SEVENTH E.V. KOMAREK, SR. MEMORIAL FIRE ECOLOGY LECTURE

FIRE—A KEY FACTOR IN THE ECOLOGY AND MANAGEMENT OF AFRICAN GRASSLANDS AND SAVANNAS

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ABSTRACT

Fire is regarded as a natural ecological factor of the environment that has been occurring since time immemorial in savannas and grasslands on the continent of Africa. The African continent is highly prone to lightning storms and has an ideal fire climate with dry and wet periods. It also has the most extensive area of tropical savanna on the earth, characterized by a grassy understory that becomes extremely flammable during the dry season. The use of fire in the management of vegetation for both domestic livestock systems and wildlife is widely recognized. Research on the effects of fire has been conducted throughout the grasslands and savannas of Africa since the early 20th century, and has focused on the effects of season and frequency of burning on forage production potential of the grass sward and the ratio of bush to grass in African savannas. In 1971, a conference was held in the United States by Tall Timbers Research Station in Tallahassee, Florida, on the theme ''Fire in Africa.'' This congress was attended by fire ecologists from throughout Africa. A major benefit that accrued from this meeting was the realization that in Africa the study of fire behavior and its effects on the ecosystem, as described by type and intensity of fire, had been largely ignored in the fire research. This led to recognition that the effects of fire must include the effects of all the components of the fire regime on the ecosystem, viz., the type and intensity of fire and the season and frequency of burning. As a consequence, a research program was initiated in South Africa in 1972, and later extended to East Africa in 1992, to characterize the behavior of fires burning in savanna and grassland vegetation and to determine the effect of type and intensity of fire on the vegetation. This research program has successfully developed a greater understanding of the effects of type and intensity of fire in African grasslands and savannas. This in turn led to the development of more effective and practical guidelines for fire regimes to be used in controlled burning for domestic livestock and wildlife management systems in grasslands and savannas. Research on the fire ecology of grasslands and savannas continues to draw scientific attention in Africa, and currently there are active research programs being conducted in the Eastern Cape Province, KwaZulu-Natal Province, and Kruger National Park in South Africa, and in the Ngorongoro Crater in Tanzania.

keywords: Africa, fire, fire behavior, fire effects, grassland, prescribed burning, savanna.

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INTRODUCTION

Fire is regarded as a natural ecological factor of the environment in Africa that has been occurring since time immemorial. It is estimated that human beings have used fire for more than 1 million y, and in Africa has extended grasslands and savannas at the expense of evergreen forests (Bond and van Wilgen 1996). The continent of Africa is highly prone to lightning storms and has an ideal fire climate comprising dry and wet periods. It also has the most extensive area of tropical savanna on the earth, characterized by a grassy understory that becomes extremely flammable during the dry season (Komarek 1971). The use of fire in the management of vegetation for both domestic livestock systems and wildlife management is widely recognized. Research on the effects of fire has been conducted throughout the grassland and savanna areas of Africa since the early 20th century (West 1965) and focused on the effects of season and frequency of burning on forage production potential of the grass sward and the ratio of bush to grass in African savannas. However, in 1971 a conference was convened by Tall Timbers Research Station in Tallahassee, Florida, with the theme ‘‘Fire in Africa.’’ This congress was attended by fire ecologists from throughout Africa. A major benefit that accrued from this meeting was the realization that in Africa the study of fire behavior and its effects on the ecosystem, as described by type and intensity of fire, had been largely ignored up until that time. This was a turning point in research on the fire ecology of African grasslands and savannas and led to the further recognition that the effects of fire must include the effects of all the components of the fire regime on the ecosystem, viz., the type and intensity of fire and the season and frequency of burning. As a result, a research program was initiated in South Africa in 1972 (Trollope 1978, Trollope and Potgieter 1985), and later extended to East Africa in 1992 (Trollope and Trollope 1999), to characterize fire behavior in savanna and grassland vegetation and to determine the effect of type and intensity of fire on vegetation. This research program has successfully developed a greater understanding of the influence of fire type and intensity in African grasslands and savannas (Trollope 1984, Trollope and Tainton 1986, Trollope and Trollope 1999, de Ronde et al. 2004). This led to the development of more effective and practical guidelines for fire regimes to be used in controlled burning for domestic livestock and wildlife management systems in grassland and savanna areas. Research on the fire ecology of grasslands and savannas continues to enjoy scientific attention in Africa, and currently the author is associated with active research programs in Eastern Cape Province, KwaZulu-Natal Province, and Kruger National Park in South Africa, and in the Ngorongoro Crater in Tanzania.

This paper presents an overview of the beneficial and significant effects that the 11th Tall Timbers Fire Ecology Conference (Tallahassee, Florida; 22–23 April 1971) has had on a greater understanding of the effects and use of fire in African grasslands and savannas. It is also a tribute to the vision and foresight that E.V. Komarek, Sr. had into the ecology of fire-dependent ecosystems and his willingness and passion to share his knowledge with society in general and in particular with communities reliant on the ecological well-being of African grasslands and savannas.

FIRE BEHAVIOR

The effect of fire on natural ecosystems involves the response of living organisms to the release of heat energy through the combustion of plant material. The manner in which and the factors that influence release of heat energy involve the study of fire behavior. Fire behavior is defined as the release of heat energy during combustion as described by fire intensity, rate of spread of the fire front, flame characteristics, and other related phenomena (Trollope 1981). In Africa there is a serious deficiency of knowledge concerning fire behavior, and limited efforts have been made to quantify the factors that influence fire behavior. Also, no attention has been paid to the dynamics of heat energy release and its subsequent effect on the ecosystem. Basically, the effect of fire on plants depends upon the amount of heat energy released, rate of release, and vertical level at which heat energy is released. The determination of such relationships helps clarify many of the apparently inexplicable effects of fire often cited in the literature. The following fire behavior parameters have been developed and identified that quantitatively describe fire behavior and its effects on savanna and grassland vegetation.

Available Heat Energy

The total amount of heat energy contained per unit mass of fuel is called the *heat of combustion*, but not all this total potential heat energy is released during a fire because some heat energy remains in unburned plant material. The net heat energy released during a fire is called the *heat yield*. Heat yield was determined for fine grass fuels in savannas in the Eastern Cape Province, South Africa, and values of 16,890 and 17,781 kJ/kg were obtained for grass fuels burning as head- and backfires, respectively (Trollope 1983). These heat yields are similar to heat yields quoted and used in the United States and Australia (Albini 1976, Luke and McArthur 1978) and were subsequently used for estimating available heat energy in all fire behavior studies conducted in southern and East Africa. In practice, the available heat energy is estimated as the plant fuel load available for combustion during a fire and is expressed in kilograms per hectare or per square meter.

Rate of Heat Energy Release

Fire intensity refers to the rate at which heat energy is released during a fire and is defined as the release of heat energy per unit time per unit length of fire front (kJ s^{-1} m^{-1}; Byram 1959). Numerically, fire intensity is the product of the available heat energy, the rate of spread of the fire front, and the mass of fuel consumed, which can be expressed as the equation

Table 1. The range of conditions under which controlled burns were applied in the Eastern Cape Province and Kruger National Park, South Africa (Trollope 1983, Trollope and Potgieter 1985). Copyright © 2002 Millpress Science Publishers. From *Forest Fire Research & Wildland Fire Safety*, by W.S.W. Trollope, L.A. Trollope, and D.C. Hartnett, "Fire behaviour a key factor in African grasslands and savannas." Reprinted by permission of Millpress Science Publishers and the authors.

Variable	Mean	Min.	Max.
Fuel load (kg/ha)	3,847	1,152	10,500
Fuel moisture (%)	32.1	7.5	68.8
Air temperature (°C)	23.8	14.3	35.8
Relative humidity (%)	36.6	4.2	82
Wind speed (m/s)	2.6	0.3	6.7
Fire intensity (kJ s^{-1} m^{-1})	2,566	136	12,912

$$I = Hwr,$$

where I = fire intensity (kJ s^{-1} m^{-1}), H = heat yield (kJ/kg), w = mass of fuel consumed (kg/m^2), and r = rate of spread of the fire front (m/s).

Albini (1976) stated that Byram's description and definition of fire intensity has proved to be very useful in fire behavior studies and quotes van Wagner (1973), who found that fire intensity was significantly correlated with the height of lethal scorching of coniferous tree crowns. Research in the Eastern Cape Province and Kruger National Park, South Africa, supports this view, as fire intensity had a highly significant positive effect on the top-kill of stems and branches of trees and shrubs in these two areas (Trollope and Tainton 1986, Trollope 1999).

Vertical Distribution of Heat Energy

A reliable indicator of the vertical distribution of heat energy released during a fire is the perpendicular height of the flames from ground level, i.e., flame height. Research in the Eastern Cape Province has shown that flame height has a significantly positive effect on the top-kill of stems and branches of trees at increasing height levels (Trollope 1983).

Factors Influencing Fire Behavior

Subsequent research showed that fire intensity and flame height were significantly correlated and both had significant effects on vegetation. Research also showed that fire intensity can best be used for describing the general behavior of fires and their effects on vegetation; consequently, this parameter was focused on in modeling the behavior of fires and their effects on vegetation. Factors influencing fire behavior were investigated in terms of those variables that need to be considered when applying controlled burns as a range management practice: fuel load, fuel moisture, relative humidity, air temperature, wind speed, and slope (Brown and Davis 1973, Luke and McArthur 1978, Cheney 1981, Leigh and Noble 1981, Shea et al. 1981, Wright and Bailey 1982). The effect of these variables on fire intensity were investigated in the Eastern Cape Province and Kruger National Park (Trollope 1978, Trollope 1983, Trollope and Potgieter 1985), where 235 controlled burns were applied to areas ranging from 0.2 to 7 ha. The range of conditions under which the controlled burns were applied is presented in Table 1.

Table 2. Effects of fuel load, fuel moisture, relative humidity, and wind speed on fire intensity (n = 200).

Independent variable	Transformation	Coefficient of determination (R^2)	Effect (%)	Significance
Fuel load	x	0.427	42.7	$P \leq 0.01$
Fuel moisture	$\sqrt{x}$	0.574	14.7	$P \leq 0.01$
Relative humidity	x^2	0.584	1.0	$P \leq 0.02$
Wind speed	$1/x$	0.600	1.6	$P \leq 0.02$
Total			60.0	

The influence of these environmental variables on fire behavior was determined by multiple regression analysis of data recorded during controlled burns where fuel load, fuel moisture, relative humidity, and wind speed were independent variables and were regressed against fire intensity as the dependent variable. Air temperature was not included in the analysis because of correlation with relative humidity, thereby not fulfilling the criteria of independence. The effect of slope was not considered because all burns were applied to relatively flat terrain.

All the independent variables had a statistically significant effect and accounted for 60% of the variation in fire intensity (Table 2). Fuel load and fuel moisture influenced fire intensity to the greatest extent, whereas relative humidity and wind speed had a significant but far smaller effect. The resulting multiple regression equation for predicting fire intensity is

$$FI = 2{,}729 + 0.8684x_1 - 530\sqrt{x_2} - 0.1907x_3^2 - 596(1/x_4),$$

where FI = fire intensity (kJ s^{-1} m^{-1}), x_1 = fuel load (kg/ha), x_2 = fuel moisture (%), x_3 = relative humidity (%), and x_4 = wind speed (m/s). The regression equation is based on the following statistics: number of cases = 200, multiple correlation coefficient (R) = 0.775 ($P \leq 0.01$), and coefficient of determination (R^2) = 0.600.

The model was tested with independent fire behavior data and found to be highly significant (r = 0.749, df = 33, $P \leq 0.01$) and accounted for 56% of the variation in fire intensity. By normal statistical standards, this coefficient of determination is rather low, and generally regression equations are used for predictive purposes only when the coefficient of determination accounts for at least 95% of the variation in the dependent variable. However, experience gained during this research suggests that it is virtually impossible to attain these levels of precision when modeling such a complex and inherently variable phenomenon as fire behavior; subsequent experience with this model showed that it provided adequate precision for formulating practical guidelines for controlled burning in grasslands and savannas both in southern and East Africa.

FIRE EFFECTS

Fire ecology refers to the response of the biotic and abiotic components of an ecosystem to a fire regime. This would include type and intensity of fire and season and frequency of burning (Trollope et al. 1990). Following the 11th Tall Timbers Fire Ecology Congress in 1971, a research program was initiated in South Africa in 1972 to determine the effect of all the components of the fire regime on vegetation, i.e., effects of type and intensity of fire and season and frequency of burn. Unfortunately, a similar research program was not known to be initiated elsewhere in Africa until 1992. An overview follows of known effects of the fire regime on grass and bush vegetation in African grasslands and savannas, based largely on the results of this research program.

Type of Fire

The most common types of fire in grassland and savanna areas are surface fires (Trollope 1983) burning either as head- or backfires. Crown fires do occur in savannas, but only under extreme conditions. Generally under these conditions they occur as passive crown fires characterized by the ‘‘torching’’ of individual trees rather than as active crown fires that are sustained by more abundant and continuous aerial fuels. Thus, type of fire determines the vertical level at which heat energy is released in relation to the location of meristematic tissues.

Trollope (1978) investigated the effects of surface fires, occurring as either head- or backfires, on the grass sward in the arid savannas of the Eastern Cape. The results showed that backfires significantly ($P \leq 0.01$) depressed regrowth of grass in comparison to headfires because a critical threshold temperature of approximately 95°C was maintained for 20 s longer during backfires than during headfires. Also, more heat was released at ground level during backfires compared to during headfires; therefore, shoot apices of the grasses were more adversely affected by backfires.

Bush (i.e., woody, shrubby vegetation) is very sensitive to various types of fires because of differences in the vertical distribution of heat energy release. Field observations in Kruger National Park and in Eastern Cape Province indicate that crown and surface headfires cause the highest amount of top-kill of stems and branches compared to that of backfires. Unfortunately, there are only limited quantitative data to support these observations. Research results were obtained from a burning trial at the University of Fort Hare in the False Thornveld of the Eastern Cape (arid savanna), where a field-scale burn was applied to a 62-ha area to control bush encroachment. The majority of the trial area was ignited as a headfire, and results showed that the phytomass of bush was reduced by 75% in the area burned as a headfire compared to 42% in the area burned as a backfire. This happened because the flame height of headfires can be up to 3 times greater than that of backfires, resulting in higher temperatures being generated above ground level (Trollope 1978). Therefore, the aboveground growing points of these plants, located in the canopies of trees and shrubs, are subjected to greater heat loads and resultant damage during headfires than during backfires. Similar results were obtained in the Scattered Tree Grassland (*Acacia–Themeda* [Edwards and Bogdan 1951]) range type in the Kenya central highlands where the effects of head- and backfires on the top-kill of savanna trees and shrubs bush were investigated (see figure 3 in Trollope et al. 2002).

Head- and backfires had significantly different effects on top-kill of trees and shrubs, with headfires generally causing a greater top-kill than backfires (see figure 3 in Trollope et al. 2002). Initially both types of fires resulted in a high top-kill of stems and branches when the bush was short, but as trees and shrubs increased in height, backfires caused a lower top-kill compared to that of headfires. This trend became more pronounced with trees >2 m in height. Headfires generate greater flame heights than backfires; therefore, fire-susceptible growing points of taller trees and shrubs are above the flaming zone of combustion during backfires compared to during headfires.

Fire Intensity

The effect of fire intensity on the recovery of the grass sward after burning was investigated in arid savannas of the Eastern Cape Province. After a series of fires ranging in intensity from 925 to 3,326 kJ s^{-1} m^{-1} (cool to extremely intense fires), no differences were detected in the recovery of the grass sward at the end of the first or second growing seasons after the burns (Trollope and Tainton 1986). Therefore, fire intensity has little influence on the recovery of the grass sward after a burn. This is a logical result because otherwise intense fires would not favor development and maintenance of grasslands.

The effect of fire intensity on trees and shrubs has been studied in arid savannas in Eastern Cape Province (Trollope and Tainton 1986) and Kruger National Park (Trollope et al. 1990). Plant mortality and total top-kill of stems and branches of bush at different heights was determined. Bush is very resistant to fire alone; in the Eastern Cape Province, the mortality of trees and shrubs after a high-intensity fire of 3,875 kJ s^{-1} m^{-1} was only 9.3%. In Kruger National Park, the average mortality of 14 of the most common bush species subjected to fires ranging in intensity from 110 to 6,704 kJ s^{-1} m^{-1} ($n = 43$) was only 1.3%. In both areas, the majority of the trees that suffered a top-kill of stems and branches coppiced from the collar region of the stem (Figure 1). A significantly greater top-kill of bush with increasing fire intensities was noted. However, the bush became more resistant to fire as the height of the trees and shrubs increased (Figure 2). Similar responses were reported in arid savannas of Eastern Cape Province (Trollope and Tainton 1986) and in the Scattered Tree Grassland (*Acacia–Themeda* savanna) in the Kenya central highlands (Trollope and Trollope 1999).

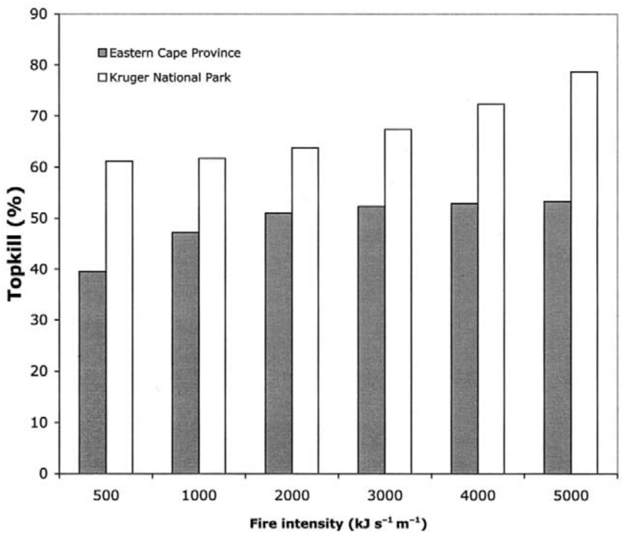

Fig. 1. Effect of fire intensity on the top-kill of trees and shrubs 2 m high in the Eastern Cape Province and Kruger National Park, South Africa. Copyright © 2002 Millpress Science Publishers. From *Forest Fire Research & Wildland Fire Safety,* by W.S.W. Trollope, L.A. Trollope, and D.C. Hartnett, ''Fire behaviour a key factor in African grasslands and savannas.'' Reprinted by permission of Millpress Science Publishers and the authors.

Season of Burning

Very little published quantitative information is available on the effect of season of burning on the grass sward. West (1965) stressed the importance of burning when grass is dormant. Scott (1971) quoted data from the Southern Tall Grassveld of KwaZulu-Natal Province, South Africa, where mean grass basal cover of plots burned in autumn, late winter, and after the first spring rains for a period exceeding 20 y, was 12.8, 13.0, and 14.4%, respectively. The absence of large differences in mean basal cover obtained with these different seasons of burning indicated that, for all practical purposes, burning when the grass sward is dormant has very little influence on the grass sward. This conclusion is supported by Tainton et al. (1977), Dillon (1980), and Everson et al. (1988), who also found that burning before or immediately after the first spring rains in KwaZulu-Natal Province had essentially the same effect on the recovery of a burned grass sward. Conversely, with grasslands burned later in the season when actively growing, causes a high mortality of tillers of *Themeda triandra*, resulting in a significant reduction in abundance (Dillon 1980, Everson et al. 1988).

The effect of season of burning on the recovery

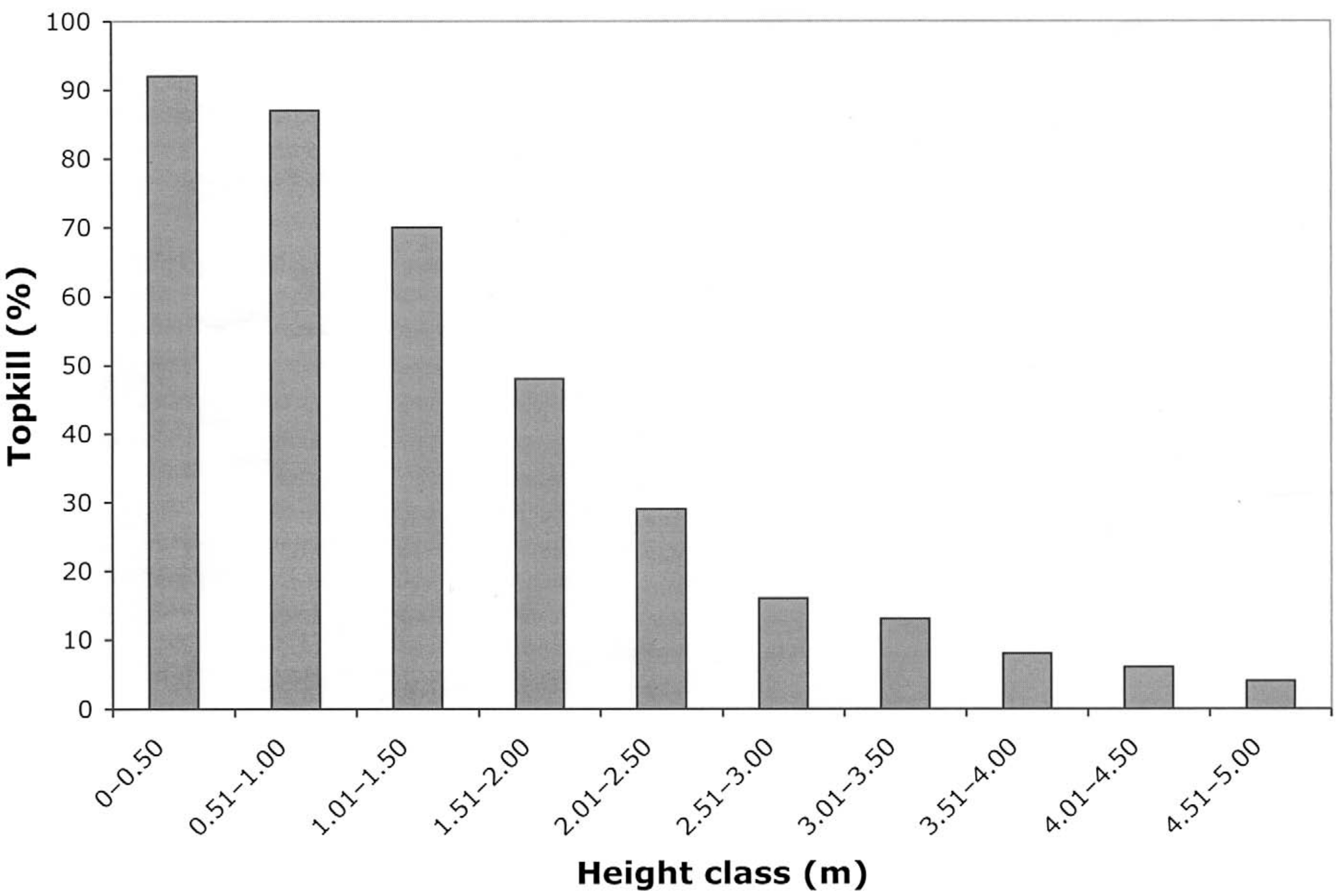

Fig. 2. Effect of height of trees and shrubs on the top-kill of bush subjected to a fire intensity of 3,000 kJ s^{-1} m^{-1} in Kruger National Park, South Africa. Copyright © 2002 Millpress Science Publishers. From *Forest Fire Research & Wildland Fire Safety,* by W.S.W. Trollope, L.A. Trollope, and D.C. Hartnett, ''Fire behaviour a key factor in African grasslands and savannas.'' Reprinted by permission of Millpress Science Publishers and the authors.

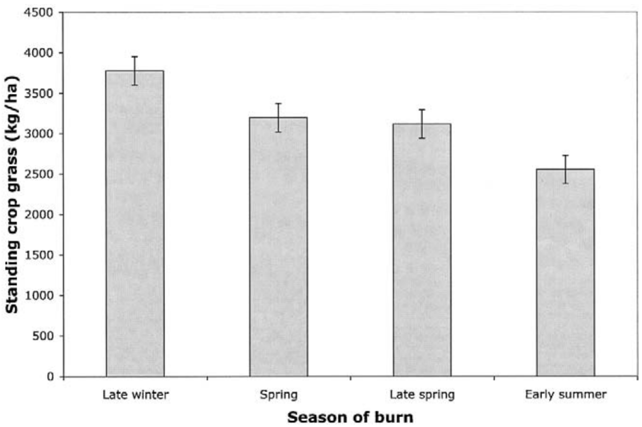

Fig. 3. Effect of season of burning on the standing crop of grass sward (kg/ha) in arid savannas of the Eastern Cape Province, South Africa (Trollope 1987). Copyright © 1987 Grassland Society of Southern Africa. From *Journal of the Grassland Society of Southern Africa,* by W.S. Trollope, ''Effect of season of burning on grass recovery in the false thornveld of the eastern Cape.'' Reprinted by permission of National Inquiry Services Centre.

of grass was also investigated in the arid savannas of the Eastern Cape Province (Trollope 1987). To determine the effect of burning the grass sward in late winter, spring, late spring, and early summer, the standing crop during the first post-fire growing season was measured.

Burning in late winter consistently resulted in a significantly greater recovery of the grass sward during the first post-fire growing season than the other treatments (Figure 3). Conversely, early summer burns that were applied when the grass was actively growing had a significantly depressive effect ($P < 0.01$) throughout the recovery period on the regrowth of the grass sward in relation to the other treatments. Burning when the grass was actively growing adversely affected recovery of the grass sward when compared with burning when the grass was dormant.

Observations and measurements made during the early summer burn showed that grass tillers were actively growing, and shoot apices were therefore probably elevated and vulnerable to fire. Furthermore, the mean rate of spread for the early summer burns was 0.11 m/s compared to 0.31 m/s for the later winter burns. This would suggest that the slow-moving early summer burn resulted in a longer duration of critical threshold temperatures compared to the fast-moving winter burn and therefore caused more damage to exposed shoot apices (Trollope 1987). Subsequent investigations have confirmed this and found that the rate of spread was significantly positively correlated ($r = 0.2669$, df $= 54$, $P \leq 0.02$) with recovery of the grass sward during the first post-fire growing season. These different sources of evidence lend support to the view that the effect of season of burning on the grass sward depends upon the physiological state of the grass at the time of the fire.

Season of burning also has an effect on the botanical composition of the grass sward. In KwaZulu-Natal Province, *Themeda triandra* declined after burning in autumn compared to burning in winter and spring, whereas *Tristachya leucothrix* increased (Bond and van Wilgen 1996).

The effect of season of burning on savanna trees and shrubs generally is confounded by fire intensity. When the trees are dormant in winter the grass is dry and supports intense fires, whereas when the trees are actively growing during summer the grass is green and fires are much cooler. West (1965) postulated that trees and shrubs are probably more susceptible to fire at the end of the dry season when plant reserves are depleted because of new spring growth. However, Trollope et al. (1990) showed that mortality of bush in Kruger National Park was only 1.3% after fires that had been applied to bush ranging from dormant to actively growing plants. Therefore, it would appear that bush is not sensitive to season of burn.

Frequency of Burning

The effect of frequency of burning on vegetation is influenced by event-dependent effects and interval-dependent effects (Bond and van Wilgen 1996). Event-dependent effects occur at the time of the fire and are influenced by type and intensity of the burn and the physiological state of the vegetation at the time of the fire. Interval-dependent effects are influenced by treatment and growing conditions that occur during the interval between burns. These two overall effects tend to confound interpretation of the effect of frequency of burning and must be considered when reporting on the effect of frequency of burning.

Frequency of burning has a marked effect on botanical composition, with species such as *Themeda triandra* being favored by frequent burning and *Tristachya leucothrix* being favored by infrequent burning in moist grasslands of KwaZulu-Natal Province (Scott 1971, Dillon 1980). Similar results have been obtained in arid savannas of Eastern Cape Province, where frequent burning favored an increase in *Themeda triandra* and a decrease in *Cymbopogon plurinodis* (Robinson et al. 1979). In East Africa, Pratt and Gwynne (1977) reported that *Themeda triandra* is a common constituent of grasslands in the Kenya central highlands on undulating plateaus and mountain flanks where fires are regular occurrences and grazing pressure is not too high. Where fires are infrequent or lacking, upland grassland tends to become dominated by *Pennisetum schimperi* and *Eleusine jaegeri,* which are coarse-tufted species of little forage value. These are interval-dependent effects of frequency of burning because *Themeda triandra* is sensitive to low light conditions that develop when the grass sward is not defoliated, and this species rapidly becomes moribund during extended intervals between fires. Conversely, species such as *Tristachya leucothrix* and *Cymbopogon plurinodis* are not as sensitive to low light conditions and survive extended periods of non-defoliation.

Conflicting results have been obtained on the effect of frequency of burning on bush. Kennan (1971) in Zimbabwe and van Wyk (1971) in Kruger National

Park both found that there were no biologically meaningful changes in bush density in response to different burning frequencies. In the False Thornveld of Eastern Cape Province, Trollope (1983) found that after 10 y of annual burning the density of bush increased by 41%, the majority in the form of short coppicing plants. Conversely, Sweet (1982) in Botswana and Boultwood and Rodel (1981) in Zimbabwe found that annual burning resulted in a significantly greater reduction in the density of bush than less frequent burning. It is difficult to draw any general conclusions from these contradictory results except to note that in all cases significant numbers of trees and shrubs were present even in the annually burned areas, irrespective of whether they had decreased or increased after burning. These variable results suggest that the effect of frequency of burning on woody vegetation is more an event-dependent effect in which factors like type and intensity of fire have had highly significant individual effects overshadowing the effect of frequency of burning per se.

The withdrawal of fire for extended periods of time appears to have a more predictable effect. For example, on the Accra Plains in southeastern Ghana, protection of moist savanna from fire for 29 y resulted in the development of forest-type vegetation with a fairly closed canopy. The fire-sensitive tree *Ceiba pentandra* became dominant (Carson and Abbiw 1990). Similar results have been obtained in the Lamto Reserve in the Ivory Coast, which receives a high mean annual rainfall of 1,300 mm and forms part of the Guinea savanna immediately adjacent to deciduous rain forest. The savanna vegetation is subjected to annual burning during the middle of the dry season. In a study investigating the exclusion of fire for 13 y, it was found that after 8 y open savanna rapidly changes into a dense, closed formation and after 13 y the first signs of forest developing occurred in the form of seedlings and saplings. In all the burned savannas of the Lamto Reserve, the pressure of forest elements on savanna vegetation is very high and fire exclusion initiates the development of forest (Menaut 1977). Similar trends have been found in the more arid savannas (500–700 mm annual rainfall) in southern Africa where in Kruger National Park fire exclusion caused both an increase in density and size of tree and shrub species (van Wyk 1971).

The effect of frequency of burning on forage production has not been intensively studied in South Africa and only limited quantitative data are available. The general conclusion is that the immediate effect of burning on the grass sward is a significant reduction of grass yield during the first post-fire growing season, but the depressive effect disappears during the second post-fire season (Tainton and Mentis 1984, Trollope 1984).

Frequent fires generally improve and maintain the nutritional quality of grassland, particularly in high rainfall areas, making it highly attractive to grazing animals. This phenomenon has been recorded throughout the savanna and grassland areas of Africa (West 1965, Tainton et al. 1977, Moe et al. 1990, Munthali and Banda 1992, Schackleton 1992). West (1965) stated that the fresh green shoots of new growth on burned grassland are very high in protein and quotes Plowes (1957) who found that the average crude protein content of 20 grasses after burning at the Matopos Research Station in Zimbabwe was 19%. This is approximately 2 times the protein content of mature grasses that have not been burned at the end of the dry season.

Apparently no information is available on the effect of frequency of burning on production and quality of browse by trees and shrubs in savanna areas.

Interactions between Fire and Herbivory

Post-burn herbivory can have a highly significant effect on botanical composition and structure of vegetation. The arid savannas of Eastern Cape Province receive a mean annual rainfall of approximately 500 mm and are an important livestock production area, particularly cattle ranching. However, during the last 50 y the grazing capacity of the rangeland has been drastically reduced by the encroachment of bush, primarily *Acacia karroo.*

An experiment was initiated in 1972 in the False Thornveld of the Eastern Cape at the University of Fort Hare to determine the role fire can play in controlling bush encroachment. Fire was chosen as a possible solution because ecologically it is recognized as a natural factor of the environment in African savannas and economically it is an indirect cost technique, making it suitable for the rehabilitation of rangeland with an inherently low economic potential. The hypothesis that fire maintains trees and shrubs at an available height and in an acceptable state for browsing animals was tested. The treatments involved applying a high-intensity fire (3,875 kJ s^{-1} m^{-1}) to a moderately encroached area of savanna (2.2 ha) dominated by *Acacia karroo* with a dense grass sward dominated by *Themeda triandra.* The high-intensity fire caused an 81.5% top-kill of tree stems and branches, but only 9.9% were killed (Trollope 1974). After the fire, follow-up treatments were superimposed on the burned area and have been maintained to date (33 y):

1) Grazing treatment (0.6 ha)—heavy grazing with cattle after the first frost in early winter (May–June) until uniform utilization of the grass sward has been achieved (approximately 10 d);
2) Browsing–grazing treatment (1 ha)—continuous stocking with goats (1 small stock unit/ha) and heavy grazing with cattle after the first frost in early winter (May–June) until uniform utilization of the grass sward has been achieved (approximately 10 d);
3) Burning treatment (0.6 ha)—annual burning at the end of winter prior to the first spring rains (July–August) (Trollope and Dondofema 2003).

These follow-up treatments have been maintained since the initiation of the experiment in 1972, and the long-term effects of the grazing, browsing–grazing, and annual burning treatments on the density of the bush were assessed in 2001 (Figure 4). Initially in

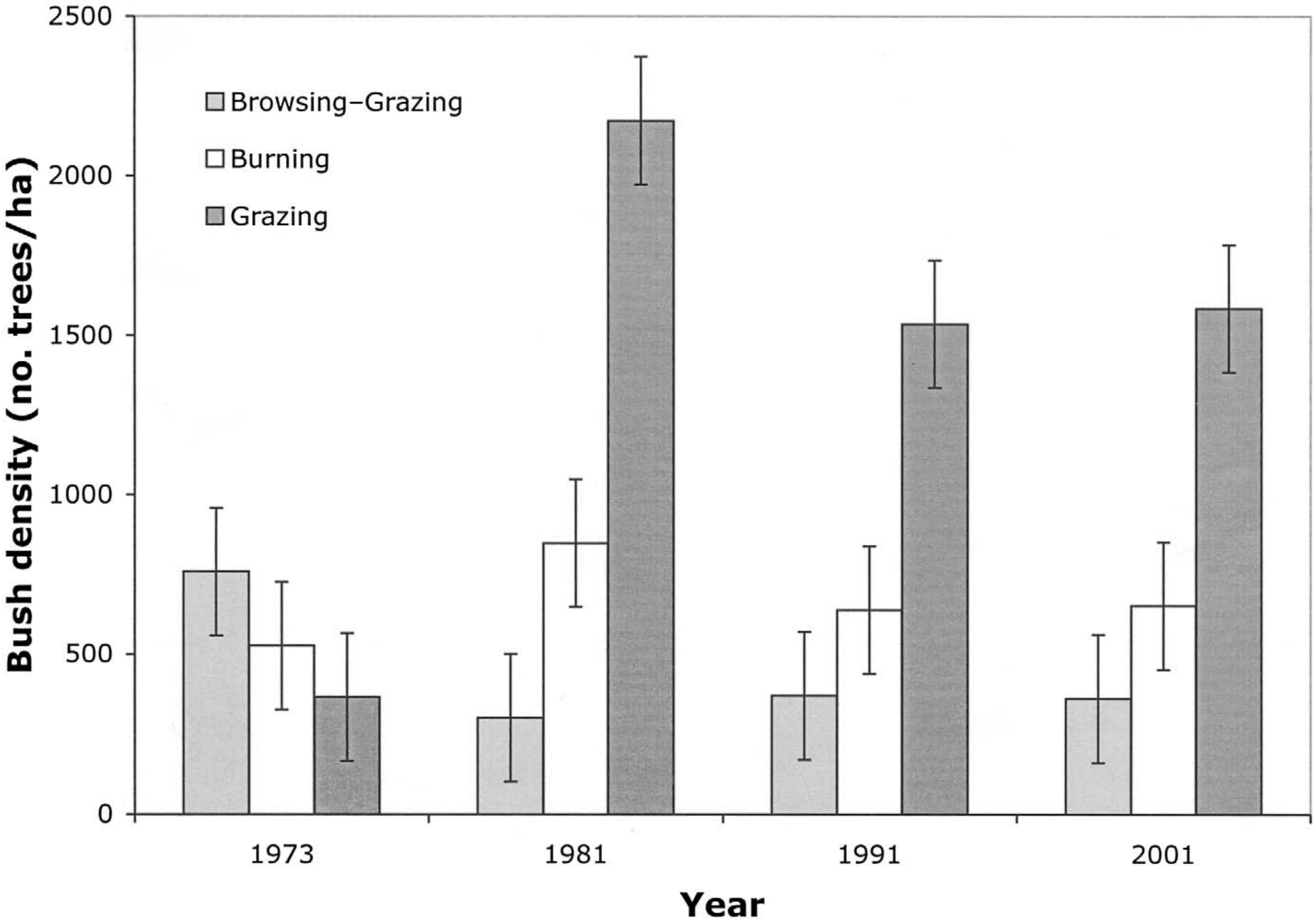

Fig. 4. Effect of grazing with cattle, browsing with goats, and annual burning on tree density (no. trees/ha) in the False Thornveld of the Eastern Cape, South Africa, 1973–2001.

1973 there were no marked differences in bush density in the different treatments. However, by 1981 distinct differences had developed and the browsing–grazing treatment had resulted in a significant reduction in density of trees and shrubs relative to 1973, and this was maintained up until the assessment in 2001 (29 y). Conversely, the grazing and annual burning treatments resulted in significant increases in density of trees and shrubs, with the grazing treatment resulting in the highest overall density of bush (Trollope and Dondofema 2003). This example illustrates the importance of the interacting effects of fire and herbivory on savanna vegetation when used as a range management practice in Africa.

FIRE MANAGEMENT

Research on the effects and use of fire in southern and East African grasslands and savannas (Trollope 1983, 1989; Trollope and Potgieter 1986; van Wilgen et al. 1990; Trollope and Trollope 1999; Trollope et al. 2000, 2003) has led to the conclusion that grass, trees, and shrubs in various localities in Africa react similarly to different components of the fire regime and, therefore, general guidelines can be formulated for prescribed burning. However, for the sake of clarity, guidelines for prescribed burning will be dealt with separately for the use of fire as a range management for domestic livestock husbandry and for wildlife management as the broad management objectives vary for these different forms of land use.

PRESCRIBED BURNING FOR DOMESTIC LIVESTOCK SYSTEMS

Prescribed burning is an important and often essential range management practice in areas used for either commercial or subsistence livestock farming. The most important factors to consider when planning a burning program are the reasons for burning and the appropriate fire regime to be applied.

Reasons for Prescribed Burning

The consensus among range scientists and progressive livestock farmers on permissible reasons for prescribed burning are 1) to remove moribund (i.e., leaf and stem material on grass plants that are overgrown and suffering from self-shading) and/or unacceptable (i.e., leaf and stem material on grass plants that is unpalatable to grazing animals) grass material, and 2) to control and/or prevent the encroachment of undesirable plants (Trollope 1989). These basic reasons for burning grassland and savanna vegetation in Africa are equally applicable to commercial or subsistence livestock farming.

An often quoted reason for burning rangeland is to stimulate an out-of-season ''green bite.'' This is often done during summer, late autumn, or late winter to provide green nutritious regrowth for grazing by livestock. This practice is unacceptable because 1) it reduces vigor of the grass sward, 2) it reduces basal and canopy cover of the grass sward, 3) it increases runoff of rainwater, and 4) it can result in accelerated soil erosion. This malpractice cannot be sufficiently condemned as it has been responsible for drastic deterioration in range condition over extensive areas of southern Africa, and unfortunate examples are evident at numerous sites in the eastern mountain grasslands of South Africa.

It has been suggested that fire can also be used to control ticks that cause tick-borne diseases in livestock, but this reason is generally discounted because ticks persist in areas that are frequently burned. However, Stampa (1959), in a study of the Karoo paralysis tick (*Ixodes rubicundus*) in the Karroid *Merxmuellera* Mountain Veld in South Africa, has shown that this parasite can be successfully controlled by altering the microclimate at the soil level and thereby creating an unfavorable habitat for this organism, resulting in its disappearance. Similar evidence has been obtained by Trollope et al. (2003) in the Ngorongoro Crater and Serengeti grasslands in Tanzania, where controlled burning by nomadic Masai pastoralists has resulted in a significantly lower incidence of ticks where this practice is applied. This latter finding has resulted in the reintroduction of prescribed burning in the Ngorongoro Crater, with beneficial results.

Finally it was shown that frequent fires favor the abundance of the productive and palatable grass species *Themeda triandra* in southern African grasslands (Scott 1971, Dillon 1980, Forbes and Trollope 1991). This raises the possibility of using fire to improve range condition by increasing the abundance of valuable forage species like *Themeda triandra.* Following appropriate research on the response of key forage species to fire, forage condition improvement could be considered as a valid reason for burning rangeland in the future.

Ecological Criteria for Prescribed Burning

The necessity for burning rangeland depends upon its ecological status and physical condition. Generally the condition of the grass sward determines whether rangeland should be considered for burning. This component reflects the ecological status of the ecosystem and the presence of or its ability to produce adequate grass fuel to carry and support a fire. Quantitative techniques have been developed in southern and East Africa to assess condition of the grass sward in relation to the need for prescribed burning (Trollope and Potgieter 1986, Hardy et al. 1999, Trollope and Trollope 1999, Trollope et al. 2000). The condition of the grass sward must be determined in terms of its botanical composition, ecological status, and basal cover, and involves classifying different grass species into different ecological categories according to their response to a grazing gradient, from high to low grazing intensities:

1) Decreaser species: Grass and herbaceous species that decrease when rangeland is under- or overgrazed;
2) Increaser I species: Grass and herbaceous species that increase when rangeland is under- or selectively grazed;
3) Increaser II species: Grass and herbaceous species that increase when rangeland is overgrazed.

Prescribed burning should not be applied if the grass sward is in a pioneer condition dominated by Increaser II grass species caused by overgrazing. Burning is generally not recommended when rangeland is in this condition in order to enable it to develop to a more productive stage dominated by Decreaser grass species. Conversely, when the grass sward is in an undergrazed condition dominated by Increaser I species, it needs to be burned to increase the fire-adapted and more productive Decreaser grass species. Finally, prescribed burning is necessary when the grass sward has become overgrown and moribund as a result of excessive self-shading. These conditions develop when the standing crop of grass is generally $\geq$4,000 kg/ha and can be estimated with the Disc Pasture Meter developed by Bransby and Tainton (1977).

The criteria used for deciding whether to burn to control or prevent the encroachment of undesirable plants are the same criteria describing the condition of the grass sward. However, grass fuel loads required for prescribed burning for this reason may differ depending on the encroaching plant species.

Fire Regime

In this discussion, the fire regime to be used in prescribed burning refers to the type and intensity of fire and the season and frequency of burning.

Type of Fire

It is recommended that fires burning with the wind either as surface headfires in grassland or a combination of surface headfires and crown fires in tree and shrub vegetation be used in prescribed burning because they cause least damage to the grass sward but can cause maximum damage to woody vegetation if required (Trollope 1999).

Fire Intensity

Research on fire behavior in Eastern Cape Province and Kruger National Park has shown that fire can be classified into categories according to fire intensity (Table 3) (Trollope 1983, Trollope and Potgieter 1985). When burning to remove moribund and/or unacceptable grass material, a cool fire of $<$1,000 kJ s^{-1} m^{-1} is recommended. This can be achieved by burning

Table 3. Fire classification according to fire intensity.

Fire intensity (kJ s^{-1} m^{-1})	Description
<500	Very cool
501–1,000	Cool
1,001–2,000	Moderately hot
2,001–3,000	Hot
>3,000	Extremely hot

when the air temperature is <20°C and the relative humidity is >50%. When burning to control undesirable plants like encroaching bush, a hot fire of >2,000 kJ s^{-1} m^{-1} is necessary. This can be achieved when the grass fuel load is >4,000 kg/ha, the air temperature is >25°C, and the relative humidity is <30%. A hot fire will cause a significant top-kill of stems and branches of bush species up to a height of 3 m. In all cases, the wind speed should not exceed 20 km/h.

Season of Burning

Research in southern Africa has clearly indicated that damage to the grass sward is minimized if burning is applied when the grass is dormant. Therefore, it is recommended that when burning to remove moribund and/or unacceptable grass material, burning should preferably be applied after the first rains of >13 mm at the commencement of the growing season, i.e., when grass is still dormant and fire hazard is low. Conversely, when burning to control encroaching plants, burning should be applied before the first rains of the growing season, i.e., when grass is very dry and dormant to ensure a high-intensity fire. The actual time of the year when prescribed burning will be applied in Africa depends on the latitude and rainfall pattern of the region.

Frequency of Burning

When burning to remove moribund and/or unacceptable grass material, frequency of burning will depend upon the rate of accumulation of excess grass litter (Trollope 1999). Field experience indicates that litter accumulation should not exceed 4,000 kg/ha and, therefore, frequency of burning should be based on the rate at which this phytomass of grass material accumulates. This approach has the advantage that the frequency of burning is related to the stocking rate of grazers and to the amount of rainfall the area receives. Generally in high rainfall areas (>700 mm/y) this will dictate a frequency of burning every 2–4 y. In more arid areas, the frequency will be much lower and, in fact, the threshold of a grass fuel load >4,000 kg/ha will generally exclude fire in these regions, particularly where condition of the rangeland is degraded and excessive grass fuel loads never accumulate.

Post-Fire Range Management

When burning to remove moribund and/or unacceptable grass material, grazing should be applied as soon as possible after the burn to take advantage of the highly nutritious regrowth of grass. It is unclear whether rotational or continuous grazing should be applied after fire. However, there is complete consensus among rangeland scientists on the necessity of applying a rotational resting system when prescribed burning is used (Zacharias 1994, Kirkman 2002). This involves withdrawing a portion of the rangeland from grazing for an extended period of at least 1 growing season or longer (6–12 mo) to maintain the vigor of grasses and enable seed production to occur for plant recruitment. The rest period is applied during the season prior to the prescribed burn. In terms of rotational grazing after a burn, great success has been obtained with the ‘‘open camp system’’ developed in KwaZulu-Natal. Grazing camps are permanently established fenced areas or paddocks on a commercial livestock ranch, i.e., the rangeland on a livestock ranch is subdivided into grazing camps that are grazed on a rotational basis. This system involves burning a camp and grazing it as soon as possible after the fire, after which the livestock are moved rotationally to other camps until such time as the burned camp is ready to be grazed again. Burned rangeland is thus maintained in a palatable and nutritious condition for as long as possible after the burn to the benefit of livestock. The same procedure is then followed in subsequent years. This system presupposes the availability of adequate camps to apply this form of grazing management. In areas where there are few grazing camps available, emphasis must be given to applying a rotational resting system. Where there are no camps, such as in communal grazing areas like the Transkei in South Africa, sufficiently large areas need to be burned to avoid overutilizing the burned area. This practice will also de facto result in a resting treatment being applied to the unburned area, which is initially less attractive to grazing animals.

PRESCRIBED BURNING FOR WILDLIFE MANAGEMENT

Prescribed burning is recognized as an important management practice for wildlife management in African grassland and savanna ecosystems and is regarded as a natural factor of the environment essential for the ecological well-being of both biotic and abiotic components (Trollope 1990, Thomson 1992, Bothma 1996). However, a wide diversity of views prevails on the most appropriate burning system to use in wildlife areas, ranging from so-called ‘‘natural’’ burning systems based entirely on lightning as the ignition source to actively applied burning systems based on rangeland condition.

Fire management systems are most developed in southern Africa. The different burning systems used are the lightning burning system, the range condition burning system, the patch mosaic burning system, and the integrated fire management system. Personal experience in southern and East African grasslands and savannas has led to the conclusion that the range condition burning system is a practical and efficient burning system to use in wildlife areas and is strongly recommended.

Range Condition Burning System

The range condition burning system was developed from a fire research program that was initiated in Eastern Cape Province in 1968 and later extended to Kruger National Park in 1982 and to East Africa in 1992 (Trollope 1971, Trollope and Potgieter 1985, Trollope and Trollope 1999). It is based on empirical results and is appropriate for use in wildlife areas because it provides a practical means of improving and maintaining species and habitat diversity of natural grassland and savanna ecosystems (Trollope 1971, Trollope et al. 1995). It can be used to remove moribund and/or unacceptable grass material, to create or maintain an optimum relationship between herbaceous and woody vegetation, if necessary, and to encourage wildlife to move to less preferred areas in order to minimize the overutilization of preferred areas. The basic philosophy of the range condition burning system is that the use of fire to achieve specific management objectives must be based on the condition of the vegetation and its known response to different components of the fire regime. Similar ecological criteria, as used for prescribed burning for domestic livestock systems, are also used to select areas for burning. This system also allows for all wildfires initiated by unplanned ignition sources, such as lightning or other causes, to burn freely if the grass sward is dominated by Decreaser and/or Increaser I grass species and is in a moribund and unpalatable condition. The effect of fire on grassland and savanna vegetation is similar irrespective of the source of ignition when burned under the same weather conditions. Finally, limits must be set on the extent of area to be burned at any one time as a precaution against inadequate forage being available for herbivorous wildlife. It is therefore recommended that not >50% of a given area be burned in moist grassland and savanna ecosystems (>700 mm rainfall/y) and not >33% in arid (<500 mm rainfall/y) grassland and savanna ecosystems.

The designated areas to be burned can be ignited either as point ignitions or as perimeter ignitions involving ‘‘block burning.’’ Point ignitions are used to develop a mosaic of different types of fires in response to changes in wind direction, air temperature, and relative humidity during the burning period. The ensuing fire mosaic will ensure a range of fire effects, which are intended to maximize habitat diversity both in grassland and woody components of the vegetation. The use of point ignitions is best suited to large conservation areas generally >20,000 ha (Brockett et al. 2001), where intensive range management is not a critical requirement. The intensity of prescribed burns will vary according to the objectives for burning similar to domestic livestock systems. Regarding season of burning it is recommended that prescribed burns be applied when the grass sward is dormant, but the ‘‘burning window’’ can extend over the entire dry season and the actual timing of fires may be varied according to objectives for burning. When burning to remove moribund grass material, prescribed burns can be applied at any time during the dormant season. When burning to reduce the density and size of trees and shrubs, fires should be applied when grass fuel is at its lowest moisture content in order to ensure a high-intensity fire. Finally, the guidelines used for controlling the frequency of burning in domestic livestock systems also apply to prescribed burning for wildlife management.

Post-Fire Range Management

Grazing after burning in wildlife areas is difficult to control. In order to prevent overgrazing, it is important to ensure that the burned area exceeds the short-term forage requirements of grazing animals that are attracted to the highly palatable and nutritious regrowth that develops after a burn (Trollope 1992). Another strategy that has been successful in southern Africa is to apply a series of patch burns at regular intervals throughout the duration of the burning window during the dormant season. This attracts grazing animals to successively burned areas, thereby spreading the impact of grazing over the entire burned area and avoiding the detrimental effects of heavy continuous grazing in any one area (Brockett et al. 2001).

GENERAL DISCUSSION AND CONCLUSIONS

An important feature of this overview of the fire ecology of African grasslands and savannas is the dependence of prescribed burning on a knowledge of fire behavior and fire effects. An attempt has been made to quantify primary factors affecting fire behavior in terms of rate of spread, fire intensity, and flame height of surface headfires. The influence of various factors contributing to fire intensity in African grasslands and savannas has also been quantified. Significant progress has been made with determining the effects of type and intensity of fires on the grass sward and tree and shrub vegetation in African grass and savanna ecosystems. This research has enabled formulating effective and practical guidelines for fire as a range management practice for domestic livestock production and wildlife management. However, research conducted to develop the fire intensity model and to determine the effects of type and intensity of fires on herbaceous and woody vegetation has been largely limited to savanna areas of the Eastern Cape Province and Kruger National Park. This emphasizes the need to extend similar fire ecological studies to other African grassland and savanna areas. The greatest limiting factors to conducting fire ecology studies are to find suitable study sites where landowners and users are prepared to sacrifice forage supplies that are normally used for sustaining either domestic livestock or wildlife populations. In addition, applying controlled experimental fires is dangerous, requiring well-developed managerial skills and suitable firefighting equipment to contain fires, all of which are not readily available over much of the African continent. Finally, competent fire ecologists are a rare commodity, not only in Africa but in the world, further limiting the implementation of a comprehensive fire research program elsewhere in Africa. The most successful attempt to test these results elsewhere in Africa has been to conduct fire behavior and fire effect trials in the Kenya central highlands. These trials lead to the conclusion that the behavior and effect of surface fires in East African grasslands and savannas were similar to that in southern African grasslands and savannas (Trollope and Trollope 1999).

Another successful attempt was to compare the behavior of fires in African grasslands and savannas with fires occurring in tallgrass prairies on the Konza Prairie Biological Station at Kansas State University in the United States. This involved recording the behavior of 45 surface headfires and 24 surface backfires applied as controlled burns to catchment units on Konza. A detailed analysis of the fire behavior data led to the conclusion that the overall behavior of surface headfires in tallgrass prairies at Konza was similar to that in grasslands and savanna ecosystems in South Africa (Trollope et al. 2004). These two independent data sets from similar types of vegetation, but in widely separated grassland and savanna areas on the earth, provide a measure of scientific support for research results that have been obtained on fire behavior and to an extent on fire effects in southern African grasslands and savannas. Nevertheless, it is strongly recommended that as much further research as possible be conducted in other African grassland and savanna ecosystems. This will contribute to a greater understanding of the fire ecology of these ecosystems, thereby leading to improved range management for both domestic livestock production and wildlife management on the African continent.

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