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STABILITY OF ECOLOGICAL SYSTEMS: VARIATION TRENDS AND CONTROL MECHANISMS IN MEDITERRANEAN GRASSLANDS[1]

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ABSTRACT.-Mediterranean grasslands are highly stable because recovery is possible after the destruction of floristic composition by discrete disturbances. Experimental evidence indicates that during the successional convergence process, pasture-herbivore interaction is the essential mechanism of stability control. Without this interaction, and regardless of the occurrence of initial changes in species composition, grasslands present a successional divergence that expresses a trend in the variation of their species composition regulated by interspecific competition.

On a regional scale, and considering the response of ecological systems after a range of disturbances, the trend is towards an increase in relative stability with altitude. This is probably related to the pattern of ecosystem change towards greater ecological persistence.

RESUMEN.- Los pastizales mediterráneos presentan una alta estabilidad porque se recuperan tras perturbaciones discretas que destruyen la estructura de su composición florística. La evidencia experimental indica que durante el proceso de convergencia sucesional la interacción ecológica del pasto con los herbívoros es un mecanismo esencial de control de la estabilidad. En ausencia de esta interacción, e independientemente de la ocurrencia de alteraciones en la composición florística inicial, los pastizales presentan un proceso sucesional divergente, que se expresa en una tendencia de variación de su composición en especies, regulada por la competencia interespecífica.

Desde una perspectiva regional, y considerando la respuesta de los sistemas ecológicos a diferentes tipos de perturbaciones, la estabilidad relativa tiende a aumentar con la altitud. Esto probablemente se relaciona con el patrón de variación de los ecosistemas hacia estilos de adaptación con una mayor persistencia ecológica.

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RÉSUMÉ.- Les parcours méditerranéens présentent une grande stabilité car ils se récupèrent après de légères perturbations qui détruisent la structure de leur composition floristique. L'évidence expérimentale indique que lors du processus de convergence de la succession, l'interaction pâturage-herbivore est un mécanisme essentiel de contrôle de la stabilité. En absence de cette interaction et, indépendamment de l'apparition d'altérations de la composition floristique initiale, les parcours présentent un processus de succesion divergent, qui s'exprime par une tendance dans la variation de la composition de ses espèces, réglée par la concurrence interspécifique.

D'une perspective régionale et étant donné la réponse des systèmes écologiques à différents types de perturbations, la stabilité relative tend à augmenter avec l'altitude. Ceci est sans doute en relation avec le modèle de variation des écosystèmes vers des styles d'adaptation à plus grande persistance écologique.

Key-words: *altitudinal gradient, experimental disturbance, floristic composition variability, recovery, succession.*

Stability is a property which, despite having different meanings and components, is always associated with the response of ecological systems to disturbance (MARGALEF, 1969; HOLLING, 1973; CONNELL & SLATYER, 1977; CONNELL & SOUSA, 1983; WESTMAN, 1986). The species composition of ecosystems is a very complex characteristic that is related to their history, current environmental factors and the influence of disturbances. It expresses the result of species dynamics, particularly dependent on their relationship with certain abiotic variables and the network of interspecific relationships. It is recognized that in a given environment, some species combinations are more probable than others, even though this composition is relatively variable: different alternative combinations can exist within a single environment. Furthermore, the composition of an ecosystem is rarely constant, and is subjected to temporal variations of varying intensity.

Species composition permits the state of an ecological system to be described by a position defined in a multidimensional space. It is interesting to elucidate the reason for the system's occupation of this position, and whether the latter is more or less variable within the hyperspace. The closer the probable states of the system in this n-dimensional space, the more stable the system (Fig. 1).

On the other hand, disturbances can produce notable changes in the structure and function of the ecosystems, and thus considerable changes in their composition. The underlying difficulty is to elucidate the degree of stability of ecological systems and to interpret the possible control mechanisms. In this sense, the observable reactions of ecosystems to disturbance permit their stability to be evaluated and their possible variation trends to be detected.

Grasslands were used in the present study to observe these reactions in their role as examples of ecosystems that permit the evolution of their composition over relatively short periods to be analyzed (VAN ANDEL *et al.*,

RELATIVE STABILITY

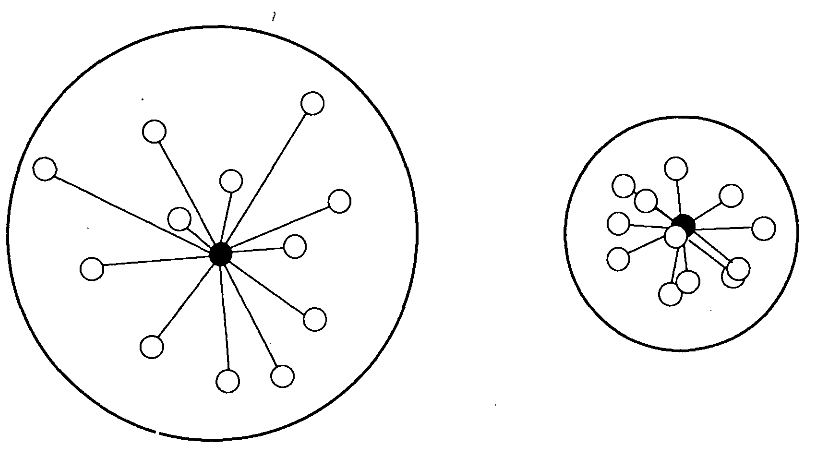

Fig. 1. Example of two ecological systems with differing degrees of relative stability. Each system is represented by a cluster of dots that represent the possible states of the system in a hyperspace which, for the purposes of simplicity, is shown in a two-dimensional projection. Lines indicate the distance from each point to a hypothetical attractor, that may be estimated as a position defined by the mean vector of the systems being considered. The most stable systems are composed of relatively similar states, represented by points near each other in the region of the hyperspace containing them. *(Ejemplo de dos sistemas ecológicos de diferente grado de estabilidad relativa. Cada sistema se halla representado por una constelación de puntos que representan los estados posibles del sistema en un hiperespacio que, por simplicidad, se representa en una proyección bidimensional. Las flechas indican la distancia de cada punto a un hipotético atractor, que puede estimarse como una posición definida por el vector promedio de los sistemas observados. Los sistemas más estables están constituidos por estados relativamente similares, representados por puntos próximos en la región del hiperespacio que los contiene.)*

1987). Previous studies have detected some characteristic behavior patterns in semi-arid Mediterranean grasslands. These express global changes in floristic composition as a consequence of meteorological variability (PECO *et al.*, 1983), and of the inherent recovery patterns after experimental disturbances of different intensity (CASADO *et al.*, 1987). The latter results indicate a capacity for rapid recovery after disturbances that profoundly alter the initial composition, and permit them to be typified qualitatively as systems with a high relative stability.

The present paper aims to assess the stability of floristic composition and to determine its control factors in Mediterranean grasslands under different climatic environments.

1. Material and methods

The study grasslands were located along a mesoclimatic altitudinal gradient of more than 1.000 m. They covered five localities on the southern side of the Guadarrama Range and its foothills (642, 891, 1215, 1449 and 1719 m.). Two contrasting geomorphological positions were differentiated at each altitude: upper zones with some slope, and lower zones that were practically flat. In all cases the orientation was southerly. At the end of 1986, three types of experimental disturbances were performed in each geomorphological sector, with potential effects on the structure and function of these ecosystems. The disturbances consisted of ploughing, fencing off and a combination of both. In each case an undisturbed grassland was used as a control plot. Four plots (5 x 8 m.) were established on each hillside zone. The frequencies of the plant species in them was registered using randomly placed quadrats of 20 x 20 cm. Except for one locality (1.449 m.), data was available on the composition before the disturbance (1986).

The medium term results, four years after the disturbance (1987-90), are presented. Some of the short term effects have been described in MONTALVO *et al.* (1989).

Ploughing caused a direct alteration of the plant community structure and had a specific location in time. On the contrary, fencing was a permanent disturbance to the normal energy flow of the ecosystem. The exclusion of herbivores, mainly farm ungulates, was a factor that could also cause effects on the floristic composition of these ecosystems.

A matrix of 256 species x 192 observations was analyzed. Each observation represented a combination of the sources of variation under consideration: altitudinal, experimental and time. Each element of the matrix represented the frequency of the plant species on each plot. The similarity of the observations was estimated using the Kulczinsky index. The overall variability of the global floristic composition of the grasslands was typified by a non-metric MDS ordination analysis (KRUSKAL, 1964; BELBIN, 1987).

A stability analysis was performed considering each ecosystem composed of a set of different states observed over time. Each state represented a point in a multidimensional space whose position was defined by its species composition.

Its relative stability was estimated as $S = \Sigma(1/d_i)/n$, where d_i was the euclidean distance between each observation i in the multidimensional space and the position defined by the mean vector of the observed states, and n was the number of observed states. In this way, rising values of S indicated higher stability (greater proximity of the points in the hyperspace). The value of n was for 16 observed states of each grassland after the disturbance (4 treatments, including the control, and 4 years for each slope zone).

The variation patterns of global floristic composition after the experimental disturbances were analyzed separately for each slope zone. The affinity between disturbed and control grasslands was estimated by calculating the euclidean distance for each year.

2. Results and discussion

2.1. *Environmental hierarchies in succession*

Figure 2 shows the effects of the sources of variation on the global floristic composition of the grasslands. Each point represents one of the observed states. Both regional and local spatial variability are greater than the one provoked by the experimental disturbances or the dynamics of the undisturbed grassland. The observation groups appearing from left to right in the Figure tend to be arranged along Dimension 1 according to their position on the altitudinal gradient. The mean value of the coordinates of the observations of each locality in this dimension has a significant high correlation with altitude ($r = 0.985$; $p<0.01$). Considering the mean value of the coordinates of the observations corresponding to each slope zone, the relationship with altitude is also significant ($r = 0.889$; $p<0.001$).

Subsets of observations corresponding to the two slope zones of each locality are segregated to differing degrees. The lower zones are consistently located towards the right of the ecological space defined by dimensions 1 and 2. The greater dampness of geomorphological or altitudinal origin seems to determine a tendency for change in the floristic composition in same direction. This result seems to express the qualitative coincidence of the local geomorphological effects with the altitudinal or regional effects on floristic composition. It suggests the predominance of the water balance as an underlying control factor in the variation pattern of the global floristic composition of Mediterranean grasslands.

The importance of the initial environmental framework is quite clear in terms of the floristic composition dynamics in the grassland. In the observation period, the effects of the experimental disturbances and the dynamics of the intact grasslands are not translated into changes that cancel the altitude and geomorphology-related variation. The identity of each ecosystem defined by this external framework thus prevails over the experimentally induced variation. This could be interpreted as the "factor" of initial floristic composition (EGLER, 1954). However, the explanation of the dynamics by means of the identity of its components does not help to fully describe successional change patterns. It apparently reflects the initial terms and the greater regional importance of the abiotic factors on the grassland composition. To a certain extent, the ecosystem is pre-adapted to the changes as it is composed of the elements that probably determine its most successful organizational possibilities.

The variation of grassland composition seems be related to the variation in water availability. On this time scale, there is a persistence of a large proportion of the species already present before disturbance. This seems to indicate its importance in determining the style of adaptation of these ecological systems that is clearly related to the altitudinal gradient (MONTALVO *et al.*, 1991).

The lack of significant deviations from this space-time scale of analysis seems to indicate the low probability of species being replaced by other previously absent types. This is probably regulated by the availability of other life forms in their vicinity and, in particular, by their dispersal and establishment possibilities, as they are potentially capable of interacting with various local factors (ecological and geographical barriers —characteristics of the present grasslands or their interchangeable states—, limitations of the physical environment, etc.). Nevertheless, the adaptive inertia represented by this regularity suggests that the differences of an external origin may persist in the subsequent ecosystems, highlighting to a greater or lesser degree the prevailing role of the physical environment, or at least of its ecologically internalized influence expressed by the species composition of these systems.

2.2. *Relative stability: global comparison*

The multiple states of the grasslands under consideration can be represented in a hyperspace (see Fig. 2 for two-dimensional projection). The close positions of each slope zone at each altitude and their location in certain regions of the ecological space, indicate a certain degree of confinement. This clearly expresses the relative similarity of their global floristic composition on this regional scale, regardless of the type of disturbance or the variation over time. From this perspective, and on this spatial scale of analysis, each of these ecosystems has a certain degree of stability, since the changes in the study period were not sufficient to detect a greater variation in their plant composition that in that of others: their floristic identity is preserved. The identified set of states is a fraction of the possible states for an environmental framework defined by the mesoclimate of the given altitude and the variation associated with the geomorphological position, and permits a comparison of the relative stability of these grasslands.

Figure 3 shows an increasing trend in stability, measured through parameter S, as altitude increases ($r = 0.694$; $p<0.05$). This trend is particularly strong on the lower zones ($r = 0.878$; $p<0.05$) in comparison with the upper zones ($r=0.666$; $p=0.220$). The lower correlation and absence of statistical significance in the latter case appears to be caused by the limited number of available localities, since to a large degree it is the result of the apparent deviation registered in the 1215 m locality.

The meaning of this measure of stability is not only conceptually, but also experimentally dynamic, and is dependent on its formal and circumstantial definition. Obviously the composition did not remain identical in any case, and thus no grassland could be described as absolutely stable. The

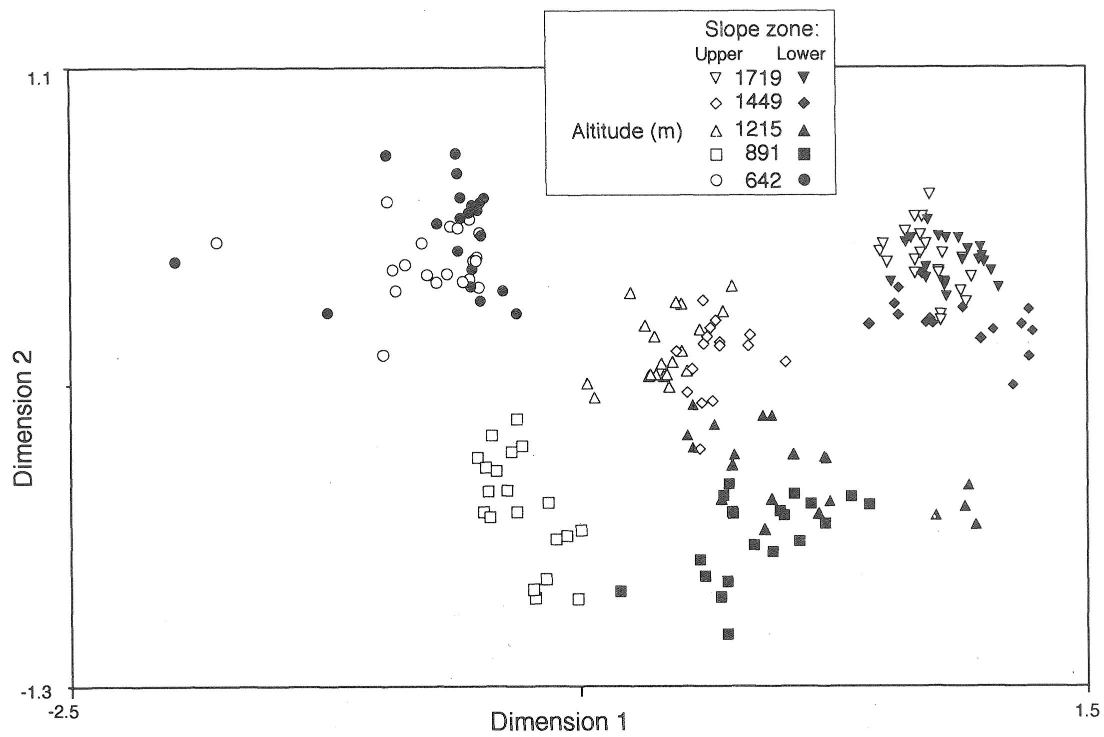

Fig. 2. Variability in the floristic composition of Mediterranean grasslands at different altitudes following the application of various types of experimental disturbance. The results express the projection of a MDS ordination analysis. A single symbol is used to represent observations between 1986-1989, from the same altitude and slope zone regardless of the type of experimental treatment. *(Variabilidad de la composición florística de pastizales mediterráneos de diferente altitud tras la aplicación de distintos tipos de perturbaciones experimentales. Los resultados expresan la proyección de un análisis de ordenación MDS. Mediante un mismo símbolo se han representado las observaciones realizadas durante el periodo 1986-1990, independientemente del tipo de tratamiento experimental.)*

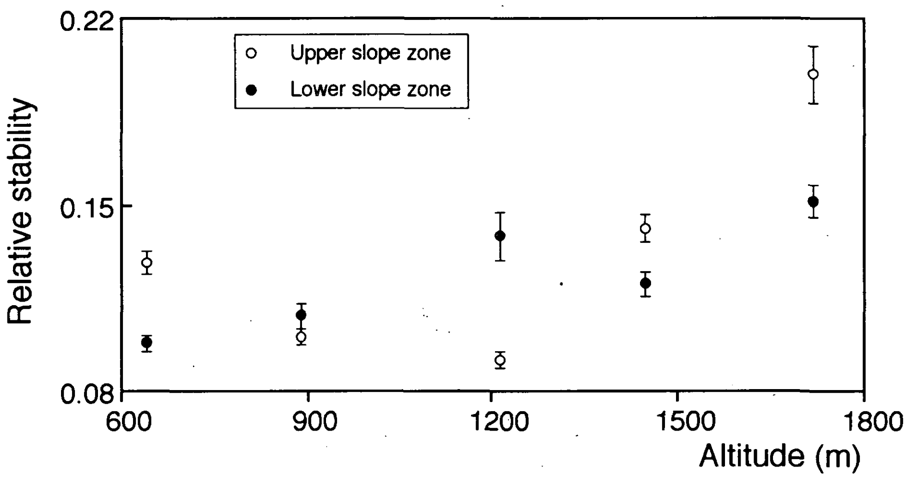

Fig. 3. Altitudinal variation of the stability of the global floristic composition of Mediterranean grasslands. Increasing values of stability represent increased similarity of composition. The set of 16 states of the system (different types of experimental treatment, including the control, in the period 1987-1990) for each slope zone and altitude were considered. See text for details of calculation. *(Variación altitudinal de la estabilidad de la composición florística global de pastizales mediterráneos. Valores crecientes de estabilidad representan una mayor similitud de la composición. Para cada zona de ladera y altitud se ha considerado el conjunto de los 16 estados del sistema observados (diferentes tipos de tratamientos experimentales, incluido el control, durante el periodo 1987-90). Véase detalles del cálculo en el texto.)*

quantification of this property permits the comparison of the relative variation detected in different grasslands, i.e., the experimental determination of the variation magnitude in the context of the disturbances and the limited observation period. Nevertheless, the trend is coherent with the altitudinal gradient of persistence (MONTALVO *et al.,* 1991): grasslands with a more persistent organization, revealed by the morphological-functional traits of their species, would have a greater stability in their composition.

2.3. *Intrinsic variation patterns*

The evolution of the floristic composition following the disturbances in each slope zone was analyzed on a local scale. The effects of the disturbances can induce dynamics that are dependent on the co-variation and the possible interaction with other external factors such as weather. Furthermore, there can be considerable changes derived from the intrinsic dynamics of the ecosystem itself. These phenomena are well known in semi-arid grasslands (eg. PECO *et al.,* 1983, CASADO *et al.,* 1987).

In order to separate or minimize the possible influences of these sources of variation, the changes in global floristic composition were contrasted, assessing the differences between each treatment and the control through the euclidean distance. Figure 4 illustrates a representative example of the sites studied.

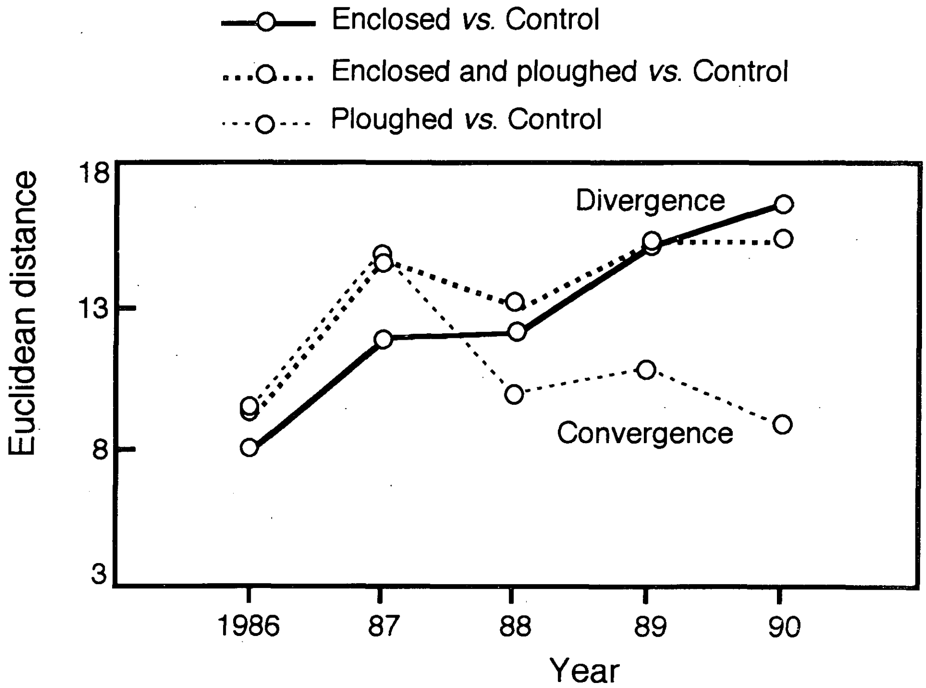

Fig. 4. Example of patterns of variation in floristic composition on a local scale. Affinity in global composition is shown, expressed by the euclidean distance between disturbed and control grasslands both before (1986) and after disturbances (1987-1990). *(Ejemplo de las pautas de variación de la composición florística a escala local. Se representa la afinidad en la composición global, expresada por la distancia euclídea, entre los pastizales perturbados y el control tanto antes (1986) como después de la realización de las perturbaciones (1987-90).)*

There are two intrinsic variation patterns in the composition of each ecosystem: recovery or transformation. The grazed and ploughed grasslands have a convergent or recovery successional change. After an initial state in which there are large differences, their plant species composition gradually appears more like that of undisturbed grassland. Three years after disturbance, the composition differences are lower and seem to remain at comparatively insignificant levels. The grazed grasslands seem to behave like stable ecosystems because, after ploughing and with the participation of the herbivores, they are capable of returning to their initial state prior to disturbance. The recovery rate tends to increase as the position on the altitudinal gradient rises. The greater ecological persistence may be associated with a greater regeneration capacity of its composition after an alteration of the initial composition. These results are consistent with those detected in semi-arid grasslands, where the most mature systems recover more quickly (CASADO *et al.*, 1987).

In contrast, the behavior of the fenced grasslands, whether ploughed or not, is the opposite. The ungrazed grasslands undergo a divergent or transformation successional process. In time there is a transition towards states with increasingly different floristic composition from the initial state. The patterns of transformation differed according to whether or not they were also ploughed. Nevertheless, in the medium term, the successional trend tended to be confused with that of the grassland that was only fenced off, and to indicate a degree of parallelism that seems to reveal the scarce importance of the initial mechanical disturbance in its dynamics. After eliminating the herbivores, the grasslands behave as unstable ecosystems, with a successional trend to differ from their initial state, and change their floristic composition.

2.4. *Stability control mechanisms*

The above-mentioned general patterns of change express organizational trends that require different mechanisms for the regulation of the transitions in the successional path. While the disturbances are the causal agents of the successional process, the mechanisms constitute its form of effective articulation. They are the driving forces that essentially represent means of explaining the observed changes. The detected experimental variability and the differences conditioned the influence of both, the environmental factors and the internal characteristics of the ecosystems, facilitate the interpretation of their combined action.

The mechanisms seem to operate together, and to have multiple interrelationships. Given that the states reached in the medium term after the successional process are different, one may easily suspect that this variability is partly determined by the operation of different mechanisms, or at least by their differing prominence according to the framework in which it develops.

The interaction between herbivores, primarily farm ungulates, and the plants that constitute the pasture, is a mechanism that regulates the structure and function of the grasslands, permitting a relative stability of their floristic composition. As an essential ecological interaction, mainly trophic, it represents a factor that maintains a high turnover rate in the ecosystem. Its role is proven explicitly in the light of the experimental comparisons.

The successional convergence of the ploughed grasslands can only be explained in terms of the plant-herbivore interaction. As the cattle graze, they contribute substantially to define the floristic composition of the system and its biomass. Herbivory is responsible for the maintenance of a relatively high turnover rate, in both the ploughed and the undisturbed grasslands. The majority of the aboveground plant biomass produced annually is consumed by herbivores, and an insignificant fraction of unconsumed grass is accumulated in winter in the form of litter, probably without either previously or subsequently affecting the composition or the normal function of the ecosystem (MONTALVO, 1991). The colonization and establishment of the plant species cannot be considered as independent processes, but rather as results of the interaction with the herbivores.

In summary, there are only two possible consequences of the suppression of a stability mechanism: its replacement by another functionally equivalent mechanism, or the intervention of other internal factors with a different purpose. If these direct a pattern of change in grasslands in various environments towards a system of different but analogous organization, one would be in possession of means to assess the mechanisms that possibly underlie such regularity.

In the ungrazed grasslands, interspecific competition between primary producers causes readjustments in their composition and relative abundance. Without predation, the plants with a superior competitive capacity grow more and usurp resources, especially radiation, in their own benefit. Several species become extinct locally or become rarer. A situation in which grazing herbivores permit a similar resource availability for most of the species and probably a very low competition, is transformed into another state of monopoly or oligopoly by a smaller proportion of species. The system undergoes a process of adaptation to the new conditions of energy flow. Produced biomass is accumulated dry after the beginning of the summer drought and the turnover rate is unquestionably lower than in grazed grasslands, since the matter persists for a longer time in the ecosystem, particularly in the form of litter (MONTALVO, 1991).

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