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in

Lindberg J.E. (ed.), Gonda H.L. (ed.), Ledin I. (ed.).
Recent advances in small ruminant nutrition

Zaragoza : CIHEAM
Options Méditerranéennes : Série A. Séminaires Méditerranéens; n. 34

1997
pages 11-25

Some aspects of the use of vegetation by grazing sheep and goats

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SUMMARY - Understanding the grazing animal/vegetation interactions is necessary as a basis for developing new effective grazing schemes, to improve the use of grazing lands for multipurpose uses. Due to the complexity of the grazing ecosystem a holistic research development approach to optimize outputs and reduce unwanted side´ effects is required. A systems approach is suggested as the best strategy. Multifloristic vegetation composition of grasslands, particularly rangelands, coupled with variation in animal species selection necessitates the application of mixed grazing. It is intended to examine some of the main biological issues involved in the sheep/goat/vegetation grazing relationships which govern the patterns of diet acquisition and its nutritive value. Emphasis is placed on selection patterns as influenced by the presence of preferred vegetation fractions, learning patterns, anti-intake/toxic factors and presence of other animals of the same or other spp. under temperate and semi-arid conditions. Parameters such as quantity of vegetation available, ease of access and distribution in the context of use of space, including water, are evaluated. A basic requirement is that grazing animals be used to maintain a sub-climax vegetation to sustain productive and protective use of grazing land resources.

Key words: Diet selection, competition, grazing, sheep, goats, review.

RESUME - *"Quelques aspects de l'utilisation de la végétation par des ovins et caprins en pâturage". Il est nécessaire de comprendre les interactions de l'animal en pâturage avec la végétation comme base pour développer de nouvelles démarches efficaces de pâturage, afin d'améliorer l'exploitation des prairies pour des utilisations polyvalentes. En raison de la complexité de l'écosystème du pâturage, une approche holistique de développement de la recherche est nécessaire pour optimiser le rendement et réduire les effets secondaires indésirables. Une approche de systèmes est suggérée comme la meilleure stratégie. La composition multifloristique de la végétation des prairies, en particulier des parcours, associée à la variation de la sélection des espèces animales, requiert l'application d'une activité mixte de pâturage. Le propos de cet article est d'examiner certaines des principales questions biologiques qui entrent en jeu dans les relations, sur pâturage, des ovins/caprins/végétation, qui déterminent le mode de mise en place du régime et sa valeur nutritive. L'accent est mis sur les tendances de la sélection car influencées par la présence de fractions préférées de végétation, des modes d'apprentissage, des facteurs toxiques et de non-ingestion, et par la présence d'autres animaux de la même espèce ou d'autres espèces sous des conditions tempérées et semi-arides. Des paramètres sont évalués tels que la quantité de végétation disponible, la facilité d'accès et la distribution dans le contexte de l'utilisation de l'espace, y compris l'eau. Une exigence fondamentale est que les animaux en pâturage soient habitués à maintenir une végétation sous-optimale afin de permettre une utilisation productive et protectrice des ressources en prairies.*

Mots-clés : *Sélection du régime, compétition, pâturage, ovins, caprins, révision.*

Introduction

Rangelands occupy 44% of the earth's land surface. In arid and semi-arid areas expansion of cultivated areas has increasingly restricted rangelands to the less productive locations such as high mountains and sparse vegetation consisting mainly of ligneous plants containing relatively high proportions of antinutritive phenolic compounds. Pressure on natural grazing land resources to satisfy needs of rapidly growing human population increases the risk of range degradation (Nolan and Connolly, 1992; Narjisse, 1995). In temperate areas emphasis has shifted from defining the upper limits for animal production to identification of improved methods of natural resource use in a more ecologically balanced and sustainable manner. This has resulted from concerns regarding ground water pollution, build up of heavy metals in the soil and aspects of animal welfare. Walker (1995) addressed the issues concerning the future maintenance of the biological integrity of grazing lands and Brown and Howard (1995) suggested improved management methods at regional and landscape levels. Product quality, uniformity and continuity and environmental protection aspects will increasingly dominate strategies for grazing land use (Nolan, 1996). Here it is intended to examine some of the main biological issues involved in the sheep/goat/vegetation relationships under grazing and how these are affected by preferential and differential selection patterns, availability and distribution of preferred vegetation fractions, antinutritive factors, presence of other animals of the same or different species and water supply.

The grazing ecosystem

The grazing ecosystem is complex with interacting biotic, edaphic, and climatic factors confounded with human intervention which in turn reflects varied social and economic influences (Cousins, 1995; Daniels, 1995). The nutritional requirements of grazing animals, in both temperate and semi-arid areas, is dominated by the vegetation menu offered, the levels and balance of nutrients contained in it, its physiological state, presence of anti intake factors, geographic distribution etc. Animal factors as preferential and differential selection, competition with other animals, level and rate of intake etc. determine how animals utilize the available vegetation resources.

A combination of woody and herbaceous spp. generally results in higher and more nutritious biomass production with improved seasonal distribution and higher animal output. Herbage usually has a higher nutritive value than browse in spring (Papachristou and Nastis, 1993) while browse is better in summer and provides green material in winter. In many rangelands senescence commences in the herbaceous vegetation early in the grazing season and its palatability and nutritive value diminish so rapidly that within a few weeks it is incapable of supporting animal maintenance requirements (Nastis, 1982). In contrast shrubby spp. contain sufficient protein and Phosphorus for maintenance throughout most of the grazing season (Cook, 1972) and their introduction even into *Agropyron desertorum* pasture improves overall forage quality (Otsyina *et al.*, 1980). Their presence also modifies the micro-climate which increases vegetation production and quality (Forti, 1971). Yiakoulaki and Nastis (1995) suggest that for optimum benefit the correct proportions of shrubby and herbaceous vegetation must be established for each area. Other equally subtle influences such as effects of companion grazers of the same or different sp. (Furstenburg *et al.*, 1995; Hardy, 1995; Nolan, 1996), patterns of vegetation availability and its geographic distribution (Connolly *et al.,* 1995; Laca and Ortega, 1995), proportion and distribution of preferred vegetation fractions (Hughes, 1993; Provenza, 1995), availability of water etc. are also important. Antinutritive factors and toxic, though sometimes palatable, components (Robbins *et al.*, 1987; Nastis and Malechek, 1988; Provenza, 1995) modify diet acquisition and nutritive value.

Under or over utilization of vegetation interferes with other products and values such as water production and conservation, wildlife, soil, recreation and landscape quality which may be socially and economically more important (Nastis, 1993). He referred to under-utilization leading to biomass accumulation in some Mediterranean countries due to reduced grazing and occurrence of fire which in turn causes ecosystem collapse. The greatest threat to maintaining vegetation communities is that immediate economic and social considerations may preclude the application of improved grazing management even where its benefits are well known (Nolan and Connolly, 1992; 1995). Only a global research approach and multipurpose use can ensure sustainability and environmental protection of range landscape.

Animal physiological characteristics (Faverdin *et al.*, 1995) seriously affect feed intake and diet selection. Grazing behaviour, coupled with animal learning processes, (Provenza and Balph, 1987; Thorhalldottir *et al.,* 1987) and plant defence mechanisms (Provenza and Malechek, 1986) modify grazing animal/vegetation relationships. Understanding of the animal state/vegetation state relationships which allow animals to capture adequate dietary nutrients is basic to selection of the correct grazing management. Research on this aspect has not progressed as rapidly as expected. Generally it remains descriptive, referring usually to a specific site and a particular plant/animal situation with experiments devoted to empirical observation, attempting to measure economically important factors. Although grazing behaviour research has long been a part of grazing studies generally it remains descriptive and does not monitor most of the complex environmental plant and internal animal-related factors. Thus little progress has been made in establishing cause and effect relationships. This paper is intended to stimulate thinking in a non-traditional manner which may prompt in-depth research into learning and dietary selection patterns.

Mixed animal species grazing research

The number and species/type of animals used also influences vegetation and animal production. Nolan (1996) referred to the inappropriateness of a commodity structured research approach as a basis for developing improved systems. This may have precluded the uptake of the European model in Africa (Nolan and Connolly, 1992). Variation in forage selection between ungulate spp. often necessitates the application of mixed animal spp. grazing in order to obtain higher animal output while maintaining ecological stability. Inter animal type complementary and competitive patterns cannot be assessed under mono grazing. The use of mono sp. grazing has limited the knowledge base and possibly precluded the adoption of much information due to difficulties for potential adopters to identify with paradigms which do not reflect their situation (Nolan and Connolly, 1995; Nolan, 1996). The successful extension of mixed cattle (C) and sheep (S) grazing systems in Ireland (Nolan and Connolly, 1989c) confirms this assertion. Nolan and Connolly (1989b) viewed the increased number of variables involved in mixed animal type grazing as increasing the options for developing improved grazing ecosystems. Animal/vegetation relationships under mixed animal spp. grazing are more important in more heterogeneous situations due to the possibility of complementary effects increasing with degree of heterogeneity (Nolan and Connolly, 1989a; Wright *et al.*, 1994).

In Ireland, mixed grazing benefits of 7% higher beef cattle and lamb growth rates at constant stocking rate or 10% increased stocking rate at constant animal growth rate were obtained. These benefits, which are greater at higher stocking rates, were attributed to complementary use of vegetation and in particular to sheep preferentially grazing cattle dung soiled herbage which cattle mostly refused. Vegetation growth rate in the cattle dung soiled areas was twice that of unsoiled areas and contained 12% and 14-16% higher DM contents of Nitrogen and Phosphorus and Potassium and about four percentage points higher *in vitro* DM digestibility. Necrotic total roundworm counts on lambs reared worm free, grazed for three weeks with mixed (C and S) and mono grazed S, showed that mixed grazing also reduced gastrointestinal roundworm burdens in lambs. Different aspects of the extension of this research to more heterogeneous semi-arid situations are discussed below.

Generally, results suggest that complementary grazing patterns could be expected to have the following benefits:

(i) Higher intake of preferred vegetation fractions leading to higher growth rate without competing with co-grazing partners.

(ii) Greater capture of vegetation resources leading to higher output per unit area of grazing land and return on investment.

(iii) More balanced use of vegetation due to each animal type using different vegetation spp. or fractions. This could be of major consequence in more heterogeneous rangeland situations in the context of combining range preservation with higher animal output.

(vi) Management flexibility due to ability to vary different animal type production timing patterns, etc., spread of income and labour requirement and economic security of two or more output categories.

Diet selection

Grazing animal diet selection is influenced by many factors (Hughes, 1993; Forbes, 1995). Nolan and Connolly (1992) have defined preferential selection as the selection by an animal type of one plant sp. rather than another and differential selection as the comparison between the preferential selection for a plant sp. by two or more animal types. Vegetation (Hodgson, 1982) and animal based (Gordon and Illius, 1992) factors modify these components. Forbes (1995) illustrated the theory and experimental designs of Emmans (1991) on diet selection by animals, where two or more food types are available, which generally indicated that they would select a diet close to their nutritional requirements. Hughes (1993) extended this optimal foraging theory to human activities, exemplified by the behaviour of hunters in capturing food. Learning processes (Provenza and Cincotta, 1993) and post-ingestive feed back mechanisms (Provenza, 1995) modify diet selection and these characteristics can be passed on from adult to young (Provenza, 1995). This latter information is vitally important where animals are exposed to toxic, but palatable, vegetation. In addition plant defence mechanisms have evolved in direct proportion to the risk from herbivores and in inverse proportion to the cost of defence. Defences are distributed among various tissues and organs in relation to the value of these parts. When the risk is high, defence mechanisms are increased and they are decreased when enemies are absent. For example, low kermes oak shrubs have more spiny leaves than the higher trees and Provenza and Malechek (1986) reported higher tannin content in the lower branches of black brush.

Animals are challenged to select their diet from a variety of locations, vegetation types etc. listed above. The theory of optimal foraging, that animals will select their optimum diet for the minimum expenditure of energy, does not hold universally. Other aspects as availability of water, altitude, etc. may modify the pattern of diet selection. The use of n-Alkanes, reviewed in Mayes *et al.* (1995), has facilitated definition of the origin of diets and their quantitative and qualitative characteristics for grazing animals mostly under temperate conditions. The development of methodology to measure diet selection for mixed animal spp. grazing semi-arid range by Nolan *et al.* (1995) and Connolly *et al.* (1995) which avoids handling of animals is discussed below.

Diet selection under mixed animal spp. grazing

Where forage is sparse and varied as in semi-arid areas small ruminants are expected to perform better than cattle. Evolutionary bulk eaters such as C tend to be fixed in their foraging strategy while the more versatile feeding behaviour of small ruminants allows more scope for selection of preferred fractions. Small ruminants showed greater ability to extend the range of plants consumed in dry season when overall vegetation availability was sparse (Nolan and Connolly, 1992). Under semi-arid heterogeneous vegetation conditions (Nolan and Connolly, 1992) grasses and *Convolvulaceae* dominated C and S diets and *Convolvulaceae* and woody spp. dominated G diet (Table 1). Woody spp. contributed less than 1% to C diet, slightly more to S diet and 43% to G diet. Under mixed grazing, where all animals were presented with the same vegetation menu, grasses contributed up to 80% of C diet and usually less than 10% of S and G diets and woody spp. generally contributed over 50% of G diet but negligibly to C and S diets. *Convovulaceae* dominated (over 60%) diets of all animal spp. in December 1990 and declined almost linearly to 10% by May 1991, but in the following year increased from a low level to between 20-40% for the remainder of the season.

Table 1. Percentage contributions of different vegetation types to the aggregated diets of cattle, sheep and goats over all periods for 1990-91 and 1991-92 combined

	Gramineae	Leguminosae	Convolvulaceae	Other forbes	Woody spp.	Other
Cattle	60	2	24	10	1	3
Sheep	28	5	37	16	3	1
Goats	10	2	33	11	43	1

Averaging over broad vegetation classification categories proved unsatisfactory as individual plant sp. also differed widely in selection preference by the different animal spp. (Table 2), woody spp. were not included for C and S diets due to their very low presence (Table 1). Overlap and disagreement between vegetation survey and dietary study spp. lists were of trivial importance and the 18 out of 40 spp. in vegetation surveys but not in diets accounted for only 3.1% of vegetation survey hits. The small number of spp. in the diets also dominated the vegetation but the order of presence differed. Overall 10 plant spp. formed 95% of diets, 7 herbaceous spp. formed 81% of diets and 3 woody spp. formed 88% of all woody spp. in diets. The seasonal changes recorded for the broader classification categories also occurred for the individual plant sp. A problem exists with the estimates where very low percentages exist in vegetation but are relatively high in diet as with *Ipomea pestigridis* in goat diets (Table 2). For woody spp. the latter was especially true with *Boscia senegalensis* mostly rejected by all animals (Table 2). It is suggested that improved methods for vegetation surveying are required and the recent 'scale-related' method in Westfall *et al.* (1996) may suffice.

In the Mediterranean zone, many herbaceous and ligneous spp. have high phenolic contents. Species such as *Cistus incanus* with low nutritive value and relatively high phenolic content were grazed in all seasons except summer but *Vicia tenuifolia* and *Vicia cracca* were avoided although they had a high DM crude protein content of 17% in spring and contributed significantly to herbage mass (Papachristou and Nastis, 1993). These spp. were consumed after senescence when the phenolic content reduced. Coexisting kermes oak was not avoided and classified as indifferent despite its high tannin content.

Table 2. Preferences (% in diet/% in vegetation) by cattle, sheep and goats for certain plant species

	% in diet			% in vegetation
	Cattle	Sheep	Goats	
Herbaceous				
Ipomea vagans	3.2	4.6	6.1	8.2
Schoenfeldia gracilis	0.9	0.5	0.1	60.5
Corchorus tridens	1.5	2.6	4.7	4.7
Ipomea pestigridis	27.5	61.0	101.8	0.1
Brachiaria zantoleuca	7.7	0.8	0.0	0.1
Woody				
Cumbretum aculeatum			1.7	13.8
Balanites aegyptiaca			0.6	10.6
Grewia bicolor			4.1	2.3
Acacia senegal			2.8	9.3
Boscia senegalensis			0.0	31.3

Overall these results suggest that relying on biomass availability as a measure of the value of pasture may be very imprecise as the plant spp. must be those which animals will accept. The relative level of each forage class in the diet throughout the year varies according to the availability and palatability of the coexisting spp. This is exemplified (Table 3) in Papachristou and Nastis (1993) where grass content of G diet was 41% in April, when grass was plentiful and luscious, while the highest proportion of forbes was 23% in May. G diets contained increased browse when shrub cover was increasing, and the grass and forbes contents showed the opposite trend. In Malechek and Provenza (1983) G selected on average 60% browse, 30% grasses and only 10% forbes. The differences between studies were due to differences in pasture composition. On the basis of dietary composition G have been classified both as browsers (Nastis, 1996) and as grazers (Somlo *et al.*, 1981). These differences may be associated with the overall classification that G tend to be opportunistic feeders depending on the vegetation menu on offer and they and S varied their diet to use an increasing range of vegetation types relative to C under conditions of sparse vegetation supply as dry season advances in semi-arid conditions (Nolan and Connolly, 1992).

Evergreen browse spp. studied by Papachristou and Nastis (1993) were indifferently consumed almost all year round, even when forage quality was high. In spring broad-leafed spp. were greatly preferred. They also found that leaves were preferred from all forage classes (56% to 80%) and stems were a minor diet component. A high preference for fruits occurred only during specific periods. They may, however, be crucial to animal nutrition at times of nutritional stress such as in late autumn (Malechek and Provenza, 1983). Most probably the post-ingestive effect, expressed as palatability, is the dominant driving force for selection of a particular vegetation fraction (Nastis, 1996) but it is not clear why some spp. are consumed even though they contain high proportions of antinutritive factors.

Table 3. Goat diet in pastures with different browse cover

Forage class	Brush cover		
	Low	Medium	High
Browse	53.0[c†]	62.0[b]	65.6[a]
Grass	22.0[a]	15.2[b]	13.1[b]
Forbes	20.3[a]	17.6[b]	16.5[b]

†The remainder up to 100% were unidentified spp.
a,b,c: Means in the same row followed by the same letter are not significantly different

Effect of stocking rate on diet selection

Increased stocking rate results in increased grazing periods and decreased walking (Mill *et al.,* 1985), but does not seem to affect the proportion of the various forage classes in the animal diet. In Malechek and Leinweber (1972) there were no differences between the diets of G on lightly (0.4 goats/ha) and heavily (11 goats/ha) stocked pasture, except in March, when larger quantities of woody spp. were consumed by the heavily stocked G. Papachristou and Nastis (1993) reported similar results in the Mediterranean zone in a comparison of 1 (medium stocking rate - MSR), 2 (high stocking rate - HSR) and 4 (very high stocking rate - VHSR) goats/ha/year. The levels of crude protein and *in vitro* DM digestibility were more or less proportional to the level of forbes and grasses in the diet. The proportion of herbaceous spp. in the diet was not significant for a given season, except spring, but browse remained the main dietary source throughout the year. Average brush content of diets increased from 53% to 60% as pasture brush cover increased from 52% to 66%.

Mixed grazing offers opportunity to limit the stocking rate of any one animal type to the level which will make optimum use of its preferred vegetation fractions and to make up the remainder required to achieve overall efficient use of vegetation with animal type(s) with preferences for the remaining vegetation fractions (Nolan, 1996).

Animal learning influences in diet selection

Preference for certain plant spp. depends on inherited gustatory and olfactory tastes but preferences can be greatly modified by animal learning. This wisdom is inherited and can be greatly improved through learning (Provenza and Balph, 1987) with some information being transferred from mother to offspring through milk (Thorhalldottir *et al.,* 1987). During the weaning stage the individual moves to independent feeding and an array of nutritional, morphological and physiological changes take place which indicate that for domestic ruminants most dietary selection habits develop (Martin, 1984). Learning through imitation is very effective during the weaning stage and through trial and error thereafter, by continual sampling and evaluating the usefulness of which food sources are most nutritionally important (Provenza and Balph, 1987). In du Toit *et al.* (1991) S sampled small amounts of a novel food and if it proved useful they gradually increased consumption, otherwise they avoid it. Also naive animals consume less black bush (*Coleogyne reamosissima*) than animals that are accustomed to it (Narjisse, 1981; Distel, 1990). These differences can be considered as part of learning. Inherited or acquired dietary habits make animals prefer familiar foods and reluctant to consume large quantities of a novel food even if it is proven to be beneficial to them. Goats learned to avoid *Pinus* leaves dosed with relatively high LiCl levels (Table 4) and continued to do so 50 days later.

Cues can be reinstated for any food if the quality changes over time since animals practice continual sampling. In Papachristou and Nastis (1993) *Vicia* spp. were avoided in spring but later on after maturation they were readily consumed. Zahorik and Houpt (1981) found that rumination of the food ingested can reinstate food cues and Meuret (1994) has shown that animals re-establish their memory every morning which explains their practice of a high degree of sampling at that time. Too much plant diversity tends to inhibit intake, probably due to time allocation to continuous sampling and assessment of the menu but later in the day animals concentrate on specific plant spp. to optimize intake and reduce the sampling activity.

Table 4. *Pinus brutia* consumption by goats dosed with various LiCl quantities

Days after dosing	LiCl dose - mg/kg liveweight			
	0	40	150	200
2	66.0	34.6	22.4	13.4
7	70.3	44.8	22.3	17.3
21	90.4	20.9	9.9	1.6
50	79.8	32.0	14.0	5.1

Antinutritive and toxic compounds

Secondary chemical compounds, such as tannins, significantly affect palatability and diet selection. Palatability depends on the animal's perceived post ingestive usefulness of a feed (Provenza, 1995) which polyphenols generally reduce. Tannins reduce the apparent digestibility of protein (Robbins *et al.*, 1987) by increasing Nitrogen excretion in faeces (Kumar and Vaithiyanathan, 1990). The low digestibility of protein has both direct and indirect effects on overall intake and digestibility. The nutritive value of browse is reduced more by high tannin than by fibre content (Makkar *et al.*, 1993). A diet containing 80% oak browse with an ADF fibre content of 31.7% and a tannin content of 6.9% was 17.4% less digestible than an alfalfa diet containing 39.6% ADF fibre and 1% tannin (Nastis and Malechek, 1988). Also Tagari *et al.* (1965) found that a *Lespedeza cuneata* (*Serica lespedeza*) diet with a similar fibre content to that of an alfalfa diet but with three times more tannin was 14.2% less digestible. The lower digestibility was attributed to the formation of protein complexes (Robbins *et al.*, 1987) which reduce microbial action for fibre digestion in the rumen. This lower digestibility is partly a result of its inhibitory effect on microbial activity and also of reduced enzyme activity (Nastis and Malechek, 1988). The latter authors found that tannin depresses pepsin activity (Table 5).

Table 5. Pepsin activity as influenced by tannin content of diets

Diet		Tannin content	Quantity of substrate liberated (μmol/min)
Alfalfa	Oak		
100	0	1.0	13.0 ± 0.2^{a}
80	20	2.4	12.9 ± 1.0^{ab}
60	40	3.2	10.4 ± 1.5^{bc}
40	60	4.8	7.9 ± 0.9^{cd}
20	80	6.9	5.6 ± 1.8^{d}

a,b,c,d: Means in the same row followed by the same letter are not significantly different

Nastis and Malechek (1988) found no difference in enzyme reduction between spring and summer oak samples although the spring samples had higher (8.9%) total tannin content than the summer (6.9%) samples. This may indicate that mature oak tannins are more effective in reducing enzyme activity than those of immature oak. Intake however was significantly lower in spring samples (36 ± 3 g/kg $Bw^{0.75}$) than in summer samples (42 ± 4 g/kg $Bw^{0.75}$). This indicates not only that microbial and *enzyme inhibition determine the nutritive value of a feed, but also that its gustatory effects are* unpleasant for the animal. Generally G offered diets with a high tannin content showed a reduced intake (Nastis and Malechek, 1988). It is important to establish a reliable assay to assess phenolic-related antinutritive compounds as a basis for improved efficiency systems which will utilize tannin rich locally produced forages.

Pasture value index (PVI)

The strong preferential and differential selections recorded in the literature quoted above suggest that pastures are varied in relation to the different grazing animal's perception of them and can be more or less suited to particular animal types depending on the vegetation spp. present. In Nolan and Connolly (1992) a novel pasture value index (PVI) was constructed from the individual plant spp. values. In their experimental design, described above, each dietary sampling gave four diet profiles for each animal type. Subsequent calculations were confined to the most frequent 10 species in the diet for a given sampling. Within each animal type an index of agreement was calculated between each of these four profiles giving 6 values which were then averaged to give within animal sp. consistency over the four profiles viz. the I_i for the ith animal type. Then each of the four profiles was compared with each of the four profiles for the second animal type giving 16 values which were then averaged to give between animal consistency over the four profiles viz. for the I_{ik} for the ith and kth animal types, $A_{ik} = I_{ik} / I_i \, I_k$. This was repeated for each of the three mixed treatments and for each sampling. Averaging for each animal type over the four days for each period to assess consistency may be improved by sampling the dietary composition of 4 individuals within a sp. category and allow improved estimation of within and between animal type complementary or competitive grazing and dietary selection patterns including use of space. This is discussed below in the context of measuring competition between different animal types.

In both grazing seasons there was greater repeatability within C than S or G and G were usually the lowest of the three (Table 6). The index tended to decline over time in the first grazing season and to rise during the second season for all animal types. The between animal type values were generally much lower than the within animal type values for the types compared. The PVI was always higher where a mixture of animals were grazing reflecting complementary use and a higher overall capture of vegetation resource (Nolan and Connolly, 1989b). In their temperate zone experiments, with S and C, this was reflected in about 13% less area to maintain the same number of animals at the same liveweight gain under mixed grazing. Complementary may be expected to be greater under more heterogeneous conditions, as found in range grazing (Nolan and Connolly, 1989a) where PVI values would be improved as vegetation heterogeneity increases. The methodology used appears to be adequate, relatively simple and of low cost.

A combination of animals may therefore change (generally positively) the PVI and this cannot be ignored in devising strategies for range use and interpretation of its productive and protective use options. This was apparent where animal performance was found to improve as PVI increased in Nolan and Connolly (1992), the relationship being better for S and G than for C. The PVI varied widely over pastures for all animal spp. and variation (maximum/minimum) was much greater for S (41.6) than for G (11.5) and C (2.3) as in Table 6 (Connolly *et al.*, 1995). They developed a PVI which would take into account that vegetation is frequently a mosaic of different patches each of which has its own value for each animal species and also that the value of the rangeland may depend upon the location of these patches in relation to other elements of the landscape as watering points or location of shelter. This tool evaluate proposed grazing or other interventions as water points etc. PVI values varied widely over plots in both years and differed markedly between animal species. Correlation between animal species PVI values indicated that C and G were less well related than either with S, suggesting that the value of pasture for S was intermediate. This reflects the dietary vegetation counts mentioned above where C and G were different with sheep intermediate. They also noted some agreement between years, greatest for G, perhaps due to the fact that the woody species component, which contributed most to goat diet, was constant over years.

Table 6. Pasture value index (PVI) for cattle (C), sheep (S) and goats (G) for nine plots and two years 1990-91 and 1991-92

Plot	1990-91			1991-92		
	C	S	G	C	S	G
1	1.06	1.15	0.64	1.09	0.58	0.38
2	1.50	2.28	1.21	1.52	2.41	0.85
3	0.95	0.52	0.38	0.98	0.59	0.70
4	0.59	0.31	1.66	0.97	1.42	1.42
5	0.82	0.59	1.23	0.93	1.34	1.53
6	0.89	0.46	0.54	0.94	0.64	0.91
7	1.07	1.70	1.93	0.86	0.87	1.27
8	1.02	0.61	0.25	1.17	0.63	0.24
9	1.11	1.38	1.16	0.56	0.52	1.71
Correlations between animal species						
	C – S	C – G	S – G	C – S	C – G	S – G
	0.88	-0.07	0.39	0.66	-0.61	0.18
Correlation over years						
	C	S	G			
	0.48	0.47	0.73			

Results indicate that small ruminants perceived a much greater variation in vegetation quality across pastures suggesting that they may be more sensitive to pasture quality than C and use this characteristic to procure a relatively higher quality diet. Anatomical differences may also have important effects on these relationships with S and G having greater ability to graze into smaller patches (Wright *et al.*, 1994). It was concluded that a pasture rated poor for one animal sp. may be rated good for a different sp. The results offer convincing evidence that from a commercial viewpoint certain fractions of the vegetation are good for certain animal types and that improved use may only be achieved through the use of mixed animal type grazing. Farmers/herders have apparently recognized this for a long time and the research challenge is to develop improved mixed grazing ecosystems.

Grazing management to improve content and forage quality of woody spp.

In Nolan (1996) partial protection of young shoots of *Acacia senegal* (A. se.), *Balanites aegyptiaca* (B. ae.), *Calotropis procera* (C. pr.), *Cumbretum aculeatum* (C. ac.) and *Acacia raddiana* (A. ra.) during establishment from C, S and G grazing for 0, 6, 12 and 18 months following planting showed that species differed in their survival rates with C. pr. lowest at 27% and A. ra. highest at 58% (Table 7). There was no significant difference between C (30%), S (41%) and G (50%) in unprotected survival. Partial protection from G grazing increased survival rate but protection from C or S had no effect. The trunk diameters of B. ae., C. ac., C. pr. and A. ra. were increased by protection being 24, 42, 19 and 33% respectively greater at 18 months for each extra 6 months protection (Table 7).

In the temperate zone most woody spp. grow rapidly in spring, when they can support animal production, but during summer, lack of new growth leads to poor quality (Nastis, 1982). In autumn re-growth depends on rainfall. This pattern of quality fluctuation can be modified, as for example, grazing of kermes oak shrublands in summer, after growth has stopped, triggers substantial regrowth which alters quality. Tsiouvaras (1984) found that clipping current growth every 15 days in summer, when soil water was limited, stimulated new growth which had higher crude protein and *in vitro* organic matter digestibility (IVODMD) as shown in Table 8.

Table 7. Percentage survival of *Acacia senegal* (S), *Balanites aegyptiaca* (B), *Combretum aculeatum* (C), *Calotropis procera* (CP) and *Acacia raddiana* (R) shoots after 18 months protection from grazing

Species	S	B	C	CP	R	SED
Survival at 18 months (%)	38	39	40	27	58	5.5
Height (cm)	8[a]	42[b]	65[b]	3[a]	41[b]	
Significance *vs* 0		***	***		***	
Trunk diameter (cm)	4[a]	24[b]	42[b]	19[ab]	33[b]	
Significance *vs* 0		**	***	*	***	

a,b: Means in the same column followed by the same letter are not significantly different
*P<0.05; **P<0.01;***P<0.001

Table 8. Two year's average twig number (twig/year), twig growth rate (cm/day) and crude protein (CP), IVOMD and CC % at various clipping intensities

Control	Percentage of current growth clipped					
	0%	20%	40%	60%	80%	100%
Twig number	1459[e]	1966[d]	2319[c]	2687[d]	2726[b]	3206[a]
Twig growth rate	31.3[c]	31.4[c]	40.0[b]	42.6[b]	39.8[b]	56.9[a]
CP (%)	9.3[b]	11.8[a]	11.6[a]	11.4[a]	11.3[a]	11.4[a]
IVOMD (%)	44.8[d]	57.6[a]	55.0[b]	54.1[b]	50.4[b]	49.8[c]
CC (%)	58.8[e]	73.4[a]	72.3[ab]	70.9[ab]	69.3[cd]	67.8[d]

a,b,c,d,e: Means in the same column followed by the same letter are not significantly different

Comparison of continuous and a 20-day rotational grazing systems showed that animal performance was much better where the substantial regrowth was allowed. In a comparison between clear-cut pasture and a pasture in which shrubby spp. were topped at 60 cm, the ungrazed twig length was longer for the topped (2.82 ± 0.08 cm) than for the clear-cut (2.12 ± 0.11 cm) indicating that accessibility is an important factor in diet selection (Papanastasis *et al.*, 1992). In these pastures utilization of *Carpinus orientalis* was more then twice as high (44%) as that of *Quercus coccifera* (20%). The liveweight gain of G (Liacos *et al.*, 1980) doubled when they were grazing kermes oak topped pastures compared with pure kermes oak stands and tripled when they were grazing in these pastures after the shrubby layer had been reduced to 30% and the proportion of herbage increased by seeding. Nolan (1995) found that grazing by S, C and mixed S + C resulted in white clover average growing season contributions to total DM of about 7%, 14% and 20% respectively using reseeded or semi-natural pastures. These results emphasize the necessity of applying a grazing system to maintain ecological balance between animals and vegetation and that many factors affect the PVI values.

Complementary/competition relationships between animal types in mixed grazing

Understanding the type and extent of complementary/competition relationships between two or more animal spp. or types communally grazing a heterogeneous vegetation facilitates the selection of the correct mix and grazing intensity of each animal type to apply for a given vegetation mosaic.

Some aspects of this problem have been discussed above. The degree of competition between grazing animal types can be estimated from the degree of overlap in vegetation use between them. Results of studies under Irish temperate and Senegalese Sahel semi-arid climatic conditions are in Nolan and Connolly (1989b; 1992) and Nolan (1996).

Nolan *et al.* (1995) developed a new index of dietary overlap between animal types (species, age groups, etc.) grazing the same area which allows tests of significance. They measured dietary composition for each animal sp. in each of 3 (C/S/G) mixed grazing treatments during 6 periods in each of two years using the methodology described above. Due to sampling variation the within animal type similarity will generally be <100. To evaluate whether a particular between animal type similarity value indicates greater difference between as opposed to within animal type it is necessary to allow for this by adjusting between animal type similarity for the average within animal type similarity. This led to the construction of a combined index of dietary association as $A_{ik} = I_{ik} / I_i I_k$. A value <1 implies that individuals of animal types i and k differ more than a pair of individuals within types i or k and a value of zero indicates no dietary overlap between animal species which should reduce interspecific competition. If close to unity, diets are very similar. In both grazing seasons there was greater similarity within C than S or G, with G usually lowest (Fig. 1). Within and between values were much less than unity. The between values were generally much lower than the within animal spp. index values for the types compared. In these data, this could partly be due to the same within sp. animals being sampled over the 4 samplings at a sampling period. Similarity tended to decline over time in the first grazing season and to rise during the second season for all animal types. For the new index the two years results show that C are about as close to S as S are to G but C and G are far apart. Thus S diet selection was intermediate between C and G. Other factors being equal, competition would be expected to be greater between animal types with a high index value, particularly in periods when forage is limited. This has implications for communal use of vegetation by these three spp. in relation to both animal performance and vegetation use patterns.

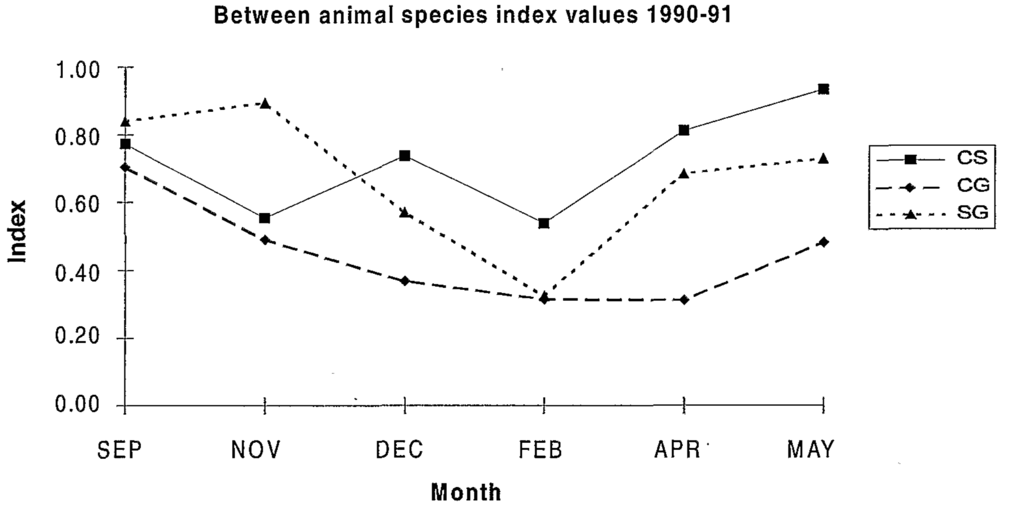

Fig. 1. Value of the index of association for comparison of diet between *versus* within animal spp. for 1990-91 and 1991-92 averaged over the three treatments. Index values are presented for C and S (CS), C and G (CG) and S and G (SG).

There was no clear within season pattern over the two years except that the index increased towards the end of dry season apparently reflecting reduced availability of preferred vegetation fractions.

Nolan (1996) interpreted these results to indicate that the grazing intensity which is likely to damage vegetation is that which applies too high a grazing intensity of the most sensitive vegetation sp./fraction. Vegetation degradation may therefore occur where some spp. or fractions are overgrazed while others are undergrazed. Mixed grazing may achieve a more balanced grazing ecosystem with increased opportunity to combine higher animal product without deleterious effects to the ability of the range to sustain vegetation and animal outputs. In Connolly *et al.* (1995) a general approach to the evaluation of the value of rangeland pastures for various grazing animals was developed which can incorporate factors such as selection by animal type, geographical distribution of vegetation resources and abiotic factors such as accessibility of water. The algorithm under development would return a value of a given area of rangeland for each of the possible animal types that could use it.

Conclusions

(i) The complexity of the grazing ecosystem requires a holistic research/development approach.

(ii) Multifloristic heterogeneous vegetation coupled with different animal type grazing selection necessitates the application of mixed grazing to combine more efficient animal production and vegetation resource sustainability. Vegetation resource capture is greater under mixed grazing.

(iii) Understanding the animal state/vegetation state relationships is the basis for the development of improved grazing ecosystems. Factors which affect the availability and intake of required amounts of nutrients are critical and the use of terms as availability and biomass need clarification.

(iv) Optimal foraging theory has to consider factors such as vegetation geographic distribution, antinutritive substances, water sources etc. to facilitate universal application.

(v) In conservation contexts stocking rate may be more usefully considered as the intensity of grazing applied to the most vulnerable vegetation species. Relative spatial and temporal availability of various forage types affect diet composition with different magnitude for different animal types.

(vi) Dietary preferences of grazing animals are greatly modified by trial and error learning. Acquired dietary preferences can be maintained long after the inducing factor is eliminated.

(vii) Pasture value index and dietary overlap measures are useful tools for evaluation of preferential and differential dietary selection and can aid the selection of the correct animal mix and overall grazing intensity to apply to a given vegetation mosaic.

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