ELSEVIER

Forest Ecology and Management 87 (1996) 127–138

Forest Ecology and Management

A qualitative successional model to assist in the management of Brazilian cerrados

Vânia Regina Pivello, Leopoldo Magno Coutinho

Dep. Ecologia Geral, Instituto de Biociências, Universidade de São Paulo, C.P. 11461, São Paulo, S.P. 05422-970, Brazil

Accepted 29 March 1996

Abstract

The Brazilian cerrado vegetation comprises a natural gradient of physiognomies, from open grassy fields to savannas and woodlands, according to soil conditions and local water availability. However, disturbances mainly caused by man tend to modify the natural distribution of cerrado physiognomies, taking them towards more primitive successional stages or even to other vegetation types.

To understand the functioning and the dynamics of cerrados submitted to disturbances and to support management decisions for conservation, an extensive amount of documented material (obtained from the literature) and non-documented information (obtained through an interview survey of 48 experts) was pulled together and analyzed, and a qualitative successional model was built, considering the following disturbances in cerrados: fire, grazing, wood cutting, weed invasion, drought and frost occurrences. This predictive model follows the 'state-and-transition' type. In the model, different communities are suggested according to the intensity, frequency and seasonality of the disturbances, as well as the combination of two or more disturbances, in a non-linear successional gradient, and the idea is to make use of them as management tools in cerrados, under proper regimes. The model is not conclusive and it is presented as a research prototype. Although every step in the model is based on literature evidence and/or expert opinion, a great amount of experimental research is necessary to validate it.

Keywords: Brazil; Savanna; Cerrado; Disturbance; Environmental management; Decision-making

1. Introduction

The Brazilian cerrados, a kind of savanna vegetation, originally covered 1.5–2.0 million km^2 of the country, representing 17–23% of the territory (Ab'Saber, 1971a; Rizzini, 1979). The extent of the cerrados comprises the core cerrado region, located in the Great Plateau of Central Brazil, as well as many patches of marginal cerrados dispersed beyond the core area (Fig. 1). Although physiognomically and structurally very similar, cerrados can be floristically distinct, according to their location (Heringer et al., 1977; Eiten, 1978, 1982; Gibbs et al., 1983; Castro, 1994).

Within the general term 'cerrado', there is a gradient of physiognomies, from the grassland type (the 'campo limpo') to a scierophylous forest (the 'cerradão'). Between these, there are three intermediate physiognomies, in increasing density of trees ('campo sujo', 'campo cerrado' and 'cerrado sensu

PII S0378-1127(96)03829-7

stricto'), which are the strict savanna forms (Fig. 2) (Coutinho, 1978, 1982). These terms are in common use by regional farmers, stock raisers and woodsmen, as well as by Brazilian scientists (Warming, 1908; Eiten, 1971, 1972; Goodland, 1971a; Coutinho, 1978, 1982, 1990; Rizzini, 1979), providing a working classification of cerrado ecosystems.

The presence of one or other physiognomy in the cerrado region is usually dependent on soil properties such as depth, fertility, drainage capacity and the occurrence of a superficial hardpan, as well as on human interferences (e.g. fire, wood cutting or cattle grazing). Cerrado sensu stricto and cerradão are found on deep, well-drained soils; cerradão usually appears in more fertile soils, and repeated cutting or burning tends to drive it towards the more open forms. Campo cerrado usually occurs in poorer or shallower soils, sometimes with lateritic concretions, or it may result from disturbed denser forms (Goodland and Pollard, 1973; Goodland and Ferri, 1979; Freire, 1979; Eiten, 1982; Furley and Ratter, 1988). Natural campo sujo and campo limpo are found either on very poor, very shallow soils, or where a hardpan exists, conditions which prevent the establishment of cerrado arboreal elements (Eiten, 1972, 1978, 1982). They can also occur as a consequence of repeated and frequent burning of more closed cerrados.

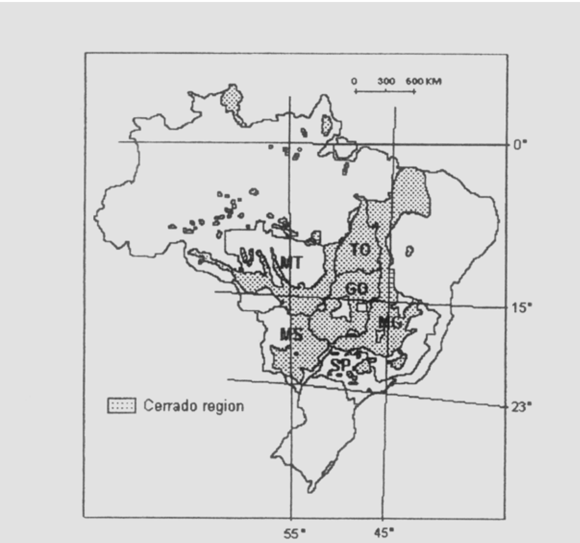

Fig. 1. The cerrado region of Brazil. MG, Minas Gerais State; GO, Goiás State; TO, Tocantins State; MT, Mato Grosso State; MS, Mato Grosso do Sul State; SP, São Paulo State.

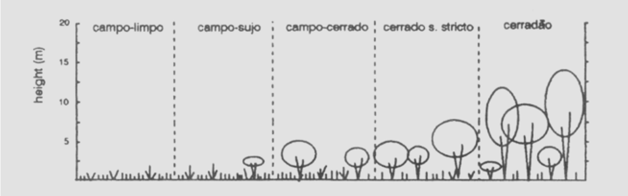

Fig. 2. Structural gradient of cerrado ecosystems (modified from Coutinho, 1982).

Within the cerrado region, patches of other vegetation types may occur interspersed among the cerrado forms, determined mainly by edaphic and geomorphological features, which govern soil fertility and water availability. Following the streams, where the water table is superficial and soils are hydromorphic, gallery forests bordered by a grassland belt, or palm fields of *Mauritia* spp in a grassy background (the 'veredas') appear, being subjected to periodical flooding. In the higher altitudes, rocky fields may occur under litholic soils. On richer soils and where there is more water available, isolated upland mesophytic forest groves are established (Fig. 3) (Ab'Saber, 1971b; Eiten, 1972, 1978, 1982; Queiroz-Neto, 1982; Cole, 1982, 1986). In many cases, however, the existing vegetation type or cerrado physiognomy does not correspond to the potential development for the area, having been modified by sporadic natural events, species competition or human actions, which can occur in isolation or simultaneously.

In most disturbed communities, the replacement sequence oscillate along a more or less predictable pattern, under average extent, frequency and intensity of the disturbance, as it also does in cerrados. However, when submitted to very frequent, broad or intense disturbances, or when there is a combination of two or more disturbances, the post-disturbance community can be either similar or very different to the original, following the multiple-pathway successional type (Noble and Slatyer, 1977; Cattelino et al., 1979; Pickett and White, 1985; Westoby et al., 1989).

The prediction of the successional path in a given ecosystem is important for management in the medium or longer term. In many circumstances, actions need to be taken in order to direct the community to a more desirable one, or to speed up

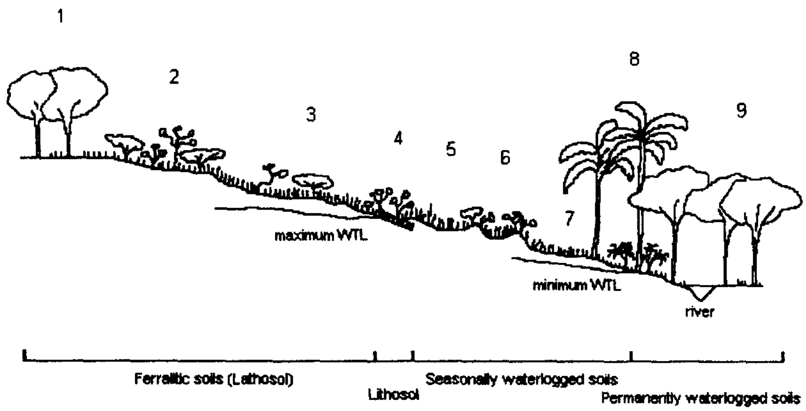

Fig. 3. Inter-relationship between topography, soil and vegetation types in the cerrado region (after Braun, 1971; Queiroz-Neto, 1982; Furley and Ratter, 1988; Oliveira Filho et al., 1989). 1, cerradão; 2, cerrado sensu stricto; 3, campo cerrado; 4, campo sujo; 5, campo limpo; 6, campo de murundus; 7, wet field; 8, vereda; 9, gallery forest; WTL, water table level.

the successional process. In extra-Amazonian Brazil, the present situation, where most native ecosystems exist as fragmented patches with limited self-recovery ability, demands management actions even in protected areas, such as biological reserves and national parks, where the 'no-action' policy has prevailed (Pivello, 1992). Specifically related to cerrado conservation areas, the main problems they are subjected to are dangerous wildfire outbreaks due to fuel build up, and weed infestation, causing the loss of typical plant and animal species (Pivello, 1992). These problems can be avoided by active management, which is not usually contemplated in management plans.

Information to set management procedures for cerrado ecosystems is still lacking and scattered, since little research has been directed to answer practical management questions. However, some information exists in experimental data or from observations of people who have day to day experience with the problems (heuristic knowledge). Therefore, the objectives of this study were:

1. to put together and to organize existing information coming from different sources (literature, experimental research and heuristics) useful for cerrado management;
2. to analyze the dynamics of cerrado ecosystems submitted to possible management actions or exposed to common natural events;
3. to propose a prototype qualitative model to predict successional trends which is simple enough to be understood and used by managers of cerrado conservation areas when making their decisions.

The model proposed here is not conclusive. Instead, it is an exploratory exercise which, gathering existing information and observations, presents possible successional trends in disturbed cerrados. Extensive experimental research is needed to validate the successional paths proposed. The building of this model could also identify all sorts of knowledge gaps for the management of cerrados, and direct research requirements.

2. Materials and methods

2.1. The study area

The study area includes the cerrados in São Paulo and Goiás States (see Fig. 1), where literature and interview surveys were carried out. Within São Paulo and Goiás States, four conservation areas were chosen as case studies—Mogi-Guaçu Biological Reserve, IBGE Ecological Reserve, Brasília National Park and Emas National Park (locations shown in Fig. 4)—which were investigated in more detail.

The predominant cerrado landscape is set on extensive plateaux, deeply dissected and fragmented in some parts, separated by flat-bottomed valleys, as well as on flat or gently rolling tablelands, with gently sloping sides (Ab'Saber, 1971a; Braun, 1971; Eiten, 1972). Climate is typically seasonal, with

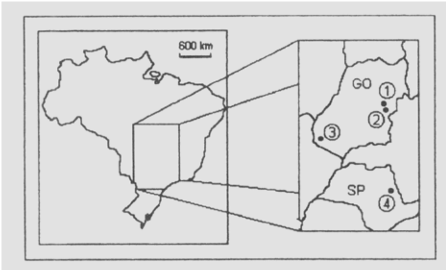

Fig. 4. Locations of the Brazilian conservation areas used as case studies. 1, Brasilia National Park; 2, IBGE Ecological Reserve; 3, Emas National Park; 4, Mogi-Guaçu Biological Reserve.

predictable alternating wet and dry periods, with the dry season in the winter. The extent of the dry season varies, according to the location, from 3 to 6 months. As in most wet savannas, cerrado soils are often deep, weathered, leached and, consequently, chemically poor, acid and ferralitic, as well as weakly structured. The predominant soil type in the cerrado region is the Lathosol (or Ferralsol) (Ranzani, 1971; Goodland, 1971b; Goodland and Ferri, 1979; Haridassan, 1982; Adámoli et al., 1987).

2.2. The knowledge acquisition process

Appropriate information necessary to develop the model, basically considering cerrado structure and functioning, management proceedings and their outcome, came from the literature, an interview survey carried out in Brazil, four case studies in Brazilian conservation areas, and personal experience of the authors.

Nineteen agricultural support organizations, advisory service offices, research institutes and universities were visited in São Paulo, Goiás and Mato Grosso do Sul States to collect documented information and to conduct most of the interviews with scientific researchers and managers of cerrado areas particularly concerned with conservation. Structured interviews were adopted (i.e. using pre-prepared questionnaires) following Byerlee et al. (1980).

2.3. The model

The model proposed follows the 'state-and-transition' model (Westoby et al., 1989), which assumes that succession is a multiple-pathway process, contrasting with earlier ideas on linear succession, suggested by Clements (Clements, 1916; Connel and Slatyer, 1977; Noble and Slatyer, 1977, 1980; Cattelino et al., 1979; Kessel, 1979; Christensen, 1985; Pickett and White, 1985; Walker, 1987; Westoby et al., 1989). In the model, each distinct stage in the community is called a 'state' and the actions that direct them to other states are called 'transitions'; states can be stationary or transient. Stationary states

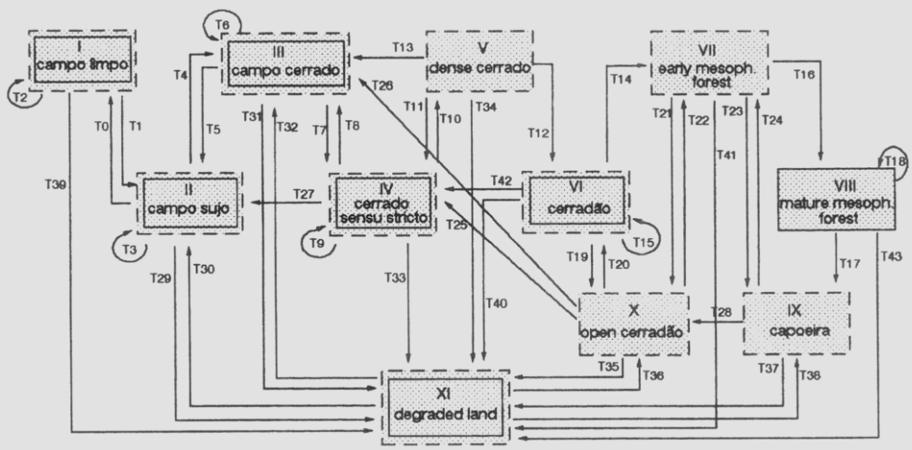

Fig. 5. A state-and-transition model for cerrado ecosystems.

Box 1 - Description of the states and transitions represented in Figure 5.

A- Catalogue of states:

State I = Campo-limpo with a few dominant fire-prone grass species. It can be a stationary state when maintained by frequent fires.

State II - Campo-sujo, scattered woody plants. A transient state if not determined by soil conditions, but it can become stationary due to fire and grazing.

State III = Campo-cerrado, with some trees. It can be maintained by periodical fires.

State IV = Cerrado-sensu-stricto, with a balanced proportion of trees and herbs.It can be maintained by periodical fires.

State V = Dense cerrado, with dominance of shrubs and trees over herbs. A transition to cerradão.

State VI = Cerradão, a forest community which combines fire-resistant and fire-sensitive species, mostly arboreal. Sometimes considered the climax stage, but probably not in the study region.

State VII = Early mesophylous forest, a transient state which has mostly forest species but still keeps cerradão species.

State VIII = Mature mesophyllous forest, a climax fire-sensitive community.

State IX = Capoeira, an open and disturbed transient forest stage impoverished by human actions.

State X = Open cerradão is considered in this region a disturbed cerradão depleted of arboreal elements. Always transient.

Stage XI = Degraded land is considered here as a highly disturbed vegetation, with a very altered species composition, either due to a strong infestation of exotics (weeds) or to soil cover depletion.

B - Catalogue of transitions:

T_1 = Early winter fire + grazing protection.

T_0, T_2 = Biennial or annual winter fires.

T_3 = Late winter or early spring fires every 1-3 years; moderate grazing.

T_4 = Fire protection; sporadic early winter fires (every 5-6 years); rainy winter + fire and grazing protection for 3-4 years; heavy grazing + early winter fire for *Melinis minutiflora* infestation; heavy grazing + herbicide for *Hyparrhenia rufa* or *Brachiaria* spp infestations.

T_5, T_8 = Frequent winter fires; wood cutting; frost + hot fire; consecutive very dry winters + hot fires; overgrazing.

T_6 = Winter fires every 2-3 years.

T_7 = Fire protection; rainy winter + fire protection; consecutive early winter fires + fire protection.

T_9 = Winter fires every 4-6 years.

T_{10} = Fire + cutting + grazing protection.

T_{11} = Mild winter fire; repeated frosts.

T_{12}, T_{14}, T_{16}, T_{18}, T_{20}, T_{22}, T_{24}, T_{36}, T_{38} = Fire + cutting protection.

T_{13} = Hot fire; repeated moderate fires; wood cutting.

T_{15} = Ground fire; mild wood cutting.

T_{17}, T_{23}, T_{26} = Fire; wood cutting; fire + wood cutting.

T_{19} = Fire; wood cutting; fire + wood cutting; repeated frosts.

T_{21} = Hot fire; repeated moderate fires; fire + wood cutting.

T_{25} = Cutting protection + periodical early fires.

T_{27}, T_{40}, T_{41}, T_{43} = Hot fires; heavy cutting.

T_{28} = Light winter fires.

T_{29}, T_{31} = Annual fires; overgrazing; strong weed invasion.

T_{30}, T_{32} = Fire + grazing protection if there is no weed invasion; periodical early winter fires if there is a fire-sensitive weed infestation; heavy grazing if there is a palatable weed infestation; herbicide treatment.

T_{33}, T_{34}, T_{35} = Hot fires; fire or cutting + strong weed invasion; heavy cutting + fire; overgrazing.

T_{37} = Hot fires; fire or cutting + strong weed invasion; heavy cutting + fire.

T_{39} = Overgrazing; strong weed invasion.

T_{42} = Selective wood cutting.

C - Opportunities and Hazards:

State I = A campo-sujo can lose all the woody elements due to very frequent fires (T_0), becoming a campo-limpo. Fire-prone species, such as Tristachya leiostachya or, in more humid soils, Imperata brasiliensis and Sorghastrum sp, may dominate the area, favouring recurrent fires (T_2). These species are not palatable and cannot be contolled by grazing pressure. The only action to return to a denser physiognomy would be fire protection, although this is difficult because of the flammability of these species.

States II, III and IV - Denser cerrados can become depleted from their arboreal elements by wood cutting or frequent fires, specially if hot or winter fires, which damage woody species (T_5, T_8, T_{27}). Fires after a frost event are usually hotter, because of the high amount of dead leaves, which will be consumed as fuel. Very dry winters decrease seed availability to germination, as well as kill seedlings, being more a problem for woody species. However, if the stresses cease and the area is protected from fire and grazing, it would evolve to denser forms (T_4, T_7). Some procedures can speed up woody species recovery and avoid weed infestations. A mild fire treatment at early winter (T4), sometimes associated with grazing, is thought to be best for achieving a denser vegetation, once total fire protection can favour a Melinis minutiflora (molasses-grass) invasion, disturbing the course of cerrado development. From a molasses-grass dominated sward, the return to the previous ecosystem can be very slow and, where it is feasible, heavy grazing could help in accelerating the process. In other cases, mild early fires every 2-3 years before this grass releases seeds (April-May) associated with grazing or not, could maintain it under control. Although it is possible to restrain molasses-grass, it cannot be eradicated from open communities, neither by burning nor by other treatment, since its seeds are always able to come from nearby. Without any management action against molasses-grass, the community can become degradaded by a strong infestation and remain as that for a long time (stateXI). As it is shade-sensitive, it will only leave the community in later successional stages, when the ground layer is well shaded, although the process may take as long as 20-30 years or more. All actions which open up the vegetation structure mey lead to site degradation when intensified (T_{29}, T_{31}, T_{33}), reducing soil cover and greatly changing species composition, favouring pioneer species. In some cases (states XI to IV and XI to V), vegetation recovery does not occur directly but through an intermediate state. Strong weed infestations may be treated by fire, heavy grazing or herbicide, according to the species.

States V, VI and X = Actions which disturb the canopy structure of dense cerrado and cerradão lead to herb establishment and to a more open physiognomy (T_{13}, T_{19}) and, according to their intensity and frequency, to weed invasion and land degradation (T_{34}, T_{35}). In this case, the best alternative for vegetation recovery seems to be total protection against fire and cutting. Cerradão and dense cerrados recovery from degraded sites might occur via previous communities (open cerradão and campo cerrado, respectively). Mild ground fires can also maintain cerradão structures, preventing them to develop to mesophylous forest, as fire-prone species are kept in the community.

State VII and IX = Protected from fire and cutting, cerradão and early mesophyllous forest can develop to a mature mesophyllous forest (T_{14}, T_{16}). As in open cerrado physiognomies, cutting or burning cerradão will open the canopy, permitting the establishment of herbaceous species, many of them from the previous cerrado successional stages (T_{19}). Depending on the remaining balance of cerrado and forest species after the disturbance, an early mesophyllous forest can either shift to an open cerradão or to a "capoeira" (T_{21}, T_{23}).

Stage VIII = A mature mesophyllous forest will perpetuate without harmful actions, such as fire and cutting (T_{18}) or become degraded (T_{17}, T_{37}).

Stage XI = A degraded land will only be able to recover if there is an available pool of native cerrado or forest species. To move to any natural seral stage it will probably take many decades.

are more stable communities, which persist for decades, while the transient states are temporary, persisting on an annual scale.

The state-and-transition model allows for disturbances of different intensities, such as distinct fire regimes, and for more than one disturbance at the same time, as usually occurs in real-life situations; it also allows the inclusion of stochastic events. It is basically qualitative and the level of detail can be adjusted according to available information.

3. Results

The model proposed below (Fig. 5 and Box 1) starts with a campo limpo not determined by edaphic conditions and where an available seed bank of species from denser cerrados exists, being therefore apt to evolve to a climax vegetation. This premise is also assumed for the other physiognomies. Fire (natural or anthropogenic), grazing, cutting, weed invasion, the occurrence of frost and of an exceptional drought, the most common events able to change cerrado structure and/or composition, were taken into account as transitions. If the disturbance is relatively light, the community is taken to a previous successional stage or, when the disturbance is severe or recurrent, it may also diverge to another vegetation type, such as degraded land. The actions able to shift cerrado communities from one state to another (shown in Fig. 5) can also be seen as options for their management.

Although the model was developed for the management of cerrados mostly in São Paulo and Goiás States, it may be applied to most cerrados within the core region.

4. Discussion

It is agreed by most authors that the typical successional pattern in cerrado ecosystems moves from the more open forms to denser physiognomies, along the gradient represented in Figs. 2 and 5, going as far as permitted by edaphic constraints (Eiten, 1972; Goodland and Ferri, 1979; Coutinho, 1982, 1990). During the succession process, the community gradually loses the heliophytes and fire-resistant species, common to open cerrado forms, and contains more and more late successional stage individuals. In São Paulo State, an open cerrado patch was able to acquire the cerradão structure about 30 years after protection from fire, grazing and cutting (Goodland and Ferri, 1979).

Cerradão has been considered the final successional stage by some authors (Eiten, 1971; Rizzini, 1979), while others believe that, in most cases, cerradão can develop to mesophyllous forest after many decades of fire and cutting protection (Cole, 1986; Furley and Ratter, 1988; Ratter, 1991; Bráulio F.S. Dias and Waldir Mantovani, personal communication). Although this hypothesis has not been adequately tested, observations show that, at least in the area considered in this study (São Paulo and Goiás States), cerradão evolves to mesophyllous forest. The existence of many species common to both communities (Rizzini, 1971) and also a continuum of soil fertility from dystrophic to mesotrophic cerradões and to mesophyllous forest suggest that cerradão is a transitional phase, which is admitted in the model (Fig. 5, states VI to VIII).

Analyzing a physiognomic gradient of cerrado forms in São Paulo State, Gibbs et al. (1983) suggested that the floristic and physiognomic differences were due mostly to human disturbances, such as burning and clearing, rather than to natural causes. Fire is one of the most important factors in opening the vegetation structure. According to the fire regime —a combination of fire type, intensity, frequency and season—a number of consequences may be expected in the community, as reported by several authors (Gill, 1975, 1977; Vogl, 1979; Coutinho, 1980; Wright and Bailey, 1982; Gillon, 1983; Frost, 1984; Trollope, 1984; Christensen, 1985; Walker, 1985; Lamprey, 1986; Frost and Robertson, 1987; Faulkner et al., 1989; Pivello, 1992; Pivello and Coutinho, 1992; Kauffman et al., 1994) and this plasticity is the main reason why fire is the most used management tool in savannas. In cerrados, fires in mid-winter (July–September) and mainly late fires (end of September to October) are recognized as damaging to trees and favouring grasses, the latter are dormant at this period. In contrast, early fires (May–June) are relatively cool and favour woody plants rather than grasses; summer fires (January–February) are usually harmful to herbs and grasses, since they severely disturb their phenological cycles (Coutinho, 1980, 1990; Pivello, 1992; Pivello and Norton, 1996).

According to fire frequency, the smaller the interval between fires, the more open the resulting vegetation structure. When fires are more frequent than the period required for the juveniles of the woody species to reach maturity, the vegetation structure will become more and more open and, after some decades without replacement of the old individuals, these species will tend to disappear. This is represented in the proposed model (Fig. 5) when you go from state VI to state I, considering also the respective transitions. On the other hand, if fires are less frequent, woody species will be able to develop and to reproduce (going from state I to VI, Fig. 5). Very frequent fires in savannas can be deleterious to the ecosystem as they reduce its pool of nutrients, but the total absence of fire can cause litter build up which retains nutrients, retarding the nutrient cycling, besides favouring wildfire occurrences (Pivello, 1992; Pivello and Coutinho, 1992). In cerrados, very frequent fires can cause severe changes in the community species composition, becoming dominated by a few fire-tolerant species (state I, Fig. 5). This is the example of the *Tristachya leiostachya* Nees, *Imperata brasiliensis* Trinius and *Sorghastrum* sp communities. Although there is no record in the literature, there are indications that campos limpos dominated by these species have developed apparently due to very frequent fires (Bráulio F.S. Dias and Leopoldo M. Coutinho, personal communication) and are self-maintained by recurrent annual or biennial burns (see Fig. 5, transition 2), which occur naturally, due to the high flammability of these species. Although possible (see Fig. 5, transition 1), it is very difficult to maintain these communities free of fire for a period long enough to permit the establishment of other species, in order to reverse the process and that is why state I may be stationary.

Fire is assumed as responsible for the 'savannization' of semi-deciduous forests in Asia (Blasco, 1983) and Cuba (Borhidi, 1988). The same seems to occur in the region of this study, where fire in mesophytic forest causes a shift to open cerradão; the younger the forest, the more cerrado species would be likely to re-establish (Fig. 5, transition 21). Burning or cutting mature mesophyllous forests would probably lead them to disturbed secondary forests (capoeira), but no longer to cerrado forms (Fig. 5, transition 17). Although frequent burnings of mesophytic forests have been assumed responsible for changing their floristic composition and shifting them to savanna environments (Ferri, 1943; Rawitscher, 1944; Beard, 1949; Rizzini, 1979), this seems to occur only when the forest is young or disturbed (Fig. 5, state VII), or even in the forest borders, because fire rarely penetrates mature forests. The same opinion is shared by Eden (1985).

Another versatile management option for savannas is through controlled grazing pressure. Light to moderate grazing stimulates herb and grass regrowth, increasing their palatability. As grazing intensity increases, the more palatable species can be depleted and tree/shrub density might increase, up to a point where trampling kills seedlings of the arboreal elements (Norton-Griffiths, 1979; McNaughton, 1979, 1984; Whiteman, 1980; Gillon, 1983; Trollope, 1984; Tothill and Mott, 1985; Ruess, 1987; Skarpe, 1991). Thus, grazing can be used to maintain open grassy savannas, for example (as suggested in Fig. 5 by transitions 3, 5 and 8), or to control exotic palatable species (Fig. 5, transitions 30 and 32). In conservation areas, however, grazing by domestic animals as a management tool must be used with caution, since domestic animals can bring diseases to the native mammals. Clipping has also been reported to reduce tillering in some grasses, especially *Melinis minutiflora* Beauvois (molasses–grass), an invader species of Brazilian cerrados (Klink, 1994).

The interaction between fire and grazing can also be another management possibility. Sometimes they cause similar and, therefore, additive effects on the community, such as increased herb palatability and regrowth, as well as litter reduction. At other times, these two factors have opposite effects: frequent or intense fires tend to decrease tree density, while grazing tends to increase it; fire usually selects for tall and rhyzomatous grasses, while grazing selects short or annual grasses (Borhidi, 1988). The combined effects of fire, grazing and herbicides can be a management option to control the most frequent invader species in cerrados: *Melinis minutiflora* Beauvois, *Hyparrhenia rufa* Nees and *Brachiaria* spp (Fig. 5, transitions 4, 30 and 32) (Pivello, 1992), all of them heliophytes and C_4 species (Klink and Joly, 1989). They are pasture grasses which spread without control in the open environments, out-competing the native species. In the natural vegetation, it has been observed that these pasture species require disturbed soils to establish (Coutinho, 1980). Although there is some controversy about *Melinis minutiflora* being fire-sensitive (Aronovich and Rocha, 1985; Costa and Brandão, 1988; Filgueiras, 1990), it is more likely that, in sites frequently burned, native cerrado herbaceous species become more vigorous and out-compete *Melinis* (Coutinho, 1976), which remains at a much lower density. This does not seem to be the case for *Hyparrhenia rufa* and *Brachiaria* spp. To control their infestations, herbicide treatment or heavy grazing could be tried (Pivello, 1992; Bráulio F.S. Dias, personal communication). Weeding is not feasible in large areas and it also disturbs the soil even more. In the longer term, the development of a denser vegetation will cause the loss of these grasses by shading.

The practice of wood cutting is common in savannas, usually associated with cattle raising. Opening up the canopy causes changes in the microclimate, allowing the propagation of heliophytes. It has been observed in sub-humid climatic regions that cutting in association with fire and sometimes with grazing can lead semi-deciduous forests to a 'savannization' process (Fig. 5, transitions 17, 21 and 23), stimulating the development of the herbaceous layer and changing the species composition (Blasco, 1983; Eden, 1985; Borhidi, 1988).

Sporadic climatic events, such as frost occurrences or unusual rainfall patterns, may also bring changes to the community. Cerrado plants are sensitive to frost, which kills young and seedlings of woody species, although not the adults (De Vuono et al., 1982; Delitti, 1984; Filgueiras and Pereira, 1989) and may delay tree/shrub development (Fig. 5, transitions 11 and 19). A very dry winter, which lasts longer than usual, results in higher fruit and seed consumption by predators and may also cause the death of seedlings, thus delaying woody encroachment. A wet winter, on the other hand, stimulates seed recruitment and woody species development (Waldir Mantovani, personal communication). Frost events also interact with fire, since the large amount of dead material caused by the frost favours hot fires which damage woody elements, opening the physiognomy (Fig. 5, transitions 5 and 8).

5. Further considerations

Management success is directly dependent on the level of knowledge about relevant environmental components and the inter-relationships which govern their dynamics. The successional development of disturbed cerrados is a poorly explored field of experimental research to a great extent because it takes a long time to follow, but also because it involves risks, since fire is always present in such ecosystems. Thus, part of the knowledge used to build the model presented came from people's experience, observations and data extracted from research designed for other purposes, resulting in a simple and rather general prototype. Even so, it can be very useful to cerrado managers and decision-makers, since it pulls together practical information that is very scattered in the literature; further research could add more useful information to the model, thus improving its performance. However, longer term investigation on successional trends in disturbed cerrados is needed to validate all the assumptions made and to predict the longer term implications of different management regimes on ecosystem development. Some of the most important topics which require urgent investigation as identified during this study are related to:

1. Historical data: records (including information from aerial photographs) on successional changes in cerrado ecosystems; records of fire occurrences in cerrados; information on management practices used by Indian peoples and their effects on the communities.
2. Surveys: detailed floristic surveys in every cerrado physiognomy, relating species to vegetation form and to environmental conditions; detailed floristic surveys in grazed lands, relating species to grazing pressure.
3. Basic biological information on phenology, reproduction, dispersal and recruitment strategies of cerrado plants.
4. Field experiments: to determine the effects of different disturbance (fire, grazing, cutting) regimes and/or pressures on soil physical and chemical properties, soil biota, plant regeneration and changes in species composition; to find methods for the control of exotic herbs; to analyze changes in plant species composition according to different grazing pressures; to analyze interacting effects of the disturbances considered.

6. Conclusions

The consequences of disturbances on cerrado environments may result in a complex of altered communities, since the cerrado landscape comprises a wide variety of ecosystems and phytophysiognomies, and the disturbance types, regimes and interactions vary in many ways.

Nowadays, almost every cerrado environment is no longer 'natural' but remains under human pressure, and, consequently, efforts must be made to relate the fragmented existing information in order to test predictions and thus diminish the huge knowledge gap concerning cerrado dynamics under disturbance regimes and its practical management. Moreover, most of the disturbances considered can be used as management tools, especially fire and grazing which are able to induce a large range of environmental responses, according to the regime adopted.

Therefore, qualitative models as presented here, even preliminary, can be very useful for the following reasons:

1. they put together fragmented information;
2. they analyze the information on a practical basis;
3. they point out knowledge gaps;
4. they stimulate corroborative experimental research.

Acknowledgements

The authors are grateful to Dr. Waldir Mantovani for the productive discussions on parts of the model.

References

Ab'Saber, A.N., 1971a. A organização natural das paisagens inter e subtropicals brasileiras. In: M.G. Ferri (Editor), III Simpósio sobre o Cerrado. Edgard Blucher/EDUSP, São Paulo, pp. 1–14.

Ab'Saber, A.N., 1971b. Contribuição à geomorfologia da área dos cerrados. In: M.G. Ferri (Editor), Simpósio sobre o Cerrado. Edgard Blucher/EDUSP, São Paulo, pp. 94–104.

Adálmoli, J., Macedo, J., Azevedo, L.G. and Madeira Netto, J., 1987. Caracterização da região dos cerrados. In: W.J. Goedert (Editor), Solos dos Cerrados. EMBRAPA-CPAC, Planaltina, pp. 33–74.

Aronovich, S. and Rocha, G.L., 1985. Gramíneas e leguminosas forrageiras de importância no Brasil central pacuário. Inf. Agropec., 11(132): 3–13.

Beard, J.S., 1949. Brazilian campo cerrado: fire climax or edaphic climax? Geogr. Res., 39(4): 664–666.

Blasco, F., 1983. The transition from open forest to savanna in continental southeast Asia. In: F. Bourlière (Editor), Tropical Savannas. Elsevier, Oxford, pp. 167–182.

Borhidi, A., 1988. Vegetation dynamics of the savannization process on Cuba. Vegetatio, 77: 177–183.

Braun, O., 1971. Contribuição à geomorfologia do Brasil Central. Rev. Bras. Geogr., 32(3): 3–39.

Byerlee, D., Collinson, M., Perrin, R., Wilkemann, D. and Biggs, S., 1980. Planning Technologies Appropriate to Farmers—Concepts and Procedures. CIMMYT, Mexico City, 71 pp.

Castro, A.A.J.F., 1994. Comparção florístico-geográfica (Brasil) e fitossociológica (Piauí-São Paulo) de amostras de cerrado. Ph.D. Thesis, Universidade Federal do Piauí, Teresina.

Cattelino, P.J., Noble, I.R., Slatyer, R.O. and Kessel, S.R., 1979. Predicting the multiple pathways of plant succession. Environ. Manage., 3(1): 41–50.

Christensen, N.L., 1985. Shrubland fire regimes and their evolutionary consequences. In: S.T. Pickett and P.S. White (Editors), The Ecology of Natural Disturbances and Patch Dynamics. Academic Press, London, pp. 85–100.

Clements, F.E., 1916. Plant Succession: An Analysis of the Development of Vegetation. Carnegie Institution, Washington, DC, 512 pp.

Cole, M.M., 1982. The influence of soils, geomorphology and geology on the distribution of plant communities in savanna ecosystems. In: B.J. Huntley and B.H. Walker (Editors), Ecology of Tropical Savannas. Springer-Verlag, Berlin, pp. 145–174.

Cole, M.M., 1986. The Savannas—Biogeography and Geobotany. Academic Press, London, 438 pp.

Connel, J.H. and Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat., 111: 1119–1144.

Costa, N.M.S. and Brandão, M., 1988. Plantas daninhas com possibilidade de serem empregadas como forrageiras. Inf. Agropec., 13(150): 17–21.

Coutinho, L.M., 1976. Contribuição ao conhecimento do papel ecológico das queimadas na floração de espécies do cerrado. Thesis, Instituto de Biociências da Universidade de São Paulo, São Paulo, 173 pp.

Coutinho, L.M., 1978. O conceito de cerrado. Rev. Bras. Bot., 1: 17–23.

Coutinho, L.M., 1980. As queimadas e seu papel ecológico. Bras. Florest., 44: 7–23.

Coutinho, L.M., 1982. Ecological effects of fire in Brazilian cerrado. In: B.J. Huntley and B.H. Walker (Editors), Ecology of Tropical Savannas. Springer-Verlag, Berlin, pp. 273–291.

Coutinho, L.M., 1990. Fire in the ecology of the Brazilian cerrado. In: J.G. Goldammer (Editor), Fire in the Tropical Biota —Ecosystem Processess and Global Challenges. Springer-Verlag, Berlin, pp. 81–105.

Delitti, W.B.C., 1984. Aspectos comparativos da ciclagem de nutrientes minerais na Mata Ciliar, no Campo Cerrado e na floresta implantada de *Pinus elliottii* Engelm. var. *elliottii* (Mogi-Guaçu, S.P.). M.Sc. Thesis, Instituto de Biociências da Universidade de São Paulo, São Paulo, 298 pp.

De Vuono, Y.S., Barbosa, L.M., Batista, E.A. and Gurgel Filho, O.A., 1982. Efeitos biológicos da geada na vegetação do cerrado (nota prévia). Silvic. São Paulo, 16A(1): 545–547.

Eden, M.J., 1985. Forest cultivation and derived savanna and grassland: comparative studies from Papua and south-west Guyana. In: J.C. Tothill and J.C. Mott (Editors), Proceedings of the International Savanna Symposium 1984. Australian Academy of Science, Canberra, pp. 260–264.

Eiten, G., 1971. Habitat flora of Fazenda Campininha, São Paulo, Brazil. In: M.G. Ferri (Editor), Simpósio sobre o Cerrado. Edgard Blucher/EDUSP, São Paulo, pp. 155–202.

Eiten, G., 1972. The cerrado vegetation of Brazil. Bot. Rev., 38(2): 201–341.

Eiten, G., 1978. Delimitation of the cerrado concept. Vegetatio, 36(3): 169–178.

Eiten, G., 1982. Brazilian 'savannas'. In: B.J. Huntley and B.H. Walker (Editors), Ecology of Tropical Savannas. Springer-Verlag, Berlin, pp. 25–47.

Faulkner, J.L., Clebsch, E.E.C. and Sanders, W.L., 1989. Use of prescribed burning for managing natural and historic resources in Chickamauga and Chattanooga National Military Park, USA. Environ. Manage., 13(5): 603–612.

Ferri, M.G., 1943. Observações sobre Lagoa Santa. Ceres, 4: 1–16.

Filgueiras, T.S., 1990. Africanas no Brasil: gramíneas introduzidas da África. Cad. Geociênc., 5: 57–62.

Filgueiras, T.S. and Pereira, B.A.S., 1989. Efeito de uma geada sobre a flora do cerrado na Reserva Ecológica do IBGE, DF-Brasil. Cad. Geociênc., 2: 67–70.

Freire, E.M.S., 1979. Influência das propriedades do solo na distribuição de comunidades de vegetação em uma topossequência, em área da 2° superfície de erosão do Planalto Central Brasileiro, na Fazenda Água Limpa, D.F. M.Sc. Thesis, Universidade de Brasília, 140 pp.

Frost, P.G.H., 1984. The responses and survival of organisms in fireprone environments. In: V. Booysen and N.M. Tainton (Editors), Ecological Effects of Fire. Springer-Verlag, Berlin, pp. 273–309.

Frost, P.G.H. and Robertson, F., 1987. The ecological effects of fire in savannas. In: B.H. Walker (Editor), Determinants of Tropical Savannas. IRL Press, Oxford, pp. 93–140.

Furley, P.A. and Ratter, J.A., 1988. Soil resources and plant communities of the central Brazilian cerrado and their development. J. Biogeogr., 15(1): 97–108.

Gibbs, P.E., Leitão Filho, H.F. and Shepherd, G., 1983. Floristic composition and community structure in an area of cerrado in SE Brazil. Flora, 173: 433–449.

Gill, A.M., 1975. Fire and the Australian flora: a review. Aust. For., 38: 4–25.

Gill, A.M., 1977. Management of fire-prone vegetation for plant species conservation in Australia. Search, 8(1–2): 20–27.

Gillon, D., 1983. The fire problem in tropical savannas. In: F. Bourlière (Editor), Tropical Savannas. Elsevier, Oxford, pp. 617–641.

Goodland, R., 1971a. A physiognomic analysis of the 'cerrado' vegetation of Central Brasil. J. Ecol., 59: 411–419.

Goodland, R., 1971b. Oligotrofismo e alumínio no cerrado. In: M.G. Ferri (Editor), III Simpósio sobre o Cerrado. Edgard Blucher/EDUSP, São Paulo, pp. 44–60.

Goodland, R. and Pollard, R., 1973. The Brazilian cerrado vegetation. J. Ecol., 61: 219–224.

Goodland, R. and Ferri, M.G., 1979. Ecologia do Cerrado. EDUSP/Itatiaia, São Paulo, 193 pp.

Haridassan, M., 1982. Aluminium accumulation by some cerrado native species of central Brazil. Plant Soil, 65: 265–273.

Heringer, E.P., Barroso, G.M., Rizzo, J.A. and Rizzini, C.T., 1977. A flora do cerrado. In: M.G. Ferri (Editor), IV Simpósio sobre o Cerrado. Itatiaia, Belo Horizonte, pp. 211–232.

Kauffman, J.B., Cummings, D.L. and Ward, D.E., 1994. Relationships of fire, biomass and nutrient dynamics along a vegetation gradient in the Brazilian cerrado. J. Ecol., 82: 519–531.

Kessel, S.R., 1979. Gradient Modelling—Resource and Fire Management. Springer-Verlag, New York, 432 pp.

Klink, C.A. and Joly, C.A., 1989. Identification and distribution of C_3 and C_4 grasses in open and shaded habitats in São Paulo State, Brazil. Biotropica, 21(1): 30–34.

Klink, C.A., 1994. Effects of clipping on size and tillering of native and African grasses of the Brazilian savannas (the cerrado). Oikos, 70: 365–376.

Lamprey, H.F., 1986. Fire and its use on manipulating vegetation. In: S. McMillan (Editor), Wildlife/Livestock Interfaces on Rangelands. O.A.U./S.T.R.C., Kenya, pp. 165–171.

McNaughton, S.J., 1979. Grassland–herbivore dynamics. In: A.R.E. Sinclair and M. Norton-Griffiths (Editors), Serengeti—Dynamics of an Ecosystem. The University of Chicago Press, Chicago, pp. 46–81.

McNaughton, S.J., 1984. Grazing lawns: animals in herds, plant form and coevolution. Am. Nat., 124(6): 863–886.

Noble, I.R. and Slatyer, R.O., 1977. Post-fire succession of plants in Mediterranean ecosystems. In: H.A. Mooney and C.E. Conrad (Editors), Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems. USDA Forest Service General Technical Report WO-3, pp. 27–36.

Noble, I.R. and Slatyer, R.O., 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio, 43: 5–21.

Norton-Griffiths, M., 1979. The influence of grazing, browsing, and fire on the vegetation dynamics of the Serengeti. In: A.R.E. Sinclair and M. Norton-Griffiths (Editors), Serengeti—Dynamics of an Ecosystem. The University of Chicago Press, Chicago, pp. 310–352.

Oliveira Filho, A.T., Shepherd, G.J., Martins, F.R. and Stubblebine, W.H., 1989. Environmental factors affecting physiognomic and floristic variation in an area of cerrado in central Brazil. J. Trop. Ecol., 5(4): 413–431.

Pickett, S.T.A. and White, P.S., 1985. Patch dynamics: a synthesis. In: S.T.A. Pickett and P.S. White (Editors), The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, London, pp. 371–384.

Pivello, V.R., 1992. An expert system for the use of prescribed fires in the management of Brazilian savannas. Ph.D. Thesis, Imperial College, University of London, 276 pp.

Pivello, V.R. and Coutinho, L.M., 1992. Transfer of macro-nutrients to the atmosphere during experimental burnings in an open cerrado (Brazilian savanna). J. Trop. Ecol., 8: 487–497.

Pivello, V.R. and Norton, G.A., (1996). FIRETOOL: an expert system to assist on prescribed burnings in cerrado (Brazilian savannas) conservation areas. J. Appl. Ecol., 33: 348–356.

Queiroz-Neto, P., 1982. Solos da região dos cerrados e suas interpretações. Rev. Bras. Ciênc. Sol., 6(1): 1–12.

Ranzani, G., 1971. Solos do cerrado no Brasil. In: M.G. Ferri (Editor), III Simpósio Sobre o Cerrado. Edgard Blucher/EDUSP, São Paulo, pp. 26–43.

Ratter, J.A., 1991. Guia para a Vegetação da Fazenda Água Limpa (Brasília, D.F.). Universidade de Brasília, Brasília, 137 pp.

Rawitscher, F.K., 1944. Problemas de fitoecologia com considerações especials sobre o Brasil meridional. Bol. Fac. Filos. Ciênc. Let. Univ. S. Paulo (Botânica), 3: 3–111.

Rizzini, C.T., 1971. A flora do cerrado–análise florística das savanas centrais. In: M.G. Ferri (Editor), Simpósio sobre o Cerrado. Edgard Blucher/EDUSP, São Paulo, pp. 105–154.

Rizzini, C.T., 1979. Tratado de Fitogeografia do Brasil. Hucitec/EDUSP, São Paulo, 2 vols.

Ruess, R.W., 1987. The role of large herbivores in nutrient cycling of tropical savannas. In: B.H. Walker (Editor), Determinants of Tropical Savannas. IRL Press, Oxford, pp. 67–91.

Skarpe, C., 1991. Impact of grazing in savanna ecosystems. Ambio, 20(8): 351–356.

Tothill, J.C. and Mott, J.C. (Editors), 1985. Proceedings of the International Savanna Symposium 1984. Australian Academy of Science, Canberra, 384 pp.

Trollope, W.S.W., 1984. Fire in savanna. In: V. Booysen and N.M. Tainton (Editors), Ecological Effects of Fire. Springer-Verlag, Berlin, pp. 149–176.

Vogl, R.J., 1979. Some basic principles of grassland fire management. Environ. Manage., 3(1): 51–57.

Walker, B.H., 1985. Structure and function of savannas: an overview. In: J.C. Tothill and J.C. Mott (Editors), Proceedings of the International Savanna Symposium 1984. Australian Academy of Science, Canberra, pp. 83–91.

Walker, B.H., 1987. A general model of savanna structure and function. In: B.H. Walker (Editor), Determinants of Tropical Savannas. IRL Press, Oxford, pp. 1–12.

Warming, E., 1908. Lagoa Santa—Contribuição para a Geographia Phytobiológica. [Reproduced in: E. Warming and M.G. Ferri, 1973. Lagoa Santa e a Vegetação dos Cerrados Brasileiros. EDUSP, São Paulo, 386 pp.]

Westoby, M., Walker, B.H. and Noy-Meir, I., 1989. Opportunistic management for rangelands not at equilibrium. J. Range Manage., 42(4): 266–274.

Whiteman, P.C., 1980. Tropical Pasture Science. Oxford University Press, Oxford, 392 pp.

Wright, H.A. and Bailey, A.W., 1982. Fire Ecology. Wiley, New York, 447 pp.