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PRELIMINARY DATA ON NUTRITIONAL VALUE OF ABUNDANT SPECIES IN SUPRAFORESTAL PYRENEAN PASTURES[1]

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ABSTRACT.– The alpine pastures of the Pyrenees have been used as summer ranges for centuries and continue to be an important forage resource for livestock husbandry to this day. Some studies attribute high nutritional values to alpine pastures, but recent surveys have revealed weight-loss in animals summering in Pyrenean pastures. There is virtually no information available with regard to the nutritional value of the species which constitute Pyrenean summer pastures. Twenty-three of the most common species were analysed chemically to determine their nutritional value and their capacity to meet livestock requirements. Monthly samplings of uneaten plants were performed from June to September in plots where species were abundant. These samples were analysed to determine neutral detergent fiber (NDF), lignin (ADL), crude protein (CP), P, K and Mg content. In vitro *dry matter digestibility (IVDMD) was calculated using the pepsin-cellulase method and metabolizable energy (ME) was estimated from it. On average, graminoids presented higher levels of NDF and lower levels of the other nutrients when compared with forbs. Month effect was significant for ADL, CP, P and K. In these cases June was the month which differed significantly from other months. Crude protein, P and K contents diminished with maturity, whereas ADL and Ca levels increased. NDF, IVDMD and Mg values remained fairly constant throughout the summer in both botanical groups. This fact is noteworthy because it may provide a constant supply of ME for herbivores during the grazing period (July to September). Dicotyledoneous forbs meet livestock requirements of all the nutrients analysed except P during the grazing period. Graminoids are deficient in ME (mainly for sheep), P and Mg, and their CP content is slightly low for the requirements of sheep. When cattle and sheep diets are based mainly on graminoids, they could suffer a nutritional deficit in alpine Pyrenean pastures.*

Key words: Chemical composition, forbs, graminoids, nutritional requirements, summer ranges, Pyrenees.

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RÉSUMÉ.– Pendant des siècles, les pâturages alpins pyrénéens ont été utilisées comme pâturages estivaux pour le bétail, et constituent encore de nos jours une importante ressource pour l'élevage. Certains travaux classiques attribuent une valeur nutritionnelle élevée aux pelouses des étages alpin et subalpin, mais des études récentes ont révélé des pertes de poids chez les animaux paissant dans les estives pyrénéennes. En pratique, aucune information n'est disponible quant à la valeur nutritionnelle des espèces constituant ces pâturages. Vingt trois espèces (13 graminoïdes et 10 dicotylédones) abondantes dans les pâturages des étages alpin et subalpin dans les Pyrénées ont été analysées chimiquement pour déterminer leur valeur nutritive et leur capacité à couvrir les besoins du bétail. On a réalisé des relevés mensuels de juin à septembre, en prélevant les plantes non consommées dans des parcelles où ces espèces sont abondantes, dans deux zones d'étude. Des analyses de laboratoire ont été réalisées pour déterminer le contenu en protéines brutes (CP), en phosphore (P), en potassium (K), en magnésium (Mg), en fibre neutro-détergente (NDF) et en lignine (ADL). La digestibilité in vitro *de la matière sèche (IVDMD) a été déterminée par la méthode de la pepsine-cellulase, et l'énergie métabolisable a été déterminée à partir de celle-ci. En moyenne, les graminoïdes ont présenté un contenu plus élevé en NDF, et plus faible pour tous les autres nutriments, que celui des dicotylédones. Les différences inter-mensuelles n'ont été significatives que pour ADL, CP, P et K, le mois de juin étant généralement le plus différent des autres. Le contenu en CP, P et K a diminué au fil de la maturation, alors que ADL et Ca ont augmenté. Les valeurs de NDF, IVDMD et Mg sont restées relativement constantes tout l'été dans les deux groupes botaniques. C'est un fait notable, car cela traduit un apport constant d'énergie métabolisable pour les herbivores pendant toute la période de pâture (juillet à septembre). Les dicotylédones couvrent les besoins des vaches et des brebis durant cette période, pour tous les nutriments sauf pour P. Les graminoïdes manquent d'énergie métabolisable, P et Mg, et leur contenu en CP est en limite si on le compare aux besoins des brebis. Vu que le régime alimentaire des vaches et des brebis est basé sur les graminées, les animaux pourraient connaître un déficit nutritionnel quand ils paissent les pâturages alpins dans les Pyrénées.*

Mots clé: Composition chimique, dicotylédones, graminoïdes, besoins nutritionnels, pâturages estivaux, Pyrénées.

RESUMEN.– Los pastos alpinos pirenaicos han sido utilizados durante siglos como estivaderos para el ganado y constituyen aun hoy un importante recurso para la ganadería. Algunos trabajos clásicos atribuyen a los pastos alpinos un alto valor nutricional, pero estudios recientes han revelado pérdidas de peso en animales que estivan en pastos de puerto pirenaicos. Prácticamente no existe información disponible sobre el valor nutricional de las especies que constituyen estos pastos. Veintitrés especies (13 graminoides y 10 dicotiledóneas) abundantes en los pastos alpinos y subalpinos pirenaicos fueron analizadas químicamente para determinar su valor nutritivo y su capacidad para cubrir las necesidades del ganado. En parcelas donde las especies eran abundantes, se realizaron muestreos mensuales de junio a septiembre en dos áreas de estudio. En el laboratorio se realizaron análisis para determinar el contenido en proteína bruta (CP), fósforo (P), potasio (K) y magnesio (Mg), fibra neutro-detergente (NDF) y lignina (ADL). Se determinó la digestibilidad in vitro *de la materia seca (IVDMD) por el método de la pepsina-celulasa y la energía* *metabolizable (EM) fue estimada a partir de ella. En promedio las graminoides presentaron mayores contenidos en NDF y menores en el resto de nutrientes que las dicotiledóneas. El efecto mes fue solo significativo para ADL, CP, P y K, siendo generalmente el mes de junio el que presentó diferencias significativas con el resto de los meses. El contenido en CP, P y K disminuyó con la madurez, mientras que ADL y Ca aumentaron. Los valores de NDF, IVDMD y Mg se mantuvieron relativamente constantes durante todo el verano en ambos grupos botánicos. Este hecho es destacable porque permite un suministro constante de EM para los herbívoros durante todo el período de pastoreo (Julio a Septiembre). Las dicotiledóneas cubren los requerimientos de vacas y ovejas durante el período de pastoreo de todos los nutrientes analizados excepto en P. Las graminoides son deficitarias en EM, P y Mg, y su contenido en CP es un poco justo para las necesidades de las ovejas. Debido a que el régimen alimentario de vacas y ovejas está basado principalmente en las graminoides, los animales podrían estar experimentando un déficit nutricional cuando pastan en los pastos de puerto pirenaicos.*

Palabras clave: Composición química, dicotiledóneas, graminoides, requerimientos nutricionales, pastos de puerto (estivas), Pirineos.

1. Introduction

The Pyrenees have a surface area of 7330 km^2 above 1700 m. This area is mainly occupied by a varied mosaic of herbaceous communities which are used as summer pasture by settled and trashumant livestock. Pyrenean summer pastures have been and continue to be an important economic resource for local populations (MONTSERRAT & FILLAT, 1990), as they provide livestock with cheap and supposedly good quality forage during the summer. It is a widespread belief among local livestock farmers that the sojourn of livestock in summer pastures is beneficial both in terms of general health and weight gain. Furthermore, some former studies support the idea that alpine plants have higher forage quality than the corresponding species in temperate areas (BLISS, 1962; JOHNSTON *et al.*, 1968; CHAPIN III *et al.*, 1975). However, after seven years of controls on summering livestock, CASASÚS *et al.* (1999) found that, although calves and cows gained live weight during their stay in summer pastures, sheep suffer a weight-loss of 4 to 7 kg. These authors attribute the losses to a low energy content of the grass.

There is little knowledge regarding the nutritional value of Pyrenean pasture species with only incomplete information available for a few of them (LABROUE & TOSCA, 1977; GARCÍA-GONZÁLEZ & ALVERA, 1986). In this study, we have selected 23 of the most abundant species in alpine pastures of the central and western Pyrenees. Some of the species studied are endemic and others, such as *Nardus stricta*, *Festuca rubra*, *Agrostis capillaris* are widely distributed. Although a greater amount of information is available for the latter, the nutritive value of Pyrenean varieties remains unknown. We have determined the nutritional value of these 23 species in terms of chemical composition and *in vitro* digestibility and calculated their seasonal variation during the vegetative period. We have then evaluated their adaptation to the nutritional requirements of the livestock which make use of them (mainly cattle and sheep). These requirements are calculated from nutritional standards extracted from the bibliography (NRC, 1985, 1996).

2. Methods

2.1 Study areas

The species were sampled in two areas (Aísa-Borau, lat 42º42'N, long 0º34'W and Ordesa, lat 42º36'N, long 0º00'), which are representative of alpine pastures of the Western and Central Pyrenees respectively (Figure 1). Actually samples were taken at mountain and subalpine vegetation belts (see Table 1). The subalpine and the upper part of the mountain vegetation belts in the Pyrenees were deforested during Middle Ages and transformed in alpine pastures (BRAUN-BLANQUET, 1948; VIGO & NINOT, 1987), therefore sometimes they are named supraforestal pastures. Main plant communities (phytosociological alliances) in the study area are the dense pastures of *Bromion erecti*, *Nardion strictae* and *Primulion intricatae* type in flat or gently sloping areas, the stony pastures on slightly steeper slopes (*Festucion eskiae, F. gautieri*) and the communities with sparse vegetation cover such as screes and crags (*Iberidion spathulatae, Saxifragion praetermissae, S. mediae*) (REMÓN & GÓMEZ, 1989; GARCÍA-GONZÁLEZ *et al.*, 1991a; ALDEZABAL, 2001). Aísa-Borau is an area covering 1800 ha at altitudes between 1600 and 2600 m composed of several pastoral units with a mean stocking rate of 0.75 LU (livestock units)·ha^{-1}·$year^{-1}$. Ordesa has a surface area of 5700 ha, an altitude range of 1800 to 3300 m and a stocking rate of 0.5 LU·ha^{-1}·$year^{-1}$. Both areas are used jointly by cattle and sheep from July to September. Cattle graze freely whereas sheep are guided by shepherds. Small herds of horses and goats normally graze freely in the same areas. Pastures are communal properties used jointly by herds and flocks from different municipalities. Mean annual temperature and rainfall are 6.2ºC and 1249 mm respectively in Aísa-Borau and 4.9ºC and 1721 mm in Ordesa (the average over 20 years in both areas). The average temperature and rainfall during the sampling period (June to September 2000) were 14.3 ºC and 291 mm respectively for Aísa-Borau, and 11.6ºC and

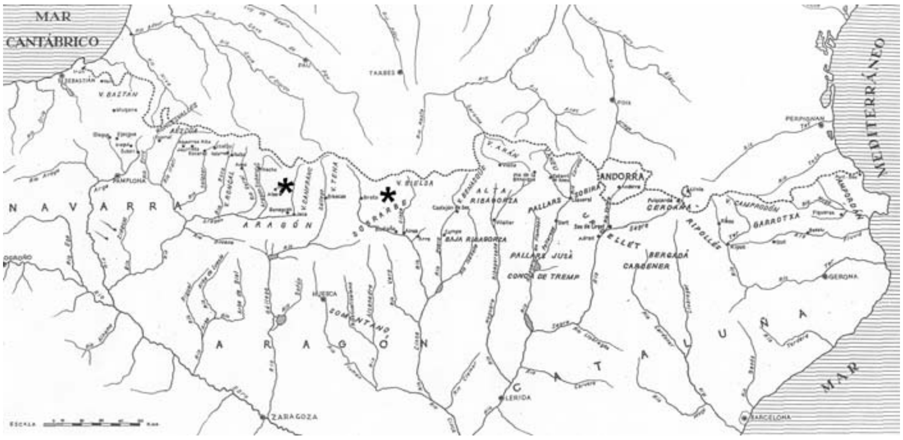

Figure 1. Simplified map of the Pyrenean range showing the position (asterisks) of the two study areas (Aísa-Borau and Ordesa).

358 mm for Ordesa. Average duration of the vegetative period (mean temperature higher or equal to 7 ºC) is of 138 days in the Aísa-Borau plots and 145 days in Ordesa (DEL BARRIO *et al.*, 1990).

2.2 Sampling

Thirteen graminoid species and ten dicotyledoneous forbs (hereafter referred to as forbs), were sampled taking into account their abundance in the summer pastures and their utilization by herbivores (Table 1). Their abundance in pastures and diets had been established in previous studies (GARCÍA-GONZÁLEZ & MONTSERRAT, 1986; GARCÍA-GONZÁLEZ *et al.*, 1991b; ALDEZABAL, 2001; GAÑÁN *et al.*, 2002). The species were sampled in communities where they were most abundant. Because of that, we needed to establish different plots representing different plant communities. Eight 1-ha unfenced plots in the Aísa-Borau area and three 1-ha unfenced plots in the Ordesa area were established (Table 1). These were representative of average environmental and herbivore utilization conditions. From the 23 species selected six (four graminoids and two forbs) were sampled simultaneously in the two study areas to detect differences in their nutritional value due to location (Table 1). The samplings were performed in the middle of each month from June to September 2000. In the majority of cases it was difficult to obtain a pure

Table 1. Scientific name, phenological stage and plot altitude (m) of collected species in the two study areas (Aísa-Borau and Ordesa). Species with an asterisk were sampled in the two areas.
Phenology, 1: vegetative growth; 2: budding; 3: flowering; 4: beginning of fruiting/seeding; 5: fruiting/seeding; 6: dispersal of fruit/seed; 7: some leaves dried; 8: senescence; 9: regrowth. Phenology number in brackets: approximately a third of the population at this phenological stage. Phenology numbers separated by commas: phenological stages in equal proportion.

AISA-BORAU AREA					
Species	**Altitude**	**June**	**July**	**August**	**September**
Achillea millefolium L.	1780	1(2)	2	3	4,5
Agrostis capillaris L. *	1780	1	3	4	7,8,9
Anthyllis vulneraria L.	1930	3(4)	5	6	7
Brachypodium pinnatum P. Beauv.	1590	1	2,3	7	6,7
Dactylis glomerata L.	1550	4	6	6,7	9
Festuca eskia Ramond ex DC.	2125	1,2	3	5	7
Festuca gautieri (Hackel) K. Richter	2125	1(2)	3	6	7
Festuca indigesta Boiss.	2125	2	3	6	7
Festuca rubra L. *	1780	2	3	6	8
Galium verum L. *	1780	1(2)	3	3,4	8,9
Helictotrichon sedenense (DC.) J. Holub*	1990	2	4	6	7,8,9
Hieracium pilosella L.	1780	1	2	2,3,4,5	4,5
Lotus alpinus (DC.) Ramond *	1930		3	5	6
Trifolium alpinum L. *	1900		4,3	5	4,7
Trifolium pratense L.	1780	1	3	4	7,8,9
Trifolium repens L.	1780	1	3,4	4	9
ORDESA AREA					
Species	**Altitude**	**June**	**July**	**August**	**September**
Agrostis capillaris L.	2000		6	6,7	7,8,9
Carex caryophyllea Latourr.	2000	1,2,3	7, 8	7, 8	8
Festuca rubra L.	2000	1(2)	4,6	7	8
Galium verum L.	2000		3	2,3,7	6,7
Helictotrichon sedenense (DC.) J. Holub	1750	2	5	7	7,8,9
Koeleria vallesiana (Honckeny) Gaudin	2000	1	5	6	7,9
Lotus alpinus (DC.) Ramond	2000	3(2)	3	3,6	4,5
Nardus stricta L.	2000	1(2)	5	7	8
Plantago alpina L.	2000	1,2	4,5	7	9
Poa alpina L.	2000	2	6,7	6,7	7,8,9
Sanguisorba minor Scop.	2000	2	2	7	9
Sesleria albicans Kit. ex Schultes	1750		7	7	7,9
Trifolium alpinum L.	2000	2	3	3,6	8,9

sample as the leaves of the species were frequently mixed with the leaves of other species. Due to this, the ungrazed leaves (or plant parts) of each species were chosen and cut by hand, selecting the different items from the other species and scattering the cuttings within their plot. The top half of graminoids and forbs to a height of 2 cm were cut to try to simulate herbivore grazing. Samplings were composed of a considerable number of individuals or leaves of each species, until these reached a minimum total fresh weight of 50 g.

For several species we had determined differences in chemical composition in the different plant parts, flowers and leaf-stem fraction. These parts were sampled separately, in addition to the whole plant. The proportion of leaves and stems in the leaf-stem fraction reflected their proportion in pastures with a frequent predominance of leaves (approximately two-thirds). Seven species of graminoids *(Dactylis glomerata, Festuca eskia, F. glacialis, Helictotrichon sedenense, Koeleria vallesiana, Phleum alpinum, Poa alpina)* and five forbs *(Achillea millefolium, Plantago alpina, Trifolium montanum, T. ochroleucon, T. pratense)* were sampled in this way during the flowering peak (July and August respectively). The botanical nomenclature follows TUTIN *et al.* (1964-80).

2.3 Chemical analyses

The samples were cleaned, dried at 60ºC for 48 hours and ground to a maximum 1 mm particle size. Using the VAN SOEST *et al.* (1991) sequential method, neutral detergent fiber (NDF) and acid detergent lignin (ADL) were determined. *In vitro* dry matter digestibility (IVDMD) was determined following the enzymatic method proposed by AUFRÉRE & MICHALET-DORAU (1990). Samples were incubated in two 24-hour phases, the first with pig stomach pepsin (Fluka, ref. 77 160) and the second with cellulases of *Trichoderma viridae* (BDH, ref. 39074) at a pH of 4.6. Metabolizable energy (ME, $MJ \cdot kg^{-1}$ DM) was estimated from the IVDMD by applying the equation ME = 0.17·IVDMD - 2.0 (SCA, 1990).

Nitrogen contents were determined using the Kjeldahl method and crude protein (CP) was calculated by multiplying the nitrogen content by 6.25. Phosphorus (P) content was determined by colourimetry of vanadomolybdophosphoric yellow, potassium content (K) by atomic emission spectrophotometry and calcium (Ca) and magnesium (Mg) content by atomic absorption spectrophotometry (AOAC, 1990).

The nutrient requirements of sheep and beef cattle were estimated from NRC (1985, 1996) recommendations, adapting them to the average conditions applicable to flocks and herds in the Spanish Pyrenees (FILLAT, 1981). Cattle requirements were estimated for adult beef cows weighing 454 kg adult weight with a peak in milk production of 4.5 kg, in an average herd with 50% of cows in their 5th month and 50% in their 10th month after calving. Sheep requirements were estimated for sheep weighing 50 kg, in flocks where half the sheep were at maintenance conditions and the other half were in their first 15 weeks of gestation.

2.4 Statistical analyses

Each chemical constituent was treated separately. The effect of the study area on the nutritional value of the species sampled in the two areas had been determined with a paired t test. The chemical composition of 23 selected species were analyzed using one-way ANOVAs (analysis of variance) to assess both the species factor (taking the months as replicates) and the month factor (taking the species as replicates). Moreover, two-way ANOVAs were conducted to assess the effects of botanical groups (graminoids and forbs), sampling dates and their interaction. One-way ANOVAs were also achieved to assess the effect of the sampling month within each botanical group and the effect of the botanical group within each month. Where significant differences existed (P 0.05), a posteriori Newman-Keuls tests were performed (SOKAL & ROHLF, 1995). A one-way ANOVA was used to compare the nutritive value of different plant parts, both for graminoids and forbs. Statistical tests were performed with Statistica 6.0 software.

3. Results

3.1 Site, species and botanical group comparisons

The species which were sampled in the two study areas did not present significant differences in any of the chemical constituents in the months of July, August and September (Table 2). However, in August and September, the content of K shows a significance level close to 0.05. In June, the sample was too small for statistical analysis. Given that in general, chemical constituents do not differ between study areas, values of species common to both areas were averaged.

Taking months as replicates, all 23 species differed from each other ($P < 0.001$) in all the chemical constituents. When considering all the species jointly, significant differences were observed ($P < 0.001$) between months for CP, P and K. In the case of the latter constituents, the month of June differed significantly from the other months ($P < 0.01$).

From the two-way ANOVAs, chemical composition between botanical groups (graminoids and forbs) revealed significant differences for all chemi-

Table 2. Mean values of chemical composition of the species sampled in both study areas (Aísa-Borau and Ordesa) throughout the summer period (as % of DM). P, probability values of paired t tests. NS, not significant; NS[a], P = 0.052; NS[b], P = 0.068.

	July			August			September		
	Aísa-Borau	Ordesa	P	Aísa-Borau	Ordesa	P	Aísa-Borau	Ordesa	P
NDF	56.1	55.5	NS	52.6	51.1	NS	55.9	55.8	NS
ADL	7.8	7.6	NS	7.3	6.6	NS	8.1	8.1	NS
IVDMD	53.8	56.3	NS	60.6	67.4	NS	59.9	61.5	NS
CP	13.5	12.7	NS	12.1	13.1	NS	10.6	10.5	NS
P	0.14	0.13	NS	0.14	0.11	NS	0.09	0.09	NS
K	1.45	1.41	NS	1.56	1.33	NS[a]	1.16	0.87	NS[b]
Ca	0.71	0.75	NS	1.05	1.94	NS	1.07	1.42	NS
Mg	0.13	0.13	NS	0.15	0.17	NS	0.15	0.18	NS

cal constituents (Table 3). Month effect was significant for ADL, CP, P and K. June showing significant differences when compared with the other months. The interaction of both factors only showed significant differences for phosphorus. Within each sampling month, significant differences exist between botanical groups in all the chemical constituents (one-way ANOVAs). Taking each botanical group separately, significant differences were observed between the months for some chemical constituents. The results of this latter analysis are shown in Figure 2.

3.2 Fiber and digestibility

NDF content in graminoids is greater (P < 0.001) than the content in forbs in all the sampling months (Figure 2) and remains relatively constant in time

Table 3. Results of two-way ANOVA between botanical groups (graminoids and forbs) and sampling date. Degrees of freedom and F value in brackets. NS, not significant; *, P < 0.05; **, P < 0.01; ***, P < 0.001.

	NDF	ADL	IVDMD	CP	P	K	Ca	Mg
Botanical groups	*** (1, 560.3)	*** (1, 36.1)	*** (1, 36.3)	*** (1, 98.0)	*** (1, 80.6)	*** (1, 23.5)	*** (1, 35.9)	*** (1, 90.1)
Sampling month	NS (3, 0.2)	* (3, 3.0)	NS (3, 2.0)	*** (3, 35.3)	*** (3, 44.4)	*** (3, 5.7)	NS (3, 1.6)	NS (3, 0.4)
Interaction	NS (3, 1.4)	NS (3, 1.8)	NS (3, 0.0)	NS (3, 0.4)	* (3, 3.6)	NS (3, 0.0)	NS (3, 1.0)	NS (3, 0.1)

Table 4. Chemical composition (% of dry matter) of graminoid species.

Species	**Month**	**NDF**	**ADL**	**IVDMD**	**CP**	**P**	**K**	**Ca**	**Mg**
Agrostis capillaris L.	June	65.8	3.3	71.6	16.8	0.18	2.35	0.27	0.12
	July	70.0	4.6	58.1	10.5	0.15	1.55	0.23	0.11
	August	63.2	4.4	60.6	11.0	0.13	1.46	0.52	0.16
	September	65.0	4.6	60.0	8.3	0.07	0.91	0.32	0.14
Brachypodium	June	74.7	5.1	50.1	15.2	0.12	1.78	0.38	0.09
pinnatum P. Beauv.	July	77.6	5.4	42.5	8.5	0.07	1.24	0.41	0.06
	August	74.1	5.0	45.1	8.6	0.07	1.42	0.47	0.08
	September	75.1	7.9	44.9	7.3	0.04	1.64	0.57	0.11
Carex caryophyllea	June	62.8	3.6	70.6	16.5	0.17	2.04	0.56	0.12
Latourr.	July	64.5	3.3	65.6	9.7	0.06	1.60	0.39	0.14
	August	59.9	3.0	67.6	8.6	0.08	1.59	0.72	0.14
	September	62.6	3.2	64.8	8.5	0.07	1.25	0.38	0.15
Dactylis glomerata L.	June	75.2	6.4	44.5	8.2	0.10	1.99	0.19	0.09
	July	72.2	6.6	38.3	5.7	0.11	1.89	0.26	0.11
	August	83.0	7.6	35.3	3.5	0.02	1.52	0.24	0.14
	September	68.6	5.6	57.5	10.3	0.09	2.80	0.42	0.20
Festuca eskia	June	68.4	5.6	54.2	15.7	0.16	1.87	0.14	0.08
Ramond ex DC.	July	69.2	5.0	47.6	9.3	0.10	1.13	0.17	0.06
	August	63.3	5.1	51.3	8.1	0.08	1.03	0.19	0.06
	September	67.1	6.3	51.6	7.6	0.04	0.82	0.24	0.07
Festuca gautieri	June	79.5	4.8	47.9	10.5	0.10	1.40	0.34	0.07
(Hackel) K. Richter	July	73.2	5.0	46.0	7.3	0.09	1.12	0.30	0.07
	August	74.4	5.1	47.1	7.5	0.07	1.17	0.44	0.08
	September	72.9	6.0	51.6	7.0	0.04	1.05	0.34	0.09
Festuca indigesta	June	73.8	6.0	47.7	10.7	0.08	1.17	0.36	0.06
Boiss.	July	73.4	6.5	47.0	9.3	0.10	1.14	0.44	0.09
	August	76.2	6.1	42.5	6.7	0.05	0.68	0.49	0.06
	September	72.4	5.5	51.7	8.8	0.06	0.76	0.45	0.08
Festuca rubra L.	June	72.6	3.8	52.8	15.3	0.16	1.64	0.27	0.10
	July	71.5	5.3	48.0	9.8	0.10	1.38	0.28	0.09
	August	66.5	4.4	56.4	10.9	0.08	1.23	0.54	0.13
	September	68.7	4.8	54.9	8.7	0.07	1.03	0.48	0.11
Helictotrichon	June	72.7	5.1	56.2	14.9	0.17	1.72	0.41	0.09
sedenense (DC.)	July	75.0	5.7	46.1	7.5	0.08	1.27	0.39	0.07
J. Holub	August	69.2	5.2	55.9	8.8	0.16	1.65	0.61	0.08
	September	70.9	4.6	52.3	6.2	0.08	1.00	0.51	0.09
Koeleria vallesiana	June	67.9	4.1	62.5	17.0	0.12	1.70	0.49	0.10
(Honckeny) Gaudin	July	72.7	5.4	51.6	8.1	0.07	1.05	0.44	0.09
	August	71.5	5.7	55.2	9.6	0.06	0.83	0.63	0.10
	September	64.3	6.2	54.8	10.0	0.07	0.99	0.36	0.09
Nardus stricta L.	June	76.2	5.0	44.9	16.4	0.16	1.16	0.18	0.09
	July	76.5	6.5	39.2	12.1	0.12	0.79	0.23	0.08
	August	75.0	5.5	48.3	8.6	0.08	0.67	0.28	0.08
	September	78.2	4.6	46.9	6.5	0.06	0.39	0.29	0.07
Poa alpina L.	June	66.0	4.1	67.4	17.3	0.19	1.65	0.36	0.11
	July	62.6	4.1	62.7	8.1	0.09	1.12	0.24	0.09
	August	53.9	3.0	77.7	11.3	0.10	1.22	0.30	0.12
	September	61.8	3.6	70.6	7.9	0.08	0.73	0.26	0.10
Sesleria albicans	July	70.5	6.5	51.1	7.8	0.07	1.11	0.45	0.08
Kit. ex Schultes	August	66.2	6.5	61.6	7.5	0.04	1.15	0.57	0.09
	September	65.1	5.7	58.3	6.6	0.05	0.85	0.65	0.09

Table 5. Chemical composition (% of dry matter) of forb species.

Species	Date	NDF	ADL	IVDMD	CP	P	K	Ca	Mg
Achillea millefolium L.	June	36.9	8.8	59.4	20.1	0.30	4.61	1.01	0.24
	July	33.5	6.8	65.0	14.2	0.15	2.84	0.98	0.25
	August	51.1	16.3	48.8	10.4	0.09	2.57	0.95	0.16
	September	40.0	8.0	65.6	13.5	0.12	3.22	1.15	0.23
Anthyllis vulneraria L.	June	43.8	7.4	61.1	14.2	0.15	2.02	2.01	0.19
	July	36.2	6.5	68.6	13.9	0.11	1.57	4.88	0.20
	August	31.3	4.9	82.5	13.4	0.09	1.21	6.56	0.19
	September	27.5	4.2	85.5	13.0	0.10	1.17	7.42	0.21
Galium verum L.	June	31.6	8.2	70.8	21.1	0.31	2.04	0.87	0.22
	July	34.6	9.5	65.8	14.4	0.16	1.46	0.93	0.19
	August	35.3	11.4	73.8	14.1	0.15	1.77	1.32	0.22
	September	39.8	11.4	68.5	12.2	0.10	1.40	1.45	0.25
Hieracium pilosella L.	June	38.3	4.7	62.9	14.0	0.17	2.84	1.01	0.23
	July	44.3	6.7	56.8	11.5	0.11	2.22	0.91	0.18
	August	41.7	6.9	60.5	10.1	0.12	2.35	0.98	0.20
	September	38.7	5.2	71.1	10.2	0.12	2.24	1.05	0.22
Lotus alpinus (DC.)	June	30.4	6.6	74.0	22.3	0.30	1.82	1.02	0.22
Ramond	July	36.8	10.3	61.2	16.6	0.16	1.67	1.92	0.20
	August	29.6	6.5	79.8	13.7	0.09	1.27	5.63	0.22
	September	37.5	9.2	54.5	12.5	0.10	1.28	3.81	0.28
Plantago alpina L.	June	36.7	5.7	71.7	21.1	0.29	2.18	1.31	0.31
	July	30.7	5.4	74.3	9.5	0.14	2.23	1.32	0.45
	August	37.6	7.2	71.4	9.9	0.12	1.98	1.52	0.37
	September	41.2	8.4	63.4	9.7	0.13	1.39	1.34	0.30
Sanguisorba minor	June	25.8	3.5	62.3	17.6	0.26	1.50	1.24	0.41
Scop.	July	26.5	3.5	58.4	15.2	0.17	0.98	1.68	0.37
	August	22.0	4.0	71.0	14.9	0.17	1.04	2.16	0.53
	September	31.0	11.4	69.4	14.0	0.15	1.48	1.46	0.52
Trifolium alpinum L.	June	39.7	6.9	64.5	26.4	0.23	1.42	0.56	0.14
	July	46.8	10.7	51.3	19.6	0.17	1.24	0.64	0.12
	August	47.2	9.9	57.6	17.0	0.14	1.26	0.81	0.13
	September	53.1	13.9	55.8	15.4	0.13	0.78	0.86	0.12
Trifolium pratense L.	June	30.8	3.0	68.4	24.1	0.19	1.79	1.15	0.25
	July	44.8	8.4	54.6	14.7	0.11	1.88	0.76	0.18
	August	55.7	12.8	48.3	9.9	0.07	2.03	1.23	0.13
	September	39.2	8.7	60.9	14.0	0.10	1.86	1.40	0.19
Trifolium repens L.	June	32.3	4.6	74.2	23.9	0.26	2.85	1.14	0.29
	July	37.7	8.1	58.6	18.5	0.20	1.94	0.79	0.15
	August	42.4	9.8	61.2	17.4	0.14	1.94	0.87	0.17
	September	34.4	5.1	67.6	16.9	0.12	1.79	0.99	0.19

in both groups ($P > 0.05$). At the species level seasonal change of NDF is very variable. Some species such as *Poa alpina, Nardus stricta, Festuca eskia, Sanguisorba minor, Trifolium alpinum, Plantago alpina, Lotus alpinus and Galium verum* increase their fiber content towards the end of the summer (Tables 4 and 5). Other species such as *Dactylis glomerata, Koeleria vallesiana, Sesleria albicans, Festuca indigesta, Trifolium repens, T. pratense, Achillea millefolium and Hieracium pilosella*, decrease their NDF content towards the end of the summer. The seasonal variation of *Anthyllis vulneraria,* whose NDF content decreases progressively throughout the summer, is worth noting. *Trifolium alpinum* is the species which has the highest mean content of NDF among forbs (47%) and *Sanguisorba minor* has the lowest (26%). Among graminoids, *Nardus stricta* shows the highest mean content of NDF (76%) and *Poa alpina* the lowest (61%).

There are differences in ADL content between botanical groups ($P < 0.001$) and between sampling months ($P < 0.05$), but not in the interaction of these two factors (Table 3). ADL content and its variability are greater in forbs than in graminoids (Figure 2). In June, ADL content is significantly lower ($P < 0.05$) than in other months. No significant differences were observed between months for graminoids or forbs from the one-way ANOVA results, although a tendency to increase was observed for lignin in forbs from June to August (Figure 2). *Carex caryophyllea* and *Poa alpina* have the lowest average lignin content (3.3% and 3.7% respectively) and *Achillea millefolium, Galium verum* and *Trifolium alpinum* the highest (10%) (Tables 4 and 5). As in the case of NDF content, *Anthyllis vulneraria* progressively decreases its ADL content from June to September (Table 5).

Average monthly values of the IVDMD of graminoids vary from 50-60% and those for forbs vary from 60-70%. Differences exist in IVDMD between botanical groups ($P < 0.001$) but not between sampling months or in the interaction of these two factors (Table 3). In both botanical groups, the maximum value appears in June, is reduced to minimum values in July and shows an increasing trend once again in August and September (see seasonal development of ME in Figure 2). The digestibility of all the species diminished in July, except in *Anthyllis vulneraria, Achillea millefolium* and *Plantago alpina* (Table 5). *Dactylis glomerata* together with *Nardus stricta,* are the species which show the lowest average digestibility values among graminoids (44 and 45% respectively), as *Trifolium alpinum* does among forbs (57%). *Anthyllis vulneraria* shows the highest IVDMD values, with an average of 74% and a maximum value of 85.5% in September. The species with the greatest IVDMD average among graminoids is *Poa alpina* (70%).

3.3 Crude protein and macrominerals

Crude protein content presents significant differences between the different botanical groups and sampling months (Table 3). Both botanical groups show a marked decrease in CP content from June to July ($P < 0.001$), which then remains fairly constant during the course of the following months. Among graminoids, *Dactylis glomerata* and *Festuca gautieri* have the lowest average CP values (6.9 and 8.1% respectively), and *Agrostis capillaris* and *Festuca rubra* have the highest (11.7% and 11.2% respectively). In the forbs group, *Trifolium alpinum* and *T. repens* stand out for their high protein content throughout the summer (Table 5).

In both botanical groups, P content decreases sharply from June to July (Figure 2). *Agrostis capillaris* (0.13%) and *Festuca indigesta* (0.07%) present the highest and lowest mean values respectively for graminoids. *Helictotrichon sedenense* undergoes a sharp increase in P content in August. Forbs, such as *Sanguisorba minor* (0.19%) and *Anthyllis vulneraria* (0.11%) show the highest and lowest mean values respectively.

Potassium content decreases throughout the summer in both botanical groups, with a sharper decrease from June to July (Figure 1). This decrease is significant in graminoids ($P < 0.01$). With regard to the species, *Nardus stricta* presents the lowest mean values (0.75%) and *Achillea millefolium* presents the highest (3.3%) (Table 4 and 5). In September, there is a notable increase in K content in *Dactylis glomerata* and *Achillea millefolium* (Table 4 and 5).

Calcium content of forbs is higher than that of graminoids in all months ($P < 0.01$). In both botanical groups Ca content increases from July to August, and in graminoids the difference is significant ($P < 0.05$). The intra-month variability of the Ca content is higher in forbs than in graminoids (Figure 2). Among forbs, *Anthyllis vulneraria* and *Lotus alpinus* stand out for their high Ca content, with mean values of 5.2% and 3.1% respectively. In graminoids, *Sesleria albicans* and *Carex caryophyllea* present the highest mean values (0.5%). The acidophilous species *Nardus stricta* and *Festuca eskia* present the lowest mean values (0.24 and 0.18% respectively).

The average values of magnesium content remain fairly constant throughout the summer in both botanical groups (Figure 2), although taken individually, the species experience fluctuations which vary from month to month. Mg content variability between months is greater in forbs than in graminoids (Figure 2). In graminoids, *Festuca eskia* presents the lowest (0.07%) and *Carex caryophyllea* the highest mean value (0.14%). In forbs, *Trifolium alpinum* is the species with the lowest (0.13%) and *Sanguisorba minor* with the highest mean content of Mg (0.46%). The latter rises to a maximum of 0.52% in August and September, a very much higher percentage than that of other species (Table 5).

3.4 Plant parts

The P content was greater in reproductive organs (spikes and flowers) than in vegetatives (leaf-stem) in the analysed graminoid ($P < 0.05$) and forb species ($P < 0.001$) (Table 6). Graminoid spikes also presented a higher lignin ($P = 0.06$) and a lower K content ($P = 0.03$) with regard to leaf-stem fraction.

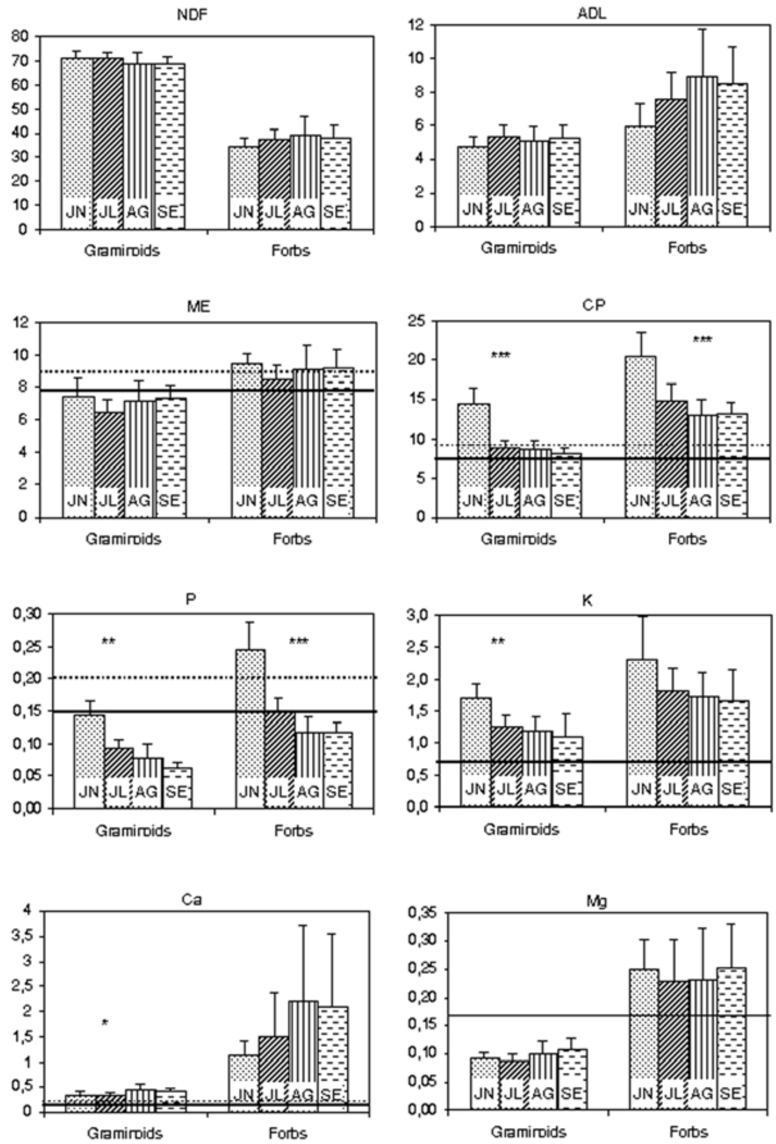

Figure 2. Mean values of the chemical constituents (as % of DM, except for ME in MJ·kg^{-1} DM) by botanical group and sampling date. Vertical bars represent 95% confidence intervals. The asterisks indicate significant differences in month factor within botanical groups (no asterisk, not significant; *, P < 0.05; **, P < 0.01; ***, P < 0.001).

In the case of forbs, CP content was higher (P < 0.05) in the flowers than in the leaf-stem fraction.

4. Discussion

4.1 Site comparison

HANLEY & MCKENDRIK (1983) found no significant differences between the same sampled species in different areas of Alaskan forests. CLARK (2003) found differences between different study areas in the North American Blue Mountains in the protein content of *Carex geyeri,* but no differences in NDF. ARZANI *et al.* (2004) did not find any differences between study areas in chemical composition of five alpine grasses in the mountains of Iran. Doubtless, differences or similarities in chemical composition of the same species in different study areas are directly related to differences or similarities in the environmental conditions of these areas. In the present study, nutritional values of species sampled in both study areas in the same maturity period were fairly constant (Table 2). This could be because the species which were common to both areas were sampled in similar plant communities (where they were most abundant) and these have similar edaphic conditions (BADÍA *et al.,* 2002). The only significant difference between species which are common to both areas is the K content. The level of K can change rapidly in plants, as a result of both mobility and leaching, with an increase in K content in the ground and a decrease in levels in the plant after rainfall (CHAPIN III *et al.*, 1975). This may have caused the differences in K, as in the Ordesa area it rained in the days immediately preceding the sampling period in August and September, whereas in Aísa-Borau it did not.

Table 6. Mean values of chemical constituents of plant parts (as % of DM) and significance of the differences (one-way ANOVA).
NS, not significant; NS[a], P = 0.064; *, P < 0.05; **, P < 0.01; ***, P < 0.001.

		NDF	ADL	IVDMD	CP	P	K	Ca	Mg
Graminoids	**Spikes**	76.2	8.9	42.3	10.2	0.18	0.90	0.17	0.09
N = 7	**Leaves-stems**	71.5	5.9	49.3	9.1	0.10	1.33	0.29	0.08
	F	1.57	4.81	0.56	0.26	6.62	6.15	3.44	0.36
	P	NS	NS[a]	NS	NS	*	*	NS	NS
Forbs	**Flowers**	53.1	12.8	49.2	14.0	0.17	1.76	0.92	0.21
N = 5	**Leaves-stems**	51.3	11.5	52.9	9.2	0.08	1.98	1.20	0.19
	F	0.11	0.28	0.44	7.89	30.75	0.77	2.99	0.17
	P	NS	NS	NS	*	***	NS	NS	NS

4.2 Fiber, digestibility and metabolizable energy

On average, graminoids show higher fiber content, lower lignin content and lower digestibility than forbs. However, MINSON (1990) indicates that graminoids in temperate areas have higher average digestibility values than legumes. In the case of arctic plants analysed by KLEIN (1990), the average digestibility of graminoids is lower than that of forbs in June, but in July the values are similar. According to SCEHOVIC (2000), "for the same level of lignification, legumes are more digestible than graminoids". In our case, graminoids present significantly lower mean IVDMD values than forbs in all months (Table 3). This could be due to the fact that although graminoids have less lignin than forbs (33% less on average), they have twice the NDF content.

General trends of seasonal variation of fiber content indicate that as the plants mature, their NDF and lignin contents increase and their digestibility decreases (ULYATT, 1981; MINSON, 1990; BRUINENBERG *et al.*, 2002). In our study, lignin seems to show a tendency to increase in forbs during the course of the vegetative period, although this increase is not significant (Figure 2). However, in both botanical groups NDF and IVDMD unexpectedly remain fairly constant. This trend has also been found in monthly fiber and digestibility variation of the main Pyrenean plant communities (GARCÍA-GONZÁLEZ *et al.*, 2006). MINSON (1990) also points out the similarity of the digestibility level during growth and later weeks ("plateau" effect) could be due to the constant value of the soluble carbohydrates. The existence of high energy contents and their steadiness throughout the vegetative period in alpine plants related to high lipid values have been mentioned by other authors (BLISS, 1962; KÖRNER, 1999).The steadiness of relatively constant IVDMD values during the vegetative period is of great interest as it allows herbivores access to a constant or slightly increasing source of energy during the grazing period (July to September).

The ME requirements estimated for standard Pyrenean cows and sheep based on NRC (1985, 1996), are 7.9 and 9.2 MJ·kg^{-1} DM respectively. The average ME of graminoids (7.1 MJ·kg^{-1} DM) would appear to be insufficient to satisfy the requirements of either animal species, whereas the average ME of forbs (9.1 MJ·kg^{-1} DM) could satisfy cattle requirements and only just meet those of sheep (Figure 2).

4.3 Crude protein

Both botanical groups show a high average CP content during the growth period (June), which decreases suddenly in the following month and then remains fairly constant throughout the rest of the summer (Figure 2). This type of variation has been frequently shown in other studies (CHAPIN III *et al.,* 1975; VAN REES & BEARD, 1984; ALLDREDGE *et al.,* 2002). At lower altitudes, protein peaks in May (HANLEY & McKENDRICK, 1983; GANSKOPP & BONHERT, 2001) whereas in higher mountain areas, peaks occur at a later stage because the vegetative period begins later and is shorter (DEL BARRIO *et al.,* 1990). Some species *(Dactylis glomerata, Trifolium repens)* experience a second protein peak at the end of the summer (Table 4 and 5) (JONES & WILSON, 1987). The fact that the grazing period in Pyrenean summer ranges begins in July instead of June, when grass CP content reaches its maximum, is probably a consequence of the trade off between CP content and pasture production which peaks in July (ALDEZABAL, 2001)

Almost all the species studied meet the protein requirement for cattle (7.2%), except *Dactylis glomerata* in July and August (Table 4). The minimum CP requirement for sheep is 9.4% (NRC, 1985) and few graminoid species reach greater values than this during the grazing period (July to September). All forbs satisfy the CP needs of both species during all the months of the study period.

4.4 Macrominerals

Forbs in this study present higher P contents than graminoids, thus coinciding with the results obtained by JOHNSTON *et al.* (1968). As a general rule, phosphorus content in growing plants is high and declines with maturity (VAN REES & BEARD, 1984; VALLENTINE, 2001). In the month of June, all the forb species and *Agrostis capillaris, Carex caryophyllea, Festuca eskia, F. rubra, Helictotrichon sedenense, Nardus stricta* and *Poa alpina,* meet the minimum daily P requirement recommended for cattle (0.15%). In June, all forbs meet the minimum P requirement for sheep (0.2%), except *Anthyllis vulneraria, Hieracium pillosella* and *Trifolium pratense.* During the remaining months, none of the species meet the minimum P requirements for either sheep or cattle, except *Sanguisorba minor.*

Potassium content in plants varies according to their phenological stage, with the lowest values occurring in maturity (VAN REES & BEARD, 1984). In this study, we observed the reduction of K content from June to July in both botanical groups. Forbs have a higher K content than graminoids (CHAPIN III *et al.*, 1975; HANLEY & McKENDRICK, 1983). On the other hand, *Nardus stricta* has a very low content (0.75%), which coincides with the results of other authors (TOSCA & LABROUE, 1981). All the species analysed, except *Nardus stricta* in September, reach minimum K requirements for sheep and cattle (0.65%).

The forbs studied stand out for their high Ca content, whereas graminoids show very low values. These results are similar to those of other authors (HANLEY & McKENDRICK, 1983; JOHNSTON *et al.*, 1968; DELPECH & DENUDT, 1978). LARCHER (1995) states that *Anthyllis vulneraria* (a calcicolous species) has a low K and Mg content and a high Ca content. These results coincide with the values found in this study. This species, together with *Lotus alpinus* has the highest Ca contents. Calcium is a limiting element for calcifugous species *(Festuca eskia, Nardus stricta)* and these always present low values of it (LARCHER, 1995). All the species studied meet the Ca requirements for cattle and sheep (0.22 and 0.25% respectively), except *Festuca eskia.*

In general, forbs have a greater Mg content than graminoids (MINSON, 1990; Mc DOWELL & VALLE, 2000), which coincides with the results of this study. DELPECH & DENUDT (1978) also obtained similar results from alpine plants in the Alps. Among forbs, *Sanguisorba minor* and *Plantago alpina,* are the species with the highest Mg content, which coincides with GARCÍA-GONZÁLEZ & ALVERA (1986). The Mg content does not present any great changes with time: variations range from 0.09 to 0.11% (graminoids) and from 0.23 to 0.25% (forbs) in this study. These variations coincide with the results presented by MINSON (1990) for temperate plants. None of the graminoids studied meet the minimum Mg requirements for cattle and sheep (0.16%), except *Dactylis glomerata* in September. All forbs studied, except clovers have enough Mg content to meet the requirements of cattle and sheep.

4.5 Plant parts

In the analysed species, spikes and flowers have almost double the P content of the leaf plus stem fraction ($P < 0.05$). They also have more ADL and lower digestibility (Table 6) although this is not significant, likely because we have considered leaf and stem fractions jointly. Forbs flowers have a greater CP content ($P < 0.05$) and spikes have a lower K content than the leaf plus stem fraction ($P < 0.03$). These results coincide, in general terms, with those observed in temperate grasses (MINSON, 1990; VAN SOEST, 1994), in arctic plants (KLEIN, 1990) and in Pyrenean pasture species (GARCÍA-GONZÁLEZ & ALVERA, 1986). LARCHER (1995) indicates that P accumulates in reproductive organs and, protein accumulates in seed, buds and storage organs. In graminoids, K tends to accumulate in young tissues and at parts of intense metabolism. Therefore, leaves have a greater K content than spikes.

4.6 Nutritional requirements of herbivores

The analysed species represent 75-80% of the total cover of Pyrenean summer pastures (ALDEZABAL, 2001; GAÑÁN *et al.,* 2002). Furthermore, their nutritional characteristics appear to remain relatively constant between different areas within the same communities (Table 1) and between years (the monthly values of the chemical components analysed in different years are highly correlated between species (GARCÍA-GONZÁLEZ *et al.,* 2004)). These species also constitute an important part of cattle and sheep diets during the summer period (GARCÍA-GONZÁLEZ & MONTSERRAT, 1986; ALDEZABAL, 2001).

Except for P, forbs covered the requirements of herbivores during the grazing season (Figure 2). Graminoids only partly covered them, depending on which chemical component was being considered. Thus, a greater or smaller proportion of forbs in the diet may determine the degree of nutritional deficit. Sheep and cattle in the study areas have a diet mainly based on graminoids (77-83%) (GARCÍA-GONZÁLEZ & MONTSERRAT, 1986; ALDEZABAL, 2001). Weighing the monthly mean values of ME of the botanical groups by a ratio of 0.8 graminoids/0.2 forbs, we would obtain that diets cover 95% of the ME needs in cattle (7.5 versus 7.9 $MJ \cdot kg^{-1}$ DM), but only 82% of the ME needs in sheep (7.5 versus 9.2 $MJ \cdot kg^{-1}$ DM). Therefore, there could be an ME deficit in Pyrenean summer pastures, particularly for sheep.

5. Management implications

Thousands of sheep graze Pyrenean summer pastures, so a precise knowledge of the pastures nutritive value is important for regional livestock husbandry. The results in the present study and those of other authors (FERRER *et al.,* 1991; CASASÚS *et al.,* 1999), seem to point to a ME deficit of alpine pastures mainly for sheep. This leads to the question of why summer pastures have been considered a good forage resource by livestock raisers for centuries. A number of possible explanations exist. Firstly, body weights of cattle and sheep have increased in the last century due to genetic selection. E. g. sheep weight was 27% lower at the beginning of the last century (SIERRA, 2002). Furthermore, productive needs are higher now than in the past because of commercial demands. FILLAT (1981) shows an increase of carcass weight in calf and cows from 1933 to 1975 in Western Pyrenees. Lower body weight and productive needs could explain that values of ME found in summer ranges were sufficient to cover livestock energetic requirements in the past, but are insufficient for the new market demands.

Secondly, it could be that the equation applied in our study to obtain an estimate of ME (SCA, 1990), was not the most suitable for Pyrenean species. We used it because it is appropriate for IVDMD estimations. Other equations (RITTENHOUSE *et al.,* 1971; ORTEGA *et al.,* 1997) gave similar results. Nevertheless, BRUINENBERG *et al.* (2002) suggest that the quality of seminatural grasslands could be higher than the value shown using equations based on the properties of improved species. More precise data of the ME content of the analysed plants seem necessary. Better estimates of their ME values should be obtained in animal experiments or new regressions in parallel animal experiments and *in vitro* laboratory analysis should be developed.

In addition, it has been argued that herbivores can improve the quality of their diet by selecting the most nutritious species or plant parts (KRYAZAKIS & OLDHAM, 1993; GANSKOPP *et al.,* 1997). For example, KLEIN (1990) indicates that the high N and P content in flowers would justify the selective consumption of floral parts by reindeer. Moderate to high consumption of flowers has also been observed in cattle, sheep and chamois *(Rupicapra pyrenaica)* in alpine pastures of the Pyrenees (GARCÍA-GONZÁLEZ & MONTSERRAT, 1986). An additional behavioural mechanism for improving diet quality in herbivores is altitudinal migration. This behaviour allows livestock access to higher pastures where the lower temperatures and the recent snowmelt delay the grass growth, keeping it at an earlier phenological stage with a higher nutritional value (MORGANTINI & HUDSON, 1989). If herbivores were to find the grass at the same stage as in the month of June, they would meet their nutritional requirements in all the nutrients (Figure 2). The spatial heterogeneity of alpine environments means that by horizontal movements, it is also possible to find areas where the snow has melted recently and the pasture is still in the first growth stages (NELLEMANN & THOMSEN, 1994). The active selection of species in early phenological stages can imply a real increase in the nutrient levels obtained by herbivores.

6. Conclusions

From the analysed graminoids and forbs, *Poa alpina* and *Trifolium repens* have the best crude protein – digestibility combination and *Dactylis glomerata* and *Hieracium pilosella* the worst respectively. Graminoid spikes have greater phosphorus content and forb flowers greater phosphorus and crude protein content than the corresponding stem-leaf fraction.

Crude protein, P and K contents diminished with maturity, whereas ADL and Ca levels increased. NDF, IVDMD and Mg values remained fairly constant throughout the summer in both graminoids and forbs. This fact is remarkable because it may provide a constant supply of ME for herbivores during the grazing period.

On average, graminoids presented higher levels of NDF and lower levels of the other nutrients when compared with forbs. Only forbs seem to cover the requirements of herbivores, with the exception of P, during the grazing season. Thus, a greater or smaller proportion of forbs in the diet may determine the degree of nutritional deficit. Cattle and sheep diets are mainly based on graminoids in the Pyrenees. Therefore, according to the results of this study, there could be an ME deficit in Pyrenean summer pastures, particularly for sheep.

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