Woody and herbaceous aboveground production of a Patagonian steppe

ROBERTO J. FERNÁNDEZ-A., OSVALDO E. SALA, AND RODOLFO A. GOLLUSCIO

Abstract

Aboveground net primary production (ANPP) of the Patagonian steppe in southwestern Chubut (Argentina) was estimated using a harvest technique to assess the herbaceous (mainly grass) component and a double sampling technique to evaluate shrub production. The latter requires the measurement of plant dimensions and the harvest of shrub biomass in small plots. This technique, by virtue of having an explicit biological model which considers both shrub size and production per unit surface of plant, allows comparisons among years, sites, and treatments. Detailed estimates of ANPP yielded a value of 79 g of dry matter (DM) m^{-2} yr^{-1} (SE = 19 g DM m^{-2} yr^{-1}) for an annual rainfall of 191 mm. Our estimates fits (± 17%) predictions of 4 models relating primary production to annual precipitation. Two thirds of production were accounted for by perennial grasses and one third by shrubs. A less detailed method, which uses only peak biomass, gave ANPP estimates for 4 additional years ranging from 21 to 75 g DM m^{-2} yr^{-1} while annual precipitation during this period ranged from 55 to 167 mm. There was a large reduction in ANPP during a year of extreme drought; however, there were no increases in ANPP during years with above-average precipitation. This suggests that the carrying capacity for the Patagonian steppe may not be linearly related to precipitation.

Key Words: Argentina, grasses, Mediterranean-type climate, primary production methods, shrubs.

Net primary production has been indicated as the most important single functional attribute of plant communities (Whittaker 1975). It represents all the energy actually available for consumers, thus setting the upper limit to secondary production. McNaughton et al. (1989) found herbivore biomass, consumption, and production to be closely associated to primary production, and suggested the latter as an integrative variable of whole-system properties. Carbon and nutrient budgets at the ecosystem scale depend upon reliable estimates of primary production.

Patagonia is a large region of approximately half a million km^2 in southern Argentina, South America. It is comprised of 5 floristic districts which are dominated to different degrees by grasses or shrubs (Soriano 1983). Few estimates of aboveground net primary production (ANPP) have been published for this huge area. Bertiller (1984) reported productivity for the Central District steppe, and Defossé et al. (1990) reported biomass dynamics for the more mesic grassland of the Sub-andean District. Ares (1978) and Soriano (1983) estimated primary production for the grass-shrub steppe of the Occidental District (of about 50,000 km^2), but they only considered the grass layer.

Our objective was to estimate ANPP of herbaceous (mainly grasses) and woody vegetation in the Occidental District of Patagonia. As grasses and shrubs have different growth habits, techniques to estimate ANPP for one life-form are not appropriate for the other. We estimated grass ANPP through a direct harvest technique and woody vegetation ANPP with a double sampling technique (Wilm et al. 1944). We performed a detailed estimate of ANPP for one year, and we used a simpler method during 4 additional years to assess interannual variability.

Methods

Study Site

The study site is located near Río Mayo, Chubut (Argentina), at 45°41′S, 70°16′W, and an elevation of 500 m. The work was performed in an area representative of the community of *Stipa speciosa* Trin. et Rupr., *S. humilis* Cav., *Adesmia campestris* (Rendle) Skottsb., *Berberis heterophylla* Juss. and *Poa lanuginosa* Poir. (Golluscio et al. 1982), which covers most of the Patagonian Occidental District (Soriano 1983). Large herbivores have been excluded from the sampling area since 1983. Average annual precipitation for a 37-year period was 136 mm and ranged between 47 and 230 mm. Precipitation is mainly rainfall concentrated during fall and winter periods. Mean monthly temperatures ranged from 2° C in July to 14° C in January. Soil is coarse textured, with pebbles which account for 47% of its weight; it has a cemented calcareous layer at a depth of about 0.4 m (Paruelo et al. 1988). Vegetation is chiefly composed of grasses and shrubs. Tussock grasses have a basal cover of 25% and are represented principally by *Stipa speciosa, S. humilis*, and *Poa ligularis* Nees ap. Steud. Shrubs, which are less than 1 m in height, have a cover of 12% and are represented mainly by *Mulinum spinosum* (Cav.) Pers., *Adesmia campestris* and *Senecio filaginoides* DC. Forbs account for less than 1% of total cover and they were not taken into account in this study.

Shrub Production

A single estimate of biomass at the end of the growing season was considered an adequate basis to estimate shrub production because current year shoots and leaves remain attached to the plant and are easily identifiable. We did not consider diameter increases of branches but only their elongation; thus, our data may have a bias towards underestimation.

Current year biomass was estimated using a double sampling techique (Wilm et al. 1944). In late January 1985, we selected 10 *Senecio filaginoides*, 10 *Adesmia campestris*, and 15 *Mulinum spinosum* individuals by employing a stratified random procedure to encompass a wide range of plant sizes. We measured, in each one of these shrubs, the height and 2 perpendicular diameters, and harvested current year biomass from a rectangular 10 × 25-cm quadrat projected vertically through the center of the canopy. Then we harvested current year growth of the entire individual.

We calculated the relationship between the direct method of harvesting the entire shrub production versus estimating it using its dimensions and the biomass of the small quadrat on the top of the shrubs. For each individual "i" of species "j", production per plant ($P\hat{P}_{ij}$) was calculated as:

$$P\hat{P}_{ij} = k_j * PPUA_j * AREA_{ij} \qquad (1)$$

Where $AREA_{ij} = 2\pi R_{ij}^2$, assuming hemispherical shape, since more complicated shapes did not significantly improve the model. $PPUA_j$ is average production per plant unit area, estimated from

---

Authors are graduate student, professor, and research scientist at Departamento de Ecología, Facultad de Agronomía, Universidad de Buenos Aires. Av. San Martín 4453, Buenos Aires 1417, Argentina.

This work was jointly funded by Consejo Nacional de Investigaciones Científicas y Técnicas of Argentina (PID 3-911901/85, PID 427/89, INT 151/87) and U.S. National Science Foundation (INT 8414037). Field facilities and rainfall data were provided by Instituto Nacional de Tecnología Agropecuaria (Argentina). M.R. Aguiar and J.M. Paruelo helped during field work. A. Soriano, A.J. Hall, W.K. Lauenroth, and S.B. Perelman provided valuable suggestions.

Manuscript accepted 15 December 1990.

the 10 × 25-cm quadrats. The term k_j is the regression coefficient (slope) obtained when relating PP_{ij}, estimated by clipping the entire shrub, to $PPUA_j$ times $AREA_{ij}$. This regression was forced through the origin. Radius (R_{ij}) was estimated as half the average between measured diameters. Unlike other models, ours has coefficients which are not only statistically but also biologically meaningful (see Hughes et al. 1987 and Etienne 1989 for reviews). Our technique, by considering both shrub size and production per unit surface of plant, allows comparisons among sites, treatments, and years (e.g., Sala et al. 1989).

Finally, shrub dry matter production per unit ground surface, PROD (g m^{-2} yr^{-1}) was estimated from:

$$PROD = \sum_{j=1}^{3} (PP_j * D_j) \tag{2}$$

where D_j is density, and PP_j is average production per plant for each species. D_j was estimated with the closest individual method (Greig-Smith 1983) applied to 4 transects of about 100 individuals each (A.H. Nuñez, unpubl.). The same data base (N = 394) was used to estimate average area per plant for each species ($AREA_j$) in order to calculate average production per plant (PP_j) from equation (1).

Grass Production

To estimate the annual production of grasses we harvested biomass 5 times throughout a year (1984/85). We chose the method of summing positive changes in live plus recent dead grass biomass to calculate production (method 7a in Singh et al. 1975). Biomass of different grass species was pooled because previous estimates showed no differences in seasonality among them (Ares 1978, Soriano 1983).

Harvest months were May, September, and November in 1984, and January and May in 1985. Twenty 0.2 × 5.0-m plots randomly located were harvested on each date. This elongated shape has more error associated with the edge effect than, for example, a circle. However, it reduces sampling variance by encompassing a large fraction of within-community heterogeneity (Greig-Smith 1983). The standard error associated with grass production estimates was calculated according to Sala et al. (1988a).

Interannual Variability

To assess the interannual variability of ANPP, we employed a less-detailed method during 4 additional years (1983/84, 85/86, 86/87, and 88/89). We estimated grass production from the annual peak in green biomass (method 1 in Singh et al. 1975). This less-detailed method provided estimates within the confidence intervals ($P<0.05$) of the more intensive method used during 1984/85.

To estimate shrub production for the 4 additional years, we harvested shrub biomass quadrats (10 × 25 cm) only for *Mulinum spinosum* (20 quadrats each year). Then we applied equations (1) and (2) using the parameters presented in Table 1, except for the value of PPUA for *M. spinosum*, which was the one corresponding to each of the 4 years listed above. Total woody production was then calculated assuming that the proportion accounted for by *Mulinum spinosum* was the same observed during 1984/85.

Table 1. Shrub production estimates for a steppe community in Patagonia, Argentina. $PPUA_j$ is production per unit area of plant of species "j", AREA is surface area per individual assuming hemispherical shape, kj is the regression coefficient (slope) of measured vs. estimated individual production, and D_j is density. $PROD_j$ is the estimated aboveground production per unit of ground area, which was obtained by multiplying the rest of the values on the same line.

Species	$PPUA_j$ g $m^{-2}yr^{-1}$	$AREA_j$ m^2 $plant^{-1}$	K_j ——	D_j plants m^{-2}	$PROD_j$ g m^{-2} yr^{-1}
Mulinum spinosum	303	0.87	0.37	0.12	11.2
Adesmia campestris	144	1.16	0.40	0.05	3.4
Senecio filaginoides	498	0.52	0.22	0.19	11.1
Total		0.72		0.36	25.7

Results

Shrub Production

The model in equation (1) adequately described individual production for the 3 dominant shrub species. Coefficients of determination (R^2) were 0.50 for *Senecio filaginoides*, 0.79 for *Mulinum spinosum*, and 0.87 for *Adesmia campestris*, and were statistically significant ($P<0.01$) for all 3 species. Total shrub production was 26 g m^{-2} yr^{-1} (SE = 7 g m^{-2} yr^{-1}) (Table 1). Values of "k_j" different from 1 accounted for imperfect hemispheric shape and non-uniform production over the canopy. No pattern was detected in the difference between values observed and predicted by the model. Residuals from regression equations appeared unrelated to shrub height ($P>0.50$).

More than 85% of shrub production was accounted for by *M. spinosum* and *S. filaginoides*. Both species yielded similar production values (Table 1), which were attained through different ways. The first species almost doubled the latter in individual plant production, and the opposite pattern was true for their densities (Fig. 1).

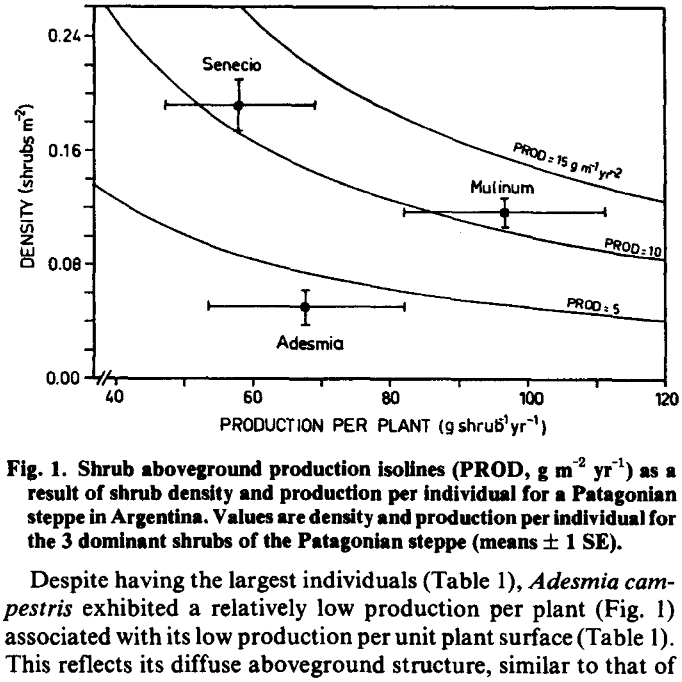

Fig. 1. Shrub aboveground production isolines (PROD, g m^{-2} yr^{-1}) as a result of shrub density and production per individual for a Patagonian steppe in Argentina. Values are density and production per individual for the 3 dominant shrubs of the Patagonian steppe (means ± 1 SE).

Despite having the largest individuals (Table 1), *Adesmia campestris* exhibited a relatively low production per plant (Fig. 1) associated with its low production per unit plant surface (Table 1). This reflects its diffuse aboveground structure, similar to that of species of the genus *Larrea*. Its low density could be the result of the high preference that sheep showed for the species (Bonvissuto et al. 1983). These 2 factors resulted in a low contribution of *Adesmia campestris* to total woody production.

Grass Production

Annual primary production of grasses was estimated to be 53 g m^{-2} yr^{-1} (SE = 12 g m^{-2} yr^{-1}). Green biomass remained constant around 10 g m^{-2} from May to September (winter) (Fig. 2). Low temperatures must have constrained production, since during this period soil water potential was above −1 MPa at 5 and 15 cm (Sala et al. 1989). A fivefold increase in green grass biomass was observed during spring and early summer (September–January) when both water availability and temperature were favorable (Fig. 2). Green biomass returned to its initial values in May, after summer drought.

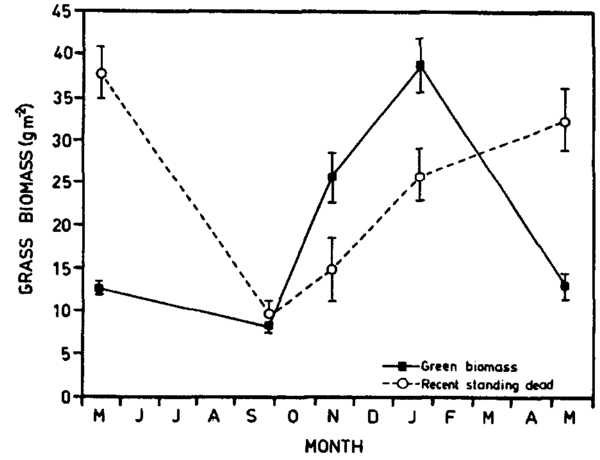

Fig. 2. Grass aboveground biomass dynamics in a Patagonian steppe in Argentina during 1984/85. Values are means ± 1 SE. Twenty 1-m² plots were harvested for each date.

Recent standing biomass had a pattern similar to that of green biomass but shifted over time. Green biomass reached a peak in early summer, while maximum standing dead occurred in fall (Fig. 2). These data suggest that the dry conditions of the Patagonian summer inhibited decomposition as well as primary production.

Interannual Variation

For the 5-year period evaluated, total ANPP yielded values ranging from 21 to 75 g m^{-2} yr^{-1}. During the year in which precipitation was the lowest (55 mm), total ANPP was significantly reduced; during the other 4 years there was not a clear response to rainfall (Fig. 3).

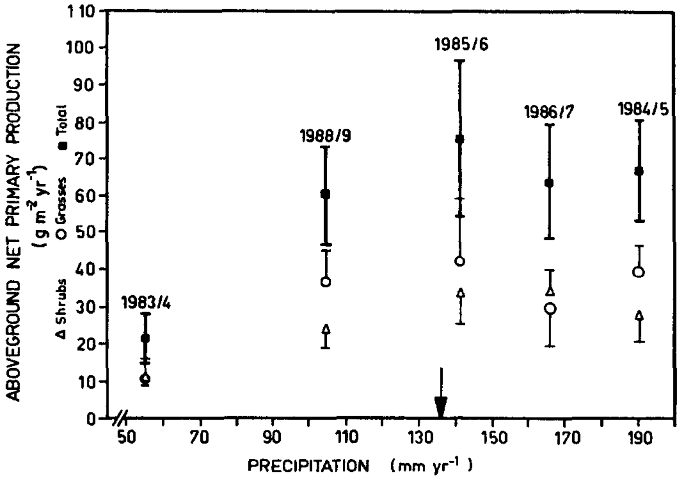

Fig. 3. Relationship between annual precipitation and primary production of grasses, shrubs, and total production in a Patagonian steppe in Argentina. Means of 20 values (except for grasses on 1983/84, for which N=10); vertical lines are 95% confidence intervals. The arrow shows average annual precipitation (N=37).

Discussion

Total aboveground net primary production was 79 g DM m^{-2} yr^{-1} (SE = 19 g m^{-2} yr^{-1}) for the 1984/85 season. This falls within the sample production range of 30–200 g m^{-2} yr^{-1} found by Noy-Meir (1973) for arid zones, and close to the lower limit of 100 g m^{-2} yr^{-1} he ascribed to semiarid zones. Predictions from 4 published models relating ANPP to annual precipitation agree (± 17%) with our data (Table 2). This suggests an efficiency in the use of rainfall similar to that of other ecosystems of the world. Rain use efficiency (ANPP/annual precipitation) was about 4 kg DM ha^{-1} mm^{-1}, which lies within the most frequent range of 3 to 6 kg DM ha^{-1} mm^{-1} reported by Le Houérou (1984) for a large set of arid and semiarid systems. The proportion of ANPP accounted for by shrubs and grasses was 33 and 67% respectively, and coincided with their relative contribution to ground cover.

Table 2. Estimated aboveground net primary production (ANPP) for 1984/85 in a Patagonian steppe, Argentina, from different models relating ANPP to annual precipitation (P, in mm).

Author and Year		Equation	Estimated ANPP (191 mm) g m^{-2} yr^{-1}
Seely	1978	ANPP = −11.3 + 0.548*P	93
Webb et al.	1978	$496 - 666 * e^{-0.0025*P}$	83
Lauenroth	1979	0.5 * (P − 29)	81
Sala et al.	1988b	0.6 * (P − 56)	81

Previous grass production estimates in this area were higher than ours. Ares (1978) estimated 96 g m^{-2} yr^{-1} for 1972, and Soriano (1983) 274 g m^{-2} yr^{-1} for 1975. These differences were not associated with annual rainfall differences (1972: 178 mm, 1975: 170 mm) but rather with the calculation method used. Both authors employed techniques including litter and old dead material, which in this steppe account for about 90% of total biomass. Singh et al. (1975) and Sala et al. (1988a) discussed the risks of using litter in estimating ANPP. When the calculation method employed by us for 1984/85 is applied to the original data of Ares (1978) and Soriano (1983), grass ANPP results in 78.9 and 45.7 g m^{-2} yr^{-1} for 1972 and 1975, respectively.

The relationship depicted in Figure 3 suggests that, on an annual basis, primary production was not constrained by rainfall in 4 out of the 5 years that were analyzed. Above-average precipitation failed to increase primary production in spite of the low amounts of water involved. Run-off is probably negligible because of the flat topography and coarse-textured soil. Nutrient limitations may be partly responsible for the lack of response to greater precipitation. However, experimental (Lauenroth et al. 1978) and modelling evidence (Seligman and Van Keulen 1989) indicate that in arid and semiarid regions water limits ANPP more frequently than nutrients do.

The winter-precipitation regime, together with the low water holding capacity of this soil, suggest that deep percolation may occur during wet years, partly explaining the lack of response in primary production to greater rainfall. We calculated that readily available water (between field capacity and permanent wilting percentage, Kramer 1969) is 120 mm. The estimate was based upon the maximum depth of roots (120 cm) (Fernández-A. and Paruelo 1988) and the water retention curves for the different horizons (Paruelo et al. 1988).

We hypothesize that the main constraints of ANPP during wet years are the root and leaf area required to absorb and transpire the above-average input of water. Even under optimum conditions, these structural characteristics of vegetation are expected to take more than 1 year to respond. They depend upon processes ranging from tillering and seedling establishment to migration and evolution of species adapted to the current Patagonian conditions (Soriano 1990).

Literature Cited

Ares, J.O. 1978. Un modelo de la dinámica de la biomasa aérea de tres especies dominantes en un pastizal patagónico. Deserta (Mendoza) 5:45-56.

Bertiller, M.B. 1984. Specific primary productivity dynamics on arid ecosystems: a case study in Patagonia, Argentina. Oecol. Generalis 5:365-381.

Bonvissuto, G., E. Moricz de Tecso, O. Astibia, y J. Anchorena. 1983. Resultados preliminares sobre los hábitos dietarios de ovinos en un pastizal semidesértico de Patagonia. IDIA (INTA, Buenos Aires) 36(supl.):243-253.

Defossé, G.E., M.B. Bertiller, and J.O. Ares. 1990. Above-ground phytomass dynamics in a grassland steppe of Patagonia, Argentina. J. Range Manage. 43:157-160.

Etienne, M. 1989. Non-destructive methods for evaluating shrub biomass: a review. Oecol. Appl. 10:115-128.

Fernández-A., R.J., and J.M. Paruelo. 1988. Root systems of two Patagonian shrubs: a quantitative description using a geometrical method. J. Range Manage. 41:220-223.

Golluscio, R.A., R.J.C. León, y S.B. Perelman. 1982. Caracterización fitosociológica de la estepa del oeste de Chubut; su relación con el gradiente ambiental. Bol. Soc. Arg. Bot. (Buenos Aires) 21:299-324.

Greig-Smith, P. 1983. Quantitative plant ecology. Third edition. Blackwell, Oxford.

Hughes, H.G., L.W. Varner, and L.H. Blankenship. 1987. Estimating shrub production from plant dimensions. J. Range Manage. 40:367-369.

Kramer, P.J. 1969. Plant and soil water relationships: a modern synthesis. McGraw-Hill, New York.

Lauenroth, W.K. 1979. Grassland primary production: North American grasslands in perspective, p. 3-24. *In:* N.R. French (ed), Perspectives in grassland ecology. Springer, New York.

Lauenroth, W.K., J.L. Dodd, and P.L. Sims. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. Oecologia 36:211-222.

Le Houérou, H.N. 1984. Rain use efficiency: a unifying concept in arid-land ecology. J. Arid Environ. 7:213-247.

McNaughton, S.J., M. Oesterheld, D.A. Frank, and K.J. Williams. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. Nature 341:142-144.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annu. Rev. Ecol. Syst. 4:25-51.

Paruelo, J.M., M.R. Aguiar, and R.A. Golluscio. 1988. Soil water availability in the Patagonian arid steppe: gravel content effect. Arid Soil Res. Rehabil. 2:67-74.

Sala, O.E., M.E. Biondini, and W.K. Lauenroth. 1988a. Bias in estimates of primary production: an analytical solution. Ecol. Model. 44:43-55.

Sala, O.E., W.J. Parton, L.A. Joyce, and W.K. Lauenroth. 1988b. Primary production of the central grassland region of the United States. Ecology 69:40-45.

Sala, O.E., R.A. Golluscio, W.K. Lauenroth, and A. Soriano. 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. Oecologia 81:501-505.

Seely, M.K. 1978. Grassland productivity: the desert end of the curve. S. Afr. J. Sci. 74:295-297.

Seligman, N.G., and H. Van Keulen. 1989. Herbage production of a Mediterranean grassland in relation to soil depth, rainfall and nitrogen: a simulation study. Ecol. Model. 47:303-311.

Singh, J.S., W.K. Lauenroth, and R.K. Steinhorst. 1975. Review and assessment of various techniques for estimating net aerial primary production from harvest data. Bot. Rev. 41:181-232.

Soriano, A. 1983. Deserts and semideserts of Patagonia, p. 423-460. *In:* N.E. West (ed), Temperate deserts and semideserts. Elsevier, Amsterdam.

Soriano, A. 1990. Missing strategies for water capture in the Patagonian semidesert. Acad. Nac. Cs. Ex. Fis. Nat. (Buenos Aires). Monografía 5:1-5.

Webb, W.L., S. Szarek, W.K. Lauenroth, R. Kinerson, and M. Smith. 1978. Primary productivity and water use in native forest, grassland, and desert ecosystems. Ecology 59:1239-1247.

Whittaker, R.H. 1975. Communities and ecosystems. MacMillan, New York.

Wilm, H.G., D.F. Costello, and G.E. Kipple. 1944. Estimating forage yield by the double sampling method. J. Amer. Soc. Agron. 36:194-203.