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Viewpoint: The state and transition model applied to the herbaceous layer of Argentina's calden forest

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Abstract

The ecological trends in the vegetation of the calden (*Prosopis caldenia* Burk.) forest of central Argentina have generally been explained with a model that assumed a unique equilibrium state or "climax." This model does not adequately explain the ecological changes that occur in the understory of the calden forest. Recently, models that present different stable states of vegetation have been suggested. These vegetation states do not change unless relatively drastic management or climatic actions occur. Observations of vegetation changes, grazing regimes, and other aspects of management permitted the development of a basic scheme to explain changes in the herbaceous layer in the calden forest, based on the state and transition model. Five stable states and 9 transitions are proposed to account for current herbaceous associations and their origins. This model seems to more accurately explain transitions between the different vegetation states in the area, some of which could not be readily explained by the "climax" model.

Key Words: succession, climax, stable states, transitions, *Prosopis caldenia*.

Previous studies of the dynamics of the vegetation of Argentina's calden (*Prosopis caldenia* Burk.) forest have been based on successional models that assume a unique stable state or "climax" plant community (Anderson 1984, Llorens and Frank 1985). It was assumed that if a disturbance caused the vegetation to change, the withdrawal of that disturbance would allow the vegetation to return to its previous state.

Successional models have not provided satisfactory explanations for observed vegetation trends under certain circumstances. Models that provide better interpretation of trends in vegetation dynamics of this region will help managers maintain or improve their natural resources and increase productivity. Westoby et al. (1989) compared the successional model to the state and transition model and identified the strengths and weakness of each. Laycock (1991) summarized a number of changes that have occurred in different grasslands of North America which did not correspond to the successional model.

The objectives of this paper are to interpret the plant community dynamics of herbaceous vegetation in the calden forest of central Argentina in relation to limitations of the successional model when applied to this region, and assess the value of the state and transition model for interpreting vegetation responses to management in the calden forest. Specific states and transitions are proposed, based upon observations and measurements of the vegetation made under different levels of management over a period of 10 years.

Description of the Area

The calden (*Prosopis caldena* Burk.) forest extends over an elongated area in the central part of La Pampa Province and the southern part of the San Luis Province in Argentina. It covers an area of approximately 4,000,000 ha. This semiarid region has been described by Parodi (1964), Cabrera (1966), Cano et al. (1980), Cano (1988) and Basso and Frank (1990). Average annual rainfall is 555 mm (Fig. 1). Elevation ranges from near sea level to 400 m. The vegetation is mostly deciduous forest dominated by calden, a leguminous tree. Originally, the calden forest was an open forest, with mature trees reaching a height of 10–12 m, with abundant open space between them. Tree foliar cover was variable, but was usually 30–50%. The density of shrubs was low. The density of calden and other woody species was lower where soil texture was more sandy, forming areas of grassland with the appearance of a savanna.

Today, the interaction of wood harvesting, overgrazing, and the exclusion of fire in the ecosystem have, over large areas, promoted the invasion of shrubs such as other *Prosopis* species, chanar [*Geoffroena decorticans* (Gill. ex Hook et Arn.) Burkart], chilladora (*Chuquiraga erinacea* Don.), creosotebush (*Larrea* sp.), molle [*Schinus fasciculatus* (Gris.) Johnston], and other species. Dispersal and improved germinability of seed by cattle may be an important factor in the increase in density of woody species. The distribution of woody species is also influenced by

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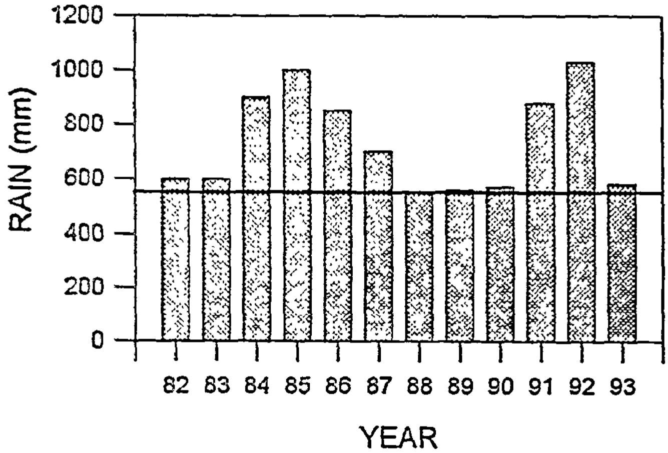

Fig. 1. Annual rainfall at Victorica from 1982 to 1993. The horizontal line represents the mean from 1922 to 1992.

topography. Shrubs are more dense on the hillsides and the typical calden forest seems to prevail in the basins between the low hills (Cano 1988). More open calden forest with larger trees can be found on the higher plateaus with finer textured soils.

Originally, the herbaceous layer was dominated by the short-grasses flechilla negra (*Piptochaetium napostaense* Speg.), flechilla fina (*Stipa tenuis* Philippi), sand dropseed [*Sporobolus cryptandrus* (Torr.) A. Gray], unquillo (*Poa liqularis* Ness ex Streudel), and California cottontop [*Digitaria = Trichacne californica* (Benth.) Henrard]. Co-occuring mid-height grass species were finestem needle grass (*Stipa tenuissima* Trinius), paja blanca (*Stipa gynerioides* Philippi), pasto puna (*Stipa brachychaeta* Godron) and balsamscale [*Elyonurus muticus* (Spreng.) 0. Kuntze]. The shorter species are generally of good forage value and are most common today in the open areas (Orquin et al. 1983) in paddocks correctly managed and not overgrazed. The mid-grasses have little or no forage value and are most common in the shade of the woody vegetation and in paddocks that have been overgrazed. Cool-season grasses are common among both the short- and mid-grasses. Generally, the cool-season species dominate except on areas with sandy soils.

The area was colonized in the last century, and sheep production predominated during the first few decades. Currently, most of the Calden Forest supports cow/calf operations. The mean stocking density for the Departamento Loventue, which is the most representative area of the calden forest, was 0.13 adult bovine ha^{-1} in 1991. This stocking density has been relatively constant over the last decade.

Sources of Information

In the early 1980's we installed a set of 250 permanent transects using the Daubenmire (1959) method. In these, we measured foliar cover, density and frequency of occurrence of all herbaceous species. The 250 transects, installed in 50 paddocks on 10 different ranches, were read every 6 months and are still read at present. The vegetation data are recorded together with information on how each paddock is grazed by the rancher. The transects were installed at the request of ranchers belonging to the Consorcio Regional de Experimentacion Agropecuaria (CREA) Carro Quemado-Luan Toro, a regional consortium for agricultural and livestock research. This CREA, the Estacion de Forrajeras Nativas de Victorica, the Agencia de Extension Rural of Victorica, and other ranchers collaborated in this research.

The initial objective of the transects was to document changes in the degree of utilization of the herbaceous vegetation. Another use of the data is to monitor trends in productivity and species composition of the region. It is somewhat difficult to draw general conclusions on regional trends because the transect network was not initially designed for that purpose. Nevertheless, the volume of information obtained over a rather long period of time gives a good indication of changes in the herbaceous vegetation in relation to management, weather, and other variables.

Complementary data were obtained from similar transects installed in enclosures at the Estacion de Forrajeras Nativas de Victorica and at the Agricultural Technical School in Victorica. We also analyzed vegetation data from enclosures and paddocks grazed continuously but which were subjected thereafter to grazing in different seasons and for varying periods of time, to simulate different grazing management schemes.

There was no year during the study in which rainfall was less than the long-term annual average (Fig. 1). Therefore, references to the relationship of climate to vegetation are for periods of normal or above-normal rainfall.

Limitations of the Successional Model in the Calden Forest

The presumed "climax" herbaceous understory would be dominated by low-growing grass species, and the mid-grasses would appear primarily in small patches beneath trees. However, mid-grass species became dominant as a consequence of overgrazing of the more palatable short-grasses.

Observations indicated that once the mid-grasses were present in a paddock, their frequency and foliar cover continued to increase slowly even after grazing was terminated. This increase in abundance of mid-grasses occurred whether grazing was interrupted by relatively short periods of rest, a single growing period, or for several years. Exclusion of grazing does not cause an expected recovery of the climax, as represented by increased dominance by short-grass species.

Some land owners graze the native vegetation only during the winter season. During the summer, cattle are grazed on weeping lovegrass (*Eragrostis curvula* L.), a perennial warm-season grass introduced from Africa. We might predict a decline in cool-season species because of winter grazing, and an increase in warm-season species. After nearly 10 years of observation, however, we find that the cover of both species remained unchanged.

Changes in the density of woody species that may be caused by grazing were also not compatible with that expected from a successional model. In the climax plant community, the calden forest appears to be an open forest. But even temporary over-grazing diminishes the cover of herbaceous species and permits the establishment of woody species (Pelaez et al. 1992), resulting in domination by shrubs. Subsequent exclusion of grazing did not preclude a continued increase in woody species.

Application of the State and Transition Model

Westoby et al. (1989) proposed that the vegetation dynamics observed on rangelands could be described by a "state and transition" model. The states are relatively stable assemblages of species occupying a site (Laycock 1991), and the transitions occur at changes between one stable state and another. Westoby et al. (1989) proposed the following requirements to implement the state and transition model: 1) description of the possible states, 2) description of the possible transitions, and 3) a description of the proposed management strategies that may produce a positive transition and avoid hazards of management or climatic conditions that cause a negative transition.

Possible states and transitions for the calden forest are described here, as well as possible management strategies for controlling vegetation dynamics. Each state has been given a number and a name based on its dominant species or by the principal characteristics of the dominant species (Table 1).

Table 1. Stable states of the herbaceous layer in the calden forest.

		Associated species	
State	Dominant species	Loamy soils	Sandy soils
1. *Poa*	*Poa ligularis*	*Stipa longiglumis* *Briza subaristata* *Stipa tenuis* *Piptochaetium napostaense*	*Poa lanuginosa* *Thelesperma megapotamicum* *Bothriochloa springfieldii*
2. Flechillal	*Piptochaetium napostaense*	*Stipa tenuis* *Aristida subulata* *Digitaria californica* *Muhlenbergia torreyi*	*Poa lanuginosa* *Bothriochloa springfieldii*
3. Mixed grass	*Piptochaetium napostaense* *Digitaria californica* *Sporobolus cryptandrus*	*Setaria leucopila* *Hordeum* sp.	*Bothriochloa springfieldii* *Setaria leiantha*
4. Mid-grass	*Stipa gynerioides* *Stipa tenuissima*	*Stipa brachichaeta* *Melica macra* *Bromus brevis* *Digitaria californica*	*Elionurus muticus* *Aristida spegazzini* *Bromus brevis*
5. Annuals	*Cenchrus pauciflorus* *Salsola kali*	*Aristida adsencionis* *Solanum eleagnifolium*	*Panicum urvilleanum*

State 1, *Poa*
The state is recognized as the only stable state or "climax" by the successional model. The state is characterised by dominance of the short cool-season grass unquillo. Associated species vary with soil texture. Flechilla grande (*Stipa longiglumis* Philippi), tembladerilla (*Briza subaristata* Lam.), flechilla negra, penacho blanco [*Bothriochloa springfieldii* (Bould.) Parodi], the perennial forb te indio [*Thelesperma megapotamicum* (Spreng.) O. Ktze.] and others occur. Some of these species are difficult to find under grazed conditions, even on rangelands where the stocking rate is low. This state is commonly found in areas distant from water or in paddocks which have a long history of light or no grazing.

State 2, Flechillal
This state is cleary dominated by the cool-season grass flechilla negra. This species provides a forage of acceptable quality for cattle during most of the year (Abiusso 1975), and especially in critical periods such as the end of the winter when the quality of other forage sources is poor (Rucci and Iglesias 1984). Most of the accomplanying species, such as flechilla fina, California cottontop and pasto hilo (*Poa lanuginosa* Poiret) are also of good forage quality. This state is frequently found on rangelands managed correctly with moderate stocking rates.

State 3, Mixed Grasses
Such areas are co-dominated by flechilla negra and warm-season species, most often sand dropseed. Other associated grasses may include cool-season species such as flechilla fina or wild barleys (*Hordeum* sp.), and the warm-season species California cottontop, bristle grasses (*Setaria* sp.), and penacho blanco. There are also a few isolated mid-grasses, sometimes occurring in patches in the shade of trees. This state is often found on correctly managed rangelands with moderate to high stocking rates. Nevertheless, the warm-season species are commonly found on sandier soils.

State 4, Mid-grasses
The mid-grass state is clearly dominated by *Stipa*, either finestem needlegrass or paja blanca or both. These species have very poor forage quality and are normally accompanied by other undesirable mid-grass species like pasto puna, paja dura (*Melica bonaeriensis* Parodi) and balsamscale. Very few species of good forage quality are found in this state, but the most common of these is California cottontop. In years with high precipitation, cebadilla (*Bromus brevis* Ness.) is common. The dominant species of this state were rarely found on well-managed rangelands (Cano 1988). This state is very common in the region, indicating that the general level of management is less than desirable.

State 5, Annuals
State 5 is dominated by aggresive annual species, such as field sandbur (*Cenchrus pauciflorus* Bentham), Russian thistle (*Salsola kali* L.), and cebadilla. It occurs on highly disturbed sites on a variety of soil types.

Catalogue of Possible Transitions

Nine possible transitions between the 5 proposed states are recognized for the calden forest (Fig. 2). The effects of each transition on forage availability are noted in Table 2 along with the management opportunities or errors that can initiate a transition and a general estimate of the rate of change for each. These transitions between states occur mainly as a result of management. In general, increases in stocking rates tend to move the vegetation towards the right in Figure 2. With the prevailing stocking densities, it appears that the most common state is the mid-grass (4), followed by the mixed grass (3) and flechillal (2) states.

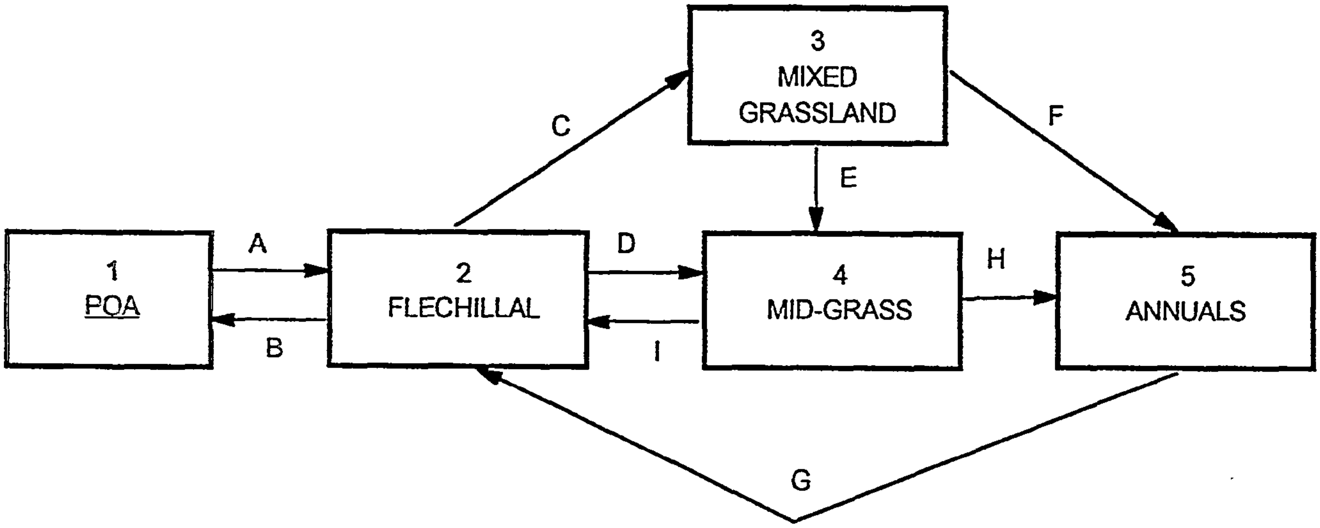

Fig. 2. Possible transitions between stable states in the calden forest.

Transitions A and B

The *Poa* (1) and flechillal states (2) or a mixture of these are common on rangelands with adequate management. Consequently, it appears that this transition seems easily reversible.

Table 2. Effects on forage production, hazards and opportunities, and rate of change of transitions between states in the calden forest.

Transition	Effect on forage production	Hazards or opportunities	Rate of change
A	Slightly unfavorable	Moderate grazing	Proportional to increase in stocking rate
B	Slightly favorable	Light grazing	Proportional to reduction in stocking rate
C	Negligible	Increase stocking rate with rotational grazing	Slow– many years
D	Very unfavorable	Increase stocking rate with continuous grazing	Relatively slow–several years
E	Very unfavorable	Erratic management, excessively long rest	Accumulative with management errors
F	Unfavorable	Destructive grazing	Relatively fast - few years
G	Favorable	Rest	Quick - only 1 year with opportune rains
H	Favorable	Heavy grazing	Quick - less than 1 year
I	Very favorable	Controlled autumn fire and high stocking rate	Quick - 1 year

Transition C

The transition from flechillal (2) to mixed grassland (3) occurs when the stocking rate is increased with rotation grazing. The temporary but frequent reduction of herbaceous cover allows the establishment of warm-season grasses in a predominantly cool-season understory, forming a mixed grassland. This transition takes place slowly, over many years.

Transition D

Observations of changing species composition under varying grazing schemes and stocking rates suggest that the transition from flechillal (2) to mid-grass (4) occurs when the stocking rate is increased under continuous grazing. Initially, the mid-grasses establish under the canopy of the caldens. Analysis of the frequency of mid-grass species suggests that these patches are relatively stable and tend to increase in size over time. This transition is relatively slow, requiring several years. It is difficult to reverse, once initiated, if no management action is taken, as is described later.

Transition E

If the herbaceous layer is in the mixed grassland state (3) and is rested from grazing through the complete growing season, the mid-grasses gradually increase in frequency and foliar cover. When grazing rests occur for excessively long periods, the mid-grasses approach dominance (Fig. 3). The mechanisms that induce this change are not yet understood. Nevertheless, this transition, in which the rest from grazing has a negative effect, has been observed many times in the vegetation transects of the Estacion de Forrajeras de Nativas de Victorica. It has also been observed that the mixed grassland state (3) remains stable if short-term grazing is alternated with short rests of only a few months. Therefore, grazing management seems to be the force that maintains the mixed grass state. Termination of rotation grazing with high stocking rates produces transition E.

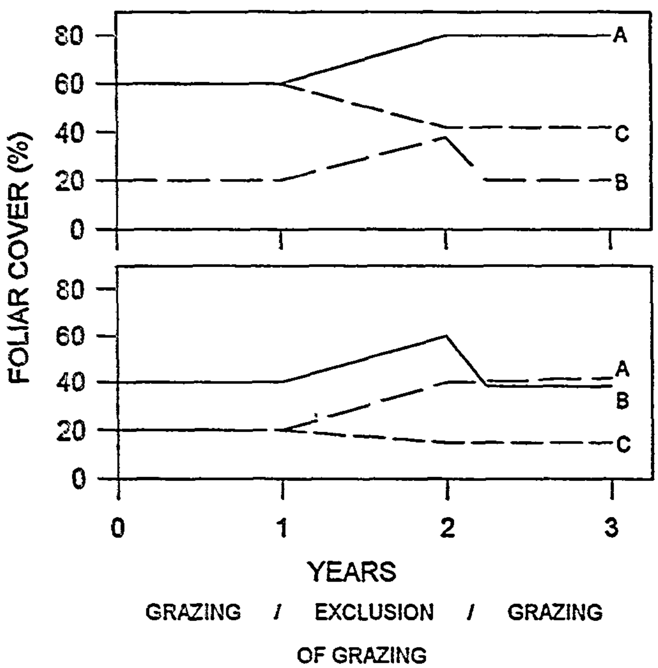

Fig. 3. Conceptual diagrams of the observed foliar cover trends of mid-grasses (line A) and short-grasses (line B) observed before, during and after a year without grazing. Line C indicates the foliar cover of the mid-grass species predicted by the successional model. The upper figure shows the expected and observed trends in paddocks in the mid-grass stable state and the lower figure shows trends in the short-grass state.

Transitions F and G

Excessive stocking rates for extended periods destroy the mixed grass state and result in bare soil soon dominated by annual grasss and weedy perennial forbs. This situation is normally found only in sacrifice areas, but is common enough to be included here. Transition G occurs if such sites are rested for a sufficient number of entire growing seasons, particulary during periods of adequate rainfall, allowing germination and establishment of the characteristic species of the flechillal (2).

Transition H

The data compiled from the transects indicate that a reduction in stocking rate does not initiate significant change in the herbaceous vegetation of the mid-grass state (4), at least over time spans of practical interest. One way to get out of this state is the use of high stocking rates, between 1 and 2 animal units ha^{-1}, for periods of 6 months or more, to force intensive utilization of the mid-grasses. This transition is possible only at the cost of weight loss by the cattle. The desirable state 2 can then be attained through transition G, as described above.

Transition I

As an alternative to destructive grazing followed by rests, fire can be used to cross the threshold from the mid grass state (4) to a flechillal (2). Frank and Llorens (1990) described a paddock in which the cover of mid-grass species was reduced substantially by a controlled fire at the end of the summer followed by grazing at a high stocking rate. Cattle readily grazed the highly palatable and nutritious mid-grass regrowth following fire, suppressing the ability of mid-grasses to compete with the fire–and grazing-tolerant short grasses. This experience has been observed frequently and consistently. Fire together with heavy grazing appears to represent the equivalent of a drastic event that converts the mid-grass community to the flechillal state via transition I over a relatively short period of time.

There is little information on the effect of fire on the woody species of the calden forest. Cano et al. (1985) and Maquieira et al. (1985) indicated that fire does not kill the woody species. Intensive fires remove the woody topgrowth, but regrowth will eventually make the forage less accessible to the grazing animal. Therefore, controlled fires must be conducted so that apical dominance of the woody species is not affected.

Mid-grasses rapidly become dominant in burned paddocks in which they occur if not grazed, perhaps because they have extensive root reserves. Consequently, transition I results only from a combination of fire and intensive grazing. This approach also provides an increase in stocking density of 1 animal unit ha^{-1} for nearly 1 year.

Discussion

Currently, significant portions of the calden forest are dominated by mid-grass species, in state 4. This is partly caused by poor livestock distribution due to a lack of fencing. The large paddocks do not allow the establishment of rotation grazing programs and result in non-uniform use and overstocking in places. This encourages the shift from flechillal to mid-grass through transition D.

It is not often possible to achieve the transition from the mid-grass to the flechillal states by the exclusion of grazing, as might be suggested by the successional model. However, it is possible to shift the vegetation from mixed grassland (state 3) to the mid-grass state (4) by excluding grazing.

Another reason for the dominance of the mid-grasses over large areas of the calden forest is the exclusion of fire in the ecosystem. It is common to have electric thunderstorms during the summer, which sometimes do not produce rain. Before settlement, in the climax state, the herbaceous layer was dominated by low-growing, cool-season species, with dry foliage during the summer. It is highly likely that frequent fires of low intensity helped model the landscape. The exclusion of fire also may encourage an increase in the density of the woody species. The exclusion of fire and the high level of herbivory which prevailed during the last century have permitted the dominance of less palatable mid-grasses. The resulting increase in the amount of fine fuel allowed the devastating wildfires which have become common in the last few years. As the vegetation has been much modified, it is now neccesary to burn under high humidity and other conditions conducive to low fire temperatures.

The current dominance by mid-grasses may also be attributable to the high frequency of years with above-average rainfall in recent decades. Ranchers and rangeland technicians relate that in 1971, the last year of a severe drought, mid-grasses suffered high mortality. Abundance of flechillal species increased in subsequent years, improving the species composition for grazing. Unfortunately, this event was not documented quantitatively.

Other factors may cause the transitions described in this paper. The microclimate may change at ground level with the taller herbaceous understory canopy and the greater woody plant density, influencing temperature, humidity, and light quality. With higher humidity and fertility and reduced light energy under the calden canopy, continuous grazing could trigger some of these transitions, since the short-grass species are more able to compete for the soil resources while the mid-grass species have an advantage over the short-grass species in competition for light (Milchunas et al. 1988). Another reason for these transitions could be a faster recovery of short grasses after grazing, compared to taller species (Coughenour 1985).

Conclusion

The successional model of vegetation change is not appropriate to explain the vegetation changes that occur in the calden forest. Other models may more reliably explain these changes. Observations of vegetation changes over a period of many years, supported by a record of grazing use and other management practices, permitted the development of a basic scheme to explain the trends of the herbaceous understory in the calden forest, based upon the the state and transition model. However, the identification of states and transitions and the conditions which initiate them are somewhat hypothetical, and additional investigations will be necessary to validate these hypotheses.

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