VII. ASSESSMENT OF BROWSE SUPPLY AND BROWSE CONSUMPTION: DISCUSSION

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Introduction

Because the majority of the herbivores in terrestrial ecosystems forage (at least) partially on the leaves, twigs, flowers, and fruits of shrubs and trees, assessment of the supply of these food items and their consumption has received considerable attention but less than has been given to the production and offtake of herbaceous vegetation.

Browse and browse supply

The assessment of browse supply and consumption encounters a variety of problems right from the start. Browse is defined rather unanimously as the current year's growth of woody plant species (leaves and twigs) and bark of trunks and branches. Supply is more difficult to define. It could simply mean the quantitative presence of leaves and twigs of woody plant species. However, supply is often understood as indicating the amount of usable or consumable browse, the classification of what is usable (or consumable) depending on the type of user, i.e., herbivore species, but also on the management objectives. For example, red deer are able to reach at higher levels and take longer twigs with a larger diameter than roe deer are, which means that the same browse supply for red deer could be larger than that for roe deer. However, both species might consume more than is desirable or acceptable from the objectives of management. The plant species involved, the potential users, and the management objectives determine the amount of browse available as a source of food. Thus, browse supply should be specified according to the species of herbivores and the woody plants concerned. Consumption is the quantitative removal of all or part of the browse.

Sampling techniques for browse supply

Shrubs and trees occur in patches as the result of differences in soil and water conditions, the degree of slope and its direction, etc. Estimation of the supply and consumption of browse per unit area requires a sampling program.

Heterogeneous landscapes necessitate stratification of the area into

(more) homogeneous subunits. The mode of stratification is partly determined by the reason for it. Although such stratification should by preference be based on criteria relevant for the consuming herbivore (e.g. occurrence and density of woody plant species), other criteria such as geomorphology, drainage patterns, and socio-ecological relationships between plant species are generally used instead. The latter criteria have more relevance for the researcher concerned with stratification.

The planning and execution of sampling of shrubs and trees for the estimation of browse supply (and consumption) raise a variety of problems. Any methodology evokes discussions. A thorough treatment of the subject is given by Perzanowski, who deals with two ways of sampling browse supply, i.e., in unfenced plots, transects, etc. and in fenced plots.

The use of unfenced plots or transects has several advantages in that it is relatively cheap and the sampling more rapid. Fenced plots have some advantages too. The latter method offers the best way to measure browse production, because consumption by herbivores is excluded. Moreover, regrowth cannot be measured accurately unless controlled clipping procedures are used.

From the point of view of forage supply for herbivores, the main disadvantage is the exclusion of browsing as a determinant factor with respect to plant growth and regrowth (pattern, rate, quantity), and plant shape. The growth pattern of shrubs and trees inside fenced plots differs from that outside such plots, e.g. as to leaf fall, time of flowering, etc.

In the first place, the rate of production differs as well. This means that the duration of exclosure will influence the amount of browse to be measured. Second, due to the high cost of fencing, fenced plots are small and variations between plots are likely to be larger than differences between estimation of browse inside and outside the enclosure. Third, the fencing itself leads to vegetational changes inside the plot, because it causes changes in microclimatic conditions and might even induce changes in the vegetation, because browse species might start to dominate less preferred species.

We conclude that fenced plots should only be used for short periods to avoid underestimation of actual production and supply.

Sampling in plots (fenced or unfenced), along transects, or by some other method means that many choices (see Chapter V) must be made. These

choices concern the location of the plots or transects (random or systematic), the number of plots or transects, the plot size/transect length, the shape of the plots (rectangular plots give less variation than e.g. circular plots, because vegetational diversity is greater), the number of sampling points per transect, and the sampling height. Statistical methods can provide a basis for such choices.

Several techniques are available to measure browse quantitatively within individual plots or at each transect point. These include (see also Chapter V):

a. Total harvesting, which gives reliable results but is time-consuming and extremely laborious.

b. Twig counting combined with weighing of a sample of twigs to estimate average phytomass per twig; this requires differentiation of twigs according to age, length, and diameter. Results are reliable and the method is less time-consuming than total harvesting.

c. Measurement of characteristic features of plants (e.g. height, crown diameter, etc.) related to browse production.

d. Photographic techniques.

e. Measurement of tree and shrub density or canopy cover (e.g. PCQ and SPM methods), both of which are related to browse production.

All but the first of these techniques rely on sampling within a plot/transect point to estimate browse production, and three of them (b, c, and e) require harvesting to relate the parameter(s) to the quantity browse.

The frequency of sampling to determine browse supply (and consumption) deserves special attention. In general, assessment of browse production and supply is carried out twice, e.g. in the autumn to estimate total production (and summer consumption) and in the spring for winter consumption. However, this approach neglects two important aspects:

1. Browse production and browse supply are not identical. During the spring all growth could in principle be consumed by a herbivore, but during the growing season annual growth of twigs and leaves would become lignified, the level of polyphenolic and other chemical digestion-inhibiting compounds could rise sharply, and therefore the consumable part of the production would show a relative decrease. Hence, supply is not a constant fraction of production, which includes the potential consumption as well.

2. Browsing influences plant growth. Because traces of browsing may disappear rapidly, a sampling frequency of twice a year or less will lead to serious underestimation of the production, supply, and consumption of browse, especially in areas with a moderate to low browsing pressure. The relative importance of these aspects differ, between plant species and management objectives.

From the foregoing it is clear that accurate estimation of browse production and supply for one or more species of herbivores demands considerable work, and that for exact measurements it is essential to follow the plant's phenological stages as closely as possible.

Assessment of browse consumption

As explained by Putman, the consumption of browse by herbivores can be assessed by vegetational and animal-based techniques, but there are no sharply defined criteria available to facilitate the choice between these two categories. For a sward-like vegetation it holds that when the offtake is above approximately 20%, vegetational techniques are to be preferred because they demand relatively less time and are more accurate than animal-based techniques.

All vegetational techniques for the assessment of browse consumption start at the level of plant species, because these species differ both physically and chemically. Twig counting is a widely applied technique (see Chapter VI) but is quite laborious. In the growing season traces of browsing may disappear rapidly, and will be missed if the sampling frequency is not sufficiently high. Because of the difficulty of distinguishing between 'old' and 'new' scars, this technique can give a bias as to species composition and thus lead to underestimation of consumption. Moreover, determination of traces at the animal-species level is often difficult too, which means that if more than one herbivore species is involved, total offtake can be assessed but not the proportion for which each animal species is responsible.

Calculation of offtake on the basis of unbrowsed twigs can evoke another source of error. These twigs are either consumable but not browsed and are for some reason actively selected or avoided by the herbivore(s). This source of error can be avoided by marking subpopulations of twigs at the start of the growing season and then following these twigs at intervals. Although this is time-consuming, it is worth doing if the effect of herbivore selection on plant quality is studied.

Signs of rooting by wild boar

Furthermore, actual offtake is the difference between browsed and unbrowsed twigs (per age, length, and diameter class) and depends on what is available 'nearby' and what has already been eaten, and thus on animal density.

Other vegetational techniques such as total plot harvesting or analysis of photographs encounter comparable difficulties.

For the assessment of browse consumption also several animal-based techniques are available. Direct observation of animals can provide valuable information about diet composition and patterns of food selection. Often wild herbivores apply 'compensatory feeding' by active selection of particular food items to optimize the digestive process. Indirectly - via bite counts per unit of time - direct observations can be used to estimate feeding rate and intake. Unfortunately observational techniques rely on prolonged visibility of the animals to be observed and visibility in daylight offers great advantages over night observations. Low density and shyness of the animals and poor visibility of their habitat are among the factors that often force the researcher to use

more indirect techniques.

Commonly used techniques include analysis of the stomach/ruminal contents and of faeces. A wealth of information has been published on these techniques (for more details about some of the advantages and disadvantages of both, see Chapter VI). A few aspects frequently discussed during the meetings should be mentioned here.

With respect to the applicability of these techniques, a useful distiction is made between qualitative aspects (plant-species composition of the diet) and quantitative aspects (intake).

It is generally agreed that analysis of both the stomach contents and (especially) the faeces provides sufficient reliable information on the diet composition of herbivores.

Stomach-content analysis has the following main disadvantages: a) data are often only available for a limited period of the year (due to hunting regulations), b) samples are small, and c) often only a small part of the diet spectrum is sampled due to differential fermentation rates of plant parts and species, and selective, non representative habitat use. Results obtained with this technique may have limited value in view of the usually small samples from identical conditions with respect to season and place.

Apart from the advantages offered by faecal-content analysis (samples available throughout the year, no restrictions on sample size), this technique encounters other problems, e.g. the identification of the producer of the faeces and the identification of plant fragments. All samples contain unidentifiable plant fragments, the proportions depending on the animal species involved (in ruminants there are more fragments unidentifiable than in non-ruminants) and on the minimum fragment size to be considered for identification (the larger this size, the more easily the fragments can be fractured, and digestible plant species will be underestimated or missed).

Assessment of intake

Calculation of total and proportional intake based on the diet composition indicated by both techniques requires knowledge of plant-species characteristics, especially the differential digestibility of plant species and plant parts, and also of the kinetics of the material during passage through the digestive tract and intestines.

The digestibility of plant species determined by in-vitro digest-

ibility trials is often taken as the basis for reconstruction of dietary intake according to the proportional presence of these plant species in the faeces. Ruminal fluid from the animal species concerned should by preference be used in these in-vitro trials. With mixed diets use must be made of inocula derived from well-adapted rumen biota to avoid in-vitro fermentation that will lead to unreliable estimates of digestion rates or no results at all. But since use of inocula is often impossible, domestic animals (sheep) are used as the suppliers. Inocula from 'grazers' like sheep and cattle are an important source of error if digestibility of browse or browse-based diets is at stake. Feeding trials might provide accurate data on plant species-specific digestibility, but even if tame animals are not difficult to obtain, the reliability of such data remains questionable. Plant-species digestibility will vary much with the quantitative composition of the diet. This digestibility is determined not only by the quantitative proportion of the plant species concerned but also by the presence of other plant species in the diet. A second and often neglected source of error is due to the more fibrous parts of the browse ingested, especially twigs and bark. In the faeces this material often has no characteristics permiting plant-species determination. In Western Europe wood structure will help identification, because the number of woody species is limited, but this material is often removed from the faeces by the treatments applied.

Another source of error in the reconstruction of dietary intake from faecal fragments can lie in the conversion of surface area of plant fragments into quantity ingested without taking into account leaf thickness, which differs between plant species and groups. Because the ratio between weight and surface of plant leaf is comparable for the majority of plant species, this source of error is probably negligible.

Fistulation and feeding trials are alternative techniques used to avoid the limitations associated with the above-described animal-based methods. Apart from their specific problems (e.g. availability of tame or tamed animals), feeding trials (cafetaria system) can indeed provide information on food choice, but it must be kept in mind that the results obtained in this way concern the choice of plant species under controlled, i.e., non-natural conditions. In nature an animal's decision to feed on plants of a certain species depends upon several factors besides the presence of those plants; for example, browse with a certain amount of secondary plant metabolites (e.g. tannins) might be taken if other

species with nutritional compensation for these compounds can be selected for. The optimization of foraging in nature is difficult if not impossible to simulate in feeding trials.

Fistulated animals need constant medical attention and care. Under free-ranging conditions, optimal care is difficult to guarantee. This explains the reluctance to use this type of research unless conditions can be tightly controlled. Moreover, the limited number of fistulated animals used might lead to bias concerning the choice and intake of plant species according to individual preferences. However, in habitats with few plant species this bias is probably small.

Rooting of wild boar imitated by the forester to stimulate forest rejuvenation

Concluding remarks

In view of the many problems involved, it is concluded that animal-based techniques for assessment of the quantitative intake of browse by herbivores should be used to supplement vegetational methods. At least for the estimation of total browse consumption, animal-based techniques should not be used.

Finally, with respect to the assessment of browse supply and consumption, two criteria are considered important: accuracy and sampling efficiency. The accuracy of the information obtained is strongly influenced by the amount of time and funds available. Optimization of both accuracy and efficiency often means the acceptance of a certain arbitrary level of inaccuracy; a certain accepted deviation from the (unknown) true value. This estimation can, however, be very precise. Much attention is often paid to a high degree of precision, but the methodology applied leads to a rather inaccurate estimation. A certain balance between accuracy and precision is just as important as an optimal balance between efficiency and accuracy.