallest plants having a zero reduction in height. The relative decrease in plant height after the faster burn was greater for each height class than that for the slower burn, for example in *Ochna pulchra* (Fig. 8a). In terms of the proportion of plants that decrease in canopy height it was found, for tree

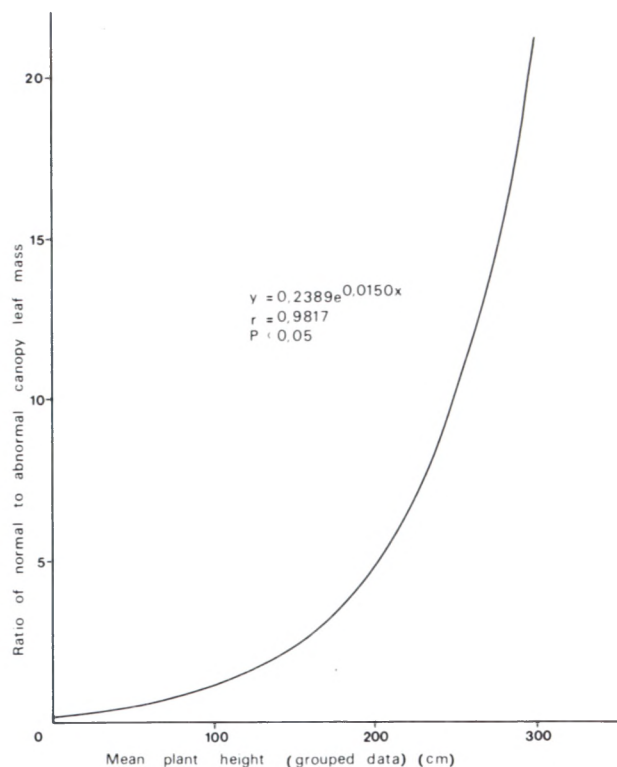


FIG. 7.—Relationship between mean plant height and the ratio of the mass of normally to abnormally formed canopy leaves for *Ochna pulchra* in both burns.

species plants, that 5% of unburnt plants, 28% of the plants of the slower burn and 50% of the plants of the faster burn decreased in height. There was therefore a similar pattern with a greater proportion of individuals decreasing in height in the faster burn area (Fig. 8b). A very similar pattern was obtained in terms of reduction in estimated canopy volume (Fig. 8c). In the multistemmed shrub species group, changes in height were more variable and less strongly correlated with height.

iv) Changes in canopy leaf biomass

Effects of the burns on the canopy leaf biomass could be determined as described earlier on the basis of application of allometric biomass prediction formulae once appropriate tests of the validity of application had been made. It was found that the allometric formulae, applied to unburned plants (stem diameter ≥ 1 cm at 20 cm height) of *Ochna pulchra*, overestimated the actual harvested canopy leaf biomass value by only 0.1%. In *Terminalia sericea* it was found that canopy leaf mass was underestimated but remained within 20% of the actual harvested amount. In *Burkea africana* it was found that canopy leaf mass was overestimated by more than 20% (in the relatively small tested sample population of the control) and the biomass prediction formulae were thus not applied to the burned *B. africana* populations. Since the allometric formulae cannot be applied to the smallest individuals, canopy leaf biomass data from unburned control plants were utilized for the lowest size classes.

In the slower burn area, *Ochna pulchra* plants under 1 m tall decreased in canopy leaf biomass by 90%, but this reduction became less marked with taller plants so that a decrease of only 26% was found for plants between 2.5 and 5 m tall. In the faster burn area the plants under 1 m tall decreased in

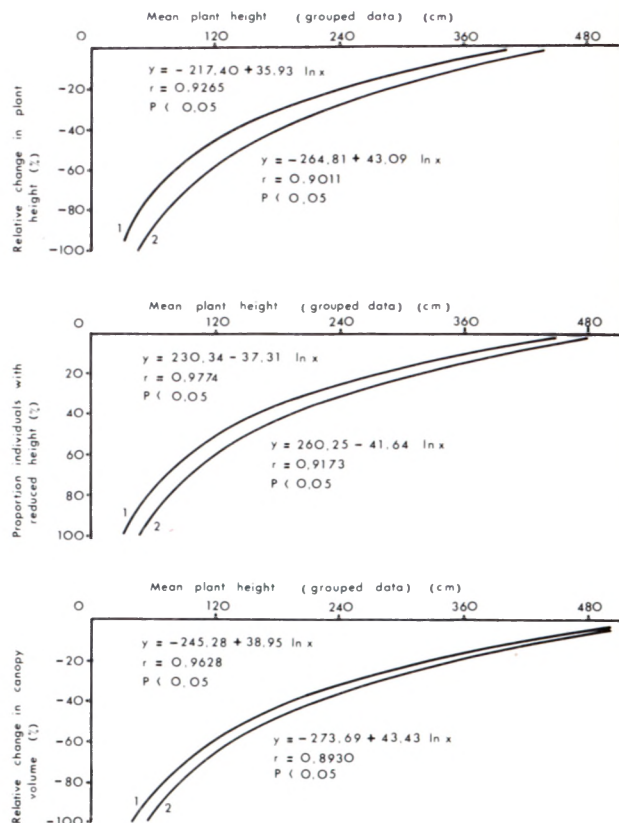


FIG. 8.—Relationships between mean plant height and: a, relative change in plant height; b, proportion of individuals that decrease in height (graph inverted for comparison); c, relative change in canopy volume for *Ochna pulchra* in (1) the slower burn and (2) the faster burn.

canopy leaf biomass by 92%, and this also became less marked with taller plants but with a 50% decrease for plants between 2.5 and 5 m tall.

In *Terminalia sericea* of both burns, trees ≥ 2.7 m tall had a canopy leaf biomass of 79% of that predicted, but for the smaller trees only 6% of the predicted value. This contrasts with the 83% of that predicted in the unburned control plants. Therefore, allowing for the shift in the prediction equation (given by the control), a reduction of at least 90% in canopy leaf mass after fire occurred for the *T. sericea* plants less than or equal to 2.6 m tall. In *Burkea africana* of both burns, stem basal area was used as a measure of plant size to relate to the harvested canopy leaf biomass. For trees up to a cross-sectional stem basal area (at 20 cm height) approaching 50 cm² canopy leaf biomass was less in burned plants than unburned plants, but for plants with a basal area of about 50 cm² or more this difference no longer held (Fig. 9). For taller plants (approximately greater than 2.5 m) *Ochna pulchra* had a greater canopy leaf biomass reduction than *Terminalia sericea* and *Burkea africana*. For smaller plants the differences were less pronounced between these three main tree species.

c) Effect of fire on basal shoot numbers

Most basal shoots that were live before the burns were killed by the fire. Although 14% of the basal shoots of control tree species plants died without fire, 91% were killed in the slower burn and 100% in the faster burn. The killing of live basal shoots by fire was independent of plant height and species. In the multistemmed shrub species plants killing of live basal shoots was virtually 100% in both burns.

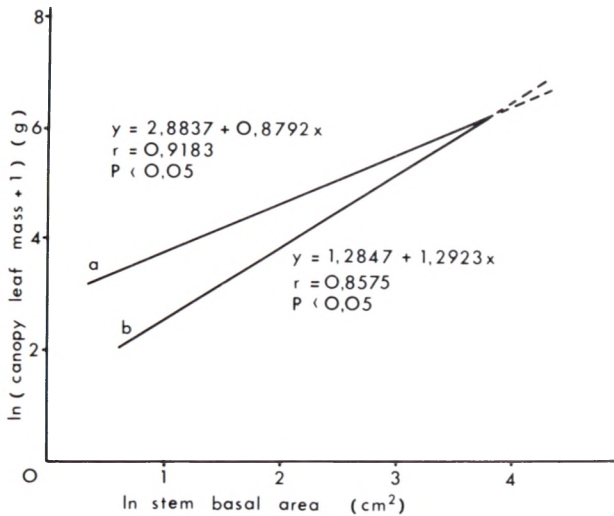


FIG. 9.—Relationship between stem basal area and canopy leaf mass for: a, unburned individuals; b, burned individuals in both burns for *Burkea africana*.

The formation of new post-fire basal shoots was a common phenomenon in burned individuals (Figs. 10 & 11) and these were virtually completely grown by December, that is, about three months after the burn (Fig. 3). Whereas a mean of 0.09 new basal shoots were formed per unburned control plant, the corresponding values were 2.42 for the slower burn and 4.55 for the faster burn. In the unburned control plants, however, new basal shoots were not formed from individuals more than 1 m tall, whereas in burned individuals these were formed irrespective of plant height, but with a tendency for fewer basal shoots to be produced per tall individual. In the multistemmed shrub species plants approximately 5% of the unburned individuals produced new basal shoots, whereas corresponding values were 93% in the slower burn area and 100% in the faster burn area.

The possible relationship between the number of live basal shoots before the fire and those formed after the fire was investigated to determine to what



FIG. 10.—Basal regeneration shoots of *Ochna pulchra* on 18th December after above-ground shoots had been either killed or removed by the burn.



FIG. 11.—Basal regeneration shoots of *Grewia flavescens* on 3rd January after all above-ground shoots had been killed and almost all removed by the burn.

degree live basal shoots were replaced after fire. Data were expressed as the ratio of the number of new basal shoots to the number of old basal shoots killed by the fire. In *Ochna pulchra* basal shoots killed were replaced by almost twice (1,88) the number of new basal shoots. In *Burkea africana* the ratio was only 1,30 which was, however, still a net increase of basal shoots per plant.

In *Ochna pulchra*, although the number of new basal shoots tended to decrease with increasing plant height class, it was found that replacement of basal shoots increased with increasing plant height. No such trend was discernible in *Burkea africana*. The basal shoot replacement relation is given in Fig. 12 for the mean of both burns. The degree of ability of these plants to produce new basal shoots after fire appears to depend on not only the size of the plant, but also on the number of basal shoots prior to the fire.

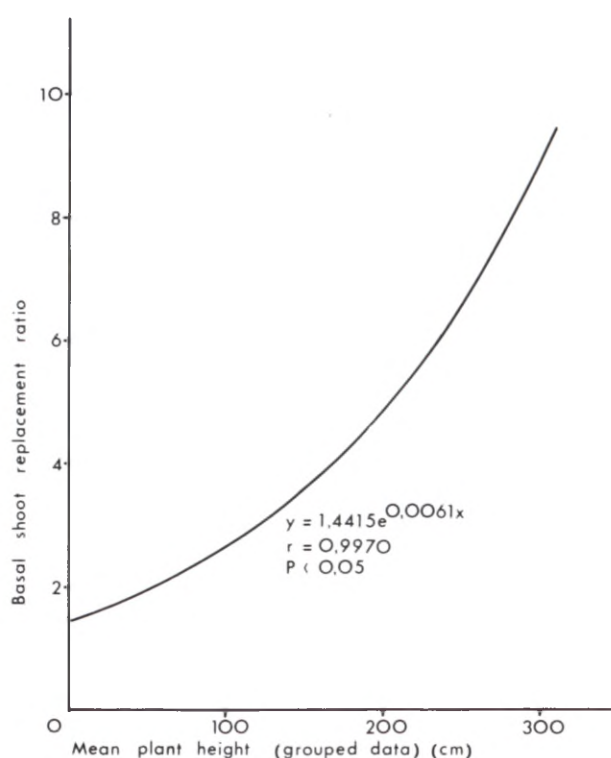


FIG. 12.—Relationship between mean plant height and the ratio of number of post burn basal regeneration shoots to number of pre-burn live basal shoots (basal shoot replacement ratio) in *Ochna pulchra*.

d) Effect of fire on production of new basal regeneration shoot biomass

Basal shoot production (over the 6 month period following the burns) averaged per individual from both burns was 9,59 g for *Ochna pulchra*, 14,52 g for *Burkea africana* and 1,09 g for *Terminalia sericea* (Table 3). In each of these populations, basal regeneration shoot mass of unburned plants was usually considerably less than 10% of basal mass in burned plants. This was also valid for the rarer species, but in some there were very small sized samples for the control, for example, there was no *Dichapetalum cymosum* in the control area. From Table 3 it can be seen that species with low values (<10 g) for basal regeneration shoot mass per individual were *Dichapetalum cymosum*, *Terminalia sericea*, *Strychnos pungens* and *Ochna pulchra*. The

species with highest values (>50 g) were *Grewia flavescens*, *Dombeya rotundifolia* and *Vitex rehmannii* with *Euclea natalensis* having the highest value of all (285,62 g). Those species with greatest basal regeneration shoot mass tended to be non-suffrutex shrub forms whereas tree growth forms usually had relatively low basal regeneration shoot mass.

In terms of mean biomass of basal shoots per individual shoot (where these were clearly distinguishable), *Lannea discolor* and *Burkea africana* had highest values while lowest values were found in *Dichapetalum cymosum* and *Terminalia sericea*.

Species may be divided into three groups according to their ratio of basal leaf mass to basal twig mass. Those with a ratio of less than 1, that is, there was more twig mass than leaf mass, included *Securidaca longipedunculata* and *Terminalia sericea*. Those with up to twice the amount of leaf mass to twig mass included the largest number of species. Those with more than twice as much leaf mass as twig mass included the two most important geoxylic suffrutex species *Dichapetalum cymosum* and *Fadogia monticola*.

Differences in mean basal shoot regeneration mass between different species were tested (for all species with more than 3 individuals) often using the non-parametric Wilcoxon test where appropriate (Table 4). At a level of significance of $P=0,05$ more than half the combinations were significantly different. Since the reaction of *Grewia flavescens* was so different in two burns, these were treated separately.

In *Ochna pulchra* in the slower burn, basal shoot regeneration per individual (4,86 g) was significantly lower than that (12,28 g) in the faster burn. In *Grewia flavescens* the corresponding values were 65,00 g and 160,02 g. This greater production of basal regeneration shoot mass in the faster burn area was also confirmed in *Burkea africana* for each height class of individuals. In *Grewia flavescens*, the live basal shoot mass per unburned individual was significantly greater ($P=0,005$) than the post fire regeneration basal shoot mass in the slower burn area, but there was no significant difference to that produced in the faster burn.

The possible relationship between degree of burn recorded in both burns and basal regeneration mass of the woody plants was shown by 63,73 g for those recorded as burned, 115,12 g for those recorded as severely burned and 107,68 g for those completely burned.

The species with the greatest range in basal regeneration shoot mass was *Euclea natalensis* (1,74 to 1143,37 g). When the population was divided into three equal size classes that is up to 0,5 m tall, 0,5–1,0 m and 1,0–1,5 m tall, the respective mean masses were 40,44 g, 248,38 g and 768,72 g and each value was significantly different from the other. There was thus a clearly greater basal shoot regeneration mass with increased plant size for this shrub species.

It was noted during observations that the individual leaf size, especially of *Ochna pulchra*, was markedly larger in basal regeneration shoots than in the canopy.

e) Relationships between plant height and woody plant biomass components after fire

Earlier reference has been made to effects of the burns on plant height and canopy volume in *Ochna pulchra* and to effects on canopy leaf mass in *Burkea*

TABLE 3.—Basal regeneration shoot mass data for the more common woody plant species

Species	Mean basal regeneration shoot mass per individual (g)	Mean mass per shoot (g)	Basal leaf/twig mass ratio
<i>Dichapetalum cymosum</i>	0,70	0,67	4,35
<i>Terminalia sericea</i>	1,09	1,05	0,45
<i>Strychnos pungens</i>	3,07	—	1,44
<i>Ochna pulchra</i>	9,59	2,56	1,47
<i>Securidaca longipedunculata</i>	10,16	1,95	0,31
<i>Burkea africana</i>	14,52	9,77	2,88
<i>Fadogia monticola</i>	16,37	3,74	2,37
<i>Lannea discolor</i>	45,61	20,73	0,86
<i>Grewia flavescens</i> (slow burn)	65,00	—	1,40
<i>Dombeya rotundifolia</i>	67,65	4,10	1,20
<i>Vitex rehmannii</i>	89,13	—	1,30
<i>Grewia flavescens</i> (fast burn)	160,02	—	1,40
<i>Euclea natalensis</i>	285,62	—	2,14

TABLE 4.—Statistical significance of differences in basal regeneration shoot biomass of different woody plant species after fire

Acacia caffra													
Burkea africana													
Combretum molle													
xxx	x	xxx	Dichapetalum cymosum										
	xxx		xxx	Dombeya rotundifolia									
	xxx		xxx	xxx	Euclea natalensis								
			xxx	xxx	xxx	Fadogia monticola							
x		x	xxx		xxx	xxx	Grewia flavescens (Slow burn)						
x		x	xxx	xxx		xxx	xxx	Grewia flavescens (Fast burn)					
	x		xxx			xxx		x	Lannea discolor				
	x		xxx	xxx	xxx	xx	xxx	xxx	xxx	Ochna pulchra			
			xxx	x	x		xxx	xxx	x		Securidaca longipedunculata		
			xxx					x				Strychnos cocculoides	
xxx	xxx	xxx		xxx	xxx	xxx	xxx	xxx	xxx	xxx	x	xxx	Strychnos pungens
xxx	x	xxx		xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	Terminalia sericea
		x	xxx			x		x		xxx	x	xxx	Vitex poare
xx	xxx	xx	xxx		xxx	xxx		xx	x	xxx	xxx	x	Vitex rehmannii

xxx : P < 0,005
xx : P < 0,01
x : P < 0,05

africana according to stem basal area. The present section aims to determine to what extent plant height governs changes in various plant biomass components after fire.

When basal leaf mass is compared to canopy leaf mass in *Ochna pulchra* it is found that the ratio of canopy leaf mass to basal leaf mass increases non-linearly with increasing tree height (Fig. 13). Plants under 1 m tall have more than half their leaf mass in the form of basal leaves; plants around 1 m tall have basal and canopy leaf mass about equal, while in

plants taller than 1 m canopy leaf mass becomes rapidly much greater than basal leaf mass.

In *Ochna pulchra* it was found for both burns together that the ratio of normally formed to abnormally formed canopy leaf mass increased exponentially with plant height (Fig. 7). For plants about 1 m tall abnormally formed leaf mass more or less equalled normally formed leaves. For plants above 1 m tall, normally produced leaf mass quickly became many times that of the abnormally produced leaf mass. In the faster burn plants, abnormally formed leaves

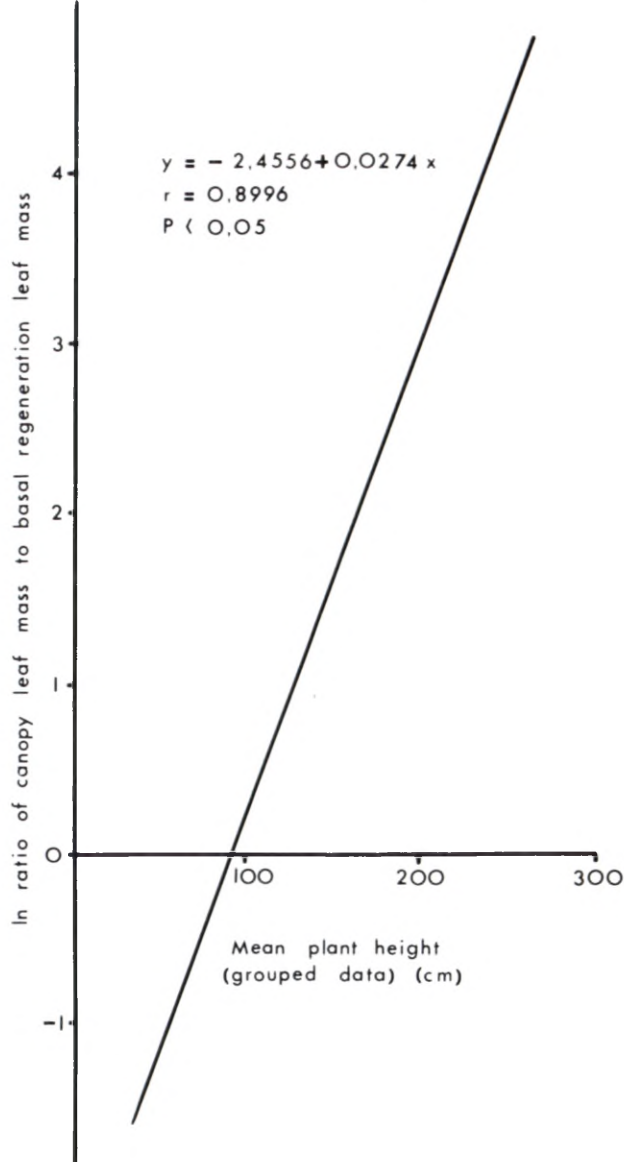


FIG. 13.—Relationship between mean plant height and ln the ratio of canopy leaf mass to basal regeneration leaf mass for *Ochna pulchra* in both burns.

contributed relatively more than in the slower burn. In the faster burn, extreme values for the ratios were also obtained, that is zero for the lowest height class and ∞ for the highest height class.

Differences in leaf mass between burned and unburned *Ochna pulchra* for both burns for each height class are indicated in Fig. 14. It can be seen that an increasing proportion of canopy leaf mass was lost after fire with decreasing plant height to a point where plants were too small to be canopied. The relationship approximates an exponential decay curve where the percentage change in canopy leaf mass decreases exponentially with lower plant height. However, in contrast to this monotonic relationship, an increasing proportion of total leaf mass is lost with decreasing height only until a height of 1–1.5 m is reached, thereupon a maximum reduction in total leaf mass having been attained, less leaf mass is lost until for smallest plants the mean total leaf mass becomes a net increase. It is also clear that it is those plants roughly 0.75–2.5 m tall, that on average have more than 50% of total leaf mass reduced by fire whereas for the smallest and largest individuals this was not so.

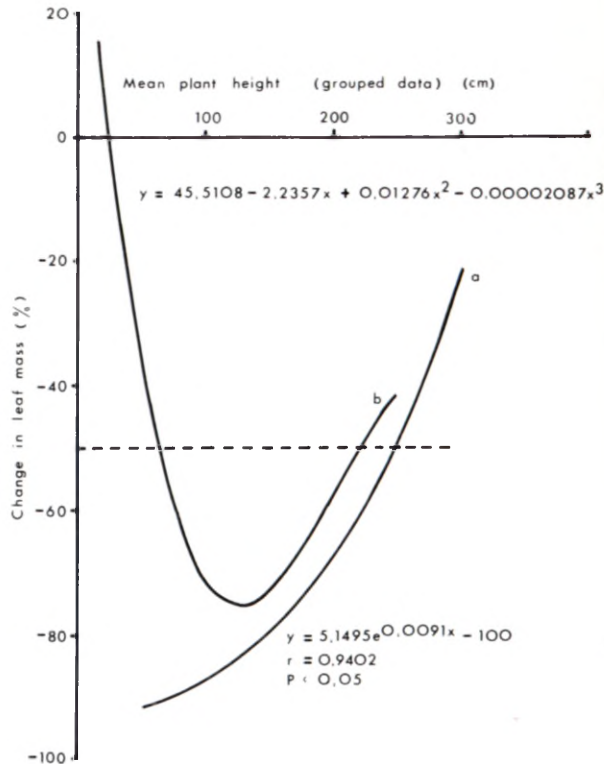


FIG. 14.—Relationship between mean plant height and: a, change in canopy leaf mass; b, change in total plant leaf mass for *Ochna pulchra* in both burns. The broken line indicates the points at which leaf mass is reduced by more than half of the total amount.

It was found tht in *Ochna pulchra*, there was an increase in basal regeneration shoot mass with height until a maximum was reached for heights about 1 to 1.5 m after which there was a decline in basal regeneration shoot mass with plant height (Fig. 15).

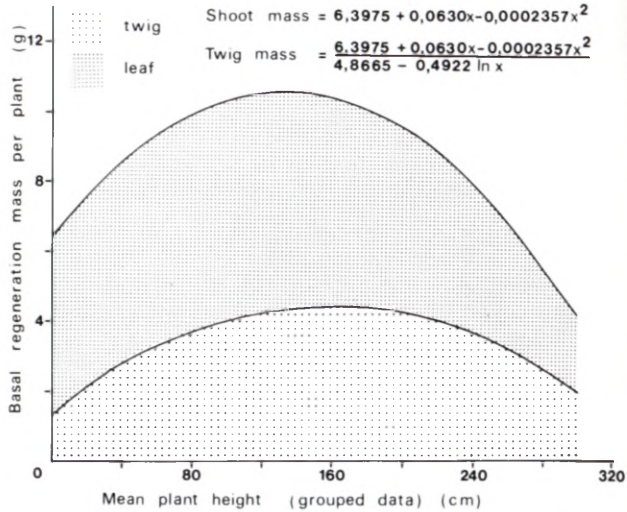


FIG. 15.—Relationship between mean plant height and basal regeneration mass showing the relative contributions of leaf and twig mass for *Ochna pulchra* in both burns (shoot mass = leaf mass + twig mass).

A relationship between plant height and the ratio of leaf mass to twig mass of the basal regeneration shoots was found for both *Ochna pulchra* and *Burkea africana* (Fig. 16). This inverse relationship

assumed the form of a logarithmically decreasing ratio with increasing tree height. There was very little distinction in the relationship between the two burns in *Ochna pulchra*. The ratio in *Burkea africana* was generally much higher than that for *Ochna pulchra* for each height class. This inverse relationship is very different to that in canopies of unburned *Ochna pulchra* where there is no such inverse relationship with plant height.

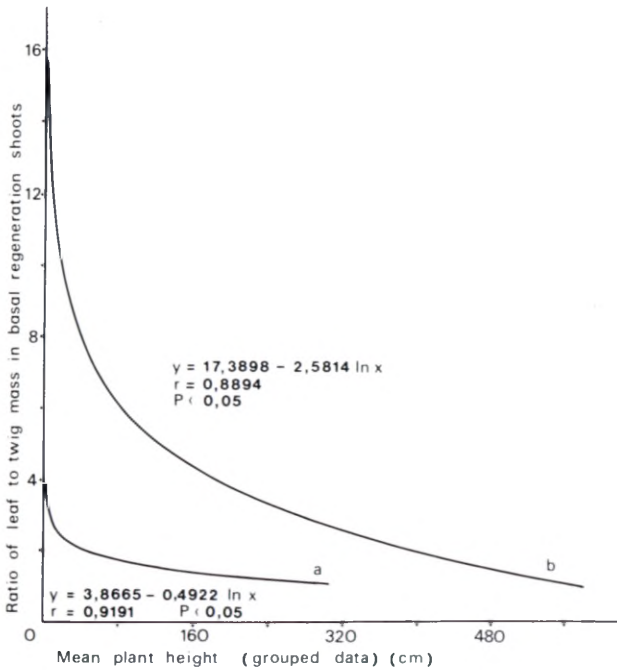


FIG. 16.—Relationship between plant height and the ratio of leaf to twig mass in basal regeneration shoots of: a, *Ochna pulchra*; b, *Burkea africana* in both burns.

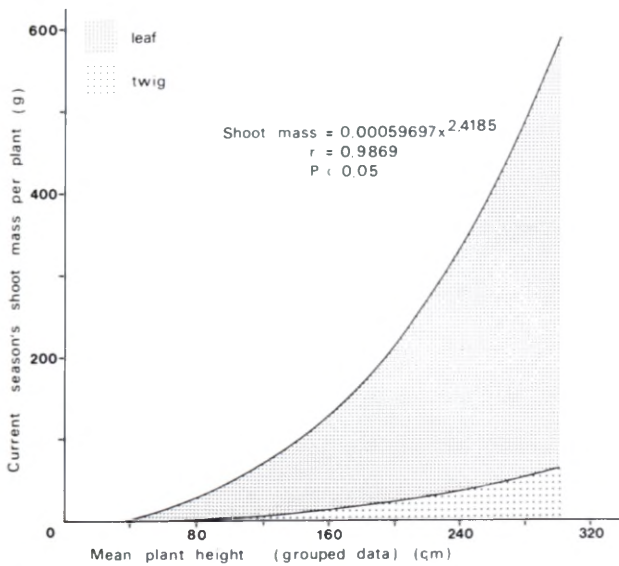


FIG. 17.—Relationships between mean plant height and current season's shoot mass showing the relative contribution of leaf and twig mass for unburned *Ochna pulchra*.

Combining the above inverse relationship equation for *Ochna pulchra* (Fig. 16) with the parabolic dependence of basal shoot mass on plant height, the result is given in Fig. 15. This may be contrasted with corresponding data in normal canopies (Fig. 17),

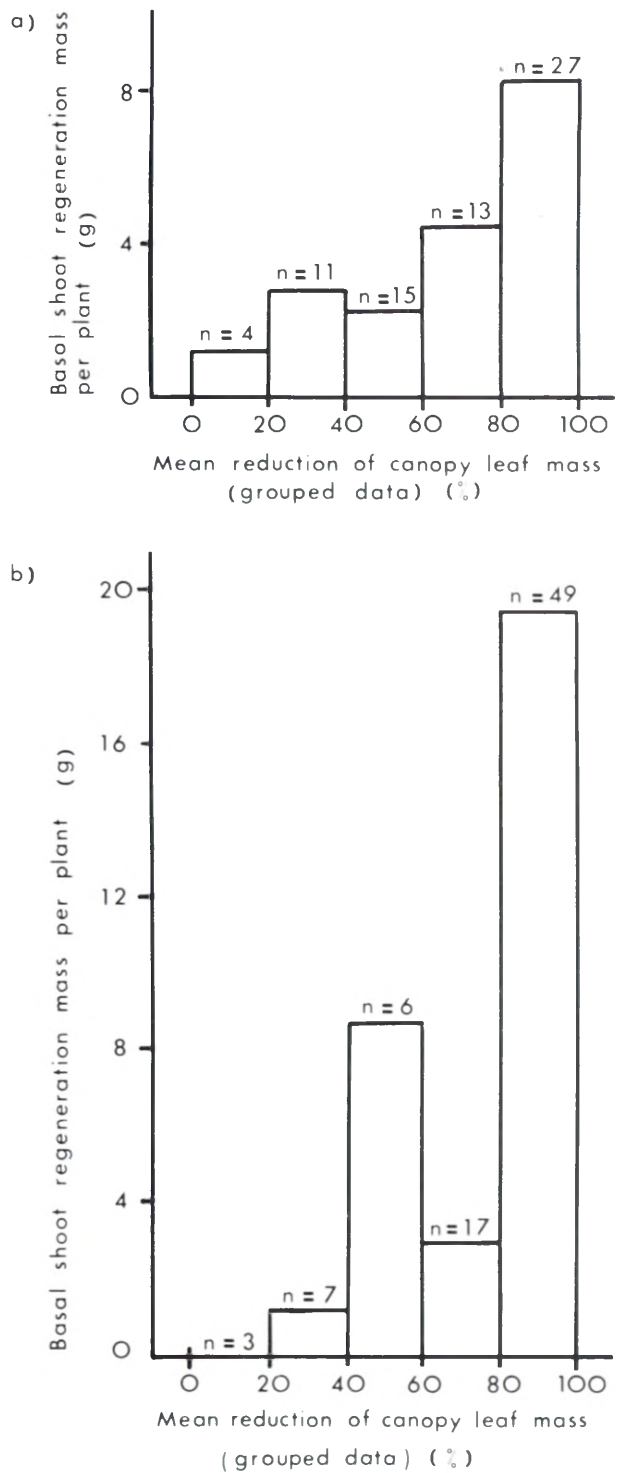


FIG. 18.—Histogram of reduction in *Ochna pulchra* canopy leaf mass against basal regeneration shoot mass per plant in: a, the slower burn; b, the faster burn. n equals the number of individuals in the sample.

obtained from randomly selected Nylsvley individuals and from published allometric biomass relations (Rutherford, 1979). It is clear that (i) the form of the relations; (ii) the relative proportion of components and (iii) changes in this proportion with plant height all differ radically between *O. pulchra* basal regeneration shoots after fire and the normal canopy shoots.

f) Other pyro-allometric biomass relations

In previous sections, much evidence has been given to show that the more damage the canopy of, for ex-

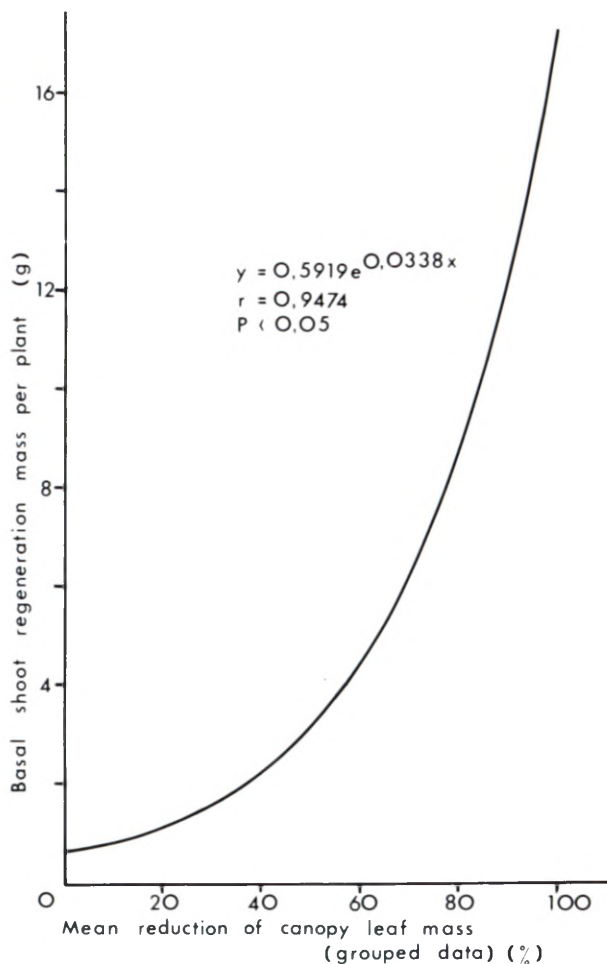


FIG. 19.—Relationship of reduction in *Ochna pulchra* canopy leaf mass and basal regeneration shoot mass per plant in both burns.

ample, *Ochna pulchra*, is subjected to, the greater the amount of basal regeneration. Now using the relative reduction in leaf biomass of canopies as a measure of canopy damage this is related to basal shoot regeneration mass to provide a more precise relationship. In deriving these relationships, individuals that were completely killed by the fire were omitted as were the very few individuals that actually increased slightly in canopy leaf mass after fire. Grouping all plants (of all heights) of *O. pulchra* into five equal classes of relative reduction in canopy leaf mass, generally increased basal shoot mass with classes of increasing reduction in canopy leaf mass (Fig. 18) was apparent in both burns. Expressed as a relation (Fig. 19) it was found that there was an exponential increase in basal shoot production with an increasing proportion of canopy leaf mass lost through fire (until a few individuals pass beyond a certain threshold and die). Particularly for the uppermost canopy leaf mass reduction class, the plants of the faster burn area produced a greater mass of basal regeneration shoots than those of the slower burn.

Although basal shoot regeneration mass was found to increase with increased damage to canopies, the concept should possibly not be extended to very small (<0.25m height) uncanopied plants of *O. pulchra*. Using the recorded degree of burn as a measure of damage to these plants, it was found that plants recorded as burned had a mean shoot mass of 10.35 g, whereas those recorded as severely or completely burned had a mass of only 5.37 g, which is significantly ($P = 0.005$) lower.

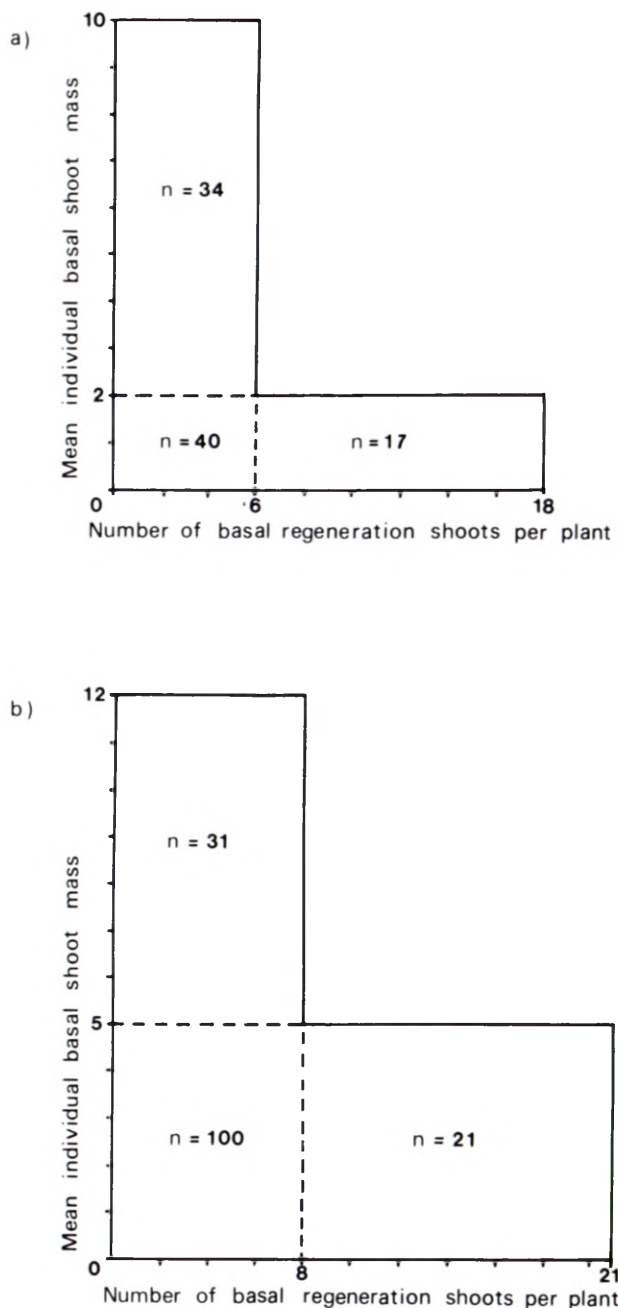


FIG. 20.—Distribution of plants of *Ochna pulchra* relative to both number of basal regeneration shoots and mean individual basal shoot mass for: a, the slower burn; b, the faster burn. n is number of plants.

Another feature that emerged for *O. pulchra* of both burns was not only an inverse but an approximately rectangular hyperbolic relation between number of basal regeneration shoots and the mean mass per basal shoot. In the slower burn area the data set was more tightly grouped (Fig. 20a) in that there was no occurrence of individuals with both more than 6 basal shoots and a mean shoot mass of more than 2 g. In the faster burn area (Fig. 20b), although the distribution was still hyperbolic, the data were more variable. In both these distributions, plant height appeared not to be important.

g) Effects of fire on standing dead individuals

Of the 45 dead standing woody plants labelled before the fire (including controls), most belonged to *Ochna pulchra*, *Burkea africana* and *Terminalia*

sericea. No significant differences in the fire effects between the two burns were found for these dead plants. The effects of fire on the height of dead standing individuals was found to tend strongly to one of two extremes, namely no reduction in height (69%) or maximum reduction to ground level (24%). All those individuals felled by the fire were under 1.5 m tall, that is, no individuals over 1.5 m tall were felled by the fire despite the observed active burning at the base of two of these a day after the fire. Eighty-six percent of those felled by fire were totally consumed. Although 24% of burned individuals were felled, this was not much higher than the 19% of individuals that fell over in the absence of fire in the six month period. There was no apparent selectivity of felling of individuals by fire or other agents according to plant species. In the main live sample individuals, basal shoots that were dead before the burn were almost always totally consumed by fire. Woody plant leaf litter on the ground, although inflammable, sometimes did not ignite fully, for example, even in thick layers in *Ochna pulchra* patches, burning was often limited to very superficial surface layers of leaves (Fig. 21).

5. DISCUSSION AND CONCLUSIONS

In keeping with common veld management practice, the experimental burns were carried out in early spring when the various deciduous plant populations were at different stages of bud break development. Although stage of bud break development at which the plant is burned may be considered possibly critical to the subsequent fire effects measured, data of Hopkins (1963) for work on selected tree species in south-western Nigerian savanna, appear to indicate that burning in the period of a few weeks before and after normal bud break, does not markedly change the period needed for recovery to start.

a) Mortality/survival of plants after the burns

That mortality was significant only in the slower burn and was also largely limited to very low tree

species plants, indicates that the effects of a slower head fire may differ to those of a faster head fire in a way similar to the different effects between a back burn and a head burn at ground level in grassland (Trollope, 1978). The apparently anomalous lower mortality with greater damage to the canopy in the faster burn, relates to the compensatory basal regeneration effect described. Therefore, even in a faster fire, with a probably more intense overall heat than in the slower burn, the mortality effects may relate to more intense heat nearer the ground and not to heat loads at canopy level. Even where fire was reported with wind twice the speed of that in the present study, mortality remained low (Stransky & Halls, 1979).

That most species in the present study had mortality after fire varying from 0 to 5% shows a fire tolerance that appears common in many other woody plants in Africa. The limitation of mortality in *Burkea africana* to very low plants, mainly seedlings, agrees well with Jackson's (1974) classification of it as a pyrophytic species. The quoted fire 'tolerance' or 'resistance' (Trapnell, 1959; Van Wyk, 1971; Lawton, 1978) for *Dichrostachys cinerea*, *Dombeya rotundifolia*, *Lannea discolor*, *Strychnos pungens* and *Terminalia sericea* is confirmed by the less than 5% mortality for each in the present study. *Ochna pulchra* was also shown in this study to be generally fire tolerant in agreement with indications of Lawton (1978) and Rushworth (1978) but not with a 'fire-sensitive' description (Geldenhuys, 1977).

The very low mortality rate after fire of multi-stemmed shrubs (omitting *Dichapetalum cymosum*), which includes the 0% mortality of *Grewia flavescens* despite its relatively high fuel loads, is paralleled in eastern Cape *Acacia karroo* Savanna where only the multistemmed plants of *Rhus lucida* recovered fully after a fire (Trollope, 1974).

b) Effects of fire on plant canopies

Data from the present study clearly show the considerable effect of fire on woody plant canopies, par-



FIG. 21.—A typical thick (>5 cm) layer of leaf litter under a patch of *Ochna pulchra* individuals: a, before the fire (5th September); b, after the fire (6th September) showing the low degree of litter burn with only a superficial layer of the litter being burned or singed. Temperature tempil plates are visible.

ticularly of the smaller plants and these findings broadly agree with results from other areas.

Whereas a two-thirds decrease in canopy volume corresponded to trees and shrubs under 5 cm DBH in *Burkea africana* Savanna in a fire treatment at Makambu, South West Africa (Geldenhuys, 1977), this decrease corresponded to 1 m tall plants of *Ochna pulchra* in the present study. The accompanying 60% reduction in plant height at Makambu was, however, not as great as the percentage reduction for the 1 m tall *Ochna pulchra*.

Although total plant mortalities may be low in both *Acacia* and *Burkea-Ochna* Savannas, it appears that in terms of canopy damage and canopy mortality the Nylsvley study species such as *Ochna pulchra* and even *Vitex rehmannii* may be less susceptible to fire than some southern African *Acacia*-dominated vegetation.

The observed high resistance of the canopy of a large individual of *Securidaca longipedunculata* to prolonged burning in the present study is in keeping with the results from the hot November burn in *Burkea africana* Savanna in South West Africa.

c) Fire and basal shoots

The present study amply confirmed an expected increase in number of basal stems per plant individual after fire. However, in contrast to some other cited findings, regeneration in terms of numbers and mass of shoots in *Terminalia sericea* after fire was far less marked and the only tree species that reacted almost as vigorously to fire as the *Terminalia sericea* in the Wankie study (Rushworth, 1975) was *Dombeya rotundifolia*. The present study's relatively great basal shoot mass in *Lannea discolor* agrees with the report for the Transvaal lowveld where after an October burn, *Lannea discolor* was one of the two species that 'sprouted well' on certain plots (Anon, 1960).

That more than half the species combinations referred to (Table 4) were significantly different with respect to mean basal shoot regeneration mass after fire appears to indicate a wide and fairly even range of values with sometimes limited variance. In the savanna plant community type studied therefore, there was no major clustering of woody plant species in terms of their basal regeneration response to fire.

Although multistemmed shrubs were (in the slower burn) somewhat more susceptible to killing of live basal shoots than were tree species, there was a clear tendency for most multistemmed shrub species, particularly non-suffrutices, to have higher mean basal regeneration shoot mass per plant than for most tree species.

The present study data point to an almost paradoxical situation regarding fire induced basal shoot regeneration of those *Ochna pulchra* plants with 100% canopy leaf mass reduction through fire. Here a plant tends either to produce the maximum mass of basal shoots or none at all (if it dies).

The ratio of number of new basal shoots to the number of old basal shoots killed by the fire, namely the basal shoot replacement ratio, is possibly a useful attribute of vegetation that is subject to recurring fire, that is where the basal shoots that are produced after one fire are affected in a subsequent fire. It is clear that successive fires may not result in a merely additive process of increasing basal shoot numbers. If the basal shoot replacement ratio is assumed to be constant with successive fires, it may be postulated

that basal shoots of *Ochna pulchra* will increase more rapidly than those of *Burkea africana* on the basis of the existing data. A finding analogous to the present study result is the determination of a positive correlation indicating that species, for example *Burkea africana*, are dependent upon the number of parent trees for regeneration in regularly burned savanna vegetation at Makambu, South West Africa (Geldenhuys, 1977).

d) Biomass and other relations after fire

That there is a positive relation between the amount of reduction in canopy leaf mass and the amount of basal regeneration is an underlying reason for the existence (in Fig. 14) of a point corresponding to an intermediate height at which plants exhibit a maximum change in total (basal and canopy) leaf mass and below which smaller plants have a reduced loss in total leaf biomass. Although the data only support a positive change in total leaf mass after fire for smallest plants, it is likely that very large trees exhibit no significant change in total leaf biomass after fire (there is no basis for upward extrapolation of curve b in Fig. 14).

One of the main findings of the present study may be described as the difference between basal shoot mass after fire and unburnt canopy shoot mass as they depend on plant height (Figs. 15 & 17). Apart from the different forms of the relation with height and the relative proportion of the biomass components, there are also the differences in this proportion with plant height (Fig. 16). Du Toit's (1972b) relation of stem diameter (mm) and mean coppice regrowth (1×10^{-1} g) of decapitated trees of *Acacia karroo* in the eastern Cape Province

$$y = -93,85 + \frac{436,20}{25,4} x$$

indicates steadily increasingly coppice mass with increasing tree size. This pattern was not attained in the present fire study since decreased canopy damage effects in the larger trees of the burn changed this relationship in the upper size range. Only where a severe crown fire is conceivable would a Du Toit type relation be expected to apply to a burned tree population.

The present study has clearly demonstrated relationships between reduction in canopy leaf mass and basal shoot regeneration mass. But it is important to note that, although in accordance with expected effects of reduction in apical dominance, increasing damage to the canopy increased basal shoot production (up to a threshold value), there was an opposite effect for very small uncanopied *O. pulchra* plants where increased damage to the plant reduced new basal shoot production. That basal shoot production, in plants with much canopy leaf mass removed by fire, was greater in the faster burn area than in the slower burn area, suggests that the fire heat intensity also had a more direct effect on stimulation of basal shoot production possibly through more effective killing of buds in the canopy.

An indication of the possible limited resources of plants in their regeneration reaction to fire is reflected by the inverse hyperbolic distribution between number of basal shoots per plant and the mean individual basal shoot mass: a compensatory effect between number and size of basal regeneration shoots in *O. pulchra*.

It was found that in several respects, the effects of the faster fire were more variable than in the slower fire, for example, the relationship between number of basal regeneration shoots (in *O. pulchra*) and mean mass per basal shoot was tighter in the slower burn than in the faster burn. This possibly parallels the findings of Trollope (1978) in eastern Cape grassland where the rate of spread of head fires was far more variable than that of back fires. In the relationships between plant height and changes in plant size (Fig. 8), the faster fire consistently had lower correlation coefficients than those for the slower fire.

Although most different types of effects of fire on the woody plants were found to depend on plant height, a few effects were found to be independent of plant height namely: the killing of live basal shoots and the burning away of old dead basal shoots. Plant height also appeared not to affect the relationship in *O. pulchra* between number of basal regeneration shoots and the mean mass per basal shoot.

The dependency or independency of fire effects according to plant species varied from the independency of the killing of live basal shoots by fire with (tree) species to the strongest dependency with species of biomass of basal regeneration shoots per plant. The consumption by fire of old dead basal shoots and the effects of fire on dead standing plants were independent of species.

It is clear that work on specific effects of fire within the savanna woody plant and plant populations creates a basis for understanding many features of short and long term fire response systems in plants. Much further work is required before an adequate understanding of such systems in populations of woody savanna plants is obtained. An undoubted limitation of current work in this field is the neglect of the role of the below ground component of the plant in governing the above ground response to fire.

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UITTREKSEL

Uitwerking van twee intensiteite van lentebrand op verskeie aspekte van houtagtige plante van 'n Burkea africana — Ochna pulchra savanne na een groeiseisoen word gegee. Mortaliteit van houtagtige plante was baie laag, byvoorbeeld in Ochna pulchra was die mortaliteit tussen 1 en 5%. In sommige soorte waar die bogrondse dele dikwels heeltemaal weggebrand het, soos in Grewia flavescens, het geen mortaliteit van individue voorgekom nie. Daar is gevind dat basale lootmassa hergroei paraboolies afhanklik is van planthoogte terwyl die verhouding tussen blaar en takkie massa van basale loot hergroei omgekeerd verander het met plant hoogte in Ochna pulchra. Dit wil voorkom dat die vermoë van Ochna pulchra plante om nuwe basale lote te vorm nie net op plantgrootte berus nie maar ook op die aantal basale lote wat voor die brand teenwoordig was. Vir lewendige Ochna pulchra plante is daar gevind dat basale lootmassa hergroei per individu eksponensiëel toeneem met groter vermindering in kroonblaar biomassa. Dié verband is ook moontlik deur direkte hitte uitwer-

kings geaffekteer. Basale lootmassa hergroei van plant soorte het baie gevarieer van 0,7 g/individu vir Dichapetalum cymosum tot 285,6 g/individu vir Euclea natalensis. Daar is 'n duidelike neiging dat nie-halfruikvormige struiksoorte 'n groter gemiddelde basale lootmassa hergroei per plant toon as dié van meeste ander boomsoorte. Daar is 'n kompenserende uitwerking in Ochna pulchra tussen getal en grootte van basale hergroeiende lote. Staande dooie houtagtige plante (voor die brand) het of omgeval as gevolg van die vuur, of is waarskynlik nie geaffekteer deur die vuur nie. Daar is ook geen selektiwiteit op grond van plantsoort nie. Resultate van die huidige studie word algemeen gestaaf deur werk op die uitwerking van vuur in savanne en sommige ander plantegroeitipes.

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