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A conceptual model relating ecological constraints to livestock production in tropical American seasonal savannas

G. Sarmiento & M. Pinillos
Centro de Investigaciones Ecológicas de los Andes Tropicales, Universidad de los Andes, 5101 Mérida, Venezuela
E-mail: gsarmi@cantv.net

Abstract

Justifications for, and restrictions to, the extensive livestock production systems prevailing in tropical American seasonal savannas are dealt with, and summarized as graphic model or flux diagrams. The crucial role of ecosystemic processes regulating the nutrient cycles is stressed, while fire is considered a key management practice. The high connectivity among the components of the system, reflected in the models, causes any given natural or man-made process to give rise to multiple and often contradictory consequences. Forage offer, quantity and quality, during the dry season, seems to be the major constraint for increasing the carrying capacity of these savannas, indirectly causing a sub-utilization of the available fodder during the rainy season and the accumulation of large amounts of dead material that is consumed by fire.

1 Introduction

Savannas and rain forests are the two most widespread ecosystems in the lowlands and middle altitude plateau of tropical America. Savannas cover almost continuous areas of hundreds of thousands of square kilometers, the major one being on the central Brazilian high plains, where they are called *cerrados* or *campos cerrados*, and the second largest in the Colombo-Venezuelan Llanos. Other extensive savanna landscapes occur in the Beni Llanos of Bolivia, in Amazonia, as scattered savanna islands within the almost uninterrupted rain forest landscape, in the low plateau of southern Venezuela and Guyana, in Roraima, northern Brazil, in the Atlantic coast of Nicaragua and Honduras, and in tropical Mexico and Cuba (Sarmiento[7,8]).

The ecological constraints to land use in savanna lands have been considered by various authors who stress the importance of water and nutrient availability and of fire as major constraints (Hadley [2], Young and Solbrig [15,16]). Solbrig [11] also points out the unstable condition of tropical savannas which he considers as non-equilibrium ecosystems. In this paper we wish to go a little further in this same direction, having taken a particular type of tropical American savanna ecosystem as a case study for discussing the limitations imposed by the ecological conditions to the intensification of a livestock economy. Our approach is systemic, in the sense that major processes related to the carbon and nutrient cycles are considered together as a network of mutually dependent elements. Therefore, the links between factors, processes and components are summarized in flow diagrams depicting the dynamic behaviour of the managed savanna. Although many data are still lacking for quantifying the transfers of energy and materials in this ecosystem, the aim of our conceptual model is to stress the major information and material links structuring the whole ecosystem. The model, obviously, takes into account only the main components more directly related to livestock production, disregarding all other ecosystem processes.

Before European settlement in the sixteenth and seventeenth centuries, the very sparse native populations inhabiting tropical American savannas had their crop fields in gallery forests and other riparian habitats, while the savannas were used for hunting and plant recollection. The most valuable large herbivores for these hunters were deer (*Odocoileus virginianus, Blastocerus dichotomus* and *Tayassu tajacu*), capybaras (*Hydrochaeris hydrochaeris*) and dantas (*Tapirus terrestris)*, all of these grazing both in open and in closed vegetation. A dramatic change in land use took place when cattle, early introduced by the Spanish and Portuguese colonizers, became so adapted to the savanna's hard ecological conditions that they started to increase in number exponentially. This semi-wild cattle was the basis of the first system of savanna use by the colonial economies, which at first exploited almost exclusively the hides and fat of the animals, in a hunting-like system of resource appropriation. Later on, the land itself, besides the livestock, became a valuable resource, and huge landholdings were the support of a quite extensive livestock economy, which provided meat and other products to the growing urban markets. This extensive form of land use persisted for hundred of years. It was only a few decades ago, when some forms of intensification, such as the introduction of Cebú breeds, cultivated pastures of exotic grasses and some basic sanitary treatments of the herd, began to spread slowly across the Llanos and cerrados (Vera and Seré[13])

Why did this traditional and apparently unproductive form of land use persist for such a long period? As predominantly herbaceous systems, dominated by perennial grasses, tropical savannas seem to be grazing lands particularly well suited to support introduced domestic grazers, such as cattle or horses. However, the strong environmental seasonality that characterizes tropical savannas severely limits the system carrying capacity, which is severely regulated by a crucial bottleneck: fodder availability during the long dry season. Besides extensive cattle raising, agriculture could be an alternative land use possibility, but both the length of the dry season and the poor soils restrict crops to the rainy season and to the most fertile soils, otherwise cropping requires exceptionally high investments in agrochemicals and other inputs associated with modern agronomic technology. As cattle raising continues to be the most important form of land use in savanna regions, therefore we shall restrict our discussion to its weakness and constraints, and possibilities for improvement.

It is quite clear now that tropical savannas result from a constellation of physical and biological factors (Sarmiento[8], Walker[14], Solbrig, Medina and Silva[12]). Rather extended periods of drought or of water excess, high fire frequency, low nutrient availability, soil acidity and aluminium toxicity, together modulate the structure, function and dynamics of savanna ecosystems. But to understand the ecological constraints impinging upon tropical savannas, it is convenient to distinguish between different types of savanna ecosystems, determined in the first instance by the soil water regime. In *seasonal* savannas, two contrasting periods, one of drought and the other of soil water availability, alternate during each annual cycle (Fig. 1). In *hyperseasonal* savannas, four contrasting periods, one of drought, an other of water availability, a third of water excess and a final period of water availability, succeed each other during each annual cycle. In *semi-seasonal* savannas, the alternation occurs between a rather long period of water excess and another of water availability, without any period of drought.

When discussing land use, it is crucial to be clear on which system we are talking about. Our interest in this paper is centreed on seasonal savannas because they are the most widespread savanna type in tropical America and the best known too.

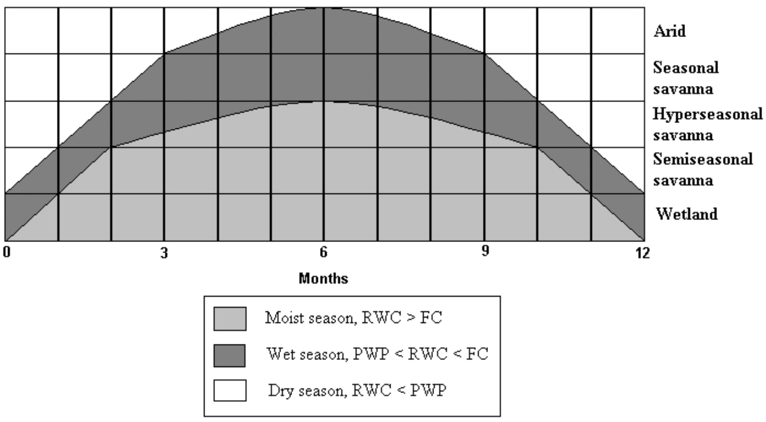
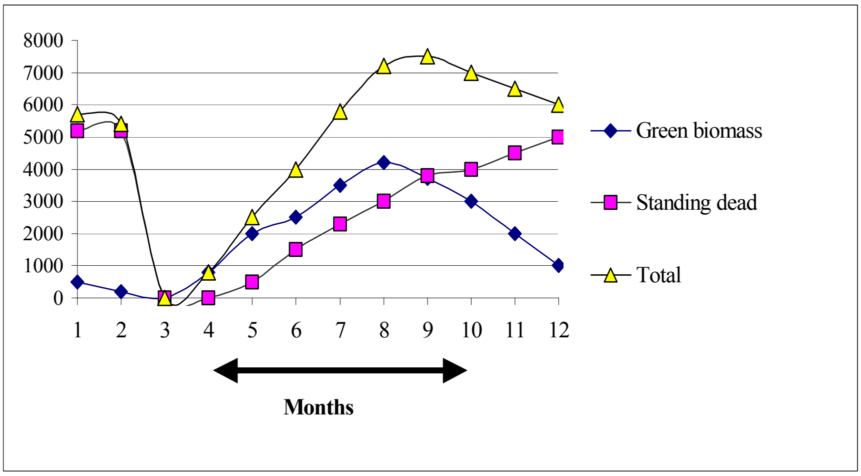


Figure 1: Differenciation of tropical savanna ecosystems according to periods of soil humidity in each annual cycle. RWC: Relative Water Content; FC: Field Capacity; PWP: Permanent Welting Point.

2 Primary productivity and the environmental offer to herbivores

The sharp environmental seasonality that characterizes seasonal savanna ecosystems is reflected, in the first instance, in the seasonality of biomass accumulation and primary production. Figure 2 shows the annual variation in herbaceous aboveground biomass in a seasonal savanna; it may be seen that the green biomass increases from the beginning of the rainy season to attain a peak towards its end of about 400 kg DW ha^{-1}, and then it steadily decreases to reach a minimum, at the end of the dry



season, of about 100 kg DW ha^{-1}.

Figure 2: Annual sequence of green, dead and total herbaceous aboveground biomass (kg DW ha^{-1}) in a seasonal savanna of the Venezuelan Llanos, burnt in March. The arrow indicates the extension of the rainy season. Data from Sarmiento[8] and San José and Medina[6].

Total aboveground biomass, instead, slightly decreases or continues accumulating, as a net result of further production and mortality of the old growth. At the end of the dry season almost the whole biomass (about 7000 kg DW ha^{-1}) is just an accumulation of standing dead straw. Net primary aboveground production (Fig. 3) sharply increases during the early months of the rainy season, to decrease then to almost nil at the end of the cycle. Seasonal patterns of primary production and biomass accumulation are directly responsible for the marked seasonal offer of green forage to cattle, since the dead standing crop has negligible palatability and nutritive value. Net primary production in tropical

American savannas under the most frequent fire regime of quasi–annual frequency, ranges from 5000 to 8000 kg DW ha-1 y^{-1}.

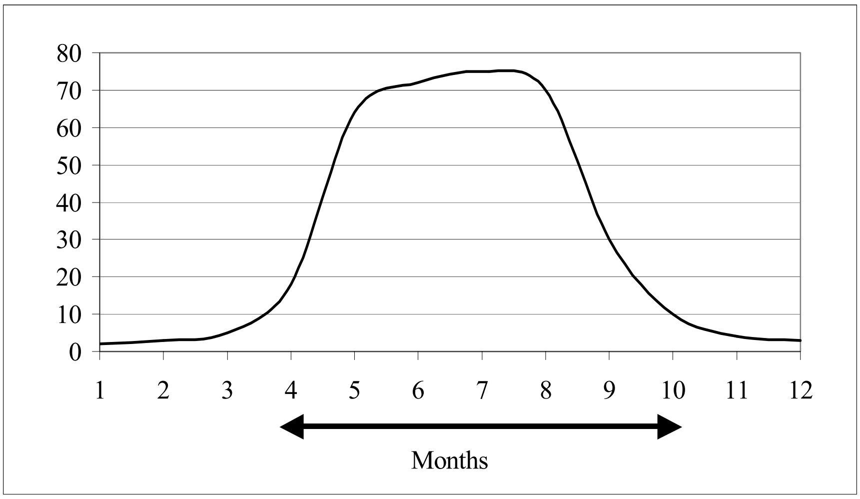


Figure 3. Annual sequence of aboveground productivity (kg DW ha^{-1} day^{-1}) in the same savanna as in Figure 2. The arrow indicates the extension of the rainy season.

As a direct consequence of the sharp seasonality of green forage production, stocking rates in these seasonal savannas are quite low. In most cattle ranches, in areas with a predominance of seasonal savannas, the carrying capacity ranges from 0.1 to 0.2 AU per hectare. After the intensive regrowth of grasses triggered by the availability of water in the topsoil, a three to four month growth period delimits the optimal grazing time when there is enough forage to allow higher stocking rates than the prevailing ones, with consumption of about half the green biomass, a threshold that insures the conservation of the natural pasture.

3 Fire

Fire has been and continues to be the most important management tool in the extensive cattle raising systems in savanna areas. Most tropical American savannas are purposely burnt with almost yearly frequency, to promote the regrowth of perennial grasses and to eliminate the standing dead biomass. From the viewpoint of plant production seasonality, fire seems to reinforce the seasonal behaviour of the unburnt system, by concentrating primary production in a still shorter time (Fig. 4).

A late dry season fire burns almost all the accumulated herbaceous aboveground plant material. A vigorous regrowth of the perennial grasses starts shortly afterwards, leading in a few months to a peak of green biomass often higher than in the unburnt grassland. But later, the decay of this green material is also more rapid than the senescence of the standing crop in the unburnt savanna.

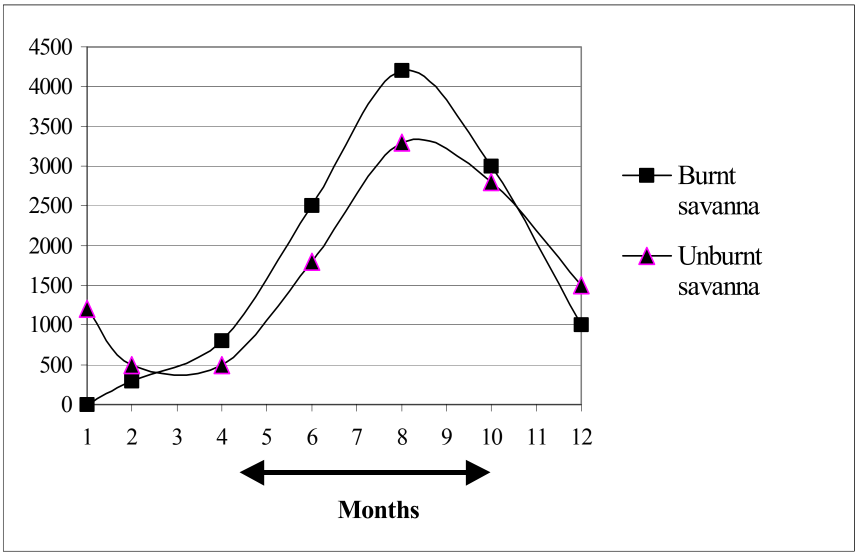


Figure 4. Accumulation of green herbaceous aboveground biomass (kg DW ha^{-1}) in an early burnt and in unburnt seasonal savanna of the Venezuelan Llanos (after San José and Medina[6]).

The nitrogen content of the standing dead material prior to burning is the lowest in the annual cycle (in the order of 0.4 – 0.5% N), due to the continuous retranslocation from the senescent leaves to the belowground plant parts. This fact drastically reduces volatilization losses, which just attain about 20 kg N ha^{-1}. The recuperation rate by translocation could be as high as 60% to 70% of the aboveground biomass' peak nitrogen content.

Two additional points concerning the effect of burning refer to the amount of biomass produced and its influence on nutrient cycling. It is still a controversial matter if in tropical savannas a causal relationship does exist linking net primary productivity with fire frequency (Solbrig et al. [12]). Given that any increase in fire frequency also increases nutrient losses, we may expect a negative correlation between fire frequency and primary productivity in the long-term; but as this is not the only effect of fire, the question is: which fire frequency maximizes plant production? This issue certainly needs further research and a systemic approach through modelling (Sarmiento & Silva[10]). In the short-term, however, the influence of fire reflects itself more on the seasonal behaviour of the productive processes than in the total amount of biomass produced. This is because burning frees the nutrient stock sequestered in the standing dead crop, allowing a fast regrowth as soon as soil water conditions become favourable.

4 Nitrogen cycling and the quality of the offer to herbivores

One of the most important ecosystemic impacts of recurrent fires is on the nitrogen cycle. In fact, a non-negligible amount of the biomass nitrogen is lost by volatilization to the atmosphere during burning; however, the amount of nitrogen circulating through the system depends on the balance between gains and losses. Among the gains, besides wet and dry deposition, biological fixation by free leaving microorganisms seems to play one of the most important roles, attaining perhaps 12 to 15 kg N $ha^{-1}y^{-1}$.

Furthermore, conservative mechanisms like nitrogen retranslocation to underground organs significantly decrease possible volatilization losses.

Whenever nitrogen plays the role of key limiting factor for growth and primary production, a generalized strategy in plant species is the translocation of this element from mature leaves to underground structures. This is a general response typical of oligotrophic systems and it applies not only to nitrogen but also to any scarce nutrient (Chapin et al.[1]). In this way, in tropical savannas, leaf nitrogen content, after reaching its annual peak during the most active period of plant growth, sharply decreases to attain quite low levels in the standing dead biomass that will be burnt with the next fire (Sarmiento [8]; Medina [5]).

In general, the final nitrogen balance of the ecosystem will depend on fire frequency: under a low frequency, biological fixation and rainfall inputs may compensate volatilization losses, while under higher frequencies, the system does not reach a steady state because losses always overcome gains.

These features of the nitrogen cycle determine that, in spite of the great accumulation of plant biomass at the end of the annual cycle, during the dry season the nutritive value and the palatability of this forage offer, greatly dependent upon its nitrogen and protein contents, descend below the minimum requirements of cattle. In other words, while the carbon, or energy offer to herbivores, follows the annual curve of total biomass, the nitrogen offer is associated with the green biomass and the primary productivity temporal patterns. In such a way, the factors limiting the carrying capacity of these savannas switch during the year, from energy availability during the wet season to both carbon and nutrient availability, particularly nitrogen, during the dry period.

Our emphasis has been on nitrogen because losses of this volatile element during burning really occur. But other nutrients, phosphorus in particular, may have a similar influence on the carrying capacity of savannas. In the quite acid soils of tropical savannas this element becomes readily immobilized. However, deep differences exist between the phosphorus and the nitrogen cycles. The phosphorus stock in savanna ecosystems is certainly quite limited, but its cycling between soil and vegetation is rather tight, without significant inputs and outputs. On the contrary, the nitrogen cycling is much more open and fragile, depending on important losses (volatilization) and gains (biological fixation).

5 The systemic constraints to land use intensification

5.1 The nutrient cycling

Taking as a reference a seasonal savanna under the actual fire frequency and stocking rates, we firstly consider the ecological constraints related to nutrient cycling (Fig. 5) and then the limitations to livestock production derived from carbon and nitrogen shortage (Fig. 6 and Table 1), then relating both aspects.

Figure 5 depicts our conceptual model of nutrient cycling in seasonal savannas. Some interactions have not been considered, such as the decomposition of the standing dead material, since it is not quantitatively significant in this ecosystem. Other processes, such as nutrient leaching from the soil, operate at a longer timescale than the management scale of a few years considered in the model.

The diagram includes major processes and components operating at the natural ecosystem level, related to nutrient fluxes from soil to producers, and from these to herbivores. The components of this conceptual model of the system relate to each other through material fluxes and positive or negative causal relationships whose temporal action depends on the number of links in the chain. The greater the number of links, the longer will be the time required to express the influence of one component on another. In the same way, the sign of the influence will depend on the arithmetic product of the involved processes: positive by positive equal positive, positive by negative equal negative, and so on (Martínez and Requena[4]). In this context, the causal relationships between components in the model represent our evaluation of the sign of the interactions operating in the ecosystem.

As the model makes evident, soil water availability is the most important regulator of the ecosystem's metabolism. It controls the photosynthetic activity and, in consequence, the forage supply to cattle; it also regulates the soil microbial activity, with strong implications for the

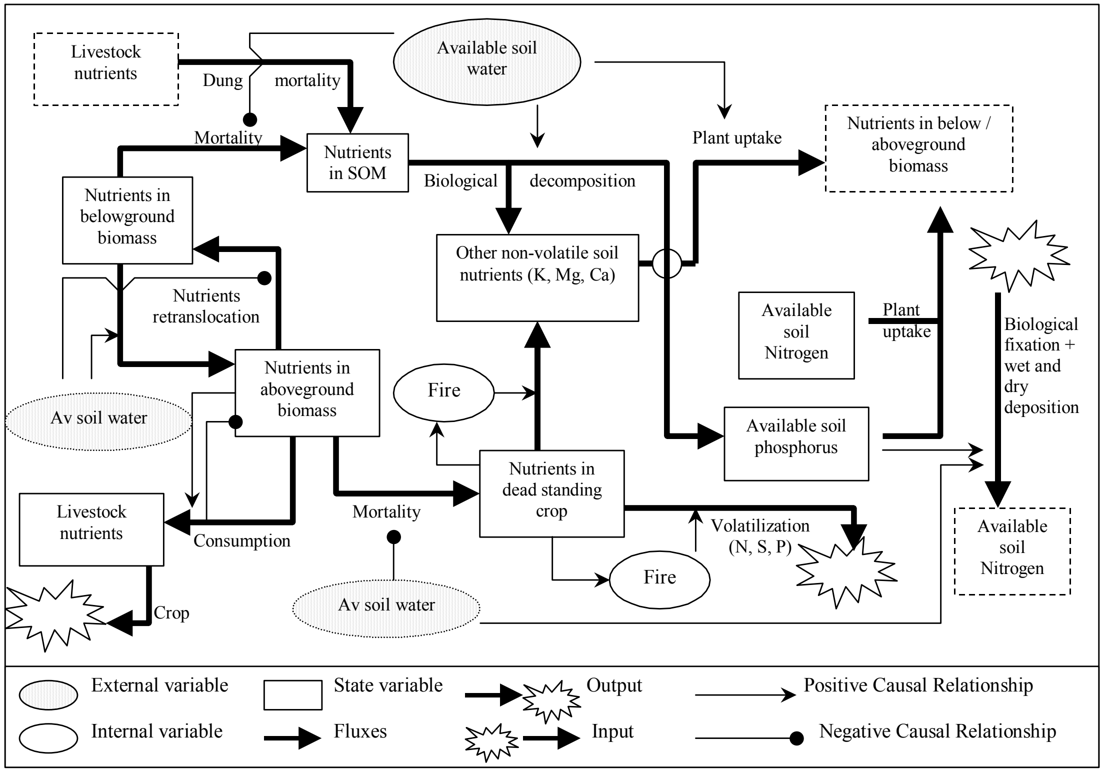


Figure 5: Flow diagram showing information and material transfers among the components of the grazed seasonal savanna ecosystem.

biological decomposition and fixation of nitrogen in this compartment; it triggers nutrient mobilization between the aboveground and the belowground biomass, and vice versa, and finally, it determines the amount of dry straw consumable by fire.

Fire releases the nutrients sequestered in the dead standing crop and it has, in this way, a positive impact on plant production; its frequency under natural conditions depends on the dead materials accumulated at the end of the dry season (Jeltsch et al.[3]) Under present–day managed conditions, however, fire acts as an external variable, since it depends on the ranchers' strategies of land use. In both cases, the positive effect on plant production is counterbalanced by its negative effect on the budget of volatile elements. Some of these volatiles, such as nitrogen, are major limitants of primary and secondary productivity. Therefore, fire is a necessary handicap, which has influenced the development of characteristic plant and animal strategies to cope with it, like nutrient translocation between aboveground and belowground plant parts.

5.1.1 Carbon and nitrogen constraints on livestock production

The offer of forage directly controls the food chain from plants to cattle. Two contrasting situations appear, depending on soil water availability. During the rainy season (Fig. 6a), the uppermost soil layers maintain rather high soil water potentials that favour grass growth. During this period, aboveground primary production may reach 7000 kg ha^{-1}, with an average monthly accumulation of green biomass in the order of 3000 kg ha^{-1}; all these figures were taking from Sarmiento[8] or from our unpublished data. The standing dead attains rather similar figures. The forage potentially available to grazers, maintaining a coefficient of utilization of 50 %, will then be 1500 kg ha^{-1}, which may feed a livestock live weight of 120 kg ha^{-1}, roughly equivalent to 0.25AU per hectare. Under these circumstances, secondary production may be in the order of 24 kg DW ha^{-1} for the whole rainy season.

By contrast, during the dry period (Fig. 6b), topsoil water potentials become quite negative, reducing grass growth to about 700 kg DW ha^{-1}, with an average green biomass of 500 kg DW ha^{-1}. With the same 50 %

Figure 6a: Primary and secondary (livestock) production in a seasonal savanna during the rainy season.

Rainy season (210 days)

↓

Continued water availability in the topsoil

↓

Active growth period of perennial grasses

↓

Aboveground primary production (herb layer)

≈ 7000 kgDW.ha^{-1}

Average green biomass	Average standing dead
≈ 3000 kgDW.ha^{-1}	≈ 3000 kgDW.ha^{-1}

↓

Potential offer to livestock

3000 * 0,5 = 1500 kgDW.ha^{-1}

↓

Cattle consumption = 1500 kgDW.ha^{-1}

Not consumed = 4500 kgDW.ha^{-1} → To dry season

↓

Average potential livestock biomass

(daily consumption 6% live weight * 210 days)

120 kg live weight.ha^{-1}

Average carrying capacity

0,25 AU.ha^{-1}

↓

Potential production 20% liveweight

= 24 kg live weight.ha^{-1}

Figure 6b: Primary and secondary (livestock) in a seasonal savanna during the dry season.

Dry season (155 days)

↓

Low topsoil water potential

↓

Water stress

↓

Reduced grass growth

↓

Aboveground primary production

≈ 700 kgDW.ha^{-1}

Average green biomass ≈ 500 kgDW.ha^{-1}

Average standing dead ≈ 200 kgDW.ha^{-1}

↓

Potential offer to livestock

(500 kgDW.ha^{-1} * 0,5 = 250 kgDW.ha^{-1}

↓

Cattle consumption = 250 kgDW.ha^{-1}

Not consumed = 4950 kgDW.ha^{-1} → To fire

Average potential livestock biomass

(daily consumption 6% live weight * 155 days)

20 kg live weight.ha^{-1}

Average carrying capacity = 0,04 AU.ha^{-1}

↓

Potential production = 4 kg live weight.ha^{-1}

utilization coefficient, the available forage could maintain about 40 kg of live biomass of grazers, with a potential production of just 8 kg DW ha^{-1}.

We may realize, then, how the forage offer during the dry season becomes the major constraint to the system's carrying capacity, determining a potential carrying capacity about six times smaller than the animal charge during the rainy season.

None of these figures take forage quality into account. If we now consider the palatability and nutritive value of the forage offer (Table 1), we see that during the period of soil water availability, nitrogen offer attains 15 kg ha^{-1}, that which an assimilation rate of 20 %, gives 3 kg.ha^{-1} of nitrogen available for animal production, enough nitrogen to build 100 kg of animal weight. Production during this period seems to be limited by carbon and not by nitrogen.

Table 1: Nitrogen stocks and transfers from plants to livestock in a seasonal savanna during the rainy and the dry seasons.

	Rainy season	**Dry season**
Green biomass kg DW ha^{-1}	3000	500
Nitrogen (N) in green biomass %	1	0.7
Total N in green biomass kgN.ha^{-1}	30	3.5
N in forage offer kg N ha^{-1}	15	1.75
N consumed kg N ha^{-1}	15	1.75
N assimilated kg N ha^{-1}	3	0.35
Potential livestock production kg live weight ha^{-1}	100	12

During the dry season, nitrogen concentration in green biomass decreases to the critical level of 0.7 %; then the total nitrogen offer in the available forage amounts to 1.75 kg N ha^{-1} of which 2%, that is 350 g, could be assimilated, enough nitrogen to build about 20 kg of animal biomass. This figure approaches the amount of animal biomass that could be produced with the available carbon, suggesting that both factors, carbon and nitrogen, are limiting secondary production during this dry period. Furthermore, a part of the green biomass, the senescent leaves, certainly fall below the critical 0.7 % nitrogen level, thus becoming unattractive to cattle.

5.1.2 Other management alternatives

Since we are talking about a productive livestock system, it is unavoidable to refer to costs, benefits and profits which, in the last instance, determine the application of one or another management practice. Of the three factors with possibilities of regulation through management practices, water, nutrients and fire, water and nutrient modifications imply high economic costs, leaving the alteration of natural fire regimes as the key management tool.

Fire frequency regulates the size of the dead standing crop compartment in tropical savannas, and then the rate of cycling of the nutrients sequestered in it. By eliminating most of the dead standing crop, burning also improves light conditions near to the soil level, optimizing in this way the primary production of the grass layer. Therefore, the elimination of the dead standing crop certainly favours forage production and improves its quality. From this angle, it is obvious, then, that the best management strategy would be to increase the fire frequency above the natural frequency as much as possible. However, this practice comes in contradiction with the long-term behaviour of the system, as we explained before, since if the system has attained a quasi-steady state with a given fire frequency, any increase in the natural periodicity of burning will alter the nutrient balance, leading the whole system to a gradual impoverishment in its nutrient pool.

Fertilization may be a way to overcome soil nutrient shortage. However, high soil acidity, as well as prevailing leaching conditions, severely limit the benefits of fertilization and greatly increase its costs. Thus, to correct soil acidity it is necessary to add huge quantities of calcium, mostly in the form of calcareous rocks, preventing in this way further phosphorus immobilization and stimulating the biological processes responsible for soil fertility.

Leaching, on the other hand, is an almost unavoidable natural process, given the high rainfall during the wet season, and the prevailing well-drained and heavy-textured seasonal savanna soils. These environmental conditions restrict the influence of the added fertilizer to a short time and they render chemical fertilization an almost prohibitive practice when applied to extensive livestock systems.

Water management through irrigation or runoff control is still more expensive since, besides increasing leaching losses, it requires costly inversions in infrastructure; irrigation becomes an economic alternative only when the land use system may be switched to intensive agriculture with all its technological paraphernalia. On the other hand, runoff control, through dykes and gauges, widely implemented in the Venezuelan Llanos, makes sense only in hyperseasonal and semiseasonal savannas where water becomes the overwhelming factor regulating the functioning of these two types of ecosystems (Sarmiento[9]).

The causal diagrams take into account the productive context of a single system: the seasonal savanna. Accordingly, we have not considered the herd management possibilities derived from temporal or spatial variations in carrying capacity conditions. Indeed, herd management represents a heavy demand in fences and it does not make sense in a homogeneous context, when just one type of savanna ecosystem occurs and where the major heterogeneity is due to the precise timing of burning. Cattle will spontaneously follow the temporal sequence of burning in savanna patches, consuming the fresh regrowth of grasses in the recently burned areas.

On the contrary, when the savanna landscape is heterogeneous, with a mosaic of the three major types of savanna ecosystems, the herd may be managed by circulating the animals among the three systems according to their different seasonal patterns of primary production and forage quality. This seasonal movement of the animals does not represent any additional cost when all types of savanna ecosystems do exist in the same productive unit and the herd can move freely from one to another. Under these particular conditions of productive complementarity among various savanna ecosystems, the seasonal displacement of cattle seems to be the best management alternative in order to avoid the dry season bottleneck, but the nutritional constraints inherent to the savanna ecosystems still remain.

In conclusion, it is clearly evident that savanna ecosystems have a very high level of connectivity among their components, and that consequently any management practice can not have not an isolated effect on any other component of the system at any given temporal scale. This renders inescapable a systemic approach in order to design the best productive alternatives in order to overcome the many ecological constraints acting upon primary and secondary production in tropical savanna ecosystems.

Aknowledgements

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References

[1] Chapin, F.S., Vitousek, P.M. & Van Cleve, K., The nature of nutrient limitation in plan communities, *American Naturalist*, 127, pp. 48–58. 1986.

[2] Hadley, M., Comparative aspects of land use and resource management in savanna environments, *Ecology and Management of the World's Savannas*, eds. J. C. Tothill & J. J. Mott, CAB, Australia, pp. 142–158, 1985.

[3] Jeltsch, F. S., Milton, W., Dean, R. & Van Rooyen, N., Analyzing shrub encroachment in the southern Kalahari: A grid based modeling approach, *Journal of Applied Ecology*, 34, pp. 1497–1508, 1996.

[4] Martínez, S. & Requena, A., *Dinámica de Sistemas 2: Modelos*, Alianza Editorial, Madrid, pp. 15 – 40, 1986.

[5] Medina, E., Nutrients: Requirements, conservation and cycles of nutrients in the herbaceous layer, Chapter 3, *Determinants of Tropical Savannas*, ed. B. H. Walker, IRL Press, Oxford, pp. 39–65, 1987.

[6] San José, J. J. & Medina, E., Producción de materia orgánica en la sabana de *Trachypogon*, Calabozo, Venezuela, *Boletín de la Sociedad Venezolana de Ciencias Naturales*, 139, pp. 347–374, 1977.

[7] Sarmiento, G., The savannas in Tropical América, Chapter 10, *Ecosystems of the world: Tropical savannas*, ed. F. Bourliére, Vol. 13, Elsevier Scientific Publishing Co., Amsterdam and Oxford, pp. 245–288, 1983.

[8] Sarmiento, G., *The Ecology of Neotropical Savannas*, Harvard University Press, Cambridge, pp. 148–206, 1984.

[9] Sarmiento, G., Ecología Comparada de Ecosistemas de Sabana en América del Sur, Chapter 1, *Las Sabanas Americanas: Aspectos de su biogeografía, ecología y utilización*, ed. G. Sarmiento, Fondo Editorial Acta Científica Venezolana, Mérida, pp. 15–56, 1990

[10] Sarmiento, G. and Silva, J. F., Un modelo de estados y transiciones de la sabana estacional de los Llanos venezolanos, *Ecotrópicos*, 10, pp. 51–64, 1998.

[11] Solbrig, O. T., Ecological constraints to savanna land use, The World's Savannas: Economic Driving Forces, *Ecological Constraints and Policy Options for Sustainable Land Use*, eds. M. D. Young & O. T. Solbrig, UNESCO, París and the Partenon Press, Carnforth, pp. 21–47, 1993.

[12] Solbrig, O. T., Medina, E. & Silva, J., *Biodiversity and Savanna Ecosystem Processes: A Global Perspective*, Springer Verlag, Berlin, pp. 37–52, 1996.

[13] Vera, R.R. & Seré, C., *Sistemas de Producción Pecuaria Extensiva. Brasil, Colombia, Venezuela,* CIAT, Cali., pp. 15–37, 1985.

[14] Walker, B., *Determinants of Tropical Savannas*, IRL Press, Oxford, pp. 1–154, 1987

[15] Young, M. D. & Solbrig, O. T., *Savanna Management for Ecological Sustainability, Economic Profit and Social Equity,* MAB Digest 13, UNESCO, Paris, pp. 3–30, 1992.

[16] Young, M. D. & Solbrig, O. T., *The World's Savannas: Economic Driving Forces, Ecological Constraints and Policy Options for Sustainable Land Use*, UNESCO, Paris and Parthenon Publishing, Carnforth, pp. 3–45, 1993.