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1 · *Fire ecology – an introduction*

> The biological response to a fire can vary widely. It will depend, first, on the physical properties of the fire – its intensity, size, frequency and time of occurrence – all of which influence the chemical potential for combustion and determine the nature of the chemicals liberated by combustion. It will depend, too, on the genetic potential stored within biota, which may also be released by a fire, and on the mechanisms or relationships for exploiting a fire that may exist within the biota. (*Pyne (1982) p. 38*)

Fire is a topic on which most people can comment. Fire is a widespread phenomenon. Most of us have seen fires in natural vegetation, or their effects; stark, blackened vegetation or a smoke pall. Because fires such as these can have damaging economic and social effects, can spoil forestry timber, can burn down houses and farms, and can kill people and animals, there has been a lot written about wildfires. Added to this wide perception of the damage that can be caused by wildfires, there has been increasing publicity given, since the 1950s, to the active use of fire as a management tool, particularly in protecting against severe wildfires. The introduction of a policy of deliberate burning as a management tool has a fascinating history, especially in the United States Forest Service (see Schiff 1962, Pyne 1982), but the ecological effects of prescribing a fixed burning regime on large tracts of land are increasingly being questioned.

To an ecologist, fire can be treated as just one of many factors in an environment. It compares with droughts, floods, hurricanes and other physical disturbances because of the direct impact it makes on organisms. Unlike these physical factors, however, fire as a disturbing force is itself influenced by the biota, particularly the plant community. Alteration of the vegetation by any of a number of factors can influence the nature of a subsequent fire. Fire has similarities to grazing as a force on vegetation because of such feedback effects.

Although knowledge of the ecological effects of fire has contributed

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to the development of ecological theory, an understanding of fire also has broader significance. First, much of the world's forestry is conducted in natural ecosystems. Ecological processes, including fire, therefore impinge on long-term forest productivity in an economic sense. Second, a substantial amount of grazing by domestic stock is carried out in grasslands, rangelands, and pastoral land. Fires in these areas affect agriculture directly by removing biomass and killing animals, and indirectly by changing plant productivity and species composition. Third, fire affects the quality and quantity of water harvested from water catchments. Fourth, an understanding of the ecological processes that permit a plant community to recover after natural disturbances, such as fire, contributes to the success of efforts made to revegetate lands following man-made disturbances. Finally, an understanding of the ecological effects of fire, both wildfire and management burning, is fundamental to conservation of plant and animal populations and representative communities in many areas.

Application of knowledge about the effects of fire to each of the management tasks listed above depends upon a sound background in ecology and access to the literature dealing with fire. There is a need for a general treatment of fire ecology for the following reasons:

1. Students embarking upon research in relation to fire should familiarize themselves with the complexities of the field, be introduced to appropriate experimental and techniques, and be made aware of the major gaps in our knowledge.
2. People working with fire as a management tool are being forced more and more to take account of the ecological implications of their management practices. For these people, this text is an introduction to what may be an unfamiliar set of ideas and literature.
3. Finally, all of us – researchers, students and land managers – need to be reminded from time to time that there is a broader perspective on ecological problems than the approach on which we usually focus.

This book is not intended to be a comprehensive review of all the detailed knowledge, from every region of the world, of the ecological effects of fires. Some of this sort of information is available in various treatments of fire ecology that have been published recently (Table 1.1). Most of these publications have a regional slant and emphasize the need for further research into various aspects of fire ecology, pointing to specific unanswered questions in each region. However, the interpretation of the *general* significance of individual studies and specific questions and the application of conclusions from one study to an

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Table 1.1. *Recent books in fire ecology*

Booysen, P. de V. and Tainton, N. M. (eds.) (1984) *Ecological Effects of Fire in South African Ecosystems*. Springer-Verlag, New York.
Chandler, C., Cheney, P., Thomas, P., Trabaud, L., and Williams, D. (1983) *Fire in Forestry* (Vols. 1 & 2). Wiley, New York.
Cowling, R. (ed.) (1992) *The Ecology of Fynbos: Nutrients, Fire and Diversity*. Oxford University Press, Oxford.
Fuller, M. (1991) *Forest Fires: An Introduction to Wildland Fire Behavior, Management, Firefighting, and Prevention*. Wiley & Sons, New York.
Gill, A. M., Groves, R. H. & Noble, I. R. (eds.) (1981) *Fire and the Australian Biota*. Australian Acacemy of Science, Canberra.
Goldammer, J. G. (ed.) (1990) *Fire in the Tropical Biota*. Springer-Verlag, Berlin.
Johnson, E. A. (1992) *Fire and Vegetation Dynamics: Studies from the Boreal Forest*. Cambridge University Press, Cambridge.
Minnich, R. A. (1988) *The Biogeography of Fire in the San Bernardino Mountains of California: A Historical Study*. University of California Press, Berkeley.
Mooney, H. A., Bonnicksen, T. M., Christensen, N. L., Lotan, J. E. and Reiners, W. A. (eds.) (1981) *Fire Regimes and Ecosystem Properties*. USDA Forest Service Gen. Tech. Rep. WO-26. Washington DC.
Mooney, H. E. and Conrad, C. E. (eds.) (1977) *Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems*. USDA Forest Service Gen. Tech. Rep. WO-3. Washington DC.
Pyne, S. J. (1984) *Introduction to Wildland Fire*. Wiley and Sons, New York.
Pyne, S. J. (1991b) *Burning Bush: A Fire History of Australia*. Holt, New York.
Trabaud, L. (ed.) (1987b) *The Role of Fire in Ecological Systems*. SPB Academic Publishing, The Hague.
van Wilgen, B. W., Richardson, D. M., Kruger, F. J. and van Hensbergen, H. J. (eds.) (1992b) *Fire in South African Mountain Fynbos*. Springer-Verlag, Berlin.
Wade, D., Ewel, J. J. and Hofsetter, R. (1980) *Fire in South Florida Ecosystems*. USDA Forest Service Gen. Tech. Rep. SE-17. Asheville, North Carolina.
Walstad, J. D., Radosevich, S. R. and Sandberg, D. V. (eds.) (1990) *Natural and Prescribed Fire in Pacific Northwest Forests*. Oregon State University Press, Corvallis.
Wein, R. W. and MacLean, D. A. (eds.) (1983) *The Role of Fire in Northern Circumpolar Ecosystems*. Wiley and Sons, New York.
Wright, H. A. and Bailey, A. W. (1982) *Fire Ecology: United States and Southern Canada*. Wiley-Interscience, New York.

understanding of fire in another region require a broad perspective. There is a great deal to be gained by contrasting different regions and one aim of this book is therefore to provide a basic framework concerning the ecological effects of fires, which can be used to direct future investigations and assist interpretation of existing information.

Although one of the aims of this book is to examine general patterns

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and principles in fire ecology, there is nevertheless a geographic bias produced by my own experiences. Thus, many examples are drawn from studies in south-east and south-west Australia, Florida and, to a lesser extent, California.

The material presented in this book is divided into sections describing the phenomenon of fire, the responses of individual organisms to fires, and the responses of populations and communities to fires.

Students and researchers in fire ecology too frequently treat fire as an isolated but repeatable event, without acknowledging that one fire is not like another. In contrast, most ecologists would view it as foolish to treat a single dry spell in summer as ecologically equivalent to a 5-year-long drought. Grubb (1985) discussed the importance of this feature of fire, and this view has been strongly emphasized for over a decade, notably in A. M. Gill's writings about *fire regimes* (see, for example, Gill 1975, 1981b). A fire has the immediate characteristics of intensity, season, extent and type (i.e. humus, ground, crown) and historic characteristics such as pre-fire climate, time since previous fires and characteristics of previous fires. These immediate and historic components are not independent, since the history can exert a strong influence on the immediate fire characteristics.

This situation, combined with the need to focus on fairly large areas for the study of many individual organisms, populations or communities, makes replicated, long-term fire studies difficult. 'Replication' must therefore often come from an examination of the results of a number of independently conducted studies of similar organisms in similar environments. Dissecting background variability from real effects of the fires is problematic, and as many factors as possible causing variation among studies must be identified. If a study does focus on a single fire in isolation, descriptive information about the particular fire must be collected and published. Knowing what characteristics of fire to measure and how to do it are therefore important parts of a study of fire ecology, even if an organism, rather than the fire, is the primary focus of attention. The phenomenon of fire is therefore included as a separate chapter (Chapter 2).

Armed with this background, the remaining chapters explore the ecology of individual organisms, populations and communities in relation to fire. In each section, the general nature of ecological studies at that level of organization are explored and then fire effects are examined in this ecological context.

In writing a book such as this, there are certain approaches, principles

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and ideas which could be emphasized. In various sections of this book, my emphases will be apparent, but they are stated explicitly here.

1. The ecological effects of fire can be extremely complex. Although experimental studies must focus on specific questions, the possibility of interaction and second-order effects must be borne in mind. In particular, plants and animals are all too often separated in ecological studies. Such an approach may miss the important effect of fire affecting, for example, an herbivore population that in turn influences the plant community.
2. Fire should not be viewed as a catastrophic event in most situations. In the context of a species, a population or a community, the response to a fire is actually a response to one of a series of recurring events. The history of past fires at a site contributes to the response to the current one. In this respect, fire may be similar to many other recurrent events affecting organisms, such as droughts, floods, cyclones and hurricanes.
3. A consideration of time-scales of fires in relation to the organisms or communities involved must underlie an understanding of the ecological effects of fire. An individual tree may see many fires in its lifetime, whereas an insect or small-mammal species may go through many generations between fires.
4. Fires in some vegetation communities may indeed be considered catastrophic because, even though fires may recur, the frequency has been so low in the past that interfire intervals have exceeded many generations of the organisms affected. Similarly, fires of unusually high intensity or completely out-of-season may have catastrophic effects even in fire-prone environments.
5. One must be wary of inferring that characteristics which permit an organism to survive a fire should be considered 'fire adaptations'. A given characteristic may have arisen in response to a selection pressure other than fire. Also, the response of a population to a single fire is not a very good estimate of the fitness of individual lineages faced with a series of fires.
6. Perhaps too much emphasis is placed on obtaining an assessment of the so-called 'natural' fire regime of an area. It is frequently stated that, in the absence of more precise information about the ecological effects of particular fire regimes, the best management plan is to mimic nature. Although attempts can been made to estimate historic fire frequencies over various time spans (e.g. pre-human, pre-

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industrial) and to include estimates of the areas burned in past fires, other components of so-called 'natural' fire regimes, such as fire intensity, season and type (i.e. crown versus ground) are much more difficult to estimate, though equally important. Furthermore, even without the assistance of modern *Homo sapiens*, fire regime is sure to have varied widely over time, and the variation is likely to have been ecologically significant in itself. In the long run, a profitable approach may be to place more emphasis on understanding just how organisms, populations and communities respond to experimentally imposed fire regimes. Anthropogenic ignitions, increasing dissection of natural landscapes and reduction of fire-hazard are realities, and direct investigation will therefore become more and more valuable than inferences based solely on the estimation of natural fire regimes in the pre-human past.

7. There are very few long-term, experimental studies of the effects of fires on any level of organization – individual organism, population or community. Long-term studies are an absolute necessity for a variety of reasons. First, many organisms in fire-prone ecosystems have long lifespans, and the effects of even a single fire may not be revealed for many years. Second, management practices are based on assumptions that certain long-term processes are operating in the community. The validity of these processes has rarely been tested by long-term, empirical study. The need for validation of models of long-term change based on short-term studies is becoming urgent. Third, ecological effects of fire are responses to a sequence of fires occurring with a certain range of frequencies, intensities, seasonalities and extents. Let us focus on any one of these, say frequency, and hold the others constant in an experimental design. An experimental comparison of low-frequency fires (i.e. one fire in 50 years) and high-frequency fires (i.e. one fire in 5 years) will clearly take many decades. For researchers in short-term positions, these comments should not be disheartening. It will be clear from the material discussed in this book that in fire ecology there is also much need for, and scope for, carefully designed and conducted shorter-term experiments.
8. My approach is largely mechanistic, in the sense that much of ecology is seeking explanations for why observed patterns are the way they are. Hence, my emphasis is on studies that are experimental and comparative, rather than solely descriptive. There is a large literature describing patterns, especially of vegetation, in relation to fire (see, for example, many of the reference books listed in Table 1.1) that is not covered thoroughly in this book.

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Some definitions

In a field about which so many people know at least a little, it is as well to consider fire terminology that differs from one place to another. Terms used to describe fires include:

wildland fire	forest fire	prescription fire
bushfire	scrub fire	controlled fire
wildfire	brush fire	hazard-reduction fire
firestorm		cool-season fire

All this can be very confusing, and the terms variously describe (i) the intensity of a fire, (ii) whether it was planned by some land management authority, and (iii) the type of vegetation in which it occurs, or some combination of these three.

The *bushfires* of Australia include fires in forests, heaths and grasslands, and this term is probably equivalent to the term *wildland fire* that is commonly used in North America. These are generic terms that describe fires in natural vegetation, but typically they are fires that were not planned, but were started by arson, accident or lightning and burn out-of-control. The term *wildfire* certainly describes a fire that is out of control.

Terms such as *forest fire* and *brush fire* typically describe the vegetation type in which a fire occurs.

Fires are deliberately lit by land management agencies for a variety of reasons. These will usually be constrained by some *prescription* that is written down and considered prior to burning. Reasons for prescribing fire include *hazard-reduction* (that is, removing some biomass so as to reduce the intensity of a future wildfire) and these fires are typically 'controlled' and, to achieve this, conducted in a *cool season* of the year. High-intensity fires may also be prescribed, at times, to maintain a vegetation type, remove invasive weeds or manipulate faunal habitat. These would also be *controlled*, though not necessarily in the cool season.

There is another suite of terms that describe some characteristics of a fire. These include: head-fire, back-fire, back burn, burning off, burning out. The first two describe the position of a fire front relative to the wind: a head-fire burning with the wind and a back-fire burning into it. Back burning, burning off and burning out are three terms that describe deliberate burning, usually conducted during fire-fighting operations.

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2 · *Fire – the phenomenon*

This chapter examines the physical and chemical characteristics of fire. A comprehensive understanding of fire at this level of detail is important for ecologists because of the two-way interactions between the characteristics of the vegetation and the nature of a fire (Fig. 2.1). The physical and chemical reactions of combustion determine the underlying nature of a bushfire; whether it ignites, how hot it burns, how it behaves. The likelihood of a fire starting, given that an ignition source is present, may depend largely on physical and chemical factors. Variability in aspects of fire behaviour such as intensity and rate of spread may be determined, to a greater or lesser extent, by factors influencing the basic physical and chemical reactions.

An understanding of these basic principles will also reveal how the existing vegetation can influence the nature of fire at a site. The characteristics of the fire, with all these interacting causes, will influence strongly the responses of particular plant and animal species (to be considered in later chapters). The responses to fires of any particular element of the biota are highly variable, making predictions difficult. It is therefore very important that the variability among individual fires is at least described adequately in experimental, ecological studies, even if fire characteristics cannot be precisely controlled.

There are several excellent book-length treatments of the physical characteristics of fire and of fire behaviour. In particular, Luke and McArthur (1978), Chandler *et al.* (1983; Vol. 1), Pyne (1984) and Johnson (1992) are valuable references that elaborate some of the information presented in this chapter. It is useful to recognize that our understanding of the factors determining fire behaviour has grown through a series of models of increasing complexity. Thus, a simple fire-triangle model, which links fuel, moisture and oxygen as primary determinants of fire intensity, has developed through relatively simple empirical models (McArthur 1966, Noble *et al.* 1980) into more complicated, computer-aided predictions, such as BEHAVE (Burgan

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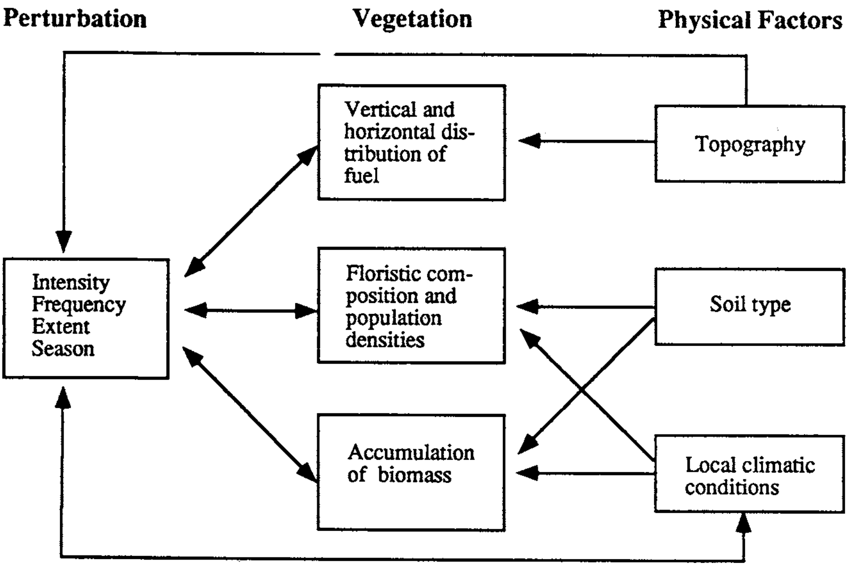

Figure 2.1 Schematic diagram illustrating the interactions between characteristics of fire, the vegetation and physical conditions (modified from Riba and Terridas 1987).

and Rothermel 1984, Catchpole and de Mestre 1986). In general, these models are based both on factors regulating the basic combustion reactions and also on an understanding of the ways in which various characteristics of climate, plant communities and the physical environment influence ignition and fire behaviour.

It is not within the scope of this book to explore these models: detailed treatments may be found in Burgan and Rothermel (1984), Catchpole and de Mestre (1986), Chandler *et al.* (1983) and other works. However, it is important for ecologists to understand combustion, and to be convinced that a description of relevant physical measures of fire is necessary in any ecological study.

In the field, many features of fuel, weather, topography and fire history interact in various ways to modify the *potential* fire characteristics, determined ultimately by the amount of energy stored as live and dead biomass per unit area. The following sections examine these interactions. The occurrence of fire is separated into two components, namely the initial ignition, or the establishment of flaming combustion, and the subsequent spread. Different, though overlapping, groups of factors control each.

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The chemical–physical reaction

The basis of fire is the physics and chemistry of combustion. Energy stored in biomass is released as heat when materials such as leaves, grass or wood combine with oxygen to form carbon dioxide, water vapour and small amounts of other substances. In some ways, this reaction can be thought of as a reverse of photosynthesis, in which carbon dioxide, water and solar energy are combined, producing a chemical energy store and oxygen. Trollope (1984) compared these processes in the following equations:

$$CO_2 + H_2O + \text{Solar energy} \rightarrow (C_6H_{10}O_5)_n + O_2 \quad \textit{Photosynthesis}$$

$$(C_6H_{10}O_5)_n + O_2 + \begin{matrix}\text{kindling} \\ \text{temperature}\end{matrix} \rightarrow CO_2 + H_2O + \text{heat} \quad \textit{Combustion}$$

In a simple form, the chemical equation for combustion can be illustrated with the complete combustion of a simple sugar, such as D-glucose (McArthur and Cheney 1972). In this case:

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + 1.28 \times 10^6 \text{ kJ}$$

Plant material is, of course, chemically much more complex than glucose, and different components of fuel (e.g. dead leaf litter, dead wood, live foliage, twigs and wood) have energy stored in a great variety of forms. However, the principle of the equation is much the same.

The term 'kindling temperature' in the above combustion equation indicates that combustion is neither a simple nor a spontaneous process. It requires the 'activation energy' of an external energy source. The process of combustion may be broken down into several stages. Wood is set on fire by first bringing to bear enough heat, from an external source, to cause pyrolysis. The colder the fuel is initially, the more kindling energy is required. Pyrolysis is the thermal alteration of the fuel, resulting in the release of water vapour, carbon dioxide and combustible gases, including methane, methanol and hydrogen. During pyrolysis, the reaction changes from being exothermic (i.e. requiring heat to proceed) to being endothermic (self-sustaining). Applying a pilot flame to the combustible gaseous products escaping from the wood and mixing with air during active pyrolysis results in flaming combustion.

Three stages of combustion in a vegetation fire can be recognized in relation to the basic principles of combustion. These are: (i) preheating, in which the fuel just ahead of the fire front is heated, dried and partly pyrolysed; (ii) flaming combustion, which results from the ignition of

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