

Forest Gaps and Isolated Savanna Trees

An application of patch dynamics in two ecosystems

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Over the past two decades, understanding of the dynamics of forests in tropical and temperate regions has developed primarily through the study of canopy gaps formed when mature trees die. The functional significance of gap-phase dynamics (Watt 1947) in mesic (moist) forests rests on two widely documented observations. First, the surrounding matrix of closed forest canopy is largely impenetrable to juveniles of most canopy-tree species, either because the saplings cannot tolerate the shade cast by canopy trees, or because young shoots are abraded as they grow into the tree crowns above them (Kelty 1986). As a consequence, most of the species that dominate old-growth forests appear to require gaps in the canopy to reach maturity (e.g., Canham 1988). Second, many species, both canopy and understory, possess a wide diversity of specialized traits that allow them to colonize the resource-rich gaps and then compete for these resources (e.g., Canham and Marks 1985, Collins et al. 1985).

Researchers have documented remarkable similarities in the processes of canopy-gap formation and closure across a wide range of forest ecosystems (see reviews in Brokaw

Discontinuities alter both the microclimate and the availability of resources crucial to component species

1985, Runkle 1985). In the paradigm that has emerged from these studies, an intact forest canopy is viewed as a closed matrix in which are embedded a population of gaps that can be described in the terms of traditional organism-level demography: birth (gap formation), growth (usually negative), and death (eventual gap closure). Although this model of patch dynamics (sensu Levin and Paine 1974, Pickett and White 1985) has proven to be a powerful tool for organizing understanding of forest dynamics, it has seldom been applied to other terrestrial ecosystems.

We propose that tropical savannas represent another important ecosystem in which the model of patch dynamics may profitably be applied. Savannas are defined as structurally simple, seasonally water-stressed communities that are dominated by a continuous layer of graminoids and a sparse overstory of trees or shrubs. The trees and shrubs are maintained at low densities by fire, large herbivores, physical stress, or competition for limited resources (Norton-Griffiths 1979, Smith and Goodman

1986); however, they form a distinct population of structural discontinuities that rise above the low-statured grassland. They break up the herbaceous matrix in a style similar to the manner in which gaps break up the forest canopy matrix, except that savanna trees project above the matrix rather than produce gaps within it (Figure 1).

There are obvious structural dissimilarities between savannas and forests, but we propose that the dynamics of both community types can productively be described in the terms of patch dynamics. In both systems, these discontinuities significantly alter both the local microclimate and the availability of resources crucial to the dynamics of many component species (Bernhard-Reversat 1982, Canham et al. 1990, Chazdon and Fetcher 1984, Monk and Gabrielson 1985). And, in both systems, the patches themselves have distinctive dynamics of birth, growth, and death.

Our goals in this article are to review and evaluate the literature on patch dynamics in forests, use this perspective to examine the emerging literature on the effects of isolated trees and shrubs in savannas, compare patch dynamics in savannas and forests, and identify promising directions for future research on patch dynamics in both systems. Although gaps in savannas formed by physical disturbance or death of herbaceous plants within the matrix are also analogous to forest gaps, they are less important to long-term dynamics of savanna communities than are patches created by overhead trees

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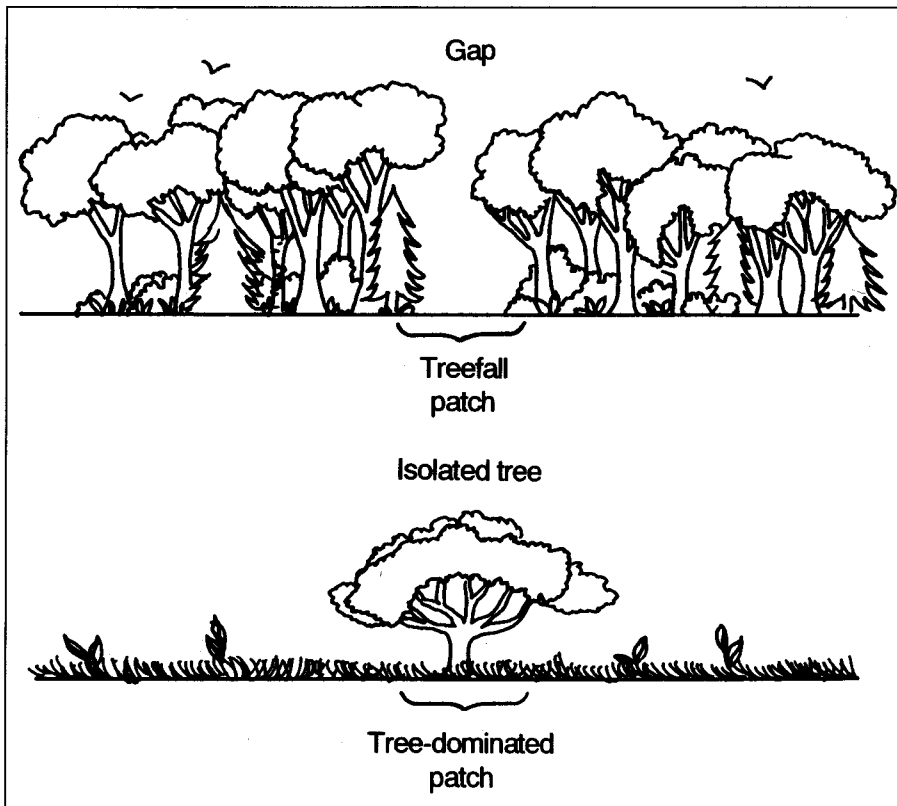


Figure 1. Gaps in forests and isolated trees in tropical savannas produce distinct understory patches. The patch is likely to have a different size and shape than does the overstory gap or tree crown.

because in savannas gaps disappear rapidly (Belsky 1986). Therefore, we do not address disturbance gaps in savannas in this article.

A synopsis of patch dynamics in forests and savannas

There is a critical distinction between an opening, called a *gap*, in a forest canopy and the area it influences, called a *patch* (Figure 1). There is a similar and equally important distinction in a sparsely wooded savanna between the tree crown, which we will call the *isolated tree*, and its zone of influence on the ground, which we will call the *tree-dominated patch*. In this section, we provide a brief synopsis of the dynamics of canopy gaps in forests. Then we describe the analogous, but less well-known, dynamics of isolated trees and shrubs in savannas.

Patch dynamics in forests. Canopy gaps are ubiquitous features of old-growth forests. They frequently occupy 5–15% of the projected area of the canopy, even after periods that

have been free of any significant disturbance. The sizes and densities of canopy gaps are remarkably similar across a wide range of ecosystems, with the majority of gaps ranging from 50 to 100 m² (roughly equivalent to the size of the crown of a single, large canopy tree). However, a significant fraction of the total area in gaps is made up of larger, less-frequent gaps in the range of 200–500 m² (Brokaw 1985, Runkle 1985).

The overall size distribution of canopy gaps is a function of two relatively distinct processes. The first process is the formation of small gaps after the death of large branches or entire crowns of single trees (Table 1). The proximate cause of this single-tree mortality is frequently some form of physical disturbance (e.g., wind or simply the weight of precipitation intercepted by canopy foliage), but it usually reflects a structural weakness in the tree due to earlier injury or loss of vigor. Although these gaps form abruptly, there are also many single-tree gaps that form slowly as canopy trees die gradually in place.

This background mortality results in the annual formation of gaps that cover 0.5–1.0% of canopy area.

In contrast, larger multiple-tree gaps are formed when discrete disturbances kill otherwise healthy trees. The sources of disturbance vary among different regions. Extreme winds associated with severe low-pressure systems (hurricanes in tropical and coastal temperate regions and extratropical cyclones in temperate regions) frequently cause extensive gap formation over large regions. Thunderstorms are a predominant cause of catastrophic windthrow in some temperate regions (Canham and Loucks 1984), but smaller-scale downdrafts (microbursts) from thunderstorms also appear to be a frequent source of localized gap formation. Local spread of disease within forests has been less widely documented, but it also appears to be an important cause of large-gap formation in some forests (e.g., Menges and Loucks 1980).

Because of their initiation by relatively infrequent disturbances, the density and age structure of large gaps tends to be much more episodic than that of smaller, single-tree gaps. The average residence time for trees in the canopy is estimated to be much shorter (less than 100–200 years) than the potential life-spans of many of the dominant tree species of old-growth forests (e.g., Runkle 1982).

Canopy gaps change in size either by shrinking, as a result of lateral growth into the gap by neighboring trees, or by expanding, as a result of deaths of trees bordering the gap (Hibbs 1982, Runkle and Yetter 1987). Given the difficulty of measuring ingrowth of canopy trees, there is relatively little data on this process. The studies of Hibbs (1982) and Runkle and Yetter (1987) suggest that gaps in temperate deciduous forests of eastern North America close radially at rates of approximately 15 cm/yr. Despite considerable evidence from the forestry literature that trees bordering large clearings are at a much higher risk of windthrow than trees within a closed forest canopy (Franklin and Forman 1987), Runkle and Yetter (1987) found that trees bordering gaps did not have significantly higher rates of mortality than trees within closed

canopies. However, even a random spatial pattern of single-tree mortality results in a significant fraction of gaps expanding in size due to the death of neighboring trees.

The rate of disappearance of gaps depends on both the size of the gap and the rate of growth by neighboring trees and by saplings within the gap. Estimates of rate of gap closure based on extrapolation of direct measurements of sapling height and lateral growth (e.g., Nakashizuka 1984, Runkle 1982) and reconstruction of growth patterns from radial growth rings of trees that successfully reach canopy size (e.g., Canham 1985) suggest that canopy gaps have relatively short life-spans of 10–30 years, although the effects of the gaps on tree size structure persist even after the gap has closed.

Patch dynamics in savannas. Isolated trees in tropical savannas are similar to forest gaps in size and in effect on canopy structure of the community. But instead of structural changes being initiated by the deaths of trees, changes are initiated by tree seedling establishment and growth (Table 1). And instead of the resulting tree-dominated patches being formed immediately, they develop slowly, starting as narrow concentric rings adjacent to the bases of tree saplings and ending as large patches extending tens of meters from the tree.

Trees invade savannas by wind- or animal-dispersed seed or by clonal spread from adjacent woodlands or forests. They normally remain as discrete, isolated individuals, particularly in areas with frequent fire. However, in regions where seed-eating birds and mammals use the tree environment, additional propagules of woody species are introduced into tree-dominated patches, which develop into shrubby thickets. Isolated trees, therefore, facilitate the formation of woodland patches, which may eventually expand and coalesce, forming extensive woodlands (Archer et al. 1988, Kellman 1979).

Because tree populations in savannas have not previously been considered in terms of patch dynamics, their density, crown size, and spatial arrangements have not been investigated. Also, because there is no predictable annual tree-ring formation,

Table 1. Comparison of the dynamics of gaps and patches formed by treefalls in forests and of isolated trees and tree-dominated patches formed by the growth of trees in tropical savannas.

Discontinuity in overhead canopy	Forest gaps	Isolated savanna trees
Formation	Rapid or gradual (episodic or gradual tree death)	Slow (seedling establishment and growth)
Expansion	Episodic (death of neighboring trees)	Gradual (crown expansion)
Closure	Rapid (through ingrowth of neighboring trees)	Rapid or gradual (tree death or crown dieback)
Life-span	Short (10–30 years)	Long (lifetime of trees, more than 50 years)
Patch colonization	Rapid	Gradual
Patch secondary succession	Limited to large gaps	Rare
Patch resource dynamics	Short-lived pulses of enhanced resources	Sustained resource enhancement

tree ages in the tropics are seldom accurately known. Although baobabs are thought to live more than 1000 years, records show that most other savanna trees live from 50 to more than 100 years, depending on the species. Trees may be killed quickly by fire, wind, or large herbivores such as elephants, or they may succumb slowly to old age or disease, paralleling the gradual closure of treefall gaps. The deaths of these trees leave distinctive, long-lived understory patches. In the few cases where the persistence of such distinct vegetation patches has been reported, patches are still identifiable after 5 years in Tsavo National Park, Kenya,¹ 13 years at the Santa Rita Experimental Range in Arizona (Tiedemann and Klemmedson 1986), and 30 years at the Forest Service San Joaquin Experimental Range in California (Holland 1980).

In terms of patch dynamics, the fundamental difference between treefall gaps and savanna trees is in the rapidity of their births and deaths. Most forest gaps form, develop, and disappear relatively quickly (10–30 years), whereas savanna trees germinate, grow, and persist from 50 to more than 100 years. As a result, isolated savanna trees constitute a more permanent element of the land-

scape. These trees are less often thought of in terms of patch dynamics, but when we adjust forest gaps and savanna trees to the appropriate temporal scale, their similarities become more apparent.

Gap dynamics versus patch environments

The first formal application of the theory of patch dynamics to natural communities occurred in marine rocky intertidal communities, where waves create bare patches of rock on a dense background of sessile organisms (Levin and Paine 1974). Given the compressed vertical structure of intertidal communities, the gap in the community matrix is spatially congruent with the patch of substrate influenced by the gap. In forests and savannas, however, the influences of gaps and tree crowns extend well beyond their vertically projected boundaries (e.g., Belsky et al. 1989, 1993, Canham et al. 1990, Runkle 1982).

Forest ecologists have focused on quantifying the biological responses of species and communities to treefall gaps and have expended much less effort measuring gap effects on forest microenvironments. However, several generalizations on the specific gap-patch systems have emerged: treefall gaps have important effects

¹A. J. Belsky, personal observation, 1993.

not only on light levels in the forest understory but on the availability of soil resources and on the microclimate; there is pronounced and predictable spatial variation in resource availability and microclimatic conditions within the patches; and different resources do not necessarily show congruent patterns of spatial and temporal variation within gaps (e.g., Canham et al. 1990, Chazdon and Fetcher 1984, Mladenoff 1987). The same generalizations are true of tree-dominated patches in savannas.

Physical conditions within patches

To justify comparisons of savanna tree-dominated and forest treefall patches, we explore the physical conditions created by forest gaps and isolated trees and the biological responses by their communities. Because the effects of forest gaps have been extensively described and recently reviewed (Denslow 1987, Pickett and White 1985, Platt and Strong 1989), we concentrate on the growing literature on savanna trees.

Light. Light conditions beneath forest gaps vary predictably with height and density of the patch vegetation, with height of the boundary trees, and with gap size. Similarly, light conditions below isolated trees in savannas vary with height, density, and diameter of the overhead crown. As a result, average light intensities below savanna trees range from 7% of full sunlight below the crowns of isolated individuals of *Quercus douglasii* (blue oak; Jackson et al. 1990) to 55% under *Acacia tortilis* (umbrella acacia; Belsky et al. 1989, 1993).

The intensity and duration of solar radiation reaching ground level is altered over areas considerably larger than the vertically projected boundaries of tree crowns and overhead gaps. On the equator in Kenya, for example, isolated trees of *A. tortilis* shade the ground from 40 m west of trees in the early morning to 40 m east of trees in the late afternoon, with zones closer to tree trunks receiving correspondingly less sunlight over the course of each day (Belsky et al. 1989). Additionally, plants growing on the north side of trees receive

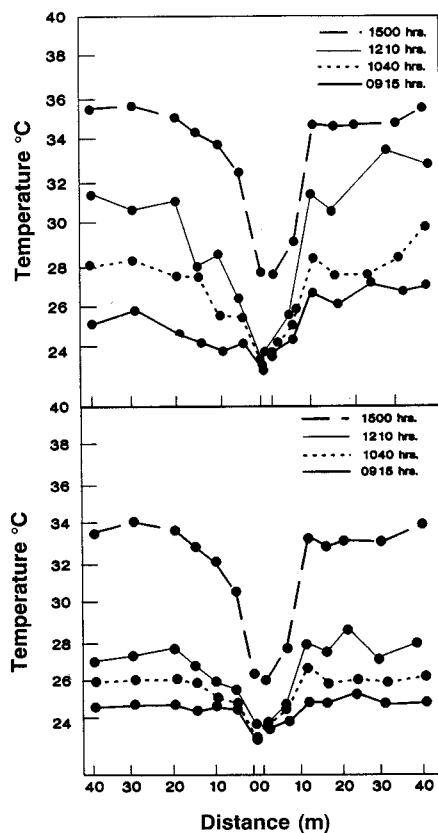


Figure 2. Soil temperatures measured at soil depths of (top) 5 cm and (bottom) 10 cm along a transect extending west (left) and east (right) of the base of an *Acacia tortilis* tree. The measurements were made at four different times: 9:15 (heavy line), 10:40 (dotted line), 12:10 (thin line), and 15:00 (broken line) in Tsavo National Park, Kenya. The base of the tree is at 0 m; the tree crown has a radius of 8 m. (Figure used with the permission of *Journal of Applied Ecology*.)

continuous shade when the sun is south of the equator, but no shade at all when the sun is north of the equator. Plants growing directly below tree crowns in the tropics, therefore, may experience little if any light reduction during the growing season, whereas other plants located beyond the edge of the crowns may receive significant light reduction.

Similarly, the area of highest light intensity may not occur directly below the forest gap. At high latitudes (north of 23.5°N and south of 23.5°S), the sun is never directly overhead. As a result, the area with the greatest photon flux in far-northern and far-southern forests may not be within the area beneath the gaps, but

several meters north or south of their boundaries (Canham et al. 1990).

Soil temperatures. Soil temperatures in forest and savanna patches vary as a function of light intensity and duration. Temperatures in forest treefall patches are commonly elevated several degrees above those found in the surrounding matrix (Minckler et al. 1973), whereas temperatures below tree crowns in savannas are similarly reduced. For example, isolated savanna trees of *Prosopis juliflora* (mesquite) in Arizona reduced soil temperatures at a depth of 2.5 cm by an average of 4°C over the year and by a maximum of 12°C in the summer (Tiedemann and Klemmedson 1977). Similarly, soil temperatures at a depth of 5 cm near isolated trees of *A. tortilis* in savannas of Tsavo National Park were commonly reduced 2–4°C in the early morning, but 8–11°C at midafternoon (Belsky et al. 1989; Figure 2).

Soil moisture. Differences in soil moisture between patches and their surrounding communities are less predictable than differences in light and temperature, because soil moisture varies with rainfall interception, soil infiltration, evaporative surface area, and relative humidity. There have been few rigorous studies of the effects of small forest gaps on soil moisture, but surface soils below forest gaps are expected to be more moist than soils of closed forests because less precipitation is intercepted by overhead canopies and less soil water is lost to evapotranspiration (Minckler et al. 1973, but see Mladenoff 1987).

Soils of tree-dominated patches in savannas have generally been reported to be more moist than soils of adjacent communities (Joffre and Rambal 1988, Kennard and Walker 1973, Parker and Muller 1982), but seasonal effects on soil moisture are complex (Vetaas 1992). Early in each growing season in Tsavo National Park, Kenya, for example, soils are dryer below tree crowns than in the surrounding grasslands due to rainfall interception (Belsky et al. 1989). Later in the growing season, soils are wetter below tree crowns as a result of cooler temperatures and reduced evapotranspiration in the shade. Still

later in the growing season, soils below tree crowns and in adjacent grasslands are equally dry as plants in both habitats use all available moisture.

Chemical and physical properties of soils. The few studies of the effects of gap formation on forest soils have yielded no general patterns. Mladenoff (1987) found measurable increases in nitrogen in treefall patches in one north temperate forest, but not in another. Vitousek and Denslow (1986) speculated that the absence of significant nutrient enrichment in tropical forest gaps is due to rapid uptake of nutrients by the remaining intact roots and by rapid adsorption of phosphorus onto charged clay particles.

The soils of savanna tree-dominated patches, on the other hand, have been extensively described. They have consistently been found to have significantly higher concentrations of organic matter and of total and available nitrogen, calcium, potassium, phosphorus, sodium, and sulfur (Belsky et al. 1989, Kellman 1979, Young 1989, Vetaas 1992) than matrix soils. Where examined, nutrient concentrations have been found to be highest adjacent to the stem and to decline with distance from the tree (Belsky et al. 1989, 1993, Bernhard-Reversat 1982, Garcia-Moya and McKell 1970, Kellman 1979). Because these soils also have greater total cation-exchange capacities, higher microbial biomasses, higher water-infiltration rates, lower bulk densities, and greater water-holding capacities than soils in adjacent communities (Belsky et al. 1989, 1993, Joffre and Rambal 1988, Kennard and Walker 1973, Young 1989), tree-dominated patches have been called "islands of high fertility" (Garcia-Moya and McKell 1970).

Patch dynamics and species diversity

Patch dynamics have widely been assumed to be essential for the maintenance of species diversity in old-growth forests (e.g., Denslow 1987). Most forest species, including shade-tolerant trees (Canham 1988), shrubs (Hibbs et al. 1980), and herbs (Collins et al. 1985), respond posi-

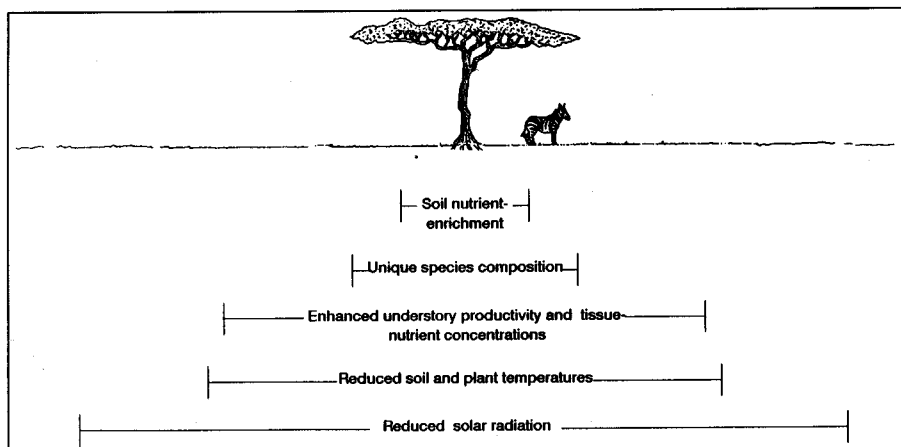


Figure 3. Zones of altered characteristics surrounding an isolated tree, *Acacia tortilis*, in Tsavo National Park, Kenya.

tively to treefall gaps. Denslow (1987) proposed that the mechanism linking patch dynamics and species diversity in forests is the partitioning of the gradient of resource availability created by natural variation in gap size.

Recent studies of interspecific variation in the effects of light levels on tree growth have provided only limited support for this view. A recently developed model with parameters derived from field data from oak-northern hardwood forests of southern New England suggests that although a range of gap sizes can indeed allow the persistence of relatively shade-intolerant species, the diversity of shade-tolerant species depends more on the limitations of species in their ability to colonize gaps than on their performance along resource gradients (Pacala et al. in press).

The effects of isolated trees on species diversity in tropical and subtropical savannas have not been explicitly discussed in terms of niche partitioning, although these trees increase community diversity both by their presence in otherwise herbaceous communities and by their creation of patches of altered resource availability (Vetaas 1992). These high-fertility, reduced-light patches allow the invasion of species that are less well adapted to the low-fertility, high-light matrix environment. The degree to which tree-dominated patches affect the dynamics of their surrounding communities has not been investigated. These patches may provide important seed sources for

species that also occur in the open grassland (source-and-sink dynamics [Pulliam 1988]) or, in the absence of fire, they may develop into woodland patches that grow and eventually replace the original grassland (e.g., Archer et al. 1988, Kellman 1979).

The patches formed by treefall gaps and isolated savanna trees provide essential habitat for specially adapted wildlife species, further increasing biodiversity in these systems. In savannas, isolated trees provide roosting sites for birds, forage for browsers, and shade for animals that seek shelter from the sun. Because below-crown herbaceous plants have also been found to be more nutritious (Belsky 1992) and remain green longer into the dry season compared to open-grassland plants (Amundson et al. in press), tree-dominated patches may also alter the movement of herbivores and their patterns of forage consumption.

Patch dynamics and ecosystem processes

Forest ecologists have focused primarily on population and community-level consequences of patch dynamics, with little attention given to the effects of patch dynamics on ecosystem processes. In contrast, savanna ecologists have concentrated more on the ecosystem-level processes of productivity and nutrient cycling than on population and community-level phenomena. This concentration most likely reflects the interests of

savanna ecologists in forage production for livestock and in habitat diversity for wildlife.

One factor that has been found to be consistently associated with isolated trees in savannas is the elevated nutrient content in soils below tree crowns. After discounting several other possibilities, Kellman (1979) speculated that the high concentrations of soil nutrients under savanna trees in Belize were due to increased wet and dry deposition on the trees. Other authors, however, attribute the nutrient loading of below-crown soils to mass transport of nutrients from deep or distant soils by tree roots, to input from perching or nesting birds, and to input from large mammals that live, rest, or graze in the tree environment (Belsky et al. 1989, Garcia-Moya and McKell 1970, Vetaas 1992, Weltzin and Coughenour 1990). The nutrient content in these patches may also be increased by reduced decomposition and leaching rates below tree crowns and by more efficient nutrient cycling (Young 1989). Because these hypotheses have not been addressed empirically, it is not known to what extent the mass transport of soil nutrients from surrounding communities increases the nutrients available to plants within the tree-dominated patches or reduces the nutrients available to plants in the surrounding matrix.

Herbaceous-layer productivity in tree-dominated patches has been found to differ from that in the rest of the savanna matrix. In some cases, understory productivity is higher in tree-dominated patches, probably due to the higher soil fertility and improved water relations of the patch species (Amundson et al. in press, Holland 1980, Tiedemann and Klemmedson 1977, Weltzin and Coughenour 1990). In other cases, productivity in tree-dominated patches is reduced below matrix levels, probably due to low germination rates in thick litter layers (Monk and Gabrielson 1985) and to low levels of solar radiation (Jackson et al. 1990, Parker and Muller 1982). Trees may also reduce understory productivity by competing for water and nutrients (Monk and Gabrielson 1985, Stuart-Hill and Tainton 1989), but this competition is not universal

(Belsky in press, Sala et al. 1989).

The probability that savanna trees reduce, rather than enhance, understory productivity increases with increasing tree density. In areas of high tree density (Belsky and Amundson 1992), trees preempt most of the light and much of the below-ground resources. These effects can also be explained in terms of patch dynamics: as tree density increases, adjacent patches interact as tree crowns shade and tree roots invade neighboring patches. At some tree density, the resources available to the herbaceous layer are reduced below critical threshold levels and herbaceous productivity declines (Obot 1988).

Limitations of discrete models of patch dynamics

Theoretical models used to describe the dynamics of forest gaps assume that gaps have discrete boundaries. And, in fact, both forest gaps and savanna tree-crowns have clearly defined, physical boundaries. But their underlying patches do not have discrete boundaries. Although researchers have commonly assumed that understory patches have the same dimensions as the overhead gaps or crowns, we have highlighted ample evidence showing that the patches are neither the same size nor the same shape as the overhead structure.

In addition, the altered levels of light, soil moisture, and nutrients in each patch are not necessarily coincident with each other. An intensive study of *A. tortilis*-dominated patches in Kenyan savannas (Belsky et al. 1989, 1993) demonstrates the difficulties of defining a single, discrete understory patch boundary (Figure 3). For isolated acacia trees, each having a crown radius of approximately 10 m, the patches of enriched soils were confined to within 5 m of the trunks. Beyond 5 m, most nutrient levels returned to background levels. In contrast, the grasses growing within 15–20 m of trunks had significantly elevated concentrations of nitrogen, phosphorus, potassium, calcium, and copper and significantly reduced concentrations of zinc and silicon dioxide compared with grasses growing further from the trunks (Belsky 1992).

Similarly, total incoming solar radiation was reduced by crown interception from 40 m west to 40 m east of the trunks, but significant differences in soil temperature were found only from 20 m east to 20 m west of the trunks. At one site, the below-crown herbaceous community had the same dimensions as the overhead crowns; but in another site, the below-crown patches extended from 5 to 13 m from the trunks. Understory productivity, on the other hand, was significantly elevated as far as 20 m from tree bases.

We suggest that two features—spatial heterogeneity of resources within the patches and continuous gradation of resources to levels characteristic of the surrounding matrix—are likely to be ubiquitous features of patches in both forested and nonforested systems. One important ecological consequence of the lack of a single, discrete patch boundary is that the response of individual plant species varies with each species's minimal resource requirements. As a result, the area of patch that is suitable for colonization and growth varies among species. This suitable size is particularly critical in forests where patches are relatively transient, and where many organisms respond to several successive gaps during their lifetimes.

Future research directions

Due to differing interests between forest and savanna scientists, there is currently little overlap in information on the biological effects of treefall gaps and savanna trees. Forest ecologists have concentrated on the effects of gaps on community dynamics and on adaptive traits, whereas savanna ecologists have concentrated on patch description and ecosystem-level processes. Both groups would clearly benefit from an exchange of ideas and techniques. The understanding of patch dynamics in forests, for example, would benefit from more studies contrasting the patch and matrix communities and from more rigorous studies of physical conditions within the patches. Similarly, the field of savanna ecology would benefit from studies investigating the effects of trees on population and community

dynamics.

To understand the contribution of treefall gaps and savanna trees to community and landscape dynamics, we need a more thorough understanding of the physical and biological properties of the component patches, including the causes and consequences of resource heterogeneity and the dynamics of nutrient enrichment and depletion. We also need to gain an understanding of ecosystem-level consequences of treefall gaps and isolated trees in their respective communities. For example, do community-wide flux rates represent simple spatially weighted averages of processes both in patches and the matrix, or are there important processes such as runoff, litter redistribution, rooting patterns, and animal foraging patterns that demand integration at spatial scales larger than the individual patch?

Few studies of forest and savanna patch dynamics have explicitly examined the interactions of the patch and the matrix. Most studies have examined species dynamics from the island-biogeographic point of view, which concentrates on the patch but ignores the matrix. The following questions concerning patch/matrix interactions need to be addressed. Are there thresholds of patch density at which the matrix community begins to disintegrate? How do the size and spatial configuration of patches within the community influence the properties of individual patches and of the patch/matrix system? How do high population densities of species in patches influence the population dynamics of the same species in the surrounding matrix? And how does patch frequency or density alter species diversity, ecosystem stability, and energy and nutrient fluxes within the system?

Finally, forest gaps and savanna trees can aid the development of general theories on patch dynamics. One unresolved question is whether the essential dynamics of such systems can be adequately described with discrete patch models or whether it is necessary that they be described by spatially explicit models that allow continuous variation.

Our comparison of savanna trees and forest gaps indicates not only

that there are striking similarities between the two community types, but it also suggests that this comparison may contribute to the investigation of patch dynamics in other terrestrial ecosystems such as prairies and deserts. Due to the longer time-scale of tree-dominated patch formation and persistence, tree-dominated patches in savannas have rarely been considered in these terms. Continued comparison of patch dynamics in forests and savannas may produce important generalities about the interplay of patch and community dynamics in terrestrial systems.

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References cited

- Amundson, R. G., A. R. Ali, and A. J. Belsky. In press. Stomatal responsiveness to changing light intensity increases rain-use efficiency of below-crown vegetation in tropical savannas. *J. Arid Environ.*
- Archer, S., C. Scifres, and C. R. Bassham. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecol. Monogr.* 58: 111-127.
- Belsky, A. J. 1986. Revegetation in the Serengeti National Park, Tanzania. II. Five years of successional change. *J. Ecol.* 74: 937-951.
- _____. 1992. Effects of trees on nutritional quality of understory gramineous forage in tropical savannas. *Trop. Grassl.* 26: 12-20.
- _____. In press. How savanna trees influence understory productivity: manipulations of shade, nutrients, and tree/grass competition. *Ecology.*
- Belsky, A. J., and R. G. Amundson. 1992. Effects of trees on understory vegetation and soils at forest/savanna boundaries in East Africa. Pages 353-366 in P. A. Furley, J. Proctor, and J. A. Ratter, eds. *Nature and Dynamics of Forest-Savanna Boundaries*. Chapman and Hall, New York.
- Belsky, A. J., R. G. Amundson, J. M. Duxbury, S. J. Riha, A. R. Ali, and S. M. Mwonga. 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. *J. Appl. Ecol.* 26: 1005-1024.
- Belsky, A. J., S. M. Mwonga, R. G. Amundson, A. R. Ali, and J. M. Duxbury. 1993. Relative effects of trees on their understory environments in high-rainfall versus low-rainfall savannas. *J. Appl. Ecol.* 30: 143-155.
- Bernhard-Reversat, F. 1982. Biogeochemical cycles of nitrogen in a semi-arid savanna.

- Oikos* 38: 321-332.
- Brokaw, N. V. L. 1985. Treefalls, regrowth, and community structure in tropical forests. Pages 53-68 in S. T. A. Pickett and P. White, eds. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York.
- Canham, C. D. 1985. Suppression and release during canopy recruitment in *Acer saccharum*. *Bull. Torrey Bot. Club* 112: 134-145.
- _____. 1988. Growth and architecture of shade-tolerant trees: response to canopy gaps. *Ecology* 69: 786-795.
- Canham, C. D., J. S. Denslow, W. J. Platt, J. R. Runkle, T. A. Spies, and P. S. White. 1990. Light regimes beneath closed canopies and treefall gaps in temperate and tropical forests. *Can. J. For. Res.* 20: 620-631.
- Canham, C. D., and O. L. Loucks. 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. *Ecology* 65: 803-809.
- Canham, C. D., and P. L. Marks. 1985. The response of woody plants to disturbance: patterns of establishment and growth. Pages 197-216 in S. T. A. Pickett and P. White, eds. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York.
- Chazdon, R. L., and N. Fetcher. 1984. Photosynthetic light environments in a lowland tropical rainforest in Costa Rica. *J. Ecol.* 72: 553-564.
- Collins, B. S., K. P. Dunne, and S. T. A. Pickett. 1985. Responses of forest herbs to canopy gaps. Pages 217-234 in S. T. A. Pickett and P. White, eds. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York.
- Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. *Annu. Rev. Ecol. Syst.* 18: 431-451.
- Franklin, J. S., and R. T. T. Forman. 1987. Creating patterns by cutting: ecological consequences and principles. *Landscape Ecol.* 1: 5-18.
- Garcia-Moya, E., and C. M. McKell. 1970. Contribution of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology* 51: 81-88.
- Hibbs, D. E. 1982. Gap dynamics in a hemlock-hardwood forest. *Can. J. For. Res.* 12: 522-527.
- Hibbs, D. E., B. F. Wilson, and B. C. Fisher. 1980. Habitat requirements and growth of striped maple. *Ecology* 61: 490-496.
- Holland, V. L. 1980. Effect of blue oak on rangeland forage production in central California. Pages 314-318 in T. Plum, ed. *Proceedings of the Symposium on Ecology, Management, and Utilization of California Oaks*. USDA Forestry Service, Pacific Southwest Forest and Range Experiment Station General Technical Report PSW-44.
- Jackson, L. E., R. B. Strauss, M. K. Firestone, and J. W. Bartolome. 1990. Influence of tree canopies on grassland productivity and nitrogen dynamics in deciduous oak savanna. *Agric. Ecosys. Environ.* 32: 89-105.
- Joffre, R., and S. Rambal. 1988. Soil water improvement by trees in the rangelands of southern Spain. *Acta Oecologica Oecol.*

- Plant*. 9: 405-422.
- Kellman, M. 1979. Soil enrichment by neotropical savanna trees. *J. Ecol.* 67: 565-577.
- Kelty, M. J. 1986. Development patterns in two hemlock-hardwood stands in southern New England. *Can. J. For. Res.* 10: 885-891.
- Kennard, D. G., and B. H. Walker. 1973. Relationships between tree canopy cover and *Panicum maximum* in the vicinity of Fort Victoria. *Rhod. J. Agric. Res.* 11: 145-153.
- Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation, and community structure. *Proc. Nat. Acad. Sci.* 71: 2744-2747.
- Menges, E. S., and O. L. Loucks. 1980. Modeling a disease-caused patch disturbance: oak wilt in the midwestern United States. *Ecology* 65: 487-498.
- Minckler, L. S., J. D. Woerheide, and R. C. Schlesinger. 1973. Light, soil moisture and tree reproduction in hardwood forest openings. USDA Forest Service Research Paper NC-89.
- Mladenoff, D. J. 1987. Dynamics of nitrogen mineralization and nitrification in hemlock and hardwood treefall gaps. *Ecology* 68: 1171-1180.
- Monk, C. D., and F. C. Gabrielson Jr. 1985. Effects of shade, litter and root competition on old-field vegetation in South Carolina. *Bull. Torrey Bot. Club* 112: 383-392.
- Nakashizuka, T. 1984. Regeneration process of climax beech (*Fagus crenata* Blume) forests. IV. Gap formation. *Jap. J. Ecol.* 34: 75-85.
- Norton-Griffiths, M. 1979. The influence of grazing, browsing, and fire on the vegetation dynamics of the Serengeti. Pages 310-352 in A. R. E. Sinclair and M. Norton-Griffiths, eds. *Serengeti: Dynamics of an Ecosystem*. University of Chicago Press, Chicago, IL.
- Obot, E. A. 1988. Estimating the optimum tree density for maximum herbaceous production in the Guinea Savanna of Nigeria. *J. Arid Environ.* 14: 267-273.
- Pacala, S. W., C. D. Canham, and J. A. Silander. In press. Forest models defined by field measurements. I. The design of a northeastern forest simulator. *Can. J. For. Res.*
- Parker, V. T., and C. H. Muller. 1982. Vegetational and environmental changes beneath isolated live oak trees (*Quercus agrifolia*) in a California annual grassland. *Am. Midl. Nat.* 107: 69-81.
- Pickett, S. T. A., and P. White, eds. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York.
- Platt, W. J., and D. R. Strong. 1989. Gaps in forest ecology. *Ecology* 70: 535.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *Am. Nat.* 132: 652-661.
- Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63: 1533-1546.
- _____. 1985. Disturbance regimes in temperate forests. Pages 17-33 in S. T. A. Pickett and P. White, eds. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York.
- Runkle, J. R., and T. C. Yetter. 1987. Treefalls revisited: gap dynamics in the southern Appalachians. *Ecology* 68: 417-424.
- Sala, O. E., R. A. Golluscio, W. K. Lauenroth, and A. Soriano. 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia* 81: 501-505.
- Smith, T. M., and P. S. Goodman. 1986. The effect of competition on the structure and dynamics of *Acacia* savannas in southern Africa. *J. Ecol.* 74: 1031-1044.
- Stuart-Hill, G. C., and N. M. Tainton. 1989. The competitive interaction between *Acacia karroo* and the herbaceous layer and how this is influenced by defoliation. *J. Appl. Ecol.* 26: 285-298.
- Tiedemann, A. R., and J. O. Klemmedson. 1977. Effect of mesquite trees on vegetation and soils in the desert grassland. *J. Range Manage.* 30: 361-367.
- _____. 1986. Longterm effects of mesquite removal on soil characteristics. I. Nutrients and bulk density. *Soil Sci. Soc. Am. J.* 50: 472-475.
- Vetaas, O. R. 1992. Micro-site effects of trees and shrubs in dry savannas. *J. Veg. Sci.* 3: 337-344.
- Vitousek, P. M., and J. S. Denslow. 1986. Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. *J. Ecol.* 74: 1167-1178.
- Watt, A. S. 1947. Pattern and process in the plant community. *J. Ecol.* 35: 1-22.
- Weltzin, J. F., and M. B. Coughenour. 1990. Savanna tree influence on understory vegetation and soil nutrients in northwestern Kenya. *J. Veg. Sci.* 1: 325-332.
- Young, A. 1989. *Agroforestry for Soil Conservation*. International Council for Research in Agroforestry, Nairobi, Kenya.

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