PERSPECTIVES

Patch dynamics integrate mechanisms for savanna tree–grass coexistence

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Abstract

Many mechanisms have been suggested to explain the coexistence of woody species and grasses in savannas. However, evidence from field studies and simulation models has been mixed. Patch dynamics is a potentially unifying mechanism explaining tree–grass coexistence and the natural occurrence of shrub encroachment in arid and semi-arid savannas. A patch-dynamic savanna consists of a spatial mosaic of patches. Each patch maintains a cyclical succession between dominance of woody species and grasses, and the succession of neighbouring patches is temporally asynchronous. Evidence from empirical field studies supports the patch dynamics view of savannas. As a basis for future tests of patch dynamics in savannas, several hypotheses are presented and one is exemplarily examined: at the patch scale, realistically parameterized simulation models have generated cyclical succession between woody and grass dominance. In semi-arid savannas, cyclical successions are driven by precipitation conditions that lead to mass recruitment of shrubs in favourable years and to simultaneous collapse of shrub cohorts in drought years. The spatiotemporal pattern of precipitation events determines the scale of the savanna vegetation mosaic in space and time. In a patch-dynamic savanna, shrub encroachment is a natural, transient phase corresponding to the shrub-dominated phase during the successional cycle. Hence, the most promising management strategy for encroached areas is a large-scale rotation system of rangelands. In conclusion, patch dynamics is a possible scale-explicit mechanism for the explanation of tree–grass coexistence in savannas that integrates most of the coexistence mechanisms proposed thus far for savannas.
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Zusammenfassung

Die Koexistenz von Bäumen und Gräsern in Savannen kann prinzipiell durch eine Reihe von Mechanismen erklärt werden, aber bis heute wird keiner von ihnen eindeutig durch Daten aus Felduntersuchungen oder Modellsimulationen belegt. Patch dynamics ist ein Mechanismus, der die Baum-Gras-Koexistenz und das natürliche Vorkommen von Verbuschung in ariden und semi-ariden Savannen erklären und möglicherweise die bisher vorgeschlagenen Mechanismen zusammenführen kann. Patch-dynamische Savannen bestehen aus einem räumlichen Mosaik von lokalen Vegetationsflächen (patches). In einer zyklischen Sukzession wechselt jeder patch zwischen Dominanz von holzigen Arten und von Gräsern. In benachbarten patches läuft die Sukzession zeitlich asynchron ab. Einige empirische Hinweise auf patch dynamics gibt es in Savannen bereits. Als Grundlage für zukünftige Tests von patch dynamics in

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Savannen entwickeln wir mehrere Hypothesen und untersuchen eine von ihnen exemplarisch: Auf patch-Ebene produzieren realistisch parametrisierte Simulationsmodelle zyklische Sukzessionen zwischen Bäumen und Gräsern. In semiariden Savannen werden diese zyklischen Sukzessionen durch Niederschläge verursacht, die in günstigen Jahren zu Massenreproduktion von Bäumen führen, während Trockenheit den Kollaps der gesamten Baumkohorte zur Folge hat. Das raum-zeitliche Muster der Niederschlagsereignisse bestimmt die Skala des Vegetationsmosaiks in Raum und Zeit. Wenn Savannen von patch dynamics bestimmt sind, ist Verbuschung eine natürliche Übergangsphase, die der baumdominierten Phase der Sukzessionszyklen entspricht. Daher wäre in diesem Fall die vielversprechendste Strategie zum Management von Verbuschungen ein großskaliges Rotationssystem bei der Beweidung. Insgesamt ist patch dynamics ein möglicher skalenexpliziter Mechanismus zur Erklärung von Baum-Gras-Koexistenz in Savannen, der die meisten der bisher vorgeschlagenen Mechanismen integrieren kann.

Introduction

Savannas are characterized by the codominance of two contrasting life forms, grasses and woody species, and are of major socio-economic importance in temperate and tropical regions (Scholes & Archer 1997). A large and growing proportion of the world's human population depends on savannas as rangelands for their livestock (Scholes & Archer 1997). Worldwide, the ecological and economic function of savannas is threatened by shrub encroachment, i.e. the increase of woody species (often unpalatable to livestock) at the expense of the grass layer (Smit 2004; Ward 2005; Wiegand, Ward, & Saltz 2005). Many theories have been put forward to explain tree–grass coexistence and the ongoing shrub encroachment in savannas (for simplicity, the terms "tree" and "shrub" will be used henceforth as synonyms for woody species in general). According to Sankaran, Ratnam, and Hanan (2004), these theories can be classified as competition-based mechanisms (e.g., Eagleson & Segarra 1985; Fernandez-Illescas & Rodriguez-Iturbe 2003; Sala, Lauenroth, & Golluscio 1997; van Langevelde et al. 2003; Walker & Noy-Meir 1982; Walker, Ludwig, Holling, & Peterman 1981; Walter 1971) or demographic bottleneck models (e.g., Higgins, Bond, & Trollope 2000; Hochberg, Menaut, & Gignoux 1994; Jeltsch, Milton, Dean, & van Rooyen 1996; Jeltsch, Weber, Dean, & Milton 1998b; Jeltsch, Weber, & Grimm 2000; van Wijk & Bouten 2001).

Walter's two-layer hypothesis (Walker et al. 1981; Walter 1971) is a prominent example of a competition-based approach that explains tree–grass coexistence with a niche separation mechanism. The two-layer hypothesis assumes that trees have access to deeper soil layers than grasses for water uptake. Thereby, intra-life form competition is vertically concentrated relative to inter-life form competition, which leads to coexistence. In the two-layer framework, shrub encroachment results from increased availability of water in deeper soil layers due to reduced grass cover, which is mainly caused by overgrazing. However, empirical and theoretical evidence for the two-layer hypothesis is equivocal. For instance, tree–grass coexistence is also reported from a field site in Namibia where the soil is too shallow to allow for a rooting niche separation (Wiegand et al. 2005). Another issue which cannot be explained by the two-layer hypothesis is the recruitment phase when the roots of tree seedlings overlap and compete directly with grass roots (Kraaij & Ward 2006; Sankaran et al. 2004; Ward 2006). Other competition-based mechanisms include phenological niche separation based on temporal separation of the regeneration niches of trees and grasses (House, Archer, Breshears, & Scholes 2003; Sala et al. 1997; Scholes & Archer 1997), a hydrologically driven model based on the trade-off between competitive ability and colonization potential (Fernandez-Illescas & Rodriguez-Iturbe 2003), and the balanced competition model where the respective superior competitor becomes self-limiting (House et al. 2003; Scholes & Archer 1997). Competition-based approaches typically assume that the tree–grass competitive balance is independent of life stage. However, there is evidence for the reverse, i.e. grasses reducing the emergence and survival of tree seedlings but being outcompeted by mature trees (Sankaran et al. 2004). Furthermore, resource competition alone was not sufficient to produce long-term tree–grass coexistence in spatial simulation models (Jeltsch et al. 1996; Jeltsch, Milton, Dean, van Rooyen, & Moloney 1998a; Jeltsch et al. 2000).

Demographic bottleneck models take life stages explicitly into account and focus on disturbances and climatic variability limiting tree recruitment and growth (Sankaran et al. 2004). In the savanna model of Jeltsch et al. (2000), disturbances such as fire, grazing, or wood cutting act as buffers preventing savannas from directional shifts towards wooded systems or grasslands. Higgins et al. (2000) explain tree–grass coexistence with

a storage effect (Warner & Chesson 1985): tree recruitment (i.e., escape of young trees from the flame zone) is pulsed in time following stochastic rainfall patterns. The longevity of trees enables them to persist over periods with precipitation patterns that are sufficient only for grass reproduction and not for tree reproduction (see Ward (2005) for a criticism of this model). Tree–grass coexistence was also promoted by explicitly including demographic structure in the savanna model of Hanan, Sea, Dangelmayr, and Govender (2008). There is agreement that in arid savannas, the primary demographic bottlenecks of woody species are germination, seedling establishment, and, in more humid areas, escape from the flame zone (Higgins et al. 2000; Jeltsch et al. 1998a; van Wijk & Bouten 2001). While competition-based models typically ignore demographic structure, demographic bottleneck models either do not include competition at all or model it only semi-quantitatively (Sankaran et al. 2004).

Whether empirical evidence is supportive or not for a specific coexistence mechanism largely depends on the system investigated. Hence, a mechanism that integrates currently proposed explanations of tree–grass coexistence is still lacking. The characteristics of such a unifying mechanism can be formulated according to the existing empirical and theoretical evidence: it should incorporate the key appropriate characteristics of both competition-based and demographic bottleneck approaches (Sankaran et al. 2004). The competitive balance between trees and grasses should depend on life stage, as well as time and environmental gradients (Sankaran et al. 2004, 2005). Competitive exclusion can theoretically be prevented by introducing life stage-dependent covariance between environment and competition into savanna models (Chesson et al. 2004). This means that a life form should experience stronger intra- than inter-life form competition if the environmental conditions are favourable for its own growth and reproduction, while inter-life form competition should dominate in conditions unfavourable for the life form.

Our aim is to propose a mechanism that meets all these criteria. Going beyond previous accounts (e.g. Wiegand, Saltz, & Ward 2006), we will show how patch dynamics as a scale-explicit mechanism can explain tree–grass coexistence in savannas and at the same time integrate the majority of the other tree–grass coexistence mechanisms suggested thus far. We will first develop the patch dynamics theory and its implications for savanna dynamics, then explore existing evidence, derive hypotheses to be tested in the future, and exemplarily present the successful test of one of these hypotheses. Finally, we will exemplify the practical consequences of a patch-dynamic view of savannas for the ecological and economic problem of shrub encroachment and offer management recommendations.

Patch dynamics

The patch dynamics mechanism was first elaborated and applied to several different plant communities in a seminal paper by Watt (1947). A patch-dynamic system consists of a spatial mosaic of patches in which the same cyclical succession of patch states occurs (Fig. 1). In different patches, the duration of successional states can vary and succession proceeds spatially asynchronously. At the landscape scale, the proportions of the different patch states are stable, giving the impression of a system at equilibrium. The landscape-scale coexistence of different communities representing the successional states depends on disturbances that prevent the persistence of a climax state (Pickett & White 1985) and on the possibility of re-invasion into early successional patch states from neighbouring patches.

Promoting patch dynamics for the explanation of community patterns is a consequence of the insight that the integration of scale concepts into ecological study is of global concern (Levin 1992; Peterson & Parker 1998). Patterns observed at one scale are likely to be caused by mechanisms operating at other (mostly smaller) scales (Levin 1992), which is inherent in the patch dynamics concept, and hierarchies of nested patches at different scales may emerge (hierarchical patch dynamics, O'Neill, DeAngelis, Allen, & Waide 1986; Wu & Loucks 1995). The spatial scale of a patch is defined by the spatial extent of the environmental drivers of the cyclical succession such as overlapping rainfall events or fires (10^{-2}–10^2 km^2, Gillson 2004), and is therefore location-specific. The spatial scale of the landscape level is at least one order of magnitude greater than the scale of the considered patch level. The temporal scale of a patch is
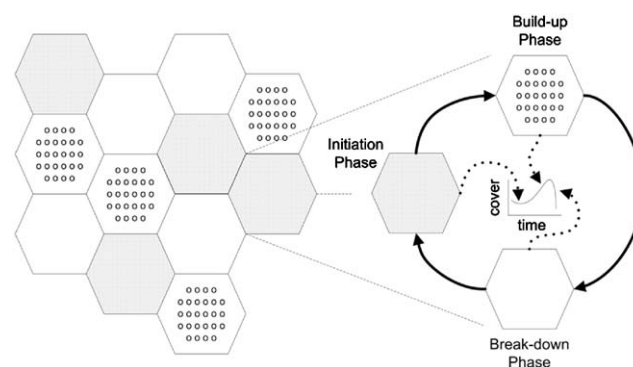

Fig. 1. Spatial and temporal overview of a patch-dynamic savanna with three patch states: patches dominated by grass (shaded hexagons), by woody species (hexagons with circles), and by bare ground (white hexagons). In each patch, cyclical succession proceeds spatially asynchronously in three phases (as depicted on the right-hand side), i.e. initiation phase, build-up phase, and break-down phase. Each phase can be attributed to a section of the curve of woody cover over time. In the example curve, the temporal extent is 35 years and maximum woody cover is 35%.

determined by the duration of the successional states, which can vary from patch to patch. The duration of a successional state is not stochastic in itself but is determined by stochastic environmental conditions such as rainfall in interaction with local soil properties. This generates the impression of stochasticity at the landscape level although a given patch will not randomly favour tree or grass establishment; rather this will depend on its current successional state.

Patch dynamics is related to the metapopulation concept (Hanski 1994; Levins 1969) where long-term persistence of a metapopulation is ensured by dispersal between patches in which local extinction may occur. While the metapopulation concept applies to populations of single species, patch dynamics can explain the coexistence of many different species or life forms. In contrast to the metapopulation approach, the patch dynamics concept specifies a particular within-patch community dynamic, i.e., cyclical succession. In line with this, Levin, Dushoff, and Keymer's (2001) theoretical model of patch dynamics is a hierarchical generalization of Levins' (1969) metapopulation model to more than one species.

Overall, the patch dynamics concept has the potential to meet all the characteristics of a unifying mechanism for the explanation of tree–grass coexistence in savannas: both competition and demographic bottlenecks (Sankaran et al. 2004) are incorporated in patch dynamics because the transformation of grass-dominated patches to tree-dominated patches is driven by life stage-dependent competition for resources such as moisture. Grasses are superior competitors until environmental conditions such as soil moisture or fire regime are favourable enough for germination and establishment of the seedlings of woody species. For instance, grasses are superior competitors as long as rain events remain short and infrequent because woody seedling germination and competitive superiority depends on frequent rain events (Ward 2009). Thereby, the transition from the grass-dominated phase to the woody phase crucially depends on the demographic bottleneck

of germination of woody seedlings. Adult woody species outcompete grasses as long as the environmental conditions and resources exceed their species-specific minimum requirements. The competitive balance also depends on time and environmental gradients, because the cyclic changes between woody species and grass dominance trace the temporal and spatial changes in environmental conditions such as precipitation or fire frequency. The promotion of coexistence by covariance between the environment and competition (Chesson et al. 2004) is also part of patch dynamics where intra-life form (i.e., tree–tree) competition increases during favourable conditions for that life form, i.e., the transformation from grass to woody species dominance, and tree–grass competition dominates otherwise. The spatial mosaic of patches and patch size are determined by overlapping favourable environmental conditions, such as the local overlap of several successive rainfall events (Wiegand et al. 2006).

Patch dynamics has the potential to integrate many of the mechanisms proposed thus far (Fig. 2). Among the demographic bottleneck models, disturbance-driven mechanisms such as fire, grazing, or wood cutting (Jeltsch et al. 2000) may provide the trigger for the break-down of woody dominance. The storage of reproductive potential over unfavourable periods (cf. Higgins et al. 2000) may prevent local extinction of woody species during break-down of the woody phase. Complete local extinction threatens the persistence of patch cycles. At the landscape scale, a competition-colonization-trade-off (Fernandez-Illescas & Rodriguez-Iturbe 2003) may be involved in maintaining the patch mosaic: whenever moisture conditions become unfavourable for competitive dominance of woody species their local populations will break down. However, propagules of woody species may experience favourable conditions in neighbouring patches. This would lead to successful germination and the start of a new phase of woody dominance in the cyclical succession there. Similarly, when grasses are outcompeted in one patch,
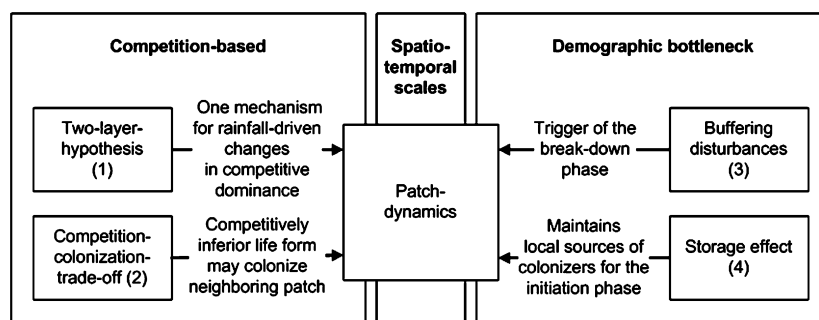

Fig. 2. Patch dynamics integrates existing competition-based theories (left box), demographic bottleneck hypotheses (right box), and spatiotemporal scales to explain tree-grass coexistence in savannas. The choice of hypotheses is merely illustrative and not comprehensive. Please refer to the text for further explanations of the hypotheses. References: (1) Walter (1971), Walker et al. (1981), (2) Fernandez-Illescas & Rodriguez-Iturbe (2003), (3) Jeltsch et al. (2000), (4) Higgins et al. (2000).

their propagules may do well in a neighbouring patch free of woody species or with declining woody population sizes. Hence, we add a spatiotemporal dimension to the original meaning of the competition-colonization trade-off (cf. Tilman 1994).

Apart from theoretical approaches, patch dynamics have also been shown to be an appropriate description for several different communities, including heathland (Watt 1947), rocky intertidal communities (Levin & Paine 1974), forests (Remmert 1991), grasslands (Coffin & Lauenroth 1990), agricultural communities (Kleyer et al. 2007) and plankton communities (Steele 1978). Empirical studies suggest that patch dynamics may also be applied to explain savanna dynamics (Gillson 2004; Wiegand et al. 2006; Wiegand et al. 2005). In a paleoecological study covering several hundred years, Gillson (2004) analysed ^{13}C isotopes and fossil pollen in a semi-arid savanna with a mean annual precipitation (MAP) of 200–700 mm to examine savanna tree dynamics at three spatial scales ($100\,m^2$, $0.1\,km^2$, and $100\,km^2$). The variation in tree dynamics at the smallest scale was much higher than the variation at the landscape scale (Gillson 2004), which can be explained by local, asynchronous cyclical successions leading to a landscape-scale equilibrium typical of patch dynamics. Wiegand et al. (2005) provided evidence for a patch-dynamic savanna based on tree size-frequency distributions at a Namibian field site. They reported negative exponential frequency distributions of tree heights at the landscape scale, indicating constant birth and death rates of individuals in stable model populations at equilibrium (Adler 1998). At the patch scale, they inferred that the position of the mode(s) of tree size-frequency distributions shifted over time indicating cyclical tree dynamics at the patch scale (Wiegand et al. 2005). Self-thinning was observed in encroached patches (Wiegand, Saltz, Ward, & Levin 2008). Competition among trees was inferred by the increase in mean nearest-neighbour distances with increasing tree size and by the reduction in the coefficient of variation in nearest-neighbour distances with increasing tree size (Ward 2005; Wiegand et al. 2005). These observations indicate that trees are spaced farther apart and are more evenly spaced as they grow. This is consistent with the expected patch-scale behaviour of a patch-dynamic savanna landscape and field data even provide evidence for hierarchical patch dynamics (Gillson 2004; Wiegand et al. 2005). In summary, field evidence for the value of patch dynamics as a scale-explicit explanation of tree–grass coexistence in savannas is accumulating.

Hypotheses for future investigations

Adding to the existing evidence, the assumption of patch-dynamic savannas generates several patch-level and landscape level hypotheses that are to be tested in future investigations. First, cyclical successions between grassy and woody dominance are expected at the patch level. Hence, a periodical increase and decrease of woody species cover should be observed at any particular location over time (Fig. 1). The period of these cycles may be subject to natural variability, which should be correlated with environmental conditions including disturbances (cf. buffering disturbances in Fig. 2; Holdo 2006). The second patch-level hypothesis predicts that intra- and inter-life form competitor removal during the build-up phase should prolong this phase, while there should be no significant effect during other phases.

Third, at the landscape level, we expect equilibrium of life forms, i.e., constant proportions of their cover over time (landscape level on the left in Fig. 1). This has already been shown for a paleoecological data set (see above, Gillson 2004), but can be explored for more recent situations by analysing series of satellite images or aerial photographs (cf. Moustakas et al. 2006). Fourth, such images can be used for formal spatial analysis to reveal the patch structure of savanna landscapes. We hypothesize that aggregated spatial patterns of woody species will emerge at scales corresponding to the patch sizes. Hence, patch sizes are defined by the scale of spatial aggregation of woody species, which is determined by the environmental drivers of cyclical succession such as overlapping rainfall events or fire (Wiegand et al. 2005). The spatiotemporal correlation between patchy environmental conditions and vegetation patches receives increasing attention (e.g. Eisinger & Wiegand 2008). Fifth, we predict spatiotemporal covariance between the location of patches of woody species and overlapping favourable environmental conditions such as rainfall. Sixth, we predict that woody patches will be bigger and closer to each other when moving from arid to mesic savannas (Fig. 3). The increased patch size is due to increasing scales of spatial aggregation of rain and fire events with increasing MAP (Fig. 3). The proximity of woody patches will increase with MAP because woody cover is expected to increase to a plateau with increasing MAP (Higgins et al. 2000; Sankaran et al. 2005). This is due to moisture limitation at low MAP and fire limitation at high MAP (Fig. 3).

Seventh, the ways in which existing tree–grass coexistence hypotheses can contribute to patch dynamics (cf. Fig. 2) pose interesting secondary hypotheses, e.g. that the landscape-level patch mosaic can be maintained by a competition-colonization trade-off as described in the *Patch dynamics* section (Fernandez-Illescas & Rodriguez-Iturbe 2003). Due to the large scales involved, testing this hypothesis may lend itself more to simulation modelling approaches than to field studies. Finally, another secondary hypothesis is that the break-down phase can be initiated by buffering
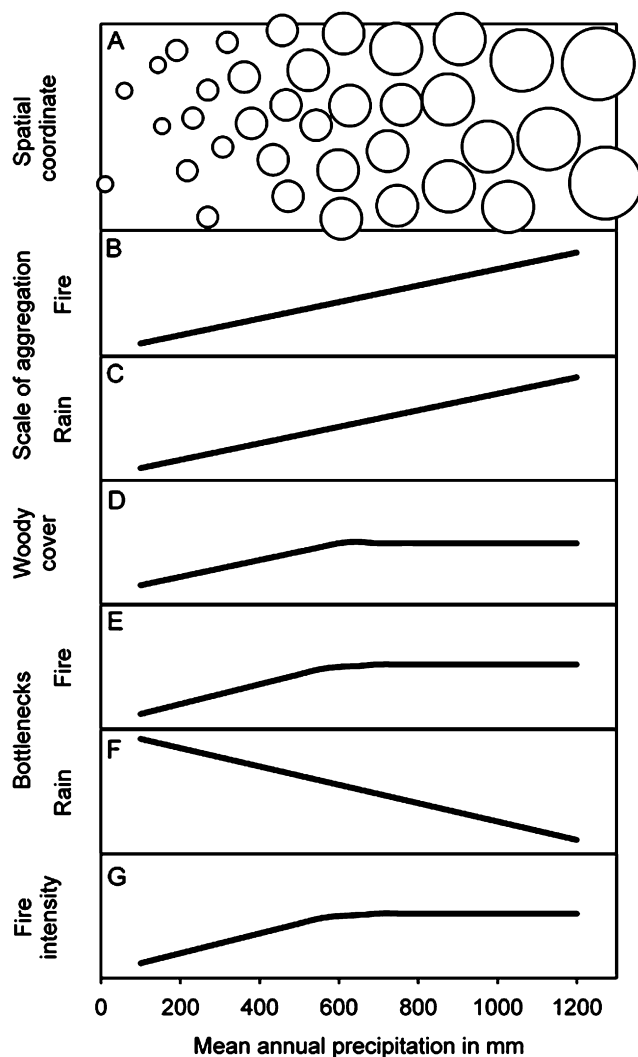
Fig. 3. Hypothesized schematic relationship between spatial and non-spatial rain, fire, and woody species parameters along a gradient of mean annual precipitation (MAP) in a patch-dynamic savanna landscape. The spatial configuration of woody patches (circles in A) shows increasing patch size with increasing MAP because the scale of spatial aggregation of fire and rain events (B, C) is increasing with MAP. The scale of aggregation represents the distance between aggregates. The spatial patch configuration in A is also affected by the relationship between average woody cover and MAP (D). Woody cover (D) depends on fire and rain bottlenecks (E, F) because whichever is most limiting (= greatest value) determines minimum woody cover. For instance, at low MAP, the rain bottleneck is most limiting and woody cover is low while at high MAP fire is more limiting than rain so that woody cover follows the plateau of the fire bottleneck curve. The fire bottleneck depends on fire intensity (G). Fire intensity increases up to a plateau because the availability of grass fuel increases with small to medium MAP and levels off at greater MAP due to increased woody cover.

disturbances such as fire (*sensu* Jeltsch et al., 2000). Increasing fire frequencies will increase the duration of grass-dominated relative to tree-dominated phases

because early break-down of established tree cohorts due to frequent fires makes the establishment of woody species less likely. This will shorten the build-up phase relative to the other phases in cyclical succession. At the landscape scale, areas with high fire frequencies will have fewer patches dominated by woody species at any given point in time, i.e. the tree–grass ratio will be lower. To give an example, we show in the following how the first hypothesis on cyclical successions at the patch-level was successfully tested with a simulation model.

Cyclical succession at the patch-level

In light of the large temporal and spatial scales involved in a patch-dynamic landscape, simulation models are a suitable tool to comprehensively test the validity of the patch dynamics approach and its implications for the explanation of tree–grass coexistence in savannas. However, before patterns can be understood at large (landscape) scales, mechanisms have to be investigated at the small (patch) scale (Wu & Loucks 1995). In a patch-dynamic system, cyclical succession is the process expected to occur at the small scale. In cyclical successions, different species or life forms replace each other in a predictable series from better colonizers to better competitors. The process is reset by the marked decline or extinction of the climax species, thereby closing the cycle. The cue triggering this decline can be inherent to the relationship between colonizers and competitors (Wiegand, Moloney, & Milton 1998) or, more commonly, is a disturbance event that occurs with sufficiently high frequency to prevent a persistent climax stage. For instance, this cue can be a drought or a fire. The occurrence of cyclical successions has been shown for a great range and diversity of plant and animal communities, such as beech forests (Rademacher, Neuert, Grundmann, Wissel, & Grimm 2004; Wissel 1992), small rodent communities (Erdakov, Maksimov, & Zolotarev 1991), alpine cushion-tussock communities (Mark & Wilson 2005), coastal marsh vegetation (Miller, Smeins, Webb, & Yager 2005), or African tiger bush (Guillaume, Huard, Gignoux, Mariotti, & Abbadie 2001). If tree–grass coexistence in savannas can be explained with patch dynamics, cyclical succession between grassy and woody dominance should occur at the patch scale (see first hypothesis above). A realistically parameterized patch-scale simulation model corroborated this hypothesis by generating robust cycles of shrub cover over 500 years for semi-arid savannas (Meyer, Wiegand, Ward, & Moustakas 2007a, 2007b). In the simplest case, the successional cycles can be divided into three phases: (1) initial phase with mass recruitment of shrubs, (2) build-up phase with shrub cohort growth, and (3)

break-down phase with simultaneous and size-dependent death of most shrubs in the cohort (Fig. 1). The three-phase concept is supported by empirical and model-based evidence, including the match of the duration of a cycle and age at death of simulated shrubs (Meyer et al. 2007a), the shift of simulated size-frequencies during the cycle (Meyer et al. 2007a), and the field evidence for senescence effects in large shrubs at a semi-arid savanna site (Meyer, Ward, Moustakas, & Wiegand 2005).

Shrub encroachment

If cyclical successions prevail in savannas, this also has implications for the management of shrub encroachment. In a patch-dynamic savanna, shrub encroachment is a natural, transient part of the successional cycle (the build-up phase). This will pose new questions related to the relative importance of overgrazing and natural causes of shrub encroachment. Hence, it is essential to identify the drivers of cyclical successions and particularly of the phase dominated by woody plants. Fire, herbivory, and pulsed resources such as nutrients or water are potential candidates for disturbance events (Holdo 2006) driving successional cycles in arid ecosystems. In particular, the potential contribution of pulsed resources to cyclical successions in arid ecosystems is promising and has not yet been well studied (Chesson et al. 2004). In a simulation model of a semi-arid savanna patch, shrub cover was not sensitive to changes in fire frequency whereas soil moisture-related parameters represented seven out of nine significantly sensitive parameters (Meyer et al. 2007b). Hence, soil moisture was a much more important driver of successional cycles (and a trigger of the break-down phase) than fire. Clearly, this result is not altogether surprising because there is seldom sufficient grass to maintain fires in arid savannas (although see Meyer et al. 2005).

Management strategies

The long-term management of shrub encroachment in savannas should be guided by the question of how to optimize the relationship between the control of shrub encroachment and its cost. Unfortunately, the manipulation of soil moisture as a major encroachment driver in a patch-dynamic arid savanna is unrealistic. Other mitigation strategies of shrub encroachment such as burning, browsing, cutting, or chemical treatment have been studied alone and in concert, but to our knowledge their relation to patch dynamics has been ignored thus far and should experience more attention in the future.

If shrub encroachment is a transient phase in cyclical succession, the most promising management option for encroached areas is a large-scale rotation system of rangelands. Other management options are inferior because once woody species have passed the critical stage of establishment, not much can be done to prevent their further increase beyond physical removal (Brown, Scanlan, & McIvor 1998). Hence, such a rotation scheme should aim to maintain natural grazing intensities in those patches that are in the grass-dominated break-down phase, but should refrain from grazing in all other patches. Encroachment managers could derive the onset of the break-down phase from knowledge of local cycle duration and precipitation thresholds for the different phases combined with observations of rainfall dynamics because the successional cycles are driven by precipitation. Estimates of local cycle duration and precipitation thresholds can be obtained from long-term vegetation observations or models (e.g., Meyer et al. 2007a, 2007b) parameterized with local data. Grazing, and particularly heavy grazing, leads to the start of the initiation phase or an extended duration of the (naturally encroached) build-up phase. The suggested management options are consistent with advice to reduce grazing intensities in high rainfall years to not weaken the competitive effect of grasses on woody species (Müller, Frank, & Wissel 2007; Müller, Linstädter, Frank, Bollig & Wissel 2007; Ward 2005; Ward 2009; Wiegand et al. 2006). We note that this is contrary to popular opinion, which posits reducing grazing intensities in dry years due to the perceived negative effects on grass availability.

Conclusions

Patch dynamics integrates many of the mechanisms thus far proposed for the explanation of the coexistence of woody and grassy species in savannas. Hence, patch dynamics may even turn out to be a unifying mechanism of tree–grass coexistence. Currently, empirical evidence in support of the applicability of patch dynamics to many savanna ecosystems is accumulating, and simulation models have shown its validity at the patch-scale. In a patch-dynamic savanna, shrub encroachment can also be a natural phase of the successional cycle and need not be caused solely by heavy grazing. Strategies for the management of shrub encroachment should therefore be adapted by implementing, for example, large-scale rotation systems that follow grass-dominated patches over space and time. Future investigations should complement the existing evidence with tests of the hypotheses developed here including a landscape-level validation of the patch dynamics mechanism, for example with models simulating landscape dynamics.

Acknowledgements

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